

ANALYSIS OF A KEY ROLE IN A CAPUCHIN
(*CEBUS ALBIFRONS*) GROUP¹

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ABSTRACT

A series of challenge situations was used to study the response patterns of group members in capuchin, rhesus, and pigtail monkey groups. Analysis and comparison of responses associated with key roles revealed important similarities in all groups despite the apparent absence of a status hierarchy among the capuchins. It is suggested that the "control animal" role is independent of the dominance or status hierarchies found in macaques. Further, it appears that it is this role and not dominance which is vital to the organization of many primate societies.

Analysis of the complex social organization of a primate group reveals a number of consistent response patterns which appear in only certain individuals within the group (Bernstein and Sharpe, 1966). These same response patterns can be recognized in other groups formed by animals of the same taxon, and often appear in similar form in several primate taxa. Such patterns may be referred to as "roles" in the restricted sense of consistent patterns of response shown by particular members of a society in specified situations. Although "role" as used by psy-

chologists and sociologists refers to human societies, the societies of monkeys and apes approach the complexity of simple human societies with specialized patterns of responses associated with particular individuals within the group.

One of the most striking response patterns, or roles, in primate societies is that of the "dominant male" in certain macaque and baboon groups. The readily observable status hierarchies in these groups have led investigators to define the role by "priority to incentives". Recent field and laboratory studies, however, suggest that other aspects of social control may be the essential elements of this role (Bernstein 1964a, DeVore and Washburn 1963, Hall 1960, Reynolds 1963, and Schaller 1963).

In a series of experiments at the Yerkes Laboratories, three groups of rhesus (*Macaca mulatta*), three groups of pigtailed (*Macaca nemestrina*), and one group of capuchins (*Cebus albifrons*) were tested in situations designed to elicit the expression of responses associated with the role of "dominant male". In addition, limited observations were made of Celebes black ape (*Cynopithecus niger*), vervet (*Cercopithecus aethiops*), gibbon (*Hylobates lar*), mixed taxa and additional rhesus, pigtail, and capuchin groups. Groups consisted of 6 to 26 animals, with a median of 11.

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The basic test situations involved challenges to the group. In addition, feeding situations were contrived to maximize competition in order to test for "priority to incentives", and agonistic episodes were observed to measure responses to intragroup sources of challenge. Data on the macaques confirmed expectations derived from other observations (Bernstein 1964a). On the basis of observations of laboratory and wild groups of capuchins (Bernstein 1964b), it was hypothesized that many of the important response patterns found in macaque "dominant males" might also be present in certain capuchin males, despite the apparent absence of a status hierarchy in the latter. This paper reports the results of a series of laboratory tests with a capuchin group.

METHOD

Subjects:

Twelve *Cebus albifrons*: three adult males, six adult females, and three immature animals were used. The group was formed in November, 1962 and tests were conducted from April to July of 1963. The stabilization of social responses prior to testing is reported in Bernstein (in press).

Apparatus:

An outdoor compound 48 x 24 x 8 ft, constructed of 2 x 4 in. welded wire over a lumber framework, was used to house the group. A 3 ft cubicle of similar construction could be extended into the compound from one side. A detailed description appears in Bernstein and Mason (1963).

Procedure:

Snake Test. The first test consisted of placing a live 4 ft snake (tentatively identified as *Elaphe obsoleta quadrivittata*) in a transparent plastic box within the 3 ft cubicle and presenting it to the group. Two observers scored all responses directed towards the snake and indicated which animals approached the box. Observations were made for 1000 sec from an enclosed observation post directly behind the cubicle, and for an additional 1000 sec from the opposite side of the compound.

Human Intruder Test. A human entered the compound and walked a fixed pattern waving a stick. Two complete circuits were completed in 100 sec and there were 10 such trials. Following this, a different human in-

truder remained passively seated in the compound for 1000 sec, then offered fruit every 100 sec, for the next 1000 sec.

Cubicle Tests. A group member was captured and placed in the 3 ft cubicle and presented to the group for 300 sec. Following this, the active human intruder entered the compound for 100 sec and departed for 100 sec, alternately, for 10 trials. During the first five intrusions observers remained in the observation post, and during the last five intrusions they moved to the opposite side of the compound. After completing this series, the subject was removed from the cubicle and held for 300 sec against the wire wall of the compound. The animal was then released into the compound and observations continued for an additional 300 sec. This procedure was repeated with each of the 12 group members.

Two observers scored all group responses and the responses of the captured animals. Approaches and contacts with the caged animal and the cage were scored in addition to social responses between animals and responses directed at the intruder or observers. Each response was scored to provide frequency counts, but duration was noted only for continuous vocalization (not more than 5 sec of silence between calls).

Complex Space Test. The final test consisted of modifying a 16 x 12 x 8 ft space in the compound by adding pieces of chain rope, nylon net, wooden platforms, swings and additional runways. A washtub of water was placed on the floor, a tether ball was hung, an infant "Busy Box" (a toy containing complex manipulanda) was attached to one wall, and several moveable pivoted platforms were placed in the space. For 2000 sec during each of the next nine days scores were kept identifying each animal in the test space, the duration of time spent in the test space, and new objects contacted. These observations continued each weekday thereafter for the next four weeks.

RESULTS

Snake Test. Presentation of the snake produced visual orientation by most animals in the group. There were 14 instances of threat directed at the snake in the first 1000 sec. The largest male accounted for 3, an immature male for 8, its mother for 2, and another immature animal for 1.

Immediately following presentation, the two older immatures approached and threatened the snake. They were joined by the mother of one of them, and the largest male which placed his arm over the back of the more active immature animal—a response interpreted as aiding (Bernstein, in press). It was repeated three times. The largest male also groomed the immature animal's mother. These were the only animals to come within 8 ft of the snake during the first 1000 sec.

During the second 1000 sec three more animals approached but showed no directed responses to the snake. The two immature animals climbed onto the cubicle with one assuming the infant riding position on the other briefly.

Human Intruder Test. During 9 of the 10 trials when the intruder was active, the largest male threatened him and produced 95 percent of the 20 discrete threats counted. Many threats were prolonged (duration greater than 10 sec) and perhaps should be considered as multiple threats. The largest male was the only group member to approach the intruder; all other animals fled each time the intruder approached with the exception of one female who failed to flee twice. Considerable vocalization including the typical alarm call occurred, but the largest male repeatedly vocalized (in a distinctive barking voice) directly at the intruder whereas only one other adult male and an immature male ever vocalized directly at the intruder, and then only once each. The youngest immature never left its mother's back and another immature also rode its mother's back briefly.

In contrast, when the passive intruder was present an adult female threatened twice with the largest male joining her in threatening the intruder once. Other animals oriented towards the intruder and there was some vocalization. One immature nursed, a second threatened a female, and most animals remained in a far corner moving slowly.

Food offers immediately attracted the largest male, two immature animals, and a female. The female climbed onto the intruder and fed and one immature took food from the intruder, whereas other animals only took food dropped on the ground. The largest male threatened the intruder once and two females threatened the observers and the intruder. One of these females

threatened twice more before taking food. Other animals took food from one another and the youngest immature moved independently near its mother.

Cubicle Tests. Caging a group member produced considerable vocalization, including alarm calling, which increased with the entry of the intruder. When the intruder was absent, group members gathered near the captive member and there was a great deal of reaching towards and contact with the caged animal. These activities and attempts to escape the cubicle decreased when the intruder was present.

Aggression towards the intruder was intensified when the captive animal was being held. Following release, the released animal often joined the group in further aggressive displays. Data are summarized in Table 1.

Examination of individual scores revealed a distinctive response pattern for the largest male. He threatened and charged the intruder 3 times more often than did any other animal, he was responsible for almost all the noisy demonstrations directed at the observers and intruder, and, he was on the ground next to the caged animal twice as often as was any other animal. Further, in addition to being in the area of caged animals, he contacted them twice as often as did any other group member whether the intruder was present or absent. He was also responsible for almost all vocalizations directed at the intruder. When confined to the cubicle, the largest male showed more aggression to the intruder and reached out towards and vocalized at the intruder more often than did any other animal. Finally, when group members were held, and following their release, the largest male was most active in threatening, charging and reaching towards the experimenters. Although he was sometimes joined by other animals, they seldom showed responses as persistently or as intensely, and did not respond when he was not present. When the largest male was confined to the cubicle, other group members clustered near him when the intruder was active.

One immature male was very vocal throughout testing and gave the alarm call continuously. He and another immature male were also most vigorous in attempts to escape the cubicle when confined. The third immature animal remained on its

TABLE 1
Response frequencies when individuals were separated from the group and restricted in space.

Response	Human active		Human hidden		Subject held		After release	
	group frequency	caged animal frequency	group frequency	caged animal frequency	group No. trials (of 12)	held animal No. trials (of 12)	group No. trials (of 12)	held animal No. trials (of 12)
Vocalization	105	55	84	46	7	11	2	6
Alarm call	72	27	56	36	5	1	2	1
Caged animal contacts	23	0	132	18	3	—	—	—
Aggressive to observers	2	0	109	30	6	—	6	5
Aggressive to intruder	44	39	—	—	—	—	—	—
Approach experimenters	35	—	—	—	5	—	2	3
Group flees	35	—	—	—	—	—	—	—
Individual flees	86	—	—	—	—	—	—	—
Group follows one animal	19	—	—	—	—	—	—	—
Backtracking	12	—	—	—	—	—	—	—
Within 3 ft. of intruder	13	—	—	—	—	—	—	—
Demonstrating	7	1	19	2	3	—	4	0
Non directed responses	1	0	7	2	0	—	0	0
High location near cage	10	—	337	—	2	—	0	0
Medium location near cage	8	—	141	—	2	—	0	0
On ground near cage	7	—	110	—	5	—	1	1
Frequency enter cage area	39	—	462	—	8	—	6	—
Struggle for release	—	12	—	19	—	4	—	—
Reaching through cage wire, no contact	1	35	0	8	7	—	0	0

Note: A dash indicates the response is not applicable.

mother's back during all trials and its mother fled the intruder more often than did any other animal. She also backtracked most often, but always did so while the largest male was between her and the intruder. (Backtracking by one or more animals was most common initially, i.e. quietly retracing the path that the full group had just covered in a noisy jumping flight from the intruder). When mother and infant were separated, both gave persistent alarm calls, but though the mother was aggressive towards the intruder when her infant was being held or confined (she showed few responses when other animals were involved) her infant showed little response when its mother was held or caged, but instead remained quietly with the group.

Trials with the human intruder became progressively less effective in producing avoidance responses. Whereas initially the group fled at the start of each approach of the intruder, they gradually tolerated closer approaches and some eventually remained

on high platforms and did not flee. Advances by the largest male also increased in frequency, as did various demonstration responses such as shaking or banging objects. The cohesiveness of the group was most notable in early trials with the group fleeing as a unit, sometimes clearly following a single animal (a second adult male).

Complex Space Test. On the first day the complex space was available to the group, only the largest male and one female spent more than 10 sec in the area. On the second day another adult male and an immature male entered for short periods, and it was not until the third day that several animals spent any time in the area. Throughout the 29 observation days, some individuals spent significantly less time in the area than would be expected by chance (333 sec of each 2000 sec observation session since the complex space occupied one-sixth of the compound). Others gradually made increasing use of the new features and one adult male was in the area over one-half of the time (averaging

1262 sec per session). The least frequent entrant was the mother of the youngest immature animal (averaging 20 sec per session). Group scores fluctuated about chance with a mean of 449 sec per session.

Intragroup Disturbances. Although intragroups fighting was not frequent, when it occurred the largest male frequently responded and interfered in the interaction. During feeding tests, however, no status hierarchy could be detected, i.e. no consistent feeding order was observed when food was available from a single location, and few aggressive episodes occurred. Food was sometimes exchanged between animals and the exchanges were reciprocal. Detailed accounts are presented in Bernstein (in press).

DISCUSSION

The data thus support the hypothesis that the consistent response pattern described as the role of the "dominant male" in macaque and baboon troop may occur in capuchin groups even when there is no evidence of a clear status hierarchy. Common responses include: assuming a position between an external disturbance and the group, attacking whatever appears to be distressing a captured group member, and approaching and terminating most cases of intragroup disturbance. Similar observations were obtained from studies of vervet, Celebes black ape, gibbon, and additional rhesus, pigtail, capuchin, and mixed taxa groups. I therefore suggest that the term "dominant male" be restricted to descriptions of a status hierarchy and another term selected for the described role. "Leader male" has been suggested, but in primate groups, animals fulfilling this role seldom travel first in group progressions, although they may exercise some control over troop movement. The key functions of this animal appear to be the control of intragroup disturbance, and the responses of the group to external challenges. "Control animal" is therefore suggested as a more appropriate term for the role.

Group members respond to the control animal in a distinctive fashion. They frequently enlist his aid in threatening both other group members and extra group targets. Further, when the control animal is confined in space, group members in distress may approach and remain in his immediate vicinity even if such approach in-

creases their proximity to the cause of their distress. Approaches to the control animal are especially notable in the case of macaques where a status hierarchy exists and social distance is ordinarily enforced with subordinates avoiding the immediate vicinity of superiors. Control animals are also far more vigorous in attacking an external source of disturbance when the challenge is directed at the group rather than to the control animal as an individual and alone. In the capuchin group reported, the largest male often permitted friendly contact with humans when he was alone, whereas when the group was present and a human disturbed them, he was aggressive towards the human. Responses included: shaking and banging of objects, vocalization and bluffing, as well as direct attack.

In the present series, the relative lack of responsiveness to the snake can be interpreted as indicating that the snake so presented was not a serious challenge to the group. Other situations were perhaps more direct challenges. Certain complex relationships between group members could be observed in the course of testing in addition to the role of the control animal, and deserve future study.

Although the largest male capuchin approached and remained near all potentially challenging stimuli more than did any other animal, he was not simply the boldest animal in the group, as was revealed during tests when a passive person offered food. The largest male did not make contact with, or take food directly from the person although other members did so. When responding to challenges, the male shook and banged objects and engaged in other activities which attracted attention to himself. The responses were similar to those observed in wild troops when approached by a human (Bernstein 1964b).

The largest male frequently remained behind when the group fled and another adult male was usually the initiator of group movements. When the largest male did travel with the group, however, the other animals followed close behind him.

The responses of the macaque groups tested can be compared with the capuchin data and although the macaques were at times more intense and more successful in aggression towards the intruder, the differential size of capuchins and macaques may account

for this. The size factor may be responsible for the relative caution with which capuchins approached new stimuli such as the complex space. The similarity of responses to challenges by control males in capuchin and macaque groups is striking and indicates that the protective function of the role is not necessarily associated with dominance or the existence of a status hierarchy. This conclusion was also supported by observations of the other groups mentioned. More data will be required, however, before any conclusions can be reached as to the differences between capuchin and macaque social organizations.

Among the macaques, and in the capuchin groups, particular animals (including some large females) at times supported the control animal in its activities. In larger groups several animals showed the same pattern of responses. In some groups, other animals, usually adult or subadult males, sometimes produced the pattern of responses associated with the control animal when it failed to respond for any reason. Removal of the control animal resulted in rapid substitution although return of the original control animal resulted in immediate resumption of the former pattern. This suggests that the functions of the control animal are essential to the society and failure to fulfill the function will elicit the responses in substitute animals.

Other roles in primate societies must also be carefully examined in order to understand the organization of a society and the differences between societies. The role of the control animal operates within the context of an organization of interrelated roles, some of which are briefly reflected in the present series of tests. We must be prepared, however, to find as much diversity in roles and role expressions as has been discovered in morphology. Morphological responses to ecological pressures have undoubtedly been paralleled in behavioral adjustments which may be reflected in the variety of organizations in primate societies.

CONCLUSIONS

Analysis and comparison of the responses of control animals in capuchin and macaque groups revealed certain important similarities in the functions of these animals. Although the responses of these animals to challenges to the group were similar in both species, no evidence of a status hierarchy could be found in the capuchin group. The control animal role in some primate groups may therefore not be associated with the attributes of dominance. The control animal role does appear to be vital to the organization of some primate societies.

The term "control animal" is tentatively suggested for the distinctive role described.

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