

## Social Context Affects How Rhesus Monkeys Explore Their Environment

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This study reports on social modulation of exploratory behavior and response to novelty by members of a captive rhesus monkey colony. The group was trained to split in half, with one subgroup composed of dominant members only, the other of subordinates. The animals were then presented the same initially novel stimuli (i.e., sand-filled metal boxes containing hidden food items) in two social contexts differing in hierarchical composition. In a combined context, all group members (i.e., both subgroups together) were simultaneously presented the stimuli. In a split context, only members of the top or bottom half of the group (i.e., each subgroup in turn) was independently presented the stimuli. Subordinates responded similarly to dominant animals in the combined context but differently in the split context, where they were far more hesitant. Rank-related differences were evident in the way animals used their home compound and in their approach and responsiveness toward the stimuli. These findings show that social context influences how animals explore novel situations, possibly reflecting different social roles or status effects on the perception of social structure. Also, despite the complexity of primate social relationships, the separation technique produced no permanent or adverse effects on the social integrity of the group. This study shows that manipulating the social environment through separation training can be a powerful tool for assessing contextual influences on behavior. *Am. J. Primatol.* 44:205–214, 1998. © 1998 Wiley-Liss, Inc.

**Key words:** exploration; response to novelty; rhesus monkeys; social roles; social context; dominance relationships

### INTRODUCTION

The presence of others influences how animals respond to their environment, and, in social species, particular individuals can play a key part in determining the behavior of group members. A primate society comprises a variety of social roles that relate to the sex, age, and rank of its members, for instance, with

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alpha males typically controlling aggression [Ehardt & Bernstein, 1992]. Demographics and social structure are also linked to differential responsiveness to novelty and exploratory activity [Chamove, 1983; Fragaszy et al., 1994]. Exploration of novel items or situations can ultimately lead to the adoption of innovative behavior. Features of the social environment interact with characteristics of the individual to influence both the rate at which a group incorporates the new behavior and the pattern of transmission [Cambefort, 1981; Huffman, 1996].

Monkeys are among the most curious of animals; however, they often show marked individual differences in their interest in and manipulation of novel objects [Glickman & Sroges, 1966]. In general, juveniles most often initiate responding to novel situations or stimuli [Menzel, 1966; Joubert & Vauclair, 1986] and engage in more manipulation of objects than do adults [Byrne & Suomi, 1996]. In addition, whereas alpha animals are first to respond to new, threatening situations [Ehardt & Bernstein, 1992], exploration of inanimate novel objects or foods is characteristic of low-ranking animals [Menzel, 1966]. When contact with novel items is initiated by subordinates, it is interpreted as compensation: subordinates face more restrictions to their activities and are thus more apt to approach new objects and exploit resources not used by higher-status animals [Katzir, 1982]. In turn, dominant animals come to rely on the initiative of subordinates, as reflected by their own reluctance.

If certain animals play specific roles, such as leading or following, then the presence or absence of these individuals should influence the exploratory behavior of others. For instance, in a social group of macaques, do dominant animals take up the slack by exploring more when subordinates are absent? The purpose of the present study was to assess rank effects on exploration and response to novel stimuli presented in familiar space and to relate potential differences to the social circumstances. Dominant and subordinate group members were tested in two social contexts. They were tested together (in a combined context involving all group members) and in separate peer groups (in a split context involving only the top or bottom half of the colony). This study reports on rank-related differences in exploratory behavior as a function of the social context.

Conducting this experiment required training animals to divide into two groups, along a border between mid-ranking matriline. Because the social organization of female-bonded macaque troops involves a complex web of dominance-subordination relations, maternal lineage, kinship bonds, and alliance ties [Wrangham, 1980], an important issue was if such a manipulation would be logistically feasible. Despite the apparent social order, rank relationships can be challenged or even altered when group composition is experimentally manipulated [Bernstein et al., 1979]. For instance, resident members of a stable group know their place and that of others within the social network, as demonstrated by the aggressive targeting of intruders and the mollifying influence of familiarity on the reception of newcomers [Bernstein et al., 1979]. Nevertheless, selective pairing of individuals can result in temporary rank reversals, such that a dominant animal can be easily outranked when sequestered with subordinates [Chapais, 1988]. Perhaps because social status needs continual reaffirmation, animals removed from a group are often harassed upon their reintroduction [personal observation].

Results of empirical studies, coupled with animal management wisdom, contribute to our understanding of dominance in social primates as the outcome of group dynamics [Wade, 1978]. On the one hand, we have gained an appreciation of the long-term stability of dominance relationships. On the other, we have witnessed social status as malleable and context-specific. The unifying view is that

status relationships are fluid—stable provided the social circumstances remain constant but more tenuous if conditions change. An experimental approach most often used in studies of primate social organization is one that challenges social stability with manipulations that typically produce changes in rank relationships. By contrast, this study was concerned with manipulating the social environment without affecting dominance relationships such that repeatedly removing entire matriline would become commonplace. This paper additionally reports on the separation technique as a tool for assessing the influence of social variables on behavior.

## METHODS

### Subjects and Housing

The subjects ( $N = 55$ ) were all the members of a captive group of rhesus monkeys (*Macaca mulatta*), comprising six matriline, including 38 females and 17 males, aged 5 months to 18 years. All animals were born, reared, and housed socially at the field station of the Yerkes Regional Primate Research Center of Atlanta, Georgia. The housing quarters consisted of a large outdoor compound (38 × 38 m), with an attached indoor area that could be partitioned into two compartments, each with independent access to the outside. Animals isolated indoors had no visual access to the outside. The daily diet of Purina monkey chow and oranges was held until after testing, which was conducted from 0800–1200 h during the nonbreeding season.

The matriarchs of the study group had lived together for over 15 years, and their descendants maintained stable social relationships. Rank relations across matriline were verified by observing subjects for aggressive and submissive behavior. A hierarchy was determined by ranking the winners of dominance–subordination encounters over losers in an order that produced the fewest reversals, with the constraint that all members of a matriline be grouped together [Drea, in press]. Nonnatal males were integrated into this matrix based on their relative ranks. The dominant subgroup included all members of the three highest-ranking matriline and one nonnatal male ( $N = 27$ ). Similarly, the subordinate subgroup comprised all members of the three lowest-ranking matriline and two nonnatal males ( $N = 28$ ). Animals in the dominant subgroup were dye-marked black on their heads for quick and easy recognition using an analine dye (#1 Nyanzol D. Flakes #21707).

### Separation Training

During 21 days, the animals were trained to separate along the border between the third- and fourth-ranked matriline. A group separation began by locking subjects outdoors and partitioning the indoor area. Because dominant animals show more relaxed responsiveness [Bartlett & Meier, 1971], subordinates were sequestered first, accommodating their tendency to bolt when approached by humans. The right-hand door to the first compartment was unlocked and swung open; then only subordinates were directed toward that doorway. Once all subordinates were inside, the left-hand door to the second compartment was unlocked and swung open, and all remaining dominant members were directed to and locked inside this compartment. Subordinates were always run clockwise, whereas dominant animals were always run counterclockwise. Traditions such as these were used to enhance training.

At first, separations required over 1 h of handling time and did not always produce perfect splits, with either dominant individuals mishoused with subordinates or vice versa. After 7 days of training, handling time was reduced to 15 min, and separations produced perfect splits every time. After 7 more days, separation time was further reduced to 4 min. Two observations merit mention. First, imperfect splits were sometimes associated with aggressive outbursts that required aborting trials. This was true whenever a dominant individual was mistakenly housed with subordinates but not if a subordinate was mishoused with dominant animals. Aggression became negligible with perfect splits. Second, aside from trainer behavior, cues for separations came to rely on certain subjects. Notably, the same individuals were consistently the first to run indoors, and other animals appeared hesitant until these leaders initiated their subgroup run. Both were adult females, but neither was the dominant matriarch of her subgroup. Ultimately, the colony could be separated, on cue and in under 2 min, by merely pointing at first one and then the other key female.

### **Habituation**

Once separations produced perfect splits, training was accompanied by habituation (i.e., for 14 days). The animals were accustomed to being separated from others by initially allowing each subgroup 1 h per day alone outdoors. During this time they received preferred food items. Over the last 7 days, time alone gradually was reduced to 15 min. The order of subgroup release alternated randomly, and subgroups were always run back into their appropriate compartment before the next stage (i.e., dominant animals were never released into a subordinate-occupied compound or vice versa). Once each subgroup had a turn outdoors, both doors were opened simultaneously, and the reunited group was fed its diet.

Early during habituation, there was a marked rank-related difference in the manner in which animals used the compound. When the dominant subgroup was released, animals appeared unfazed by the absence of subordinates and immediately dispersed throughout the outdoor enclosure. By contrast, when the subordinate subgroup was released, its members appeared behaviorally constrained by the absence of dominant members. They remained near the indoor area and did not venture into other parts of the compound. Since the focus here was to make separations as rewarding as possible, subordinates were coaxed into traversing the compound by baiting the ground with favored foods. Initially, subordinates refused desirable food items placed easily within their reach, failing to take advantage of unimpeded foraging opportunities, and then only gradually accepted the food. Without such enticement, it is likely that the rank-related differences in response to novel stimuli (see Results) would have persisted longer or been more dramatic.

### **Response to Novel Stimuli**

Following training and habituation, the animals were presented the stimuli in two social conditions on each of 27 days. Three 15 min trials were conducted daily: one per combined condition and two per split condition. The stimuli were closed metal boxes (31 cm wide × 37 cm high × 21 cm deep), each with a central opening (8 × 8 cm) for manual investigation [Drea & Wallen, 1995]. Four boxes were used per subgroup (i.e., eight during combined testing, four during split testing). Each box was filled with 10 cm of sand and contained peanuts hidden at the bottom. Boxes were hung 1 m above the ground, on the outside of the fence,

with the openings facing the compound. The site for presentation of boxes was a 9 m stretch of the fenced enclosure farthest from the indoor area. Initially, these boxes were novel to the subjects, though gradually their novelty wore off over consecutive presentations.

After a group separation and while subjects were sequestered indoors, boxes were prepared and installed. Opening both animal doors simultaneously permitted combined testing of the whole group; opening only one door allowed split testing of a given subgroup. After each trial, boxes were removed and their contents tallied. Testing order across conditions was randomized and separated by 1 h. During this time, the group was reunited outdoors (thus, the group was separated twice daily). Within the split condition, subgroup testing occurred sequentially, in random order, and separated by 10 min. Thus, a possible testing sequence was as follows: first separation, combined testing, group reunion with 1 h break, second separation, first split testing of the dominant subgroup, 10 min break, second split testing of the subordinate subgroup, group reunion.

Upon release, subjects could repeatedly visit boxes and search their contents. Several monkeys could climb the fence and position themselves near boxes; however, only a single monkey at a time could insert an arm, through the fence, into the box opening to manually search for peanuts. Data were collected from an observation tower, and the identity of subjects approaching within 1 m of boxes was scored.

## Analyses

The dependent variable for assessing rank-related differences in exploration was the number of subjects per subgroup that approached the boxes. The 27 presentation days were divided into nine time periods, with the value for each period representing the mean for 3 consecutive days. On several days, certain low-ranking individuals were removed from the group for unrelated health-care reasons. Since the average number of subordinates present throughout the study was 27.6, compared to the average of 27 dominant animals, no correction for subgroup number was made for statistical analyses. A three-factor repeated-measures analysis of variance (ANOVA) was used to determine if participation differences existed between the two subgroups in the two social contexts across the nine time periods. Animals typically habituate to novel conditions after repeated exposure, so one prediction was that both subgroups would eventually show similar response patterns. Thus, planned comparisons of means for each subgroup per social context were made within the last period using F-tests for simple effects. Comparisons of subgroup participation within earlier intervals were made using Newman-Keuls' multiple-range tests. All comparisons used the error estimate for the three-way interaction.

## RESULTS

Animals showed differences in their exploration of boxes, and these differences related to their rank and to the social context (Fig. 1). Analyses revealed that, overall, more dominant than subordinate members visited the apparatus ( $F(1,18) = 76.33$ ;  $P < 0.001$ ), more subjects visited the apparatus in the combined than in the split context ( $F(1,18) = 20.89$ ;  $P < 0.001$ ), and more animals visited boxes in the later than the earlier time periods ( $F(8,18) = 5.50$ ;  $P < 0.001$ ). The three-way interaction ( $F(8,18) = 4.22$ ;  $P < 0.005$ ) showed that response differences between the subgroups, in the different social contexts, changed over time.

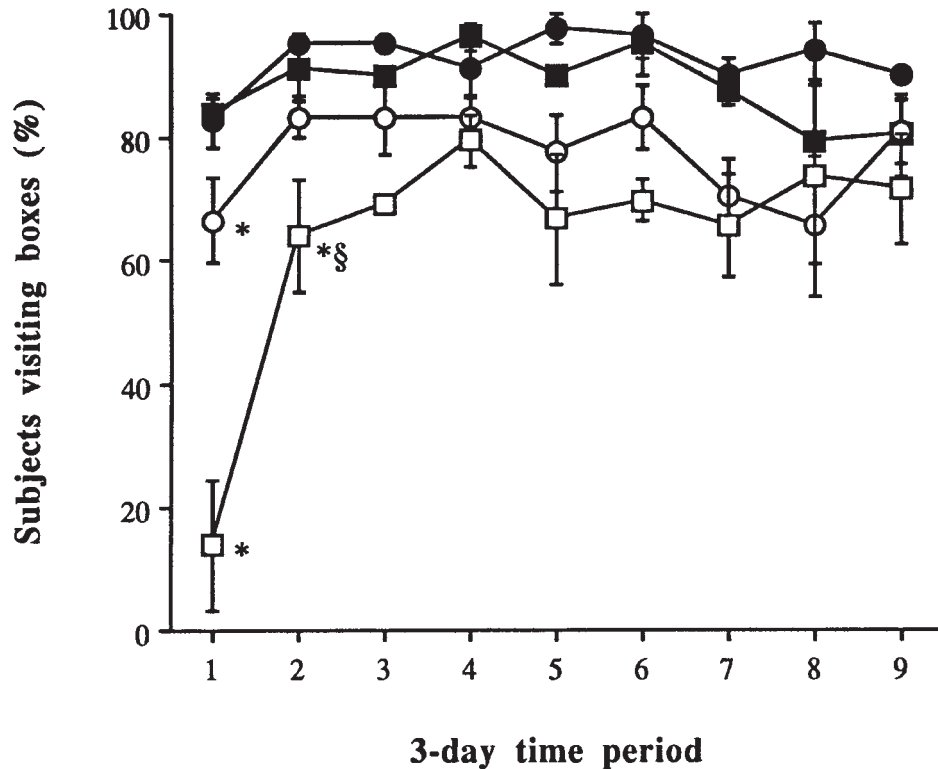


Fig. 1. Percentage of subjects from a captive rhesus monkey group that visited novel boxes across 27 presentation days. Each data point represents the mean ( $\pm$  SE) for a 3 day period. Values are given for the combined context, when dominant (●) and subordinate (○) subgroups were tested together, and for the split context, when dominant (■) and subordinate (□) subgroups were tested separately. Significant participation differences occurred in the first and second time intervals: \* < split dominant, combined dominant,  $P < 0.01$ ; § < combined subordinate,  $P < 0.01$ . There were, however, no differences by the last interval.

For instance, in each of the first two time periods, equal numbers from the dominant subgroup interacted with the apparatus in both contexts, whereas more individuals from the subordinate subgroup visited the apparatus in the combined than the split context ( $P < 0.01$ ). Additionally, in the first 3 day period, more dominant than subordinate animals participated in each context, but by the second period dominant animals outnumbered subordinates in the split context only ( $P < 0.01$ ). Investigation of individual responses in the first period showed that, on average, 80% of subordinates visiting the apparatus in the combined condition failed to do so in the split condition. This average dropped to 31.3% by the second period. These results showed that subordinates were less likely to explore novel objects in the absence of dominant animals.

Though subgroups initially differed in their responsiveness toward the boxes (i.e., when boxes were maximally novel), there were no differences between subgroups after 27 days of repeated exposure (i.e., when boxes had become familiar items). As predicted, planned comparisons made within the last period showed no differences, either between subgroups ( $F(8,18) < 0.8$ ; NS) or within subgroups ( $F(8,18) < 2.1$ ; NS). Thus, members of both subgroups were eventually equally responsive, approaching and interacting with the boxes and retrieving most of the available peanuts in both social contexts. These data showed that although

subordinates altered their behavior in response to social context, they eventually overcame their inhibition.

## DISCUSSION

Unlike previous studies that showed low-ranking animals to be the initiators of responding in novel situations [Menzel, 1966; Katzir, 1982], this study found subordinates to be either just as responsive as dominant animals or far more hesitant. Rank-related differences in behavioral responses were striking, unexpected, and expressed in several ways. First, there was a difference in tolerance of mishoused animals, with subordinates being less tolerant of mishoused dominant animals than vice versa. Second, there was a difference in locomotion and spatial distribution, with subordinates being less active in the absence of dominant members, showing reluctance to disperse into familiar space and initially failing to use the compound in which they had spent their entire lives. Finally, there was a difference in exploration, with subordinates showing less interest than dominant animals in food rewards and less approach to novel objects.

Although top-ranking animals are typically more conservative when approaching new objects, this study found dominant animals to be reliable initiators. Furthermore, their rates of exploratory behavior did not change across social circumstances and thus were not affected by the presence or absence of subordinates. By contrast, the extent of exploratory activity displayed by subordinates depended on the social situation. Subordinates showed no hesitation in the presence of dominant animals, but perhaps the most counterintuitive finding was that the absence of dominant animals had an inhibitory effect. Subordinates did not initially revel in their freedom from social constraints. Moreover, whereas previous studies showed that subordinate animals quickly react to fine changes in their familiar environment [Joubert & Vauclair, 1986], the present study found that subordinate hesitancy persisted for days, despite a period of habituation and the continued opportunity for uninterrupted access to favored foods. This study shows an overriding effect of social context on approach and avoidance of novel situations. Whereas the presence of higher-ranking animals was socially enhancing, their absence was socially inhibiting. Both social processes affect interest in and manipulation of novel objects by young monkeys [Fragaszy & Visalberghi, 1990; Fragaszy et al., 1994].

One possible explanation for the inhibition displayed by subordinates is that they anticipated reprimands from dominant animals; however, this explanation is insufficient for several reasons. First, there was no evidence of physical retribution. Levels of aggression were negligible and unchanging throughout the study, fights did not erupt upon reintegration of the two subgroups, and no subjects sustained wounds at any time. Second, whereas fear of retaliation would have been constant (or gradually fading, given that dominant animals were never released unexpectedly into a subordinate-occupied compound), the pattern of subordinate hesitancy was discontinuous, appearing during habituation, subsiding, and then reappearing during exposure to novel stimuli. Finally, subordinates participated more in the presence of dominant animals, when competition was the greatest and aggression was most likely. This finding was consistent with Bartlett and Meier's [1971] observation that animals are more likely to be present when those responding are high-ranking. Limited aggression, a fluctuating pattern of hesitancy, and differential performance by social context suggest more that subordinates depend in some way on the presence or leadership of dominant individuals.

An alternative interpretation for the asymmetrical responsiveness of subgroups is that the absence of dominant animals provided a more salient cue to subordinates than vice versa. Dominance relations within a social network play an important role in shaping behavior [Drea, in press] and determining the partners with which individuals interact [Berman et al., 1997]. In addition, hierarchical organizations demand social monitoring, so glancing at conspecifics comprises a large part of vigilance behavior in social primates, which is similarly influenced by maternal rank [Caine & Marra, 1988; Alberts, 1994]. Potentially, individuals of lower status engage in more social monitoring, both to avoid aggression and to maintain affiliations [Chance, 1967; Strayer & Garipey, 1986], thereby developing a social savvy. Unequal honing of certain social skills may explain why male immigrants who were subordinate in their natal troop integrate into host troops more successfully than those who were dominant in their natal troop [Berard, 1989]. Subordinates may also use dominant animals for “social referencing” [Russell et al., 1997], seeking information from them to evaluate a situation or object and regulating their behavior based on the information received. Regardless of the reason subordinates attend to dominant animals, the argument here is that, because of their constant monitoring, subordinates were exquisitely tuned to the momentary absence of higher-ranking animals. By contrast, dominant animals, who do not reciprocate this social monitoring, were unaffected by temporary separations. Subordinates nevertheless came to recognize the absence of higher-status animals as a positive signal [Hearst, 1984] and within days adjusted to the new situation.

The present study also established a new animal handling technique for repeatedly and temporarily separating a captive rhesus colony into subgroups and showed that, under certain circumstances, it is possible to manipulate social structure without changing social relationships. Since familiarity facilitates animal introductions and is associated with reduced aggression [Bernstein et al., 1979], success with the current procedure may have partly owed to the long history of stable relationships within the study group. In addition, free-ranging troops usually fission between genealogies [Chepko-Sade & Sade, 1979], so training success also may have owed to dividing the colony along a border between matriline. The only cases of escalated aggression associated with separations occurred early in the study, whenever dominant subjects were mishoused. It is possible that aggression erupted because the alpha animal, who often terminates intragroup fighting [Ehardt & Bernstein, 1992], could not interfere to keep aggression in check; however, if this were the case, one would expect conflicts always to be more frequent or intense in the subordinate subgroup. Instead, these outbursts are consistent with previous findings that isolating high-status animals promotes the opportunity for temporary rank reversals, supporting the notion that dominant animals are vulnerable without allies [Chapais, 1988]. The reduced tolerance of members of a different subgroup also suggested that animals recognized individuals as either belonging or not belonging.

Context- and rank-specific responding to novel stimuli, coupled with observations on group separations, show that the influence of social structure varies depending on where in the hierarchy an animal lives. Social primates learn from and about one another [Byrne & Whiten, 1988], and community members recognize the similarity of relations or associations between individuals [Gouzoules et al., 1984; Byrne & Whiten, 1988; Dasser, 1988; Cheney & Seyfarth, 1990]. Animals that use their knowledge of affiliations and status relationships may more effectively cope with social challenges or avoid confrontational situations and would be expected to alter their behavior in response to changes to their social

structure. The finding that subordinate sensitivity to the absence of dominant members was not reciprocated suggests that, based on status, changes in social structure affect individuals differently.

## CONCLUSIONS

1. Rhesus monkeys showed rank-related differences in their response to novelty that were context-specific. The present findings differ from prior studies in that subordinate animals were less likely than dominant animals to explore novel situations, especially in the absence of higher-status group members.

2. Whereas subordinates were influenced by alterations in social structure, gauged by the presence or absence of dominant individuals, dominant animals were unaffected by similar changes. These findings show that for some animals approach-avoidance behavior is socially mediated. Differences possibly reflect patterns of social attentiveness or the perception of social structure, consistent with the notion that monkeys have knowledge of social relations.

3. Socially housed, captive rhesus monkeys can be trained to separate, temporarily and repeatedly, into smaller subgroups without permanent consequences to their social structure. This technique can become a useful tool for studying a variety of questions relating to the influence of social context on behavior.

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## REFERENCES

- Alberts, S.C. Vigilance in young baboons: Effects of habitat, age, sex and maternal rank on glance rate. *ANIMAL BEHAVIOUR* 47: 749-755, 1994.
- Bartlett, D.P.; Meier, G.W. Dominance status and certain operants in a communal colony of rhesus macaques. *PRIMATES* 12:209-219, 1971.
- Berard, J.D. Life histories of male Cayo Santiago macaques. *PUERTO RICO HEALTH SCIENCES JOURNAL* 8:55-59, 1989.
- Berman, C.M.; Rasmussen, K.L.R.; Suomi, S.J. Group size, infant development and social networks in free-ranging rhesus monkeys. *ANIMAL BEHAVIOUR* 53:405-421, 1997.
- Bernstein, I.S.; Rose, R.M.; Gordon, T.P.; Grady, C.L. Agonistic rank, aggression, social context, and testosterone in male pig-tail monkeys. *AGGRESSIVE BEHAVIOR* 5:329-339, 1979.
- Byrne, G.; Suomi, S.J. Individual differences in object manipulation in a colony of tufted capuchins. *JOURNAL OF HUMAN EVOLUTION* 31:259-267, 1996.
- Byrne, R.W.; Whiten, A. *MACHIAVELLIAN INTELLIGENCE: SOCIAL EXPERTISE AND THE EVOLUTION OF INTELLECT IN MONKEYS, APES, AND*

- HUMANS. Oxford, UK, Clarendon Press, 1988.
- Caine, N.G.; Marra, S.L. Vigilance and social organization in two species of primates. *ANIMAL BEHAVIOUR* 36: 897-904, 1988.
- Cambefort, J.P. A comparative study of culturally transmitted patterns of feeding habits in the chacma baboon *Papio ursinus* and the vervet monkey *Cercopithecus aethiops*. *FOLIA PRIMATOLOGICA* 36: 243-263, 1981.
- Chamove, A.S. Role or dominance in macaque response to novel objects. *MOTIVATION AND EMOTION* 7:213-228, 1983.
- Chance, M.R.A. Attention structure as the basis of primate rank orders. *MAN* 2:503-518, 1967.
- Chapais, B. Rank maintenance in female Japanese macaques: Experimental evidence for social dependency. *BEHAVIOUR* 104:41-59, 1988.
- Cheney, D.L.; Seyfarth, R.M. *HOW MONKEYS SEE THE WORLD*. Chicago, University of Chicago Press, 1990.
- Chepko-Sade, D.; Sade, D.S. Patterns of group splitting within matrilineal kinship groups: A study in group structure. *BEHAVIORAL ECOLOGY AND SOCIOBIOLOGY* 5:67-86, 1979.
- Dasser, V. A social concept in Java monkeys. *ANIMAL BEHAVIOUR* 36:225-230, 1988.
- Drea, C.M. Status, age, and sex effects on performance of discrimination tasks in group-tested rhesus monkeys. *JOURNAL OF COMPARATIVE PSYCHOLOGY* (in press).
- Drea, C.M.; Wallen, K. Gradual acquisition of visual discrimination tasks in a social group of rhesus monkeys (*Macaca mulatta*). *ANIMAL LEARNING AND BEHAVIOR* 23:1-8, 1995.
- Ehardt, C.L.; Bernstein, I.S. Conflict intervention behaviour by adult male macaques: Structural and functional aspects. Pp. 83-111 in *COALITIONS AND ALLIANCES IN HUMANS AND OTHER ANIMALS*. A.H. Harcourt; F.B.M. de Waal, eds. Oxford, Oxford University Press, 1992.
- Fragaszy, D.M.; Visalberghi, E. Social processes affecting the appearance of innovative behaviors in capuchin monkeys. *FOLIA PRIMATOLOGICA* 54:155-165, 1990.
- Fragaszy, D.M.; Vitale, A.F.; Ritchie, B. Variation among juvenile capuchins in social influences on exploration. *AMERICAN JOURNAL OF PRIMATOLOGY* 32:249-260, 1994.
- Glickman, S.E.; Sroges, R.W. Curiosity in zoo animals. *BEHAVIOUR* 26:151-188, 1966.
- Gouzoules, S.; Gouzoules, H.; Marler, P. Rhesus monkey (*Macaca mulatta*) screams: Representational signalling in the recruitment of agonistic aid. *ANIMAL BEHAVIOUR* 32:182-193, 1984.
- Hearst, E. Absence as information: Some implications for learning, performance, and representational processes. Pp. 311-332 in *ANIMAL COGNITION*. H.L. Roitblat; T.G. Bever; H.S. Terrace, eds. Hillsdale, NJ, Lawrence Erlbaum Associates, 1984.
- Huffman, M.A. Acquisition of innovative cultural behaviors in nonhuman primates: A case study of stone handling, a socially transmitted behavior in Japanese macaques. Pp. 267-289 in *SOCIAL LEARNING IN ANIMALS: THE ROOTS OF CULTURE*. C.M. Heyes; B.G. Galef, Jr., eds. San Diego, Academic Press, 1996.
- Joubert, A.; Vauclair, J. Reaction to novel objects in a troop of Guinea baboons: Approach and manipulation. *BEHAVIOUR* 96:92-104, 1986.
- Katzir, G. Relationships between social structure and response to novelty in captive jackdaws, *Corvus monedula* L., I. Response to novel space. *BEHAVIOUR* 81:231-263, 1982.
- Menzel, E.W., Jr. Responsiveness to objects in free-ranging Japanese monkeys. *BEHAVIOUR* 26:130-150, 1966.
- Russell, C.L.; Bard, K.A.; Adamson, L.B. Social referencing by young chimpanzees (*Pan troglodytes*). *JOURNAL OF COMPARATIVE PSYCHOLOGY* 111:185-193, 1997.
- Strayer, F.F.; Garipey, J.L. The structure of social attention and its coordination with cohesive and dispersive activities in captive groups of squirrel monkeys. Pp. 99-110 in *CURRENT PERSPECTIVES IN PRIMATE SOCIAL DYNAMICS*. D.M. Taub; F.A. King, eds. New York, Van Nostrand Reinhold, 1986.
- Wade, T.D. Status and hierarchy in nonhuman primate societies. Pp. 109-134 in *PERSPECTIVES IN ETHOLOGY, VOL. 3: SOCIAL BEHAVIOR*. P.P.G. Bateson; P.H. Klopfer, eds. New York, Plenum Press, 1978.
- Wrangham, R.W. An ecological model of female-bonded primate groups. *BEHAVIOUR* 75:262-300, 1980.