

## BRIEF REPORT

### Acute Changes in Social Composition and Agonistic Behavior in Male Vervet Monkeys (*Cercopithecus aethiops sabaesus*)

JAMES E. DILLON,<sup>1</sup> MICHAEL J. RALEIGH,<sup>2-4</sup> MICHAEL T. MCGUIRE,<sup>2,4</sup> AND DEBORAH B. POLLACK<sup>2,4</sup>

<sup>1</sup>Department of Psychiatry, University of Michigan School of Medicine, Ann Arbor;

<sup>2</sup>Department of Psychiatry and Biobehavioral Sciences, School of Medicine, University of California at Los Angeles; <sup>3</sup>Neurobiochemistry Laboratory, Brentwood Veterans Administration Medical Center, Los Angeles; <sup>4</sup>Nonhuman Primate Laboratory, Veterans Administration Medical Center, Sepulveda, California

Among nonhuman primates the composition of social groups influences the interactions of group members. We assessed the effects of acute changes in social composition on behavior among 15 adult male vervet monkeys (*Cercopithecus aethiops sabaesus*). Subjects were observed in their basal social groups which comprised 3 adult males, 2-4 adult females, and offspring; and in two subgroups consisting of either two or three adult males.

Agonism and vigilance increased in smaller groups relative to basal conditions, while subjects in two-male groups displayed more aggression than those in three-male groups. These findings suggest that, among male vervet monkeys, acute disruption of stable social groups increases aggressive behavior, and that the amount of agonism is influenced by the composition of the consequent subgroups. © 1992 Wiley-Liss, Inc.

**Key words:** aggression, social composition, social disruption, vervet monkeys, affiliative behavior

#### INTRODUCTION

Although the influence of social context on social behavior has long been a focus of behavioral research with nonhuman primates, the variables of group size and subgroup composition have received only moderate attention in experimental studies. For many primate species the pattern of interaction between two animals may be modified by the presence of a third [Hinde, 1983]. For example, heterosexual pairs of hamadryas baboons interact more when presented with a third male [Kummer et al., 1974]. Similarly, male-female pairs of titi monkeys draw closer together when confronted with unfamiliar pairs [Anzenberger et al., 1986]. Female pairs of rhesus macaques groom less, maintain a greater distance from one another, and are more aggressive when exposed to a male [Winston, 1985]. When a

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Address reprint requests to James E. Dillon, Child and Adolescent Psychiatric Hospital, University of Michigan Medical Center Box 0390, 1500 East Medical Center Drive, Ann Arbor, MI 48109-0390.

new monkey is introduced into a nuclear group of rhesus monkeys, increased huddling among group members accompanies aggression toward the stranger [Bernstein, 1964].

Other investigators have examined how behavior is influenced by the size and gender composition of the group, by the age-sex class and kinship affiliations of interacting dyads and interfering animals, and by the social rank of third parties. McGuire et al. [1978], for example, found that familiar juvenile vervet monkeys exhibited more affiliative behavior and lower activity levels with increasing peer group size. The presence of males may affect interactions among female subjects, as shown by Strayer et al. [1975], who reported higher rates of interfemale affiliative behavior in groups of squirrel monkeys containing males than in exclusively female groups. Conversely, Vaitl [1977a,b] observed in the same species that the presence of adult females and infants reduced aggression among remaining adult males. Among rhesus monkeys, the age-sex class of participants affects the likelihood of a third animal influencing the agonistic interactions between dyads, adult males being most likely to interfere against other adult males or adolescent males [Bernstein & Ehardt, 1986]. The influence of acute changes in social composition has not been extensively examined in adult male vervet monkeys (*Cercopithecus aethiops sabaues*). We observed subjects of this species in stable heterosexual social groups and in subgroups consisting of both two and three adult males. Following Vaitl, we predicted that removal of adult females and offspring would result in increased agonism among remaining adult males. Following McGuire et al.'s [1978] observations of increased affiliative behavior in larger groups of juvenile vervets, we anticipated that two-male groups would exhibit higher rates of agonistic behavior than three-male groups.

## MATERIALS AND METHODS

### Subjects

Fifteen adult male vervet monkeys (*C. a. sabaues*) from five social groups were studied. All were healthy, had fully erupted canines and third premolars, and weighed between 6.4 and 12.4 kg. Each social group comprised three adult males (the focal subjects), two to four adult females, and immature offspring. Apart from births, the compositions of the groups had been stable for at least 6 months prior to the experimental procedure.

Dominance rank was assigned according to the relative success of subjects in spontaneous intermale agonistic encounters, as described previously [Raleigh & McGuire, 1989]. Rank had been stable for at least 6 months prior to the experiment.

### Housing and Care

Animals were housed at the Nonhuman Primate Laboratory, Sepulveda Veterans Administration Medical Center, Sepulveda, CA, in outdoor enclosures measuring approximately 5 × 5 × 3 m and bounded by steel mesh on the roof and three sides, and by a nightroom at the rear [see Raleigh et al., 1984]. During observations nonparticipating group members were confined to squeeze cages within fully enclosed nightrooms having dimensions of approximately 2 × 2 × 4 m. Nightrooms were separated from outdoor enclosures by a wooden wall. Apertures connecting outdoor enclosures to nightrooms were sealed by a metal barrier to prevent any physical or visual communication between experimental subjects and nonparticipating subjects.

TABLE I. Behavioral Repertoire

Behavior	Description
Approach	Moving within 1 m of another and sitting down or remaining in proximity for at least 5 seconds
Aggress	All threats, genital displays, and contact aggression
Submit/avoid	Submit: crouching, hopping back, screaming, exaggerated chewing movements, or pawing the ground in response to another animal; Avoid: moving more than 1 m away from another approaching animal
Lipsmack	Rapid, repetitive smacking of the lips
Locomotion	Number of crossings of an imaginary grid dividing an enclosure into four rectangular spaces of equal size
Vigilance	Orientation to external stimuli characterized by a tense, erect posture; all aggression directed outside an enclosure
Rest	Sitting or lying in a relaxed posture

### Behavioral Observations

The behavioral repertoire, described in Table I, is based upon Stuhsaker's [1967] ethogram for this species. A focal subject sampling technique was used. For social interactions involving more than one animal we noted whether the focal subject was the initiator or the recipient.

Interrater reliability was assessed before and after the experiment according to a procedure described elsewhere [Raleigh et al., 1981]. For each behavior interrater reliability exceeded 85% agreement between all pairs of observers.

All observations were conducted in July and August 1986, between 0745 and 1130 hours.

### Design

Each group was observed in five social composition conditions on a single day. The following conditions were presented in random sequence: whole group; two males only (first pair); two males only (second pair); two males only (third pair); and three males only. The entire group was placed in the nightroom prior to the release of animals participating in each experimental condition. The order of observation of focal animals in each condition was randomized, and each animal was observed for three 5-minute intervals in each condition. Observations were commenced within 2 minutes of the formation of the groups.

### Data Analysis

Fifteen minutes of focal observation in the whole-group and in the three-male conditions and 30 minutes of focal observation in the two-male conditions are reported for each subject. Behavior rates are reported in events per hour per monkey and subsequent analyses are based upon these rates. Rates of social behavior reflect only interactions between adult males.

All statistical analyses were performed with the Statistical Package for the Social Sciences X, version 2.1 (SPSSX) [SPSS Inc., 1986].

Analysis of variance for repeated measures was carried out using the MANOVA program of SPSSX. The analysis employed a three-level within-subjects factor, social composition (whole group, three-male, and two-male conditions); a two-level between-subjects factor, social status (dominant and subordinate); and two planned orthonormalized contrasts. One contrast compared the whole group

**TABLE II. Mean Behavior Frequency and Analysis of Variance for Groups of Different Social Composition**

	Frequency: events/hour (standard error)			Significance of F-ratio
	Two males	Three males	Whole group	
Approaches initiated	1.9 (0.6)	1.6 (0.8)	4.3 (2.9)	NS
Approaches received	2.3 (0.9)	2.7 (1.1)	1.9 (1.0)	NS
Aggression initiated	10.0 (2.9)	4.3 (2.3)	0.3 (0.3)	<.001*,**
Aggression received	9.3 (3.8)	3.5 (2.6)	0.0 (0.0)	.007*,**
Submits/avoids initiated	11.2 (3.3)	6.7 (2.5)	0.5 (0.4)	.003**
Submits/avoids received	9.9 (2.0)	9.3 (2.4)	2.4 (1.1)	.012**
Lipsmacks initiated	6.1 (2.5)	5.6 (2.9)	1.3 (0.8)	.019**
Lipsmacks received	5.3 (1.9)	5.1 (3.2)	0.0 (0.0)	.008**
Locomotion	70.7 (16.6)	45.3 (7.9)	55.2 (24.4)	NS
Vigilance	12.0 (3.5)	8.0 (3.1)	3.2 (0.8)	.005**

\*Two-male group is significantly different from the three-male group,  $P < .05$ .

\*\*Whole group is significantly different from two- and three-male groups,  $P < .05$ .

with subgroups and the other compared the two-male condition with the three-male condition. Square-root transformations of variables were employed when these resulted in distributions better approximating normality as judged from statistics of skew and kurtosis.

## RESULTS

Table II shows the mean rate and standard error of each behavior in the three social composition conditions and displays the significance ( $P$ ) of the F-ratio for the social composition factor in the analysis of variance. There are no statistically significant effects of social status and no significant interactions between social composition and social status at the .05 level for any behavior.

Intermale approaches initiated and received are not significantly affected by social composition.

Aggression initiated and received varies significantly across social composition conditions. Rates of aggression are higher in the subgroups than in the whole group; furthermore, subjects in two-male groups exhibit more than twice the rate of aggression shown in three-male groups.

Submits/avoids and lipsmacks initiated and received are significantly influenced by social composition, reflecting principally the difference between the whole group and subgroup conditions.

Locomotion is not significantly affected by social composition. Vigilance, including threats and displays directed outside the animal's social group, increases significantly in the small group conditions.

## DISCUSSION

These results indicate that acute disruption of stable social groups of vervet monkeys promotes agonism among males placed in temporary subgroups consisting of two or three males. Thus, in this experiment aggression between adult vervet males increases as group size decreases, suggesting a specific effect of the size or composition of the subgroups created by acute social disruption. The alterations in aggressive and submissive behaviors are not secondary consequences of a generalized increase in all activities. Neither locomotion nor approaching differ between the whole group and subgroup conditions. These observations suggest that the rate of intermale agonistic behavior may be particularly sensitive to

environmental alterations. Interestingly, in a companion experiment (unpublished), we found that the highest rates of locomotion and aggression directed outside the social group occurred in single, isolated males.

In this experiment social status did not explain individual differences in behavior following acute social disruption. In contrast to the rigid linear hierarchies observed in similarly housed macaques, the relative ranking of subordinate vervet males in stable social groups may often be ambiguous [Raleigh et al., 1983]. Increased aggression in two-male groups in this experiment may partly reflect increased interactions between subordinates in the absence of the dominant male. In this social context, the behavior of subordinates may tend to resemble that of dominant males, obscuring differences between ranks seen in groups that have not been disrupted. An interesting question meriting future study is how preexisting relationships between animals in stable groups influence the behavior of individuals during times of social disruption.

This study emphasizes the importance of social context, including social composition and social disruption, in assessing primate behavior. It suggests that the rates and patterns of social interactions among familiar vervet monkeys are strongly constrained by social context. Relative and absolute rates of behavior may change dramatically when social context is changed [Dillon et al., 1988; Keddy-Hector et al., 1989; Vaitl et al., 1978]. The observations are in accord with McGuire et al.'s [1978] study of juvenile vervets, which reported increased affiliative behavior and decreased locomotion in peer groups of increasing size, and with Vaitl's [1977a] report of increased aggression among adult male squirrel monkeys following removal of females and juveniles.

These findings apply to acute changes in social composition of brief duration. Such changes may also be present in free-ranging conditions, where the proximity of different animals may shift rapidly, resulting in the formation of transient functional subgroups. Unlike free-ranging conditions, however, these experimental manipulations are involuntary and occur outside an appropriate ecological context. Whether similar phenomena occur in stable, undisrupted subgroups of males may be the subject of future research.

## CONCLUSIONS

1. In adult vervet males, agonistic behavior and vigilance increase when the composition of a stable social group is acutely altered by removal of females and juveniles.
2. Vervet males from stable social groups exhibit more aggression in acutely formed two-male than three-male groups.
3. Social context, including size, composition, and recent history of disruption of social groups, is potentially an important variable influencing primate social relationships. Descriptions of primate social behavior may be valid only for a particular social context.

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