39. Mehra, M. S., Pathak, P. C. and Singh, J. S., Nutrient movement in litter fall and precipitation components for Central Himalayan forest. *Ann. Bot.*, 1985, **55**, 153–170.
40. Sanford, R. L., Apogeotropic roots in Amazon rain forest. *Science*, 1987, **235**, 1062–1064.
41. Lipps, R. C. and Fox, R. L., Subirrigation and plant nutrition. II. The utilization of phosphorus by alfalfa from the surface to the water table. *Soil Sci. Soc. Am.*, 1956, **20**, 28–32.
42. Sharma, J. C. and Sharma, Y., Effect of forest ecosystems on soil properties – a review. *Agric. Rev.*, 2004, **25**(1), 16–28.
43. Fontaine, S., Barot, S., Barre, P., Bdioui, N., Mary, B. and Rumpel, C., Stability of organic carbon in deep soil layers controlled by fresh carbon supply. *Nature*, 2007, **450**, 277–280.
44. Basile-Doelsch, I., Amundson, R., Stone, W. E. E., Borschneck, D. and Bottero, J. Y., Mineral control of carbon pools in a volcanic soil horizon. *Geoderma*, 2007, **137**, 477–489.
45. Raina, A. K. and Gupta, M. K., Soil and vegetation studies in relation to parent material of Garhwal Himalayas, Uttarakhand (India). *Ann. For.*, 2009, **17**(1), 71–82.

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Patterns of dominance relationships among the females of a captive female-only group of lion-tailed macaques (*Macaca silenus*) during the course of the introduction of a new adult male

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Lion-tailed macaques are generally considered to have more despotic than egalitarian dominance relationships; however, research lacks any conclusive evidence. In the present study, we examined dominance relationships among the females (of which the genealogical relationships were known) of a captive female-only group of lion-tailed macaques (*Macaca silenus*) during the course of introduction of a new adult male to the group at the Wels Zoo, Wels, Austria. We determined the structure of dominance hierarchy and the corresponding changes in dominance relationships, possibly mediated by an increase in sexual competition among the females. When the females were housed together without any adult male for over four months following the death of the former breeding male, the dominance hierarchy almost followed the principle of youngest ascendency. When a new male was housed for 26 days in an enclosure adjacent to that of the females (such that the females and the new male could interact with each other through a wire mesh between their enclosures), changes in dominance hierarchy were observed. During this phase, there was a temporary change in the dominance hierarchy, leading to a higher degree of aggression of the nursing female and an increase in its dominance rank. This is corroborated by the fact that when the new male was housed together with the females in the same enclosure, it resulted in infanticide and subsequently, the nursing mother lost the higher rank. We consider the implications of the present study in the captive management and breeding of long-tailed macaque.

Keywords: Captive management, dominance, hierarchy, lion-tailed macaque, rank instability.

THE asymmetrical outcome of intragroup agonistic interactions, that is, dominance hierarchy, is a defining characteristic of macaque societies[1]. According to some studies[2–4], such asymmetrical outcomes owe to limited resources among females. de Waal[5] found that these can vary with the degree of social bonding, tolerance and reconciliation after aggressive conflicts. While comparing the strength of dominance hierarchies between the females of different species of macaques, Flack and de Waal[6] defined four distinct categories: despotic, tolerant, relaxed and egalitarian, the degree of asymmetry in agonistic interactions increasing from egalitarian to despotic. Similarly, on the basis of certain aspects of their social behaviour (particularly the frequency of inter-individual agonistic and socio-positive interactions), Thierry[7] attempted to classify 22 species in *Macaca* genus along the egalitarian–despotic continuum. According to Kutsukake[8], when females of a group acquire dominance ranks relative to one another, creating a linear distribution of social dominance, the hierarchy is termed as 'linear'; whereas when a daughter's dominance rank is determined by her mother's, the former never outranks the latter, and sisters rank inversely in the order of their age, the dominance hierarchy is termed as 'reverse' or following the 'principle of youngest ascendency'. Reverse dominance hierarchies are commonly observed in female-bonded species, typically comprising genetically related individuals

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with a high degree of nepotism among them. Examples include provisioned groups of Japanese macaques (*Macaca fuscata*) and rhesus macaques (*Macaca mulatta*)[9]. Moreover, dominance relationships might vary across diverse subgroups of a population, as reported for male and female Barbary macaques[10], across diverse communities of the same species, or be species-typical.

Under free-ranging conditions, lion-tailed macaques inhabit environments with limited resource availability[11,12]. Consequently, there is high competition among females to acquire those resources[13]. One would thus expect that lion-tailed macaques (which are generally considered to have a female-bonded social structure[14]) would show consistent, transitive and stable dominance relationships, resulting in linear and strict dominance hierarchies. Consistent with this expectation, but challenging Thierry's[7] classification of lion-tailed macaque in the relaxed category (i.e. species considered to have more egalitarian than despotic dominance relationships), Singh *et al.*[13] reported despotic dominance relationships and correspondingly, despotic access to grooming partners, in free-ranging female lion-tailed macaques. However, on the whole, because of lack of adequate and accessible data, there has been no formal agreement on the nature of dominance relationships among lion-tailed macaques. More studies are therefore required.

In the present study, we examined the dominance relationships among the females (of which the genealogical relationships were known) of a captive female-only group of lion-tailed macaques during the course of introduction of a new adult male. We determined the structure of dominance hierarchy and the corresponding changes in dominance relationships, possibly mediated by an increase in sexual competition among the females. We expected that the females would show more despotic than egalitarian dominance relationships in the absence of any adult male, that is, strictly linear and stable dominance hierarchy, and that the introduction of the new male would result in a temporary instability in dominance relationships among the females.

The subjects were five female lion-tailed macaques (lineal–consanguineous relatives, including one female with a male infant; Figure 1) and an adult male lion-tailed macaque that was introduced to this female-only group. Initially, the females were housed together in an indoor enclosure with access to an outdoor facility at the Wels Zoo in Wels, Austria for over four months following the death of the former breeding male (observed for 9 days). Then, a new adult male was housed in an enclosure adjacent to that of the females (such that the females and the new male could interact with each other through the wire mesh between their enclosures; observed for 26 days). Finally, the male was permanently housed together with the females in the same enclosure (observed for 42 days).

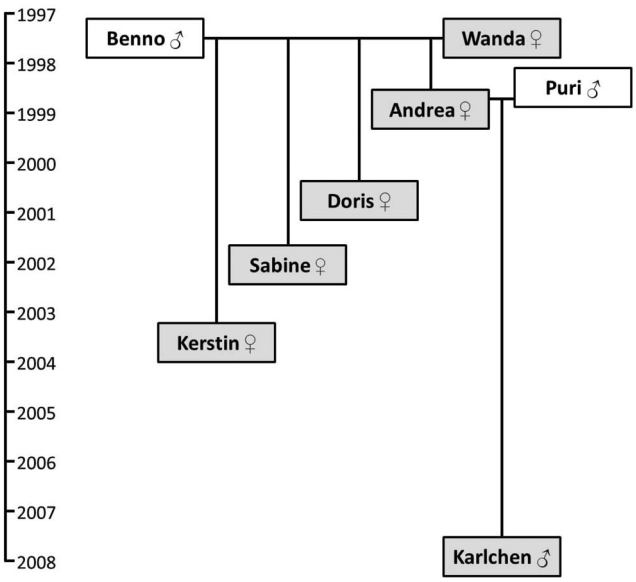

Figure 1. Genealogy map of the female lion-tailed macaques (the study subjects are highlighted in grey).

Table 1. Catalogue of the agonistic, socio-positive and sexual interactions recorded among the lion-tailed macaques

Socio-positive interactions
Body contact
Allogrooming
Sexual interactions
Present to mount
Inspect
Inspect (touch or smell) genitals
Inspect genital + call
Tug/squeeze/lift tail
Tug/squeeze/lift tail + call
Copulate/mount
Copulate/mount
Copulate/mount + call
Copulate/mount + bite
Interfere with copulation/mounting
Agonistic interactions
Chase
Chase
Chase + agonistically call
Mimic
Threat
Guarded threat
Threat + agonistically call
Agonistic with body contact
Grab, pull
Hit
Bite
Guarded attack (with body contact)
Guarded attack + agonistically call
Agonistic without body contact
Displace
Attack
Agonistically call

Table 2. Average level of sexual swelling of the female lion-tailed macaques; average minutes spent per hour by the females on sexual interactions with the new adult male and dominance status of the females based on the outcomes of dyadic agonistic interactions among them, in the three observational conditions

Individual	Average level of sexual swelling	Average minutes spent per hour on sexual activities		Dominance	
		Active	Passive	Scale score	Rank
Females housed without any adult male (61 10-min focal sessions per female between 0900 and 1800 h)					
Wanda	2.50	–	–	1.78	1
Andrea	0.00	–	–	0.30	4
Doris	0.00	–	–	0.00	5
Sabine	0.50	–	–	0.94	3
Kerstin	0.50	–	–	1.08	2
A new male (Höllander) housed in an adjacent enclosure (92 10-min focal sessions per female between 0900 and 1800 h)					
Wanda	2.53	0.48	0.43	1.36	1
Andrea	0.00	0.00	0.00	0.47	2
Doris	0.00	0.08	0.00	0.00	5
Sabine	0.95	0.37	0.53	0.41	3
Kerstin	1.74	1.02	1.22	0.32	4
The new male housed in the same enclosure (88 10-min focal sessions per female between 0900 and 1800 h)					
Wanda	2.40	0.43	1.33	1.85	1
Andrea	1.50	0.23	2.06	0.81	4
Doris	1.60	0.60	1.30	0.00	5
Sabine	1.85	0.43	0.82	0.91	3
Kerstin	1.85	0.57	0.50	1.34	2

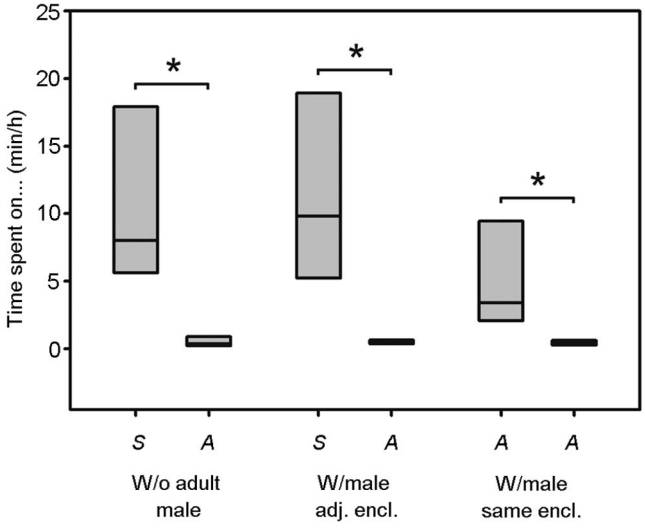

Figure 2. Time spent by the female lion-tailed macaques and the new adult male on socio-positive and agonistic interactions in the three observational conditions. S, Socio-positive; A, Agonistic. *$P < 0.05$.

We determined the time spent in socio-positive, sexual (active, i.e. directed by the females towards the new male; passive, i.e. directed by the new male towards the females), and agonistic interactions (Table 1) between the females and the new male using the focal animal sampling method[15] with a focal sampling period of 10 min (see Table 2 for a detailed description of the observation schedule).

At the start of each observation day, we graded the sexual swellings of the females in the anal region from 0 to 3.0, no swelling of skin in the subcaudal region; 1, semi-spherical swelling of skin in the subcaudal region ca. 2 cm in diameter; 2, semi-spherical swelling of skin in the subcaudal region ca. 4 cm in diameter; 3, semi-spherical swelling stretching from the subcaudal to the upper anal region. We used these grades to determine the average level of sexual swellings by dividing the total of the obtained grades by the total number of observation days.

We recorded the outcomes of all dyadic agonistic interactions among the females (Table 1). They were subjected to measurement of dominance in non-human primates[16] in order to obtain dominance scale scores on an interval scale. We used the obtained scale scores to determine absolute dominance ranks.

We performed statistical analyses on SPSS 20. We used Mann–Whitney *U*-tests to compare the time spent by the females on socio-positive and agonistic interactions in the three housing conditions.

Under all three housing conditions, the females spent more time on socio-positive interactions (mainly comprising of body contact and allogrooming) than on agonistic interactions: during the week before the new adult male was introduced ($U(8) = 0$, $z = 2.507$, $P = 0.012$), when it was housed in the enclosure adjacent to that of the females ($U(8) = 0$, $z = 2.507$, $P = 0.012$), and when the new male was housed together with the females in the same enclosure ($U(8) = 0$, $z = 2.507$, $P = 0.012$) (Figure 2). Also, there were no noticeable agonistic interactions between the females and the new male after the latter was introduced to the group. Regardless of the overall socio-positive

relationships among the females, and between the females and the new male, the four-month-old male offspring (Karlchen) of Andrea was found dead with canine wounds nine days after the new male was housed together with the females in the same enclosure. Since these wounds had traces of large canine teeth, apparently this was an infanticide by the new male (typically, infanticide victims in nonhuman primates are bitten deeply[17]).

Table 2 describes the average level of sexual swellings of the females; average minutes spent per hour by the females on sexual interactions with the new adult male, and the dominance status of the females based on the outcomes of dyadic agonistic interactions among them, in the three observational conditions. During the week before the new adult male was introduced, the youngest female–Kerstin–ranked immediately below her mother, Wanda, but above Andrea and Sabine, the two of her three lineal–consanguineous relatives (and Sabine ranked above Andrea). The dominance hierarchy almost followed the principle of youngest ascendency. Doris, which ranked below her older sister, Andrea, however, was an exception. When the new male was housed for about 26 days in the enclosure adjacent to that of the females, changes in the dominance hierarchy were observed: the nursing mother, Andrea, outranked both Kerstin and Sabine, thereby reorganizing the dominance hierarchy. During this phase, the dominance ranks followed a largely direct relationship with age (again, with an exception: Doris). When the new adult male was housed together with the females in the same enclosure, the observed changes in the dominance hierarchy reverted back. There was almost a direct correspondence between the level of sexual swelling and the dominance rank when the females were housed without any adult male ($r_s = 0.949$, $P = 0.014$) and when the new male was housed together with the females in the same enclosure ($r_s = -0.872$, $P = 0.054$). This, however, was not the case when the new male was housed in the enclosure adjacent to that of the females ($r_s = 0.462$, $P = 0.434$).

We observed that the inter-individual relationships among the females (which were more socio-positive than agonistic when the females were housed together without any adult male) remained socio-positive among them and with a new adult male introduced to the group. In a female-only group of lion-tailed macaques comprising members of a single matriarchy (which was the case with the present study group), a largely age-reversed dominance hierarchy is likely to develop merely out of the demographic structure, given that mothers consistently support their youngest daughters whenever there are conflicts between the daughters; resulting in stable matriarchal lines which are expected to be transitively dominant over each other[18,19]. Previously, to explain reverse dominance hierarchies among female Hanuman langurs (*Semnopithecus entellus*), Hrdy and Hrdy[20] suggested that reverse dominance hierarchy may be an adaptive feature of group organization, *sensu* allocating the females of higher reproductive value to higher dominance ranks.

Studies on several non-human primate species, for example, Hanuman langur[21], Japanese macaque[22], rhesus macaque[23], yellow baboon (*Papio cynocephalus*)[24] and chimpanzee (*Pan troglodytes*)[25], have demonstrated that the dominance status of a female markedly affects her survival and reproduction. This is because high-ranking females obtain priority access to limited resources and consequently are more likely to reproduce successfully than low-ranking females[26,27]. Consistent with these observations, when the new adult male was housed in the enclosure adjacent to that of the females, Kerstin and Sabine (which previously showed higher average level of sexual swellings and occupied higher dominance ranks in the dominance hierarchy compared to Andrea) spent considerably more time on sexual interactions with the new male (herein, a limited resource) – both directed by them towards the new male and directed by the new male towards them. During the same period, there was also a temporary change in dominance hierarchy which can be explained on the basis of the potential infanticide by the new male in the adjacent enclosure, leading to a higher degree of aggression of the nursing female, Andrea, and an increase in its dominance rank. This is corroborated by the fact that when the new male was housed together with the females in the same enclosure, it resulted in infanticide and subsequently, Andrea lost its higher rank. Previously, infanticide and attempts of infanticide by males have been reported in several non-human primate species, mostly in situations where a new adult male takes over a group by either driving away or incapacitating the former dominant male[28]. Females of the species that are more vulnerable to infanticide, for example, hamadryas baboons (*Papio hamadryas*), respond to infanticide by showing an immediate receptivity towards the new breeding male through the development of sexual swellings[29–31]. On the whole, the present observations provide an anecdotal observation on how the sudden introduction of a new adult male, especially to a female-only group, can result in temporary changes in the dominance structure among females, as previously reported[32] in a group of Japanese macaques. We argue that a multiplicity of factors underlies such changes in dominance relationships and dominance hierarchy, occurring within a short duration following the introduction of a new adult male.

The observed reverse dominance hierarchy, together with the knowledge of the genealogical relatedness of the females in the present study, show that the dominance relationships among female lion-tailed macaques are more despotic than egalitarian, as has been observed in the nepotistic and female-bonded societies of rhesus macaques and Japanese macaques[9]. Our observations support the proposition of Singh *et al.*[13] and have implications for the captive management and breeding of lion-tailed macaques. This is a species for *ex situ* breeding

under the Species Survival Plan (SSP), the European Endangered Species Breeding Programme (EEP) and the Coordinated Breeding Programmes of India (the native country of the species). Although comprehensive husbandry guidelines have been prepared[33] and several behavioural aspects related to management of the species, for example, male–male relationships, have been studied[34], any additional information may be further incorporated in the captive management and breeding of this endangered species. The present study provides insights into the relationships among female lion-tailed macaques in a critical situation: introduction of a new adult male can result in risk of inter-individual conflicts and agonistic encounters, which can subsequently result in infanticide. Despite an apparent increase in female–female sexual competition and a temporary instability in the dominance hierarchy, the overall relationships among the females and the newly introduced male might remain socio-positive. Nonetheless, there is a high risk of infanticide.

1. Thierry, B., Singh, M. and Kaumanns, W. (eds), *Macaque Societies*, Cambridge University Press, Cambridge, 2004.
2. Wrangham, R. W., An ecological model of female-bonded primate groups. *Behaviour*, 1980, **75**, 262–300.
3. van Schaik, C. P., The ecology of social relationships amongst female primates. In *The Behavioral Ecology of Humans and Other Mammals* (ed. Standen, V. F.), Blackwell, Oxford, 1989, pp. 195–218.
4. Sterck, E. H. M., Watts, D. P. and van Schaik, C. P., The evolution of female social relationships in nonhuman primates. *Behav. Ecol. Sociobiol.*, 1997, **41**, 291–309.
5. de Waal, F. B. M., The integration of dominance and social bonding in primates. *Q. Rev. Biol.*, 1986, **61**, 459–479.
6. Flack, J. C. and de Waal, F. B. M., Dominance style, social power, and conflict management: a conceptual framework. In *Macaque Societies* (eds Thierry, B., Singh, M. and Kaumanns, W.), Cambridge University Press, Cambridge, 2004, pp 157–181.
7. Thierry, B., Social epigenesis. In *Macaque Societies* (eds Thierry, B., Singh, M. and Kaumanns, W.), Cambridge University Press, Cambridge, 2004, pp. 267–289.
8. Kutsukake, N., Matrilineal rank inheritance varies with absolute rank in Japanese macaques. *Primates*, 2000, **11**, 321–335.
9. Chapais, B., How kinship generates dominance structures: a comparitive perspective. In *Macaque Societies: A Model for the Study of Social Organization* (eds Thierry, B., Singh, M. and Kaumanns, W.), Cambridge University Press, Cambridge, 2004, pp. 186–204.
10. Preuschoft, S., Paul, A. and Kuester, J., Dominance styles of female and male barbary macaques. *Behaviour*, 1997, **135**, 731–755.
11. Kumar, A., *The Ecology and Population Dynamics of the Lion-tailed Macaque (Macaca silenus) in South India*, Ph D thesis, Cambridge University, Cambridge, 1987.
12. Sushma, H. S. and Singh, M., Resource partitioning and interspecific interactions among sympatric rainforest arboreal mammals of the Western Ghats, India. *Behav. Ecol.*, 2006, **17**, 479–490.
13. Singh, M., Krishna, B. A. and Singh, M., Dominance hierarchy and social grooming in female lion-tailed macaques (*Macaca silenus*) in the Western Ghats, India. *J. Biosci*., 2006, **31**, 369–377.
14. Preuschoft, S. and van Schaik, C. P., Dominance and communication. In *Natural Conflict Resolution* (eds Aureli, F. and de Waal, F. B. M.), University of California Press, Berkeley, 2000, pp. 77–105.
15. Lehner, P. N., *Handbook of Ecological Methods*, Garland Press, New York, 1979.
16. Singh, M., Singh, M., Sharma, A. K. and Krishna, B. A., Methodological considerations in measurement of dominance in primates. *Curr. Sci.*, 2003, **84**, 709–713.
17. Hausfater, G. and Hrdy, S. B., *Infanticide: Comparative and Evolutionary Perspectives*, Transaction Publishers, Rutgers, USA, 2008.
18. Chapais, B., Prud'homme, J. and Teijeiro, S., Dominance competition among siblings in Japanese macaques: constraints on nepotism. *Anim. Behav.*, 1994, **48**, 1335–1347.
19. Hausfater, G., Cairns, S. J. and Levin, R. N., Variability and stability in the rank relations of nonhuman primate females: analysis by computer simulation. *Am. J. Primatol*., 1987, **12**, 55–70.
20. Hrdy, S. and Hrdy, D., Hierarchical relations among female Hanuman langurs (Primates: Colobinae, *Presbytis entellus*). *Science*, 1976, **197**, 913–915.
21. Ellis, L., Dominance and reproductive success among nonhuman animals: a cross-species comparison. *Ethol. Sociobiol.*, 2010, **16**, 257–333.
22. Gouzoules, H., Gouzoules, S. and Fedigan, L., Behavioural dominance and reproductive success in female Japanese monkeys (*Macaca fuscata*). *Anim. Behav*., 1987, **30**, 1138–1150.
23. Sade, D. *et al.*, Population dynamics in relation to social structure on Cayo Santiago. *Yearb. Phys. Anthropol*., 1977, **20**, 252–262.
24. Altmann, J., *Baboon Mothers and Infants*, Harvard University Press, Cambridge, 1980.
25. Pusey, A., Williams, J. and Goodall, J., The influence of dominance rank on the reproductive success of female chimpanzees. *Science*, 1997, **277**, 828–831.
26. Fedigan, L. M., Dominance rank and reproductive success in primates. *Yearb. Phys. Anthropol*., 1983, **26**, 91–129.
27. Silk, J. B., Social behaviour in evolutionary perspective. In *Primate Societies* (eds Smuts, B. *et al.*), Chicago University Press, Chicago, 1987, pp 318–329.
28. van Schaik, C. P. and Janson, C. H., *Infanticide by Males and its Implications*, Cambridge University Press, Cambridge, 2000.
29. Colmenares, F. and Gomendio, M., Changes in female reproductive condition following male take-overs in a colony of hamadryas and hybrid baboons. *Folia Primatol.,* 1988, **50**, 157–174.
30. Zinner, D. and Deschner, T., Sexual swellings in female hamadryas baboons after male take-over: 'deceptive' swellings as a possible female counter-strategy against infanticide. *Am. J. Primatol*., 2000, **52**, 157–168.
31. Swedell, L., Two takeovers in wild hamadryas baboons. *Folia Primatol.*, 2000, **71**, 169–172.
32. Singh, M., D'Souza, L. and Singh, M., Hierarchy, kinship and social interaction among Japanese monkeys (*Macaca fuscata*). *J. Biosci*., 1992, **17**, 15–27.
33. Kaumanns, W., Krebs, E. and Singh, M., An endangered species in captivity: Husbandry and management of the lion-tailed macaque (*Macaca silenus)*. *myScience*, 2005, **1**, 43–71.
34. Kaumanns, W. and Singh, M., Social relationships among lion-tailed macaque (*Macaca silenus*) males in differently structured social units. *Curr. Sci.*, 2012, **102**, 1451–1455.

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