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Nicholas S. Thompson

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THE MOTIVATIONS UNDERLYING SOCIAL STRUCTURE IN *MACACA IRUS*

BY NICHOLAS S. THOMPSON

Department of Psychology, Swarthmore College

Variability among individuals has always been an interesting aspect of the social behaviour of macaques and their close relatives. Each age class, each sex, each individual troop member has characteristic modes of behaviour. Such behavioural differences are more than the necessary consequence of morphological differences. Differences between the sexes and between ages within the sexes are found not only in those activities closely associated with reproduction, but in characteristic patterns of play, aggression, and association as well.

C. R. Carpenter, author of a classic series of field monographs on the social behaviour of various primates, was the first to worry about the relationship between individual differences and troop structure. He has often pointed out (Carpenter 1942) that while in theory a description of the social behaviour of a wild troop of monkeys with N members is not complete until the behaviour of each of the N(N − 1)/2 dyadic combinations of animals has been described, in practice the problem of description is simplified because troops of monkeys are structured. That is, one can predict a great deal about the individual behaviour of a troop member if one knows his age and sex. As Carpenter wrote: 'When one begins a detailed analysis of a naturalistic group of monkeys or apes it is found that the group is *organized*, that it has structure and pattern and that limits (boundaries) are set to possibilities of movements and relations of each individual'.

Carpenter's comment raises a crucial question: Does the group's pattern of organization set limits on individual behaviour in the sense that the structure of a human organization sets limits on the individual behaviour of its members; or does the group's pattern of organization grow out of the differences in the inclinations of individuals belonging to different age and sex classes? For instance, do adult females behave like adult females because they are restrained within the centre of the troop and there subjected to stimulation which provokes characteristically adult female behaviour, or are females inclined to perform characteristic patterns of behaviour which tend to bring them together in the centre of the troop and thus incidentally contribute an element to the troop's structure?

A first approach to this problem is to study a group of monkeys without ever convening it. If one studies the N(N − 1)/2 dyads of a group of monkeys which has never met as a group and finds a group structure which is reminiscent of group structures in the wild, then one is in a better position to argue that the group's structure is the summation of the individual differences of the animals within it, and does not coercively create those individual differences.

A group of monkeys was convened in just such a way during a study of acquaintance in irus macaques. Preliminary analysis of these data (Thompson 1967) revealed very striking sex differences which closely paralleled sex differences observed in the wild. The data confirmed the notion that individuals carried within them the propensities which produced group structure.

Accordingly, the data were analysed to discover what these underlying behavioural propensities might be. The results of this analysis are the subject of this report.

Method

The method is described in detail on pp 307–308 of *Animal Behaviour*, Volume 15 (1967) and will only be summarized here. The procedures of the experiment were carried out on sixty-one of the sixty-six dyads which were formed from a group of six male and six female irus macaques varying in age from juveniles to young adults. (Five pairings were eliminated because they were cagemate pairs.) The estimated ages and weights of these animals are important to the discussion which follows and so are presented in Table I. Note that the weight variation among males is much greater than that among females.

The procedures consisted essentially in placing each pair in an observation cage for two 10-min periods spaced approximately 2 months apart. Behaviour during the observation periods was filmed at a rate of one frame per sec and at a shutter speed of $\frac{1}{30}$th sec. The film record was analysed for eight behaviour categories. These as well as other terms necessary to the discussion

Table I. Description of Subjects

Sex	Identification number	Avg. weight (kg)	Est. age (months)
Males	72	5·36	52
	75	4·60	26
	64	2·64	26
	66	3·10	24
	68	1·80	22
	70	2·30	20
Females	71	4·42	42
	73	3·07	38
	65	2·24	27
	69	2·15	27
	67	2·30	26
	63	2·25	22

are defined in Table II. All behaviour categories are mutually exclusive except tail up, which could be scored concurrently with any other behaviour. To be scored, a given behavioural act had to be identified in a minimum of two consecutive frames. Behaviours continuing beyond the 2-sec minimum were scored once for each 5-sec period in which they occurred.

Thus the animal which performed only one behaviour and performed it throughout his 20 min of observation could theoretically achieve a maximum count of 240 for that behaviour.

Results and Discussion

The goal of the data analysis was to infer from the behaviours observed in the encounters the behavioural tendencies underlying them. The basic criteria for inferring a behaviour tendency were the frequency of a behaviour and the extent of its relationships with other behaviours. If a

Table II. Definition of Terms

Term	Symbol	Definition
Fight	F	Biting or rough handling of one animal by another. Rough handling defined as any manipulation of such force as to cause the filmed image of the manipulated animal's head and/or body to be blurred.
Chase	C	On three successive frames, one animal is moving towards the other while the latter is moving away.
Mount	M	The 'normal' dorsoventral sexual mount (Altmann 1962, fig. 40, p. 416). Mounter places hands on the other's haunches and grasps the other's ankles with his hind feet.
Atypical mount	N	One animal brings his genitals into contact with the body of another in a manner other than typical mount. The mount may be atypical in that the mounter approaches in an inappropriate region of the body (head, back etc.) or approaches the appropriate region in an inappropriate fashion (pulling the other animal down on top of him etc.)
Inspect	I	Bringing the nose close to or manipulating with hand or mouth the genital region of another. Behaviours scored in this category ranged (with all intergradations) from grooming of the anogenital region to picking at it with the index finger of one hand to mouthing or smelling it.
Present	P	Standing still on four feet for two successive frames with tail raised or averted from the genital region and with hind quarters oriented toward the other animal (cf. Altmann 1962, fig. 38, p. 414).
Groom	G	Manipulating with two hands the fur of another.
Tail up	T	Raising the tail so that its whole length is above an imaginary extension of the animal's backbone line. The tail may not be supported by cage structures or other animals (cf. Altmann 1962, fig. 53, p. 435).
Distance	D	An arbitrary measure of the closeness of two animals varying from 0 (touching) to 4·5 (in opposite corners).
Weight	W	The average weight of an animal measured biweekly over the 3 months of the experiment.
active	subscript a	refers to the frequency with which the animal performed a behaviour.
passive	subscript p	refers to the frequency with which an animal had a behaviour performed on him.

Table III. Weight and Sex as Factors Determining the Frequency of Behaviour. Rate of performance per pairing on each of nine variables by males and by females and by the heavier and lighter members of same-sex pairs in male–male, male–female, and female–female pairings.

	Male–male pairs			Male–female pairs			Female–female pairs		
Category	by heavier	by lighter	by both†	by male	by female	by both†	by heavier	by lighter	by both†
Fight (F)	?	?	24·60	1·54*	0·00	1·53	?	?	0·46
Chase (C)	?	?	2·46	2·58*	0·00	2·58	?	?	0·33
Mount (M)	3·00	1·80	4·80	23·03*	0·00	23·03	0·00	0·00	0·00
Atypical Mount (N)	4·13*	0·00	4·13	5·35*	0·00	5·35	0·00	0·13	0·13
Inspect (I)	1·20	0·33	1·53	11·83*	2·32	14·16	2·06	4·33	6·40
Groom (G)	2·06	1·86	3·93	7·45	7·96	15·41	5·93*	22·00	27·93
Present (P)	0·60	0·33	0·93	0·29*	2·25	2·54	0·86	2·53	3·40
Total	?	?	42·38	52·07	12·53	64·60	?	?	38·65
Tail up (T)	18·06*	57·40	75·46	17·29*	30·70	48·00	11·86	16·53	28·40
Distance	?	?	2·44	?	?	11·96	?	?	2·37

? = indicates that the performer of the behaviour could not be determined.

† = differences between these three columns are significant at the 0·05 level of significance or better for all categories but distance.

* = indicates a difference between heavy and light performance or between male and female performance significant at the 0·05 level or better by the median test.

behaviour occurred very frequently and was highly and frequently correlated with other behaviours, weight, and distance, then it was thought to have a basic behaviour tendency underlying it. This approach required information about the frequency of various behaviours (Table III) and about interrelations among behaviours (Tables IV–VII).

The method by which Tables IV–VII were generated is complex and requires explication. The frequency of the six males' performance of each behaviour was correlated with the frequency of their performance of every other behaviour in male–male pairs and separately in male–female pairs. Similarly the frequency of the six females' performance of each behaviour was correlated with the frequency of their performances of every other behaviour separately in male–female and female–female pairs. This procedure yielded the four intercorrelation matrices presented in Tables IV–VII:

correlations across males in male–male pairs;

correlations across males in male–female pairs;

correlations across females in male–female pairs; and

correlations across females in female–female pairs.

Correlations of 0·83 or better are significant at the 0·10 level, of 0·89 at the 0·05 level, and of 0·94 at the 0·02 level.

In the presentation which follows, data from Tables III–VII will be brought to bear on each category in its turn.

Tables IV–VII. Correlation matrices showing the rank order correlations found among behavioural and other measures. Correlations were computed across males in male–male pairs, across males in male–female pairs, across females in male–female pairs, and across females in female–female pairs. Correlations 0·75 or greater are shown in italics. Correlations of 0·83(*) or better are significant at the 0·10 level, of 0·89(**) at the 0·05 level, and of 0·94(***) at the 0·02 level.

Table IV. Males with Males

	Chase	Tail up		Mount		Atypical mount		Inspect		Present		Groom		Distance	Weight
	total	active	passive	active	passive	active	passive	active	passive	active	passive	active	passive	joint	active
Fight total	−0·54	+0·49	−0·66	+0·67	*+0·84**	−0·52	+0·34	+0·27	+0·49	+0·31	+0·35	+0·15	+0·52	−0·66	−0·66
Chase total	+0·31	+0·20	−0·09	−0·64	+0·03	−0·27	+0·03	−0·18	*−0·83**	−0·09	−0·46	−0·09	+0·37	+0·37
Tail up active	−0·66	*+0·81*	+0·49	*−0·88**	+0·44	+0·70	+0·43	−0·68	+0·71	+0·21	*+0·76*	−0·66	−0·66
Tail up passive		*−0·75*	*−0·75*	+0·70	−0·03	−0·27	+0·06	+0·15	−0·53	−0·15	−0·33	+0·49	+0·49
Mount active			+0·62	*−0·89***	+0·41	+0·74	+0·46	−0·31	*+0·85**	+0·37	+0·74	*−0·81*	*−0·81*
Mount passive				−0·68	+0·51	+0·40	+0·68	+0·20	+0·54	+0·52	+0·59	*−0·75*	*−0·75*
Atyp. mnt active					−0·65	*−0·87**	−0·26	+0·49	*−0·94****	−0·61	*−0·87**	*+0·88**	*+0·88**
Atyp. mnt passive						*+0·83**	*+0·90***	−0·15	+0·68	*+0·83**	*+0·90***	*−0·85**	*−0·85**
Inspect active							+0·71	−0·49	*+0·94****	+0·74	*+0·94****	*−0·88**	*−0·88**
Inspect passive								+0·23	+0·66	*+0·84**	*−0·77*	*−0·79*	−0·42
Present active									−0·43	−0·03	−0·36	+0·12	+0·12
Present passive										*+0·75*	*+0·84**	*−0·88**	*−0·88**
Groom active											+0·68	*−0·76*	*−0·76*
Groom passive												*−0·94****	*−0·94****
Distance joint													*−1·00****
Weight active													

Intercorrelations across the six male animals of weight, distance, and of the behaviour frequencies performed by (active) and performed on (passive) the males in male–male pairings. Total frequencies are used with the categories Fight and Chase because active and passive roles were impossible to ascertain in male–male fight and chase.

Table V. Males with Females

	Chase	Tail up		Mount	Atypical Mount	Inspect		Present		Groom		Distance	Weight
	active	active	passive	active	active	active	passive	active	passive	active	passive	joint	active
Fight active	+0·29	−0·43	+0·29	+0·64	+0·21	+0·38	+0·40	+0·43	+0·34	+0·60	*+0·78*	−0·64	+0·41
Chase active	+0·03	*+1·00****	+0·14	+0·90**	−0·37	−0·06	−0·15	+0·64	−0·41	−0·03	+0·09	*+0·77*	
Tail up active	+0·03	*−0·83**	−0·03	−0·60	−0·55	−0·18	+0·03	*−0·81*	*−1·00****	*+0·94****	−0·43		
Tail up passive	+0·14	*+0·90***	−0·37	−0·06	−0·15	+0·64	−0·41	−0·03	+0·09	*+0·77*			
Mount active	+0·20	+0·14	*+0·81*	−0·15	+0·09	+0·46	*+0·83**	*−0·77*	+0·60				
Atyp. mnt active	−0·23	−0·13	−0·49	*+0·77*	−0·19	+0·03	+0·03	*+0·90***					
Inspect active	+0·03	+0·35	−0·39	*+0·81*	+0·60	−0·71	−0·03						
Inspect passive	+0·12	−0·40	+0·13	+0·55	−0·64	+0·23							
Present active	−0·63	+0·04	+0·18	−0·26	−0·44								
Present passive	−0·06	+0·03	+0·27	+0·64									
Groom active	*+0·81*	*−0·75*	+0·12										
Groom passive	*−0·94****	+0·43											
Distance joint	+0·37												
Weight active													

Intercorrelations across the six male animals of weight, distance, and of the behaviour frequencies performed by (active) and performed on (passive) the males in male–female pairings.

Table VI. Females with Males

	Chase	Tail up		Mount	Atypical Mount	Inspect		Present		Groom		Distance	Weight
	passive	active	passive	passive	passive	active	passive	active	passive	active	passive	joint	active
Fight passive	+0·74	+0·69	+0·06	−0·38	−0·06	−0·67	+0·38	+0·60	−0·58	−0·06	+0·10	+0·23	−0·20
Chase passive	+0·33	+0·58	+0·06	−0·06	−0·40	+0·72	+0·43	+0·12	+0·29	+0·68	−0·29	−0·46	
	Tail up active	−0·38	−0·58	−0·32	*−0·93***	−0·15	+0·25	−0·52	−0·46	−0·31	+0·58	+0·52	
		Tail up passive	*+0·83**	−0·14	+0·26	+0·61	−0·03	+0·54	*+0·89***	*+0·87**	*−0·94****	−0·66	
			Mount passive	−0·31	+0·43	+0·20	−0·41	+0·54	*+0·89***	+0·58	*−0·94****	−0·37	
				Atyp. mnt passive	+0·60	−0·09	+0·72	−0·03	−0·03	−0·17	+0·09	−0·20	
					Inspect active	−0·06	+0·03	+0·43	+0·43	+0·16	+0·49	−0·37	
						Inspect passive	+0·03	+0·38	+0·23	*+0·88**	−0·38	*−0·84**	
							Present active	−0·43	+0·06	−0·13	+0·14	−0·17	
								Present passive	+0·31	+0·67	−0·60	−0·26	
									Groom active	+0·55	*−0·94****	−0·49	
										Groom passive	−0·72	*−0·75*	
											Distance joint	−0·54	
												Weight active	

Intercorrelations across the six female animals of weight, distance, and of the behaviour frequencies performed by (active) and performed on (passive) the females in male–female pairings.

Table VII. Females with Females

	Tail up	Inspect		Present		Groom		Distance	Weight
	passive	active	passive	active	passive	active	passive	joint	active
Tail up active	−0·46	*+0·83**	−0·03	*+0·84**	−0·20	+0·66	−0·03	−0·66	−0·54
	Tail up passive	−0·43	−0·60	−0·32	−0·43	−0·31	−0·31	+0·37	+0·26
		Inspect active	+0·03	*+0·90***	+0·20	*+0·93***	+0·03	*−0·94****	*−0·83**
			Inspect passive	+0·06	+0·37	−0·23	*+0·89***	+0·08	+0·14
				Present active	−0·17	*+0·79*	+0·23	*−0·81*	*−0·81*
					Present passive	+0·23	+0·03	−0·31	−0·14
						Groom active	−0·23	*−0·99****	*−0·93***
							Groom passive	+0·09	+0·03
								Distance joint	*+0·94****
									Weight active

Intercorrelations across the six female animals of weight, distance, and of the behaviour frequencies performed by (active) and performed on (passive) the females in female–female pairings.

Mounting

The data strongly suggest that males are animated by some behavioural tendency which females do not share. Four behaviours—fight, chase, mount, and atypical mount—are performed almost exclusively by males; indeed, three of these—fighting and the forms of mounting—account for more than 60 per cent of male behaviour time, whereas they account for less than 2 per cent of female behaviour time. (Whenever the phrase 'behaviour time' is used, it refers to the sum of time devoted to all categories, except the non-exclusive category, tail up.)

Of these four, mounting appears to be the most important. Over all their pairings males mounted more frequently than they performed any other behaviour. Mounting represents more than 10 per cent of their interactions with each other and almost 50 per cent of their interactions with females. Not only is mounting frequent but it is frequently correlated with other measures. In the first three correlation matrices, Ma or Mp can be found highly correlated with Ta, Pp, Ip and Gp positively and with D, W, and Na negatively. (Ma doesn't appear on Tables VI and VII nor Mp on Tables V and VII because females did not mount.)

Because of the frequency of mounting in males and because of the pervasiveness of its relationships to other variables, a tendency to mount seems to be one of the primary motivations underlying behaviour in dyadic confrontations. This tendency occurs only in males and occurs in all males about equally. It is the only motivation proposed which distinguishes the two sexes and must, therefore, carry the burden of explaining all of the observed differences between male and females.

Grooming

Although females never mounted one another, they did spend a substantial proportion of their time in close interaction with one another. In pairings with other females, females spent 10 per cent of their total time and 70 per cent of their behaving time engaged in grooming. Over all their pairings, females performed grooming at a rate almost equal to that of all other behaviours combined. Grooming was also performed by males and received by males. Over 10 per cent of males' behaviour with other animals of both sexes consisted in grooming, and males gave grooming to females almost as often as they received it. Grooming like mounting is a pivotal variable. In Tables IV–VII Ga and Gp are involved in no less than thirty-one correlations above 0·75 with twelve of the seventeen other variables, notably Ia, Ta, and D.

Thus grooming, like mounting, seems to have

its own motivational tendency. Presumably the grooming tendency affected all animals regardless of sex, but its effects were less evident in males because of their conflicting mounting tendency.

Distance

Thus far in the analysis, only tendencies which bring animals together have been discussed. In fact, the monkeys spent most of their time apart and not engaging in any scoreable interaction whatsoever. Presumably they had some tendency which opposed or abated the tendencies for mounting and grooming.

The nature of this spacing tendency is shown in the correlation matrices. The variable distance (D) is found on all four diagrams to be highly and negatively correlated with mounting (Ma) and with the frequency of grooming (Ga) or the frequency of being groomed (Gp).

But high proximity and high frequencies of proximity-related behaviour are not distributed equally among animals. Correlations with weight (W) show that heavy animals of both sexes were found less often in proximity with members of their own sex, that heavy males engaged females more in behaviours suggestive of conflict such as chasing and atypical mounting and that heavy females did less inspecting of males than lighter females. In short, heavy animals showed less evidence of social integration than light animals.

The social difficulties of the larger animals could be explained either as a characteristic of them or as a characteristic of the response of smaller animals to them. Taken alone, the distance, grooming, and mounting data seem to suggest that large animals were less socially motivated than small animals, But large males were responsible for most of the chasing and atypical mounting and seemed—subjectively—to give every indication of trying to be in proximity with their smaller partners. Thus the larger animal's greater distances were probably caused not by a social apathy on their part but by some sort of social antipathy directed at them by smaller animals.

These relationships of distance with the other variables indicate that each animal has a spacing tendency. This tendency is excited by the sight of another animal and is proportional in its strength to that animal's proximity and size.

Fighting, Atypical Mounting, Chasing

Atypical mounting, fighting, and chasing are the range of responses which are shown by males motivated to mount when they encounter partners motivated to avoid them.

A male's tendency to mount may express itself in two forms; typical and atypical. The typical form requires the mounted animal to stand still and support at least part of the weight of the mounting animal. It thus requires the co-operation of the mounted animal. Atypical forms can be accomplished without the co-operation of the mounted animal. The mounted animal is cornered and forcibly held down while the pelvic thrusts are administered.

The circumstances which promote mounting and those which promote atypical mounting were understandably very different. Normal mounting was negatively correlated with weight and positively correlated with a number of variables which—like normal mounting itself—imply a degree of coordination and cooperation among animals. Atypical mounting among males, on the other hand, was negatively correlated with proximity-related variables; with partners of either sex, atypical mounting was *positively* correlated with weight.

Atypical mounting thus seemed to be the response of large animals to the spacing tendency which they elicited from small animals. Unable to secure the co-operation of the smaller animal, the larger satisfied his mouting tendency forcibly.

Many of the differences between male–male and male–female pairing arose because males were less willing to be mounted than females. A male has two reasons for avoiding a mount—his spacing tendency and his own mounting tendency which is physically incompatible. A female has but one reason. This difference accounts for the fact that females were mounted more than males, that fighting was more prevalent among males than among females, and that atypical ('uncooperative') mounting made up a much higher proportion of total mounts in male–male than in male–female pairings. It also explains a qualitative difference in the conflicts seen in male–male and male–female pairs. Male–male conflicts were face-to-face conflicts whereas male–female conflicts were face-to-rump conflicts. Females avoided much of the conflict simply because they chose not to face and fight their adversary but to flee him and be chased. Flight put them in a more appropriate position for male mounting and resulted in a very rapid resolution of the conflict.

Tail Up

The data suggest that raising the tail signifies

the arousal of the spacing tendency described above. Like the inferred spacing tendency it occurred in all animals and was most frequent in the smaller of most pairings. Like the inferred spacing tendency, tail raising appeared to be activated by proximity: high positive correlations of proximity or proximity-related variables with frequency of raising the tail occurred in males with males and in females with partners of either sex. Like the inferred spacing tendency, tail raising was activated by attempts on the part of males to enforce proximity on females. Correlations between male chasing and female tail raising were perfect and positive in male–female pairs; correlations between female tail raising and male atypical mounting and male weight were also high and positive.

One important exception was observed to the close positive relationships between proximity-related measures and frequency of tail up. In males interacting with females, frequency of male tail raising was negatively correlated with proximity. Here, because of the very great importance of male mounting drive in bringing about contact between males and females, the order of causality was reversed. Males whose approach tendencies were not expressed must have been males with strong spacing tendencies, and thus frequently hold their tails erect. This interpretation of tail raising as an indicator of spacing tendency may help in part to explain an ambiguity in the field literature (see review by Marler 1965). In wild macaques, tail raising is seen both in dominant animals approaching subordinates and in subordinate appeasing dominants. The common denominator of both situations may be that a decrease in distance is anticipated by the gesturing animal.

Present and Anogenital Inspect

Both presenting and anogenital inspecting occurred in circumstances which closely resemble those which elicited grooming. Both were particularly frequent in pairs that included at least one female and both were correlated with grooming wherever they appeared. Although similar in these respects, the two behaviours differed markedly in the amount that they were performed by males; anogenital grooming was frequently performed by males, presenting rarely.

Presenting and inspecting are clearly related to the grooming and mounting tendencies, but the exact nature of this relationship is not clear from the data.

Conclusions

The data suggest that at least three basic motivations underlie behaviour in dyadic encounters: a grooming tendency, a mounting tendency, and a spacing tendency. The grooming and mounting tendencies tend to bring animals together; the spacing tendency to drive them apart. The mounting tendency is active only in males; the spacing tendency is activated by the sight of another animal and is proportional in its strength to that animal's size and closeness.

The social structure of natural macaque groups probably arises in part from the action of these three motivations. Natural groups of acquainted individuals have a similar social structure to synthetic groups of strangers convened dyadically. The distribution of frequencies of various social behaviours among size and sex classes is remarkably similar in the two situations (Thompson 1967). Where patterns of behaviour are similar, presumably the motivations underlying them are also similar.

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