scendants of migrants from north China. The Ainu are probably descended directly from the Jomon population.

In addition, the dentition of the Anyang Chinese and the Jomon, including features not reported here, are still similar enough to conclude that both populations were derived from an earlier proto-Mongoloid gene pool in eastern Asia. Neither Ainu nor Jomon have dentitions supportive of a Caucasoid origin hypothesis. The dentitions of the Chinese and Jomon, placed as they are at approximately 3000 years ago, have two to three times as many significant trait frequency differences as do the Chinese-Japanese or Ainu-Jomon pairs (Table 2). This hints at a pre-Yayoi period of 6,000 to 9,000 years (10,000 to 7,000 B.C.) of genetic isolation between the Asian mainland and the Japanese island populations. Such a period would date approximately from the time of the flooding of the continental shelf connecting Japan and the mainland. It was not until Yayoi times that identifiable genetic links were reestablished; these appear to have been minor. Table 1 suggests a low but almost equal amount of gene flow in both directions between the Ainu and Japanese. The magnitude and nature of the microevolutionary dental differences between north China and Japan by 1000 B.C. are worth remembering when considering various dates, sources, and migration numbers for the peopling of the New World and Pacific areas, as well as when considering the origin and antiquity of the Mongoloid geographic race.

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References and Notes

1. F. Weidenreich, *Palaeontol. Sinica N. Ser. D* (No. 1) (1937).
2. C. G. Turner II, thesis, University of Wisconsin–Madison (1967).
3. E. F. Harris, C. G. Turner II, J. H. Underwood, *Archaeol. Phys. Anthropol. Oceania* **3**, 218 (1975).
4. H. M. Yang, personal communication.
5. K. Hanihara, personal communication.
6. K. Kobayashi, K. Yoshida, T. Umehara, Y. Baba, in *Anthropological and Genetic Studies on the Japanese*, S. Watanabe *et al*. Eds. (Univ. of Tokyo Press, Tokyo, 1975).
7. Tokyo National Museum exhibits of Japanese prehistory.
8. W. Howells, *The Pacific Islanders* (Scribner's, New York, 1973).
9. H. Suzuki, *J. Fac. Sci. Univ. Tokyo Sect. 5* **3**, 279 (1969).
10. C.-M. Hsieh, in *The Pacific Basin*, H. R. Friis, Ed. (Special Publication 38, American Geographical Society, New York, 1967).
11. T. S. Wei, *Chin. Culture* **1**, 124 (1958).
12. G. R. Scott, thesis, Arizona State University (1973).
13. H. L. Bailit, *Dent. Clin. North Am.* **19**, 125 (1975).
14. J. F. Katich and C. G. Turner II, in *Actas del XLI Congreso Internacional de Americanistas, Mexico* (1975), vol. 1, p. 192.
15. C. G. Turner II, in preparation.
16. C. G. Turner II and K. Hanihara, *Am. J. Phys. Anthropol.*, in press.
17. M. Suzuki and T. Sakai, *Am. J. Phys. Anthropol.* **22**, 65 (1964).
18. ———, *J. Anthropol. Soc. Tokyo* **73**, 1 (1965).
19. ———, *ibid.* **64**, 87 and 135 (1956); ibid. **65**, 54 (1956).
20. K. Hanihara, T. Masuda, T. Tanaka, *J. Anthropol. Soc. Nippon (Zenruigaku Zasshi)* **82**, 75 (1973).
21. M. Suzuki and T. Sakai, *J. Anthropol. Soc. Tokyo* **63**, 1 (1954).
22. C. G. Turner II and G. R. Scott, *The Dentition of Living Easter Islanders, Eastern Polynesia* (Mouton, The Hague, in press); E. F. Harris, C. G. Turner II, H. L. Bailit, in preparation.
23. Preparation of this paper was made possible by a Richard Carley Hunt Fellowship from the Wenner-Gren Foundation for Anthropological Research. The An-yang Chinese data were gathered with permission and help from members of the Institutes of History and Philology, and Archeology, Academia Sinica, Taiwan, specifically, H. M. Yang, Li Chi, W. L. Ch'u, T. Jiang, and K. S. K. Ho. The Ainu and Jomon materials of the University Museum, University of Tokyo, were made available by K. Hanihara. This report is the sixth of a series on dental anthropology of the Pacific basin and adjoining areas (*3, 14–16, 22*).

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Hierarchical Relations Among Female Hanuman Langurs (Primates: Colobinae, *Presbytis entellus*)

Abstract. *Female hierarchies are stable over short periods but fluctuate from year to year. In general, young females rise in rank over older and often larger female relatives, even though old females remain active in troop defense. This previously undescribed dominance system can be plausibly explained with reference to inclusive fitness theory and the concept of reproductive value.*

Although hierarchical relationships are nearly universal among social mammals, little is known about factors determining rank. There are two known systems of status determination: rank determined by size (and therefore age) (*1*), and rank determined by genealogy (*2*). Among the better studied primate species such as Japanese and rhesus macaques, for which longitudinal information is available, daughters rank just below their mothers with younger daughters above older daughters. Once established, these positions in the hierarchy are relatively permanent and may have important consequences for a female's reproductive success (*3*). In both size-determined and nepotistic ranking systems, the dominant animal, either by virtue of greater size or powerful relatives, simply defeats subordinates when challenged. We propose a third type of ranking system for langurs, in which females are ranked in accordance with reproductive value (*4*). Individual reproductive value declines with age, and older female langurs defer to younger ones. Since such a system depends to a large extent on the compliance of low-ranking animals, it is only expected to occur in groups composed of close relatives.

Hanuman langurs are semiterrestrial primates that feed on fruit, seeds, and leaves. Ranging from high altitude in the Himalayas southward to Sri Lanka, langur populations can be found throughout the subcontinent of India. Langur troops are composed of overlapping generations of close matrilineal relatives accompanied by one or more fully adult males who have entered the troop from outside. The ouster and replacement of resident males has been observed at all sites where observations have continued over two or more years (*5, 6*). Whereas the male composition of a langur troop is transient, females remain together throughout their lives in the same home range. Previous studies described hierarchical relations among these females as unpredictable and poorly defined (*5, 7, 8*). Nevertheless, analysis of female-female displacements recorded during five annual 2- to 3-month study periods between 1971 and 1975, totaling 1503 hours of observation, at Mt. Abu, Rajasthan, reveals that the direction of displacements among females in this population is predictable over short periods.

"Displacement" occurs when one animal approaches another and the animal approached withdraws. Typically, approach occurs in conjunction with threats or actual contact. In most observed displacements (83 percent) the displaced animal relinquished access to some exhaustible food resource. Of the displacements related to food, some 33 percent occurred naturally while 67 percent were provoked by artificial provisioning (*9*). Displacements also occurred over positions that did not directly involve access to food (11 percent of observed displacements) and over access to infants (6 percent). Direction of displacement was consistent regardless of context.

Observations on female-female displacements were concentrated on three troops living in the vicinity of Abu town. The B-5 troop was composed of a maximum of 24 individuals (in 1972 and 1973) and as few as 18 (in January 1974, just after a male takeover). The B-3 troop contained as many as 22 individuals (in 1971) or as few as 15, including nine adult females (in 1972 just after a takeover). The B-6 troop contained five to seven adult females accompanied by variable numbers of adult males and infants (as many as 15 animals altogether, or as few as seven). All displacements recorded in focal-female samples and casual daily records (*10*) for which both partners could be identified were summarized in a matrix constructed for each study period for which there was sufficient information. The displacement hierarchy for all females more than 2 years old in B-5 troop in 1975 is shown in Table 1. Of 555 displacements recorded for the three troops, 15 (2.7 percent) did not conform to a linear arrangement. In B-6 troop between June and September 1972 there were four reversals in 88 interactions (4.5 percent). The B-6 and B-3 troops had no reversals in 144 interactions during February and March 1973. The B-3 troop had one reversal in 52 (1.9 percent), and B-5 had four reversals in 121 interactions (3.3 percent) in December 1973 and January 1974. There were six reversals in 150 interactions (4.0 percent) in B-5 in April and June 1975. These findings support the hypothesis that dominance relations among langurs can be predicted over short periods (*11*).

Marked changes in the ranks of individuals occurred between years. Several factors, including reproductive state, body size, mother's rank, and age, were considered in relation to these changes. No association could be found between changes in rank and changes in reproductive status. In troops B-3 and B-6, for example, the same female (in both cases, a young adult) remained in the alpha position through three study periods passing through various reproductive states, including cycling, pregnancy, lactation, and weaning, without apparent change in rank. Nor was any relationship between rank and body size apparent. In both B-5 (Table 1) and B-3, young females who had not yet attained full body size repeatedly displaced heavier animals.

Even though effects of kinship could not be fully assessed in the 4 years of our study, it was clear that langur females do not inherit a fixed rank beneath their mothers as has been reported for macaques. In 1975, rank positions 1, 2, 3, 4, and 8 in B-5 troop and 1, 2, 3, 5, and 6 in B-3 were occupied by young females known since they were nulliparas. Two of these females definitely rose in rank above their mothers and at least three others probably did so (*12*). Even after a female reached full adulthood, her rank was not fixed from year to year (Table 1).

Of the variables considered, direction of rank change was best (but not completely) predicted on the basis of age. In B-5 troop, females A, B, and C who ranked 9th, 10th, and 11th as juveniles in January of 1974 improved their positions in the following year so that by April of 1975, as subadults on the verge of giving birth to their first offspring, they occupied the top three positions in the female hierarchy. By using the postulate that young females rise in rank at the expense of their elders, we correctly predicted this change in writing prior to the study period (*13*, p. 223). Similar rises in rank by females ranging in age from juvenile to young adulthood were observed in the B-3 troop. In 1973 a primiparous female rose to the alpha position and remained there through 1975. Between 1973 and 1974, an 8th-ranking subadult rose to third place and remained there as a young mother in 1975.

In contrast to the fluctuations in B-5 and B-3 troops, the female hierarchy in the small B-6 troop remained comparatively stable. Only one change was recorded in the top or two bottom positions of the hierarchy in the years between 1972 and 1975; the oldest and lowest ranking female in the troop (Sol) disappeared and was presumed dead. The history of this troop during the period between 1971 and 1975 was marked by at least five different male takeovers, at least one temporary invasion by a male band, and a high incidence of infanticide (*6*). Infant mortality in B-6 troop during the first four study periods was at least 83 percent, and thus far no females born in the troop have survived past infancy. Although an extreme case, this situation illustrates the rank stability that is possible when maturing females are removed.

As would be consistent with a system in which young females rise in rank at the expense of their elders, the lowest

Table 1. Rank, previous rank, estimated age, weight, and displacement matrix for females of troop B-5 between April and June 1975. Females are listed so as to keep the number of times a female is displaced by a female listed beneath her as small as possible. Because a few females never displaced each other, a second score is calculated: the number of cells in which a female was displaced subtracted from the number of cells in which she displaced other females. If this second rule failed to differentiate between them, the females are tied.

1975 Rank	Female	1974 Rank*	Estimated age†	Weight (kg)‡	Displaces female													Total number of displacements
					A	B	C	D	E	F	G	H	I	J	K	L	M	
1	A	9	51 months	9.5		5	6		5		5	1	4	4	10	8	1	49
2	B	10.5	51 months	9.3			2	2				2	4	1	4	1	3	19
3	C	10.5	47 months					2				5	2		1		4	14
4	D	5	Young adult						2	2	1	1					1	7
5	E	12	Middle-aged	11.4						3	2	2	5	4	2	2	6	26
6	F	1	Young to middle-aged	11.8				1	1		1		2	1				6
7	G	6	Middle-aged	11.8		1								1	2	5	1	10
8	H	7	48 months	7.9			2		1						5	2		10
9	I	4	Middle-aged											1			1	2
10	J	3	Middle-aged	11.6											1	2	2	5
11	K	Too young	29 months	6.8												2		2
12	L	Too young	28 months	5.8														
13	M	8	Old adult															
Total number of times displaced						6	10	5	9	5	9	11	17	12	25	22	19	150

*The second-ranking female, together with her infant, disappeared from the troop prior to the 1975 study period. †Ages of females known since infancy are measured in months. Young adult female "D" was nulliparous in 1972, giving birth for the first time in January 1973 (probably around the age of 4 to 5 years). A female parous at the outset of the study but not obviously old at that time, is referred to here as middle-aged (that is, 9 years or more). The designation "old" is reserved for females with a particular complex of bodily and facial features, including deep creases encircling eyes and teeth worn almost to the gums; old females from Abu closely resemble photographs of captive Colobinae known to be 20 years or older (*11*). ‡Weights were obtained by luring animals onto a platform hanging from a scale. All animals were weighed between 7 and 8:30 a.m. except for female "G" who was weighed at 4 p.m.

ranks in the hierarchy in each of the three troops were occupied by the very young or else by old females. In general, very young animals were ignored by high-ranking females, while old females avoided interactions with troopmates. In 478 waking minutes that female "M," the oldest female in B-5 troop, was the object of focal-animal sampling during the 1975 study period, she approached another animal only once. She, in turn, was approached on 21 occasions and was displaced on 19 of these. In all three troops, old females tended to move and forage apart from other troop members and occasionally spent periods of several hours, or (as in the case of Sol in 1974) whole days away from the troop. Similar peripheralization of old females was mentioned in the initial langur study by Jay (*8*). One explanation for the solitary tendencies of old females is the interference they suffer from other females who routinely displace them and who occasionally attempt to take food from their mouths. In contrast to the "timidity" of old females, younger females frequently approached and initiated interactions with other troops members, and almost never left the troop.

Despite their apparent disinclination to compete and their disadvantaged position within the troop, old females participated vigorously in aggressive encounters with other troops, in defending the troop from dogs and harassment by humans, and in protecting troop infants from assaults by infanticidal males. In at least seven assaults on a B-6 infant by an adult male, the two oldest and lowest ranking females in the troop audaciously and repeatedly intervened to defend the infant. The infant's own (young adult) mother played almost no active role in defense of her offspring (*6*) (cover). Similarly, when a B-3 subadult kidnapped an infant from a neighboring troop, the two oldest among the B-3 females came forward to meet the mother from the other troop and prevented her from retrieving her infant (*14*). Because of their low reproductive value, such old females have less to lose from risk-taking, in terms of future reproduction, than do younger animals. Of four old females at Abu, one was observed with an infant once during 5 years for which she was identified, two were seen with an infant once each in 4 years of observation, while the fourth (Sol) was never seen with an infant in any of four study periods up until her death. In contrast, young and middle-aged females produced infants roughly once every 2 years. This pattern appears to be due to differences in fecundity, not to differences in mortality; old, middle-aged, and young mothers lost 33 percent of 3 births, 29 percent of 21, and 38 percent of 16, respectively (*15*).

One explanation for a ranking system that favors youthful females, combined with a defense system in which old females take greater risks, is provided by Hamilton's theory of inclusive fitness (*16*). A langur near the end of her reproductive career has low reproductive value and may stand to gain more in terms of genetic representation in future generations by "altruistically" investing in close matrilineal relatives than by pursuing an egoistic course. By contrast, young females entering their reproductive prime may stand to gain in fitness by outcompeting female relatives for available resources and by selfishly leaving troop defense to other animals.

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References and Notes

1. V. Geist, *Mountain Sheep: A Study in Behavior and Evolution* (Univ. of Chicago Press, Chicago, 197 M. W. Schein and M. H. Fohrman, *Br. J. Anim. Behav.* **3**, 45 (1955); P. R. Grant, *Anim. Behav.* **18**, 449 (1970).
2. D. Sade, in *The Functional and Evolutionary Biology of the Primates*, R. Tuttle, Ed. (Aldine, Chicago, 1972), p. 378; M. Yamada, *Primates* **4**, 43 (1963).
3. L. Drickamer, *Folia Primatol.* **21**, 61 (1974).
4. Reproductive value refers to the extent to which a female of a given age will directly contribute to the gene pool of succeeding generations; R. A. Fisher, *The Genetical Theory of Natural Selection* (Dover, New York, 1958).
5. Y. Sugiyama, in *Social Communication among Primates*, S. Altmann. Ed. (Univ. of Chicago Press, Chicago, 1967), p. 221; S. M. Mohnot, *Mammalia* **35**, 175 (1971).
6. S. B. Hrdy, *Folia Primatol.* **22**, 19 (1974); in preparation.
7. P. Jay, in *Primate Behavior*, I. DeVore, Ed. (Holt, Rinehart & Winston, New York, 1965), p. 197.
8. ——, thesis, University of Chicago (1963).
9. Provisioning by local inhabitants and by the researcher undoubtedly increases the frequency of aggressive interactions among langurs. Nevertheless, langurs living near Hindu temples and towns have been tolerated, revered, and very probably provisioned since at least the 5th century B.C. when the epic *Ramayana*, celebrating the exploits of Hanuman the monkey god, was compiled. Furthermore, at Abu and elsewhere, langurs are forced to compete among themselves for scarce resources whenever there is a severe drought, a regular occurrence throughout much of this species' range.
10. J. Altman, *Behaviour* **48**, 1 (1974).
11. By comparison, percentages of reversals recorded for single troops of Amboseli baboons and rhesus macaques at Cayo Santiago were 0.4 percent of 1638 interactions recorded over 14 months, and 1.0 percent of 5159 interactions over 24 months. These data indicate that relations between baboon and macaque females are more stable than those among langurs over long time periods; G. Hausfater, *Dominance and Reproduction in Baboons (Papio cynocephalus): A Quantitative Analysis* (Karger, Basel, 1975); E. Missakian, *Primates* **13**, 169 (1972).
12. There were ten young females in B-5 and B-3 troops who rose to the top portion of the hierarchy. Two of these ranked above parous females known to be their mothers. By a process of elimination, we deduce that at least three others ranked above their mothers, provided that their mothers had not died just prior to the beginning of the study in 1971.
13. S. B. Hrdy, thesis, Harvard University (1975).
14. Kidnapping of infant by subadult and rebuff of real mother by low-ranking old females was recorded on 16-mm film.
15. These data suggest that langurs again differ from rhesus macaques, a species in which mothers lose a disproportionate number (up to 45 percent) of first- and second-born infants compared to 21 percent of offspring born to females 7 years or older (*3*). These differences could be due to the greater opportunities that langur nulliparas have to practice caretaking skills on newborns (*13*).

W. D. Hamilton, *J. Theor. Biol.* **7**, 1 (1964).

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Acetylcholine Hot Spots: Development on Myotubes Cultured from Aneural Limb Buds

Abstract. *The hypothesis that neural induction plays a role in the development of acetylcholine hot spots (high-sensitivity regions) was tested by electrophysiological mapping of the distribution of acetylcholine sensitivity of myotubes derived from aneural hindlimb buds of chick embryos. Hot spots were found. Therefore, hot spot development is not dependent on prior contact with nerve processes.*

A current problem in developmental biology is that of identifying the interactions between developing nerve and muscle which are important in synapse formation. During development, embryonic skeletal muscle fibers are sensitive to acetylcholine (ACh) everywhere on their surfaces (*1*). After innervation occurs, the extrasynaptic sensitivity disappears, and ACh receptors in the adult are confined largely to the synaptic region (*1, 2*). Embryonic muscle fibers grown in vitro are also sensitive everywhere to ACh (*3, 4*). The excellent visual resolution possible with monolayer cultures permits detailed iontophoretic mapping of ACh sensitivity. Although the fibers in such cultures are sensitive to ACh over their entire surface, receptor distribution is not uniform. Rather, small discrete patches of elevated ACh sensitivity, called hot spots, appear. These are about 10 μm in diameter, are scattered at intervals of several hundred micrometers along the length of a fiber, and have a sensitivity about five times higher than background (*5–7*).

The functional significance of the ACh hot spots is unknown. Since they occur on uninnervated myotubes in primary