

SOCIAL MONITORING REINFORCES SOCIAL DOMINANCE RELATIONSHIPS IN BROWN
CAPUCHIN MONKEYS (CEBUS APELLA)

by

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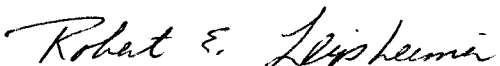
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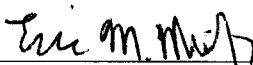


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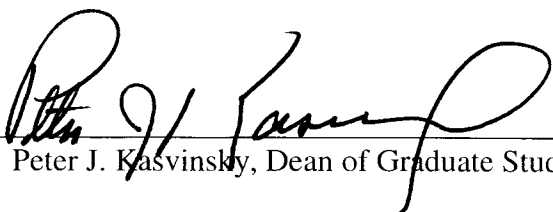
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ABSTRACT

The visual system provides an important means of communication for many non-human primate species, through which primates both convey and perceive information. This system may be particularly adept at communicating information related to social dominance relationships. To test this concept, the relationship between social monitoring and social dominance status in a captive group of brown capuchin monkeys (*Cebus apella*) was examined. We tested the hypothesis that differential social monitoring, or visual attention, is a mechanism by which brown capuchin monkeys maintain social organization. Dominance status was determined based on the directionality of aggressive behaviors, and social monitoring was quantified using focal animal sampling. The results of the aggressive behavior analysis revealed that the study group could be organized into three dominance tiers comprised of both males and females. Individuals in the dominant tier received significantly more social looks than individuals in both the middle tier and the bottom tier. Subordinate individuals engaged in the most social monitoring and also received the majority of the aggressive behaviors. Conversely, individuals that received the most looks directed the largest number of aggressive behaviors at others. The results indicate that social monitoring behavior is related to social dominance relationships, and that individuals employ social monitoring for within-group vigilance. The results suggest that social monitoring is an important mechanism by which social organization is maintained.

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INTRODUCTION

Maintenance of social organization is important for social animals that need to regulate competition and cooperation between group members. The communication of information pertinent to social relationships is critical in this regard (O'Brien, 1993). It is thought that many social species communicate information important to the maintenance of social organization visually (Adolphs, 1999; McNelis and Boatright-Horowitz, 1998; Moore et al, 1991; Watts, 1998). For example, some group-living animals use visual communication to forewarn competitors, to show affection, to reassure allies, to solicit play, to communicate recognition, to convey mating receptivity, or to convey cooperation (Drickamer et al, 2002; Mendres and de Waal, 2000; Anderson et al, 1995). Complex social relationships may have selected for visual abilities that could both communicate emotional disposition and analyze the behaviors of others (Bernstein, 1981; Tyack, 1993; O'Brien, 1993). By using visual communication, individuals within groups could communicate social information without risk of predator detection, as would be more likely through olfactory or auditory signaling (Emery, 2000).

The importance of the visual channel for the communication of social information is well documented in primates (Perrett, 1999; Keating and Keating, 1982; Kyes and Candland, 1987; van Honk et al, 2000; Visalberghi and Adessi, 2001; Haude et al, 1976; Mendelson et al, 1982; Rowell, 1972). High socio-cognitive abilities enable primates to engage in extremely complex social interactions. Most primates live in groups characterized by sophisticated social behaviors not seen in other social mammals, including coalition forming, reciprocity, and tactical deception (Emery, 2000; Rowell, 1972). Such complex social interactions are possible due to an increased reliance on the visual channel for conveying and perceiving information over other sensory processes.

Visual communication enables primates to communicate information at a level of complexity not available through other communicatory channels because psychological states can be conveyed and directed toward specific individuals instantaneously, and several signals can be sent and received at the same time (Perrett, 1999; Emery, 2000; Rowell, 1972). Information conveyed through the eyes often directly expresses emotional disposition. For example, for most primates direct eye contact is used to communicate a threat, and gaze aversion is used to diffuse a challenge (Emery et al, 1997; Mendelson et al, 1982; Adolphs, 1999; Haude et al, 1976; Rowell, 1972). Primates also perceive emotional disposition visually through the observation of gestures, body position, and facial expressions of others (Emery, 2000).

Given the neuroanatomy of the primate eyes and brain, it is not surprising that the eyes play such an important role in the communication of social information. Primate eyes are capable of resolving high levels of detail, including small differences in shape and slight movements that occur as optic and facial expressions change (Rowell, 1972). The primate brain has over 30 regions specialized for visual processing, including areas which contain neurons selectively responsive faces and eyes (Konishi, 1999; van Honk et al, 2000). These neurons respond especially acutely to direct eye contact. Some neurons are also selectively responsive to certain positions of the head (turned front, profile, head elevation), which enables primates to determine another individual's direction of attention (Perrett, 1999). Likewise, some neurons are responsive to positions of other parts of the body, which is also communicative of attention. The evolutionary development of these neuroanatomical adaptations underscores the importance of perceiving and processing information about directionality of attention and emotional disposition in primates (for a review see Emery, 2000).

Primate brains also produce neurophysiological responses to eye gaze (Emery, 2000). There are direct neuronal connections between the eyes and the hypothalamus, regulator of the body's neuroendocrine responses, and the amygdala, part of the limbic system responsible for emotion. These connections function in producing emotive responses to stimuli perceived visually (van Honk et al, 2000). Most primates have evolved the ability to perceive and understand aggressive challenges from direct eye contact, angry facial expressions, and body position without having to engage in a physical encounter (van Honk et al, 2000). Threats perceived visually, or the receipt of aggression, results in activation of the body's flight or fight stress response. Once the threat is perceived, the body produces a range of hormones that aid in mobilizing energy and cause behavioral responses.

The amygdala activates the hypothalamic pituitary adrenal (HPA) axis, which responds in two ways to stressors (Stavisky et al, 2001; Bahr et al, 2000; Kimura et al, 2000). Acute stress mediates the short-term release of epinephrine, which is rapidly broken down by the body. Chronic stress induces the production of corticotrophin-releasing hormone in the hypothalamus, which is then carried to the anterior pituitary (Kimura et al, 2000). In response, the anterior pituitary releases adrenocorticotrophic hormone (ACTH) that is carried via the blood to the cortex of the adrenal gland. ACTH then promotes the synthesis and secretion of glucocorticoids, cortisol being the major representative hormone (Emery, 2000). Over time, chronic stress leads to elevated baseline levels of plasma cortisol (Wallner et al, 1998). High basal levels of cortisol are associated with submissive, socially avoidant behavior and anxiety during social challenge situations (van Honk et al, 2000; Stavisky et al, 2001). Chronic elevated levels of cortisol produces a variety of dysfunctions, including immune system suppression,

reproduction suppression, hypertension, and changes in metabolic and gastrointestinal functions (Wallner et al, 1999; Bahr et al, 2000). Stressors can be visual stimuli. In humans, visual attention directed toward angry faces causes increases in cortisol, raising blood glucose levels. In contrast, visual attention directed away from angry faces causes decreased cortisol production (van Honk et al, 2000). The perception of, and reaction to visual stimuli, may depend on the personality of individual animals, resulting in low and high adreno-glucocorticoid responses in different individuals (Wallner et al, 1998). The visual perception of social information, particularly threat, thus results in neuroendocrine activity that operates in shaping response behaviors.

Interestingly, primates prefer to look at the eyes of conspecifics over other facial areas and body parts. For example, rhesus monkeys prefer to view the eyes of other monkeys when viewing different primate faces (Keating and Keating, 1982). Similarly, hamadryas baboons presented with slides of various facial regions of other baboons gave significantly more attention to the eye region (Kyes and Candland, 1987). These studies indicate that the eyes are a preferred focal point of attention for primates. It is suggested that the reason the eyes are the primary focus of attention is because they provide information about intent. The eyes are thought to provide the first indication of the attitude and intent of another individual, the perception of which is vital for perceiving potential threats from individuals within the group (Kyes and Candland, 1987).

Given the neuroanatomical, physiological and behavioral adaptations associated with the visual system in primates, it is likely that visual communication plays a vital role in not only communicating social information but also in maintaining social organization. Group social organization in most primate species is based on dominance relationships. Social dominance is defined as a relationship between two individuals based on a past

history of interactions, where one individual predictably causes a submissive response in another individual through agonistic behavior (Bernstein, 1981). If visual communication functions to maintain group social organization, primates must communicate dominance relationships and awareness of status differences between individuals visually (Emery, 2000).

Chance (1967) argues that it is through the amount of attention given to different individuals within a group that social organization is maintained. The most dominant animals in a social hierarchy often receive the most attention, or social monitoring, from the less dominant animals. Social monitoring occurs through repeated glances towards, or seeking out of, the dominant individual (Chance and Jolly, 1970). Frequent social monitoring satisfies the subordinate animal's need to know the location of the dominant animal at all times and serves as a submissive gesture communicating the anxiety induced in the subordinate animal by the dominant animal's aggressive disposition. As such, a subordinate animal's constant direction of attention toward a dominant animal is the most active component of the dyadic relationship (Chance, 1967; Rowell, 1974). Dominant animals conversely give less attention to subordinate animals.

Chance (1967) proposes that within the group, a chain of attention develops which fosters bonds between individuals, with dominant animals occupying central positions, both visually and spatially. Relationships are understood by the way in which individuals orient themselves with respect to dominant animals, both spatially and in the context of different behaviors. Individuals whose attention is focused exclusively on dominant animals become segregated from the rest of the group but form bonds with one another (Chance, 1967). Differential visual attention therefore reinforces social

dominance relationships through social and spatial distance and the communication of anxiety.

Most authors agree that social dominance relationships in non-human primates result from previous learning experiences of the individuals involved, although such learning may also include observed interactions and indirect social experiences (Chance and Jolly, 1970; Rowell, 1972, 1974; Bernstein, 1981;). Submissive behavior is thought to occur due to the memory of previous aggression by the dominant individual, related fear and anxiety, and the need to monitor the dominant individual's position and psychological state to prevent attacks (Chance and Jolly, 1970; Haude et al, 1976). The learned relationships are then periodically reinforced through either aggressive acts by dominants or submissive gestures by subordinates (Bernstein, 1981). Open aggression is rare once a dominance relationship is established, as a slight movement of intent or a threat display may be sufficient for a dominant individual to assert its position (Slater, 1999). Submissive or terminating responses at the outset of an aggressive encounter may also be sufficient for submissive individuals to avoid full-scale fights (Rowell, 1974).

From a cognitive standpoint, some argue that submissive gestures reflect perceived vulnerability to aggression resulting from previous experiences with certain individuals (or observations of interactions between other individuals) and discrimination learning that submissive behaviors have an appeasing effect on potential aggressors (Maestriperi, 1996). Other theories hold that submissive gestures communicate status awareness. This assumes that individuals possess self-awareness. Moreover, this also assumes that individuals attribute knowledge to others—that subordinates understand that dominants know they are superior in rank. By using submissive signals, subordinates attempt to influence the knowledge of others and influence their behavior (Maestriperi,

1996). A third theory proposes that submissive behaviors reflect a combination of fear and intention to modify the behavior of dominants, rather than awareness of status differences. This debate extends to interesting theoretical discussion concerning the attribution of mental states and theory of mind in non-human primates and other animals with high socio-cognitive abilities (Itakura and Anderson, 1996; Maestripieri, 1996).

The purpose of this study was to verify Chance's arguments regarding the role of visual attention in the social behavior of brown capuchin monkeys (*Cebus apella*). Specifically, our hypothesis was that differential visual attention, or social monitoring, is a mechanism by which brown capuchin monkeys maintain social organization. Largely because of the difficulties of measuring visual gaze in the field, the hypothesis that social organization is maintained by differential visual attention has been confirmed only in a few studies (Emery, 2000; McNelis and Boatright-Horowitz, 1998). A recent study investigating visual attention and dominance relationships in patas monkeys has confirmed that visual attention maintains social organization in this Old World species (McNelis and Boatright-Horowitz, 1998).

Brown capuchins were used in this study largely because visual communication is important to this species, particularly in agonistic encounters. We also worked with a captive group in order to test the method of measuring visual gaze set forth by McNelis and Boatright-Horowitz (1998), and to study the behavior of a New World species in this regard. Wild brown capuchins maintain strong cohesive, female-bonded social groups (Izawa, 1980; Janson, 1990; Di Bitetti and Janson, 2001). Wild groups typically include three to 30 individuals, usually in a ratio of one to two males for every four females (Janson, 1990). Group membership remains stable for years, although sub-adult males may leave the group. Females remain in the group until sexual maturity, at which time

they may remain or transfer out (Janson, 1990). Wild brown capuchin monkeys have been reported to exhibit decisive dominance hierarchies (Ross, 1988; Izawa, 1980), although some researchers have also reported that hierarchical order for male individuals other than the alpha male could not be determined (Lynch et al, 2000). Izawa (1980) reported that hierarchies exist among both sexes, and that ranking for both sexes corresponds with age order (i.e. the oldest individuals are the most dominant), although ranking between the sexes could not be clearly discerned (Izawa, 1980).

Aggressive encounters in wild brown capuchins are mild and rare; high tolerance is generally prevalent within the group (Ross, 1988; Izawa, 1980). Aggressive encounters that do occur appear to be related to contests over food, but not mates (Janson, 1985, 1990; Izawa, 1980). Dominant males control access to food through aggressive behavior (DiBitetti and Janson, 2001). Subordinate males tend to avoid contact with higher-ranked individuals by staying in the group periphery (Janson, 1990; Izawa, 1980). Low ranked females do not avoid high ranked females to the degree that low ranked males avoid high ranked males. Most aggressive encounters of wild brown capuchin groups involve threat displays using facial expressions, especially stares (Ross, 1988; Izawa, 1980).

Threatened individuals assume a submissive facial expression and then turn their faces away from challengers or change their position. Threatening between adult females is more frequent than threatening between males or between males and females, and includes open-mouth expressions, chasing and threatening vocalizations. In a study investigating the capacity of capuchin monkeys for cooperation, it was shown that visual contact was necessary for the individuals to complete the cooperative task, suggesting that capuchins do communicate visually and can understand the intentions of others communicated through the eyes (Mendres and deWaal, 2000). Capuchin monkeys have

also been shown to utilize information from the gaze, head and eye orientation of others, and could learn to use the gaze of a human to locate an object in an object-choice task (Itakura and Anderson, 1996).

In the present study, we examined the role of visual communication in the social dynamics of this primate species. The results of this study will lead to a better understanding of the role of vision in primate social dynamics, specifically in the maintenance of social organization.

METHODS

Subjects

The subjects for this study were nine captive-born brown capuchin monkeys, *Cebus apella* (four males, five females) (Figure 1). The monkeys were housed in a social group in an indoor cage, approximately 3 m x 4 m x 3 m, on the Hiram College campus (Figure 2). Subjects were well habituated to the presence of human observers. Ages of the monkeys ranged from 12 months to 25 years old. Sex, body weights and ages of the capuchins at the time of the study are listed in Table 1. The study received the approval of the Hiram College Institutional Animal Care and Use Committee (IACUC).

Procedure

Study 1

One observer was seated outside the cage. Group social structure was determined based on the directionality of aggressive behaviors between dyads. Focal animal sampling with continuous recording was used to determine social dominance relationships (Martin and Bateson, 1993). The observer continuously recorded the behavior of each subject during 10-min intervals over 16 sessions, resulting in 160 minutes of observation per subject. The observer recorded aggressive behaviors directed at the focal subject, (the recipient), and the acting individual, (the actor). The observer also recorded aggressive behaviors by the focal subject, and the target of those actions. Aggressive behaviors occurred when there was an interaction in the form of a fight and physical contact such as biting, but not when animals engaged in rough play. Aggressive behaviors also included lunges toward the target and threat vocalizations.

Study 2

Figure 1. Nine brown capuchin monkey study subjects.



NI



CA



GA



SO



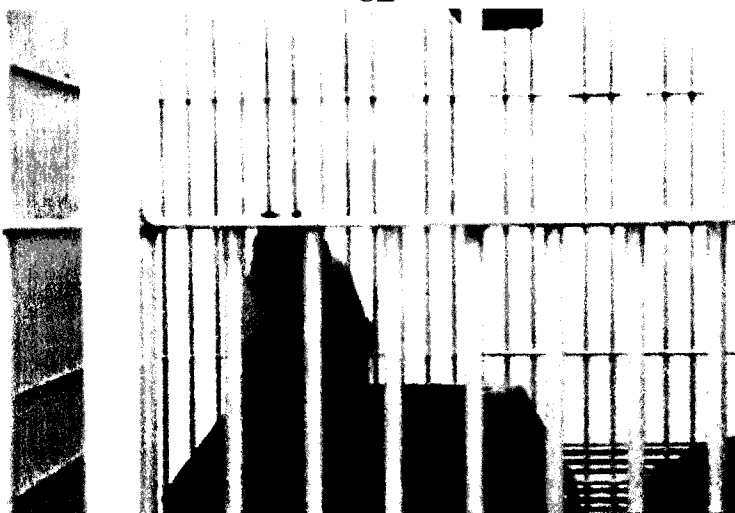
MI



NO



CZ



IS



VI (far right)

Figure 2. Indoor group cage at Hiram College. The monkeys often sit on perches and play with toys provided for enrichment.



East view



West view

TABLE 1
AGE, WEIGHT AND SEX OF SUBJECTS

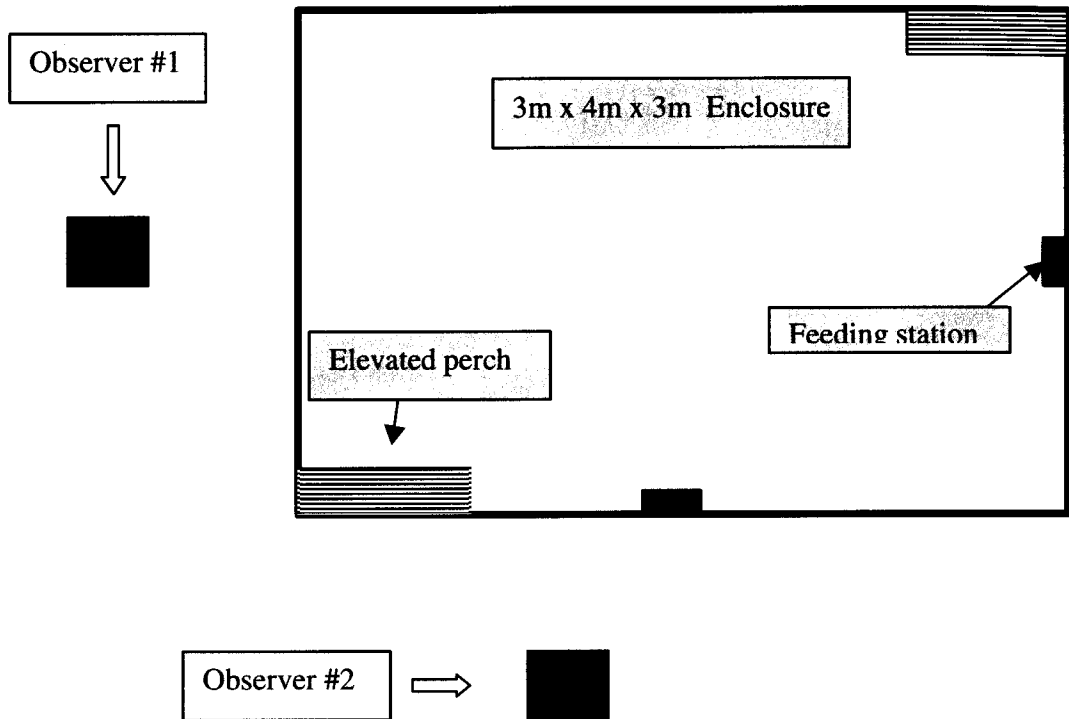
SUBJECT	AGE	WEIGHT(KG)	SEX
NINA (NI)	25	2.41	F
VINCENT (VI)	15	3.89	M
ISABELLE (IS)	14	2.24	F
NOEL (NO)	11	2.45	F
MIRO (MI)	9	6.93	M
GEORGIA	3.5	2.26	F
CARLOS	2.5	2.16	M
SOSA (SO)	1	----	M
CRUZ (CZ)	1	----	F

Differential visual attention towards other group members was determined for each subject. Two observers sat outside the cage, facing the cage at predetermined locations on adjacent sides of the cage so that their respective viewing angles differed by 90° (Fig. 3). The observers wore headphones and listened to a pre-recorded audiotape which provided a tone every 5-s to cue the observers to make a recording.

The study was conducted in 16 sessions of 1 hour each through a span of eight weeks. Instantaneous focal animal sampling was used to observe behavior. Each individual was observed for 5-min during each 1-h session, and recordings were made every 5-s resulting in 960 observations for each subject. The study was designed to include 960 observations per subject over a period of eight weeks in order to ensure sample size would be large enough to identify trends that might statistically significant. McNelis and Boatright-Horowitz (1998) found statistically significant correlations with 600 observations per subject. Sessions took place once a day between 8:00 am and 4:00 pm, two days per week. The order of subjects observed was determined at random before each session.

The observers recorded whether a subject was looking at a social target, and the identity of the target, immediately upon hearing the 5-s cue. A look was defined as any gaze directed to another member of the group. A look could be directed either to the eyes of the target, to the target's body generally or to any body part. However, looks were not included when the subject was grooming the target. Grooming was defined as touching the target with apparent intent to investigate the fur, skin, or other part of the body. Because of the rapid movement of capuchin visual gaze, looks occurring just before the

Figure 3. Diagram of observation area showing the monkey enclosure and relative positions of two observers at a 90° angle from one another.



tone were not included. However, looks occurring at the tail end of the tone were included. The observers differentiated social looks from non-social looks, and only matching data between the two observers was used in analysis. In the event the observer could not see the subject when the tone sounded, the observer recorded a dash (-). In the event the subject was not looking at any social target, or if the subject was looking at the observer, the observer recorded a zero (0). In the event the subject was looking into space or staring, and another individual entered the subject's field of vision, this was recorded as a zero (0) unless there was a change in the subject's vision indicating the individual had become an affirmative target of the subject's gaze. The observers both observed the same subject during each 5-min interval, and only matching data between the two observers was used in analysis. If, however, one observer recorded a social target and the other observer recorded a dash (-), the social target recorded was used in analysis.

In order to prevent possibly biasing the subjects to the presence of the observers, the observers entered the monkey room 15 minutes prior to beginning recordings for each observation session to habituate the monkeys to their presence. In order to ensure reliability, the observers trained for one month prior to beginning formal observations. During the training period, the observers verified that they were both consistently recording in the same way across sessions, and that they were both recording the same behavior in the same way (Martin and Bateson, 1993). In each training session, the observers practiced observing visual gaze and recording its target every 5-s over 5-min sessions for each subject. The percentage of recordings that were in agreement between the two observers was determined by dividing the number of correct recordings by the total number of recordings. If either observer was not able to make a determination of

the direction of gaze, the observation was not included in the analysis. Training sessions were conducted until acceptable between-observer reliability levels were achieved, using Cohen's Kappa $\kappa > .85$, (Boinski et al, 1999; McNelis and Boatright-Horowitz, 1998). High reliability measures indicate acceptable levels of concurrent validity. The total number of looks per subject was determined by adding the number of looks and non-looks over all 16 sessions.

Analysis

Data were analyzed using SPSS software, v. 8.0 (SPSS 1998). Non-parametric Spearman rank correlation statistics (r_s) were used to analyze relationships between variables (Martin and Bateson, 1993). Two methods were used to determine dominance ranks. First, dominance indices were calculated for each individual by dividing the number of aggressive behaviors by the actor by the actor's total number of interactions with other animals (Lehner, 1996). Secondly, dominance matrices were arranged so that the individual that always acted aggressively was at the top and the individual that never acted aggressively was at the bottom. The other animals were arranged in order so that the minimum number aggressive encounters appeared on the left side of the matrix (Martin and Bateson, 1993). We used Landau's index of linearity (h) to measure the degree to which dominance hierarchies based on aggressive encounters and visual attention were linear. A strongly linear hierarchy is shown where h is greater than 0.9 (Martin and Bateson, 1993). Dominance rank was determined for the entire group, and separate dominance ranks were determined for males and for females. This dominance rank data was used in correlation analyses with visual attention data. One-way ANOVAs were used to compare the amount of social looking between dominance tiers.

Post-hoc analyses were conducted with the Tukey test. Significance was ascribed if $P < 0.05$. Additional analyses are described in the text as needed.

RESULTS

Dominance Rank

Due to symmetrical dyadic relations and intransitive triadic relations, the social structure was nonlinear ($h = 0.39$). Although no ordinal ranking could be constructed for all nine subjects or for males and females, through dominance matrices, (Fig. 4), dominance indices (DI) calculated for each individual support the construction of a three-tiered non-linear hierarchy (Table 2). The uppermost tier, comprised of subjects that received no aggressive behavior from other individuals, includes NO, GA, and MI. Having won all aggressive interactions, NO, GA, and MI each have a dominance index of 1.0. Subjects occupying the second tier, characterized by subjects that both received aggressive behavior and directed aggressive behavior at others, have dominance indices ranging between 0 and 1 ($DI_{SO} = .62$; $DI_{CA} = .08$; $DI_{CZ} = .06$). The lowest tier is comprised of IS, VI and NI, who received aggressive behavior but did not direct aggressive behavior at others. These subjects share dominance indices of 0 due to their failure to direct any aggressive behavior at other individuals.

This three-tiered social hierarchy appears to be related to age but not to body weight or sex. Subjects occupying the first tier range from 45 to 132 months, falling in the middle of the group age span. Second tier individuals are the youngest, ranging from 10 to 33 months, and third tier individuals are the oldest ranging from 156 to 300 months. Note that there is no age overlap at all amongst the tiers. Body weights (BW) of the two females occupying the first tier ($BW_{NO} = 2.45$ kg; $BW_{GA} = 2.26$ kg) are almost identical to the two females occupying the third tier ($BW_{NI} = 2.41$ kg; $BW_{IS} = 2.24$ kg). The first

Figure 4. Two dominance matrices constructed based on aggressive behaviors result in different possibilities for linear hierarchical structure due to intransitive relationships. It was therefore impossible to construct a linear hierarchy for this group..

	NO	GA	MI	SO	CA	CZ	IS	VI	NI	Total number of aggressive behaviors directed at others
NO		0	0	1	37	0	0	12	2	52
GA	0		0	0	3	1	17	0	15	36
MI	0	0		27	10	9	0	0	0	46
SO	0	0	0		21	3	1	8	13	46
CA	0	0	0	0		1	0	5	1	7
CZ	0	0	0	0	0		1	0	0	1
IS	0	0	0	0	0	0		0	0	0
VI	0	0	0	0	0	0	0		0	0
NI	0	0	0	0	0	0	0	0		0
Total number of aggressive behaviors received	0	0	0	28	71	14	19	25	31	

	MI	NO	GA	CZ	IS	VI	SO	NI	CA	Total number of aggressive behaviors directed at others
MI		0	0	9	0	0	27	0	10	52
NO	0		0	0	0	12	1	2	37	36
GA	0	0		1	17	0	0	15	3	46
CZ	0	0	0		1	0	1	0	0	46
IS	0	0	0	0		0	0	0	1	7
VI	0	0	0	0	0		1	0	0	1
SO	0	0	0	0	1	8		13	21	0
NI	0	0	0	0	0	0	0		0	0
CA	0	0	0	1	0	5	0	1		0
Total number of aggressive behaviors received	0	0	0	14	19	25	28	31	71	

TABLE 2

THREE-TIERED HEIRARCHY BASED ON DOMINANCE INDICES

TIER	SUBJECT	AGE	DOMINANCE INDEX
1	NO	25	1.00
1	GA	14	1.00
1	MI	13	1.00
2	CA	11	0.08
2	SO	9	0.62
2	CZ	3.5	0.06
3	VI	2.5	0.00
3	NI	1	0.00
3	IS	1	0.00

tier male has a greater body weight ($BW_{MI} = 6.93$ kg) than the male occupying the third tier ($BW_{VI} = 3.89$ kg). The second tier is comprised of individuals having the lowest body weights, up to 2.16 kg. The dominant tier is comprised of one male and two females, the middle tier is comprised of two males and one female, and the subordinate tier is also mixed-sex with one male and two females.

Aggressive Behavior

We found no significant correlations between the number of aggressive behaviors subjects directed at other individuals and either their age ($r_s = -0.5$, $n = 9$, $P = 0.17$), or body weight ($r_s = 0.70$, $n = 9$, $P < 0.07$). There was a significant negative correlation, however, between the number of aggressive behaviors subjects received and body weight, ($r_s = -0.85$, $n = 9$, $P < 0.01$), but not age ($r_s = 0.06$, $n = 9$, $P = 0.87$).

Differences between males and females in the number of aggressive behaviors directed at females were not significant (Mann Whitney U $P = .532$), nor were differences between males and females in the number of aggressive behaviors directed at males (Mann Whitney U $P = .371$). There were also no significant differences between males and females in the number of aggressive behaviors received from females (Mann Whitney U $P = .707$) or from males (Mann Whitney U $P = .260$).

Individuals did differ in the number of aggressive behaviors directed at specific individuals. In fact, individuals appeared to preferentially choose other individuals as specific targets for attack. For example, NO directed 52 aggressive behaviors toward conspecifics. Of those, 71% were directed towards CA, 23% were directed towards VI, 4% were directed towards NI, and 2% were directed towards SO. NO did not act aggressively towards any of the other monkeys. In contrast, GA directed 36 aggressive behaviors towards others. Of those, 47% were directed at IS, 42 were directed at NI, 8%

were directed at CA, and 3% were directed at CZ. Interestingly, 96% of the aggressive behaviors by NO were directed at males, and 92% of GA's aggressive behaviors were directed at females. Moreover, 100% of aggressive behaviors by the dominant male MI were directed at middle tier juveniles (Fig. 5). The significant negative correlation we found between the number of aggressive behaviors subjects received and body weight is likely a result of the fact that all three dominant tier individuals directed aggressive behaviors at juveniles and the large body weight of MI, rather than an indication that individuals with low body weight are generally attacked more. Despite the findings related to body weight, we found no general patterns across the group that could explain why some individuals were attacked more than others. CA received the most aggressive behaviors overall (39%), followed by NI (16%) and SO (14.8%) (Fig. 6).

Social Monitoring

Significant differences were found between dominance tiers in the number of looks received ($F = 25.03$, $df = 2$, $P < 0.001$) (Fig. 7). Post-hoc analyses indicate that individuals in the most dominant tier received significantly more social looks than individuals in both the middle tier (Tukey $P < 0.035$) and the bottom tier (Tukey $P < 0.001$). Middle-tier individuals also received significantly more looks than bottom-tier individuals (Tukey $P < 0.024$). Similarly, there were significant differences between dominance tiers and the number of looks given ($F = 14.72$, $df = 2$, $P < 0.005$) (Fig. 7).

The number of looks given by bottom-tier individuals was significantly greater than the number of looks given by top-tier individuals (Tukey $P < 0.005$) and the number of looks given by middle tier individuals (Tukey $P < 0.019$). However, middle-tier

Figure 5. Comparison of aggressive behaviors by NO, GA and MI directed at other individuals.

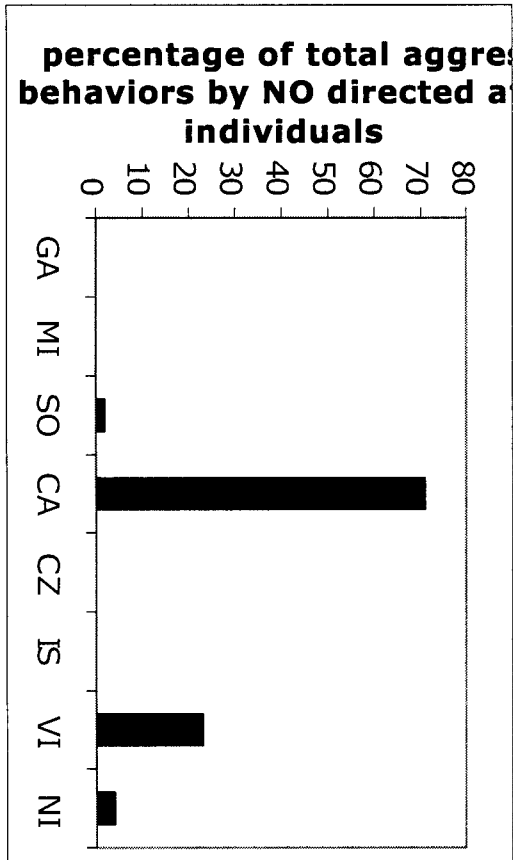
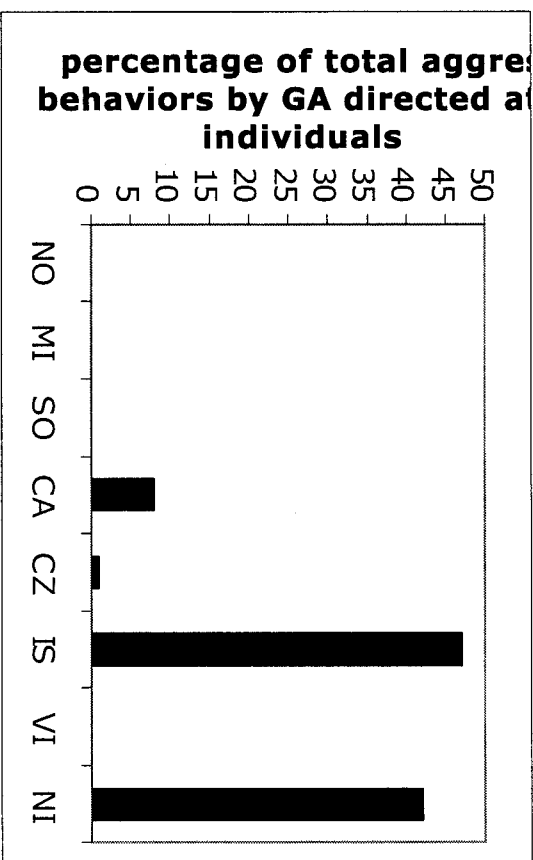
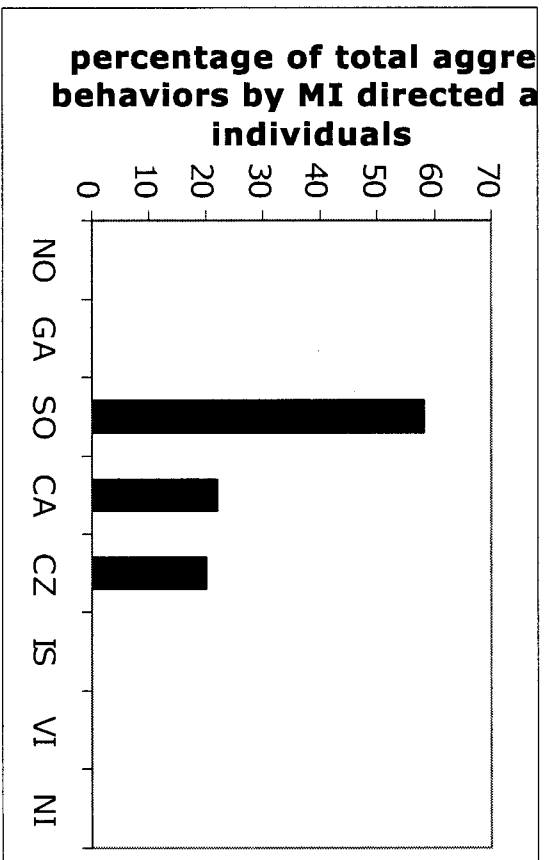


Figure 6. Percentage of total aggressive behaviors received for each individual.

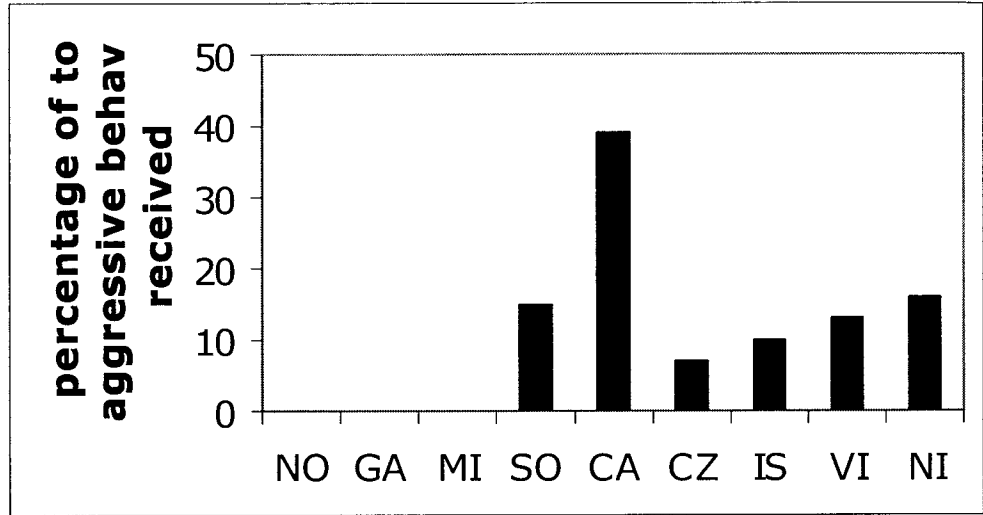
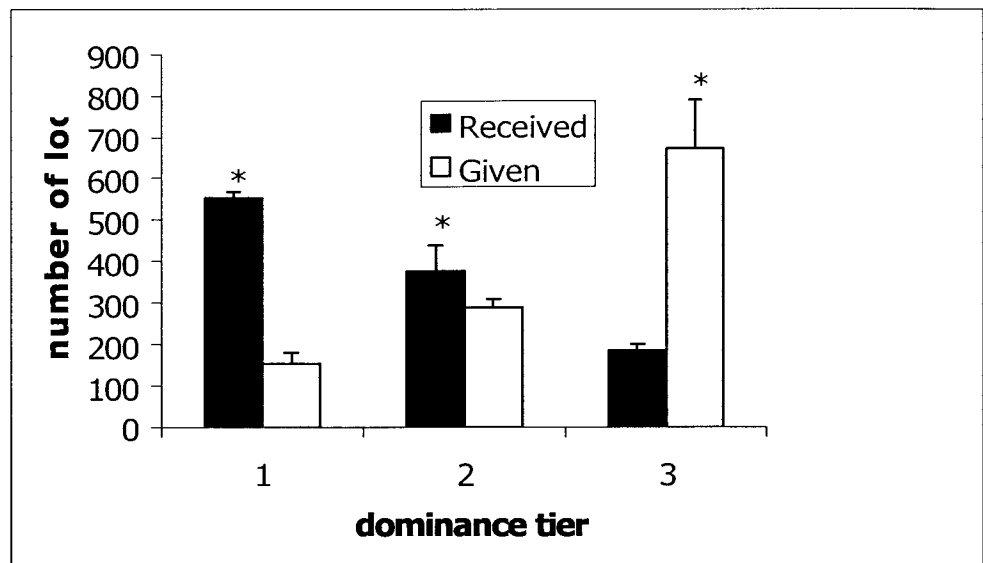


Figure 7. Mean number of looks received and given for subjects occupying each dominance tier. Asterisks denote significance where $P < 0.05$.



individuals did not give significantly more looks than top-tier individuals (Tukey $P < 0.414$). Based on the number of looks given and received, group social structure is linear ($h = 0.89$)

There is a significant negative correlation between the number of looks given and the number of aggressive behaviors directed at others ($r_s = -0.80, n = 9, P < 0.008$) (Fig. 8). Furthermore, there is a significant positive correlation and the number of looks received and the number of aggressive behaviors directed at others ($r_s = 0.85, n = 9, P < 0.004$) (Fig. 9). There is also a significant positive correlation between the number of looks given and the number of aggressive behaviors received from others ($r_s = 0.72, n = 9, P < 0.026$). However, the correlation between the number of looks received and the number of aggressive behaviors received from others is not significant ($r_s = -0.62, n = 9, P = 0.071$).

The total number of looks made by each subject during the study was calculated by adding the number of social looks and non-social looks over all 16 sessions. The percentage of total looks that were social is set forth in Figure 10. There are significant differences between dominance tiers in the percentage of looks individuals gave that were socially directed ($F = 17.21, df = 2, P < .003$) (Fig. 11). Using post-hoc analyses, we determined that third-tier individuals engaged in significantly more social looking than both first-tier individuals (Tukey $P < 0.003$), and second-tier individuals (Tukey $P < 0.025$). We did not find a significant difference, however, in the amount of social looking between first and second-tier individuals (Tukey $P = 0.155$). The percentage of social looks is not significantly correlated with the number of aggressive behaviors received, ($r_s = 0.64, n = 9, P = 0.061$), although there is a significant

Figure 8. Number of aggressive behaviors directed at others for nine brown capuchin monkeys relative to number of looks at other individuals.

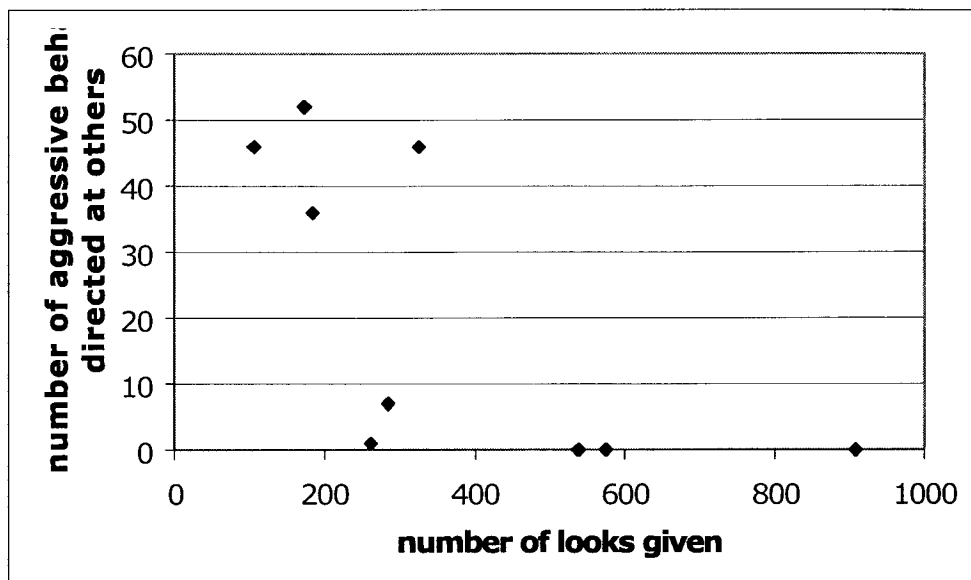


Figure 9. Number of aggressive behaviors directed at others for nine brown capuchin monkeys relative to number of looks received from other individuals.

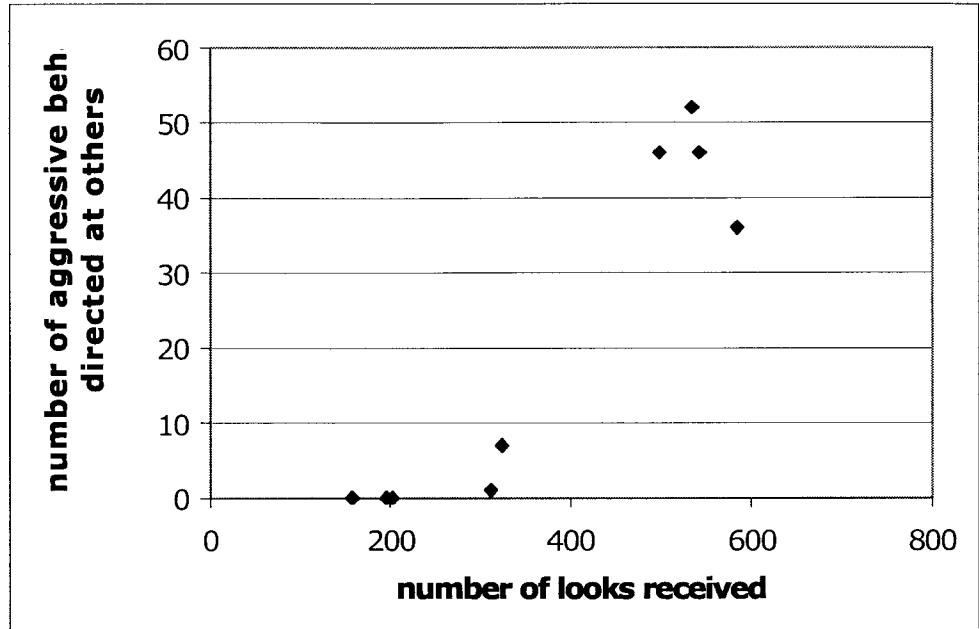


Figure 10. Percentage of looks directed at a social target for nine brown capuchin monkeys.

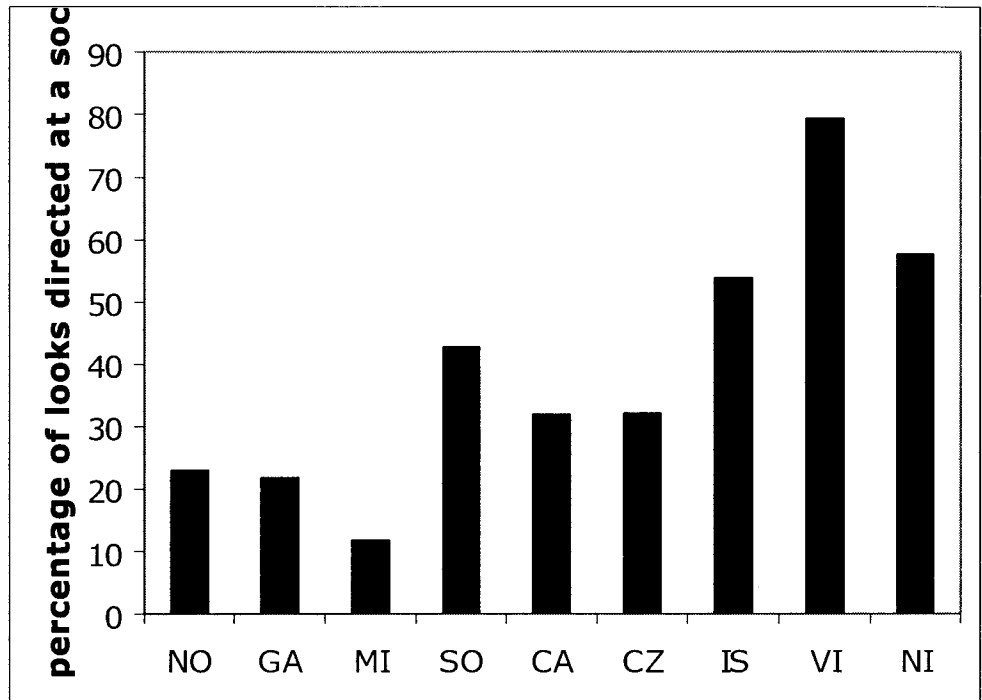
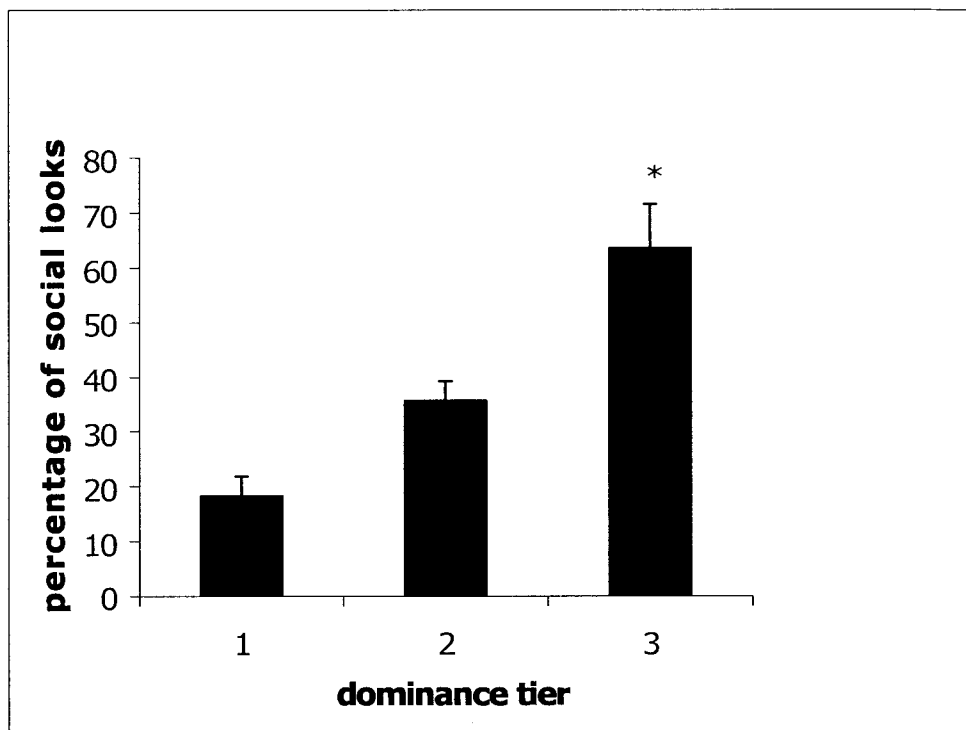


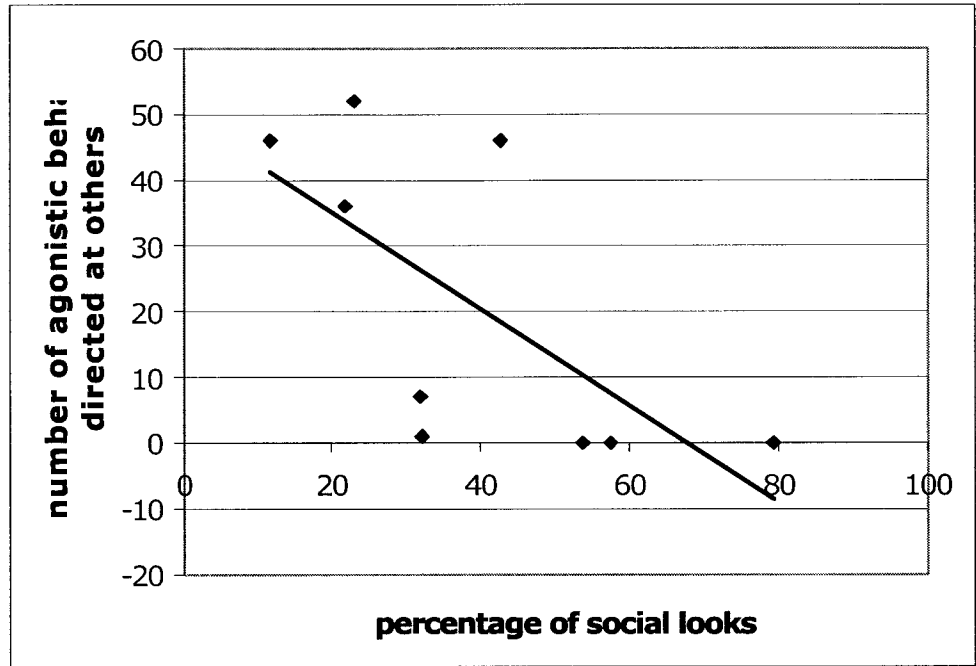
Figure 11. Percentage of looks directed at a social target for subjects occupying each dominance tier. Asterisks denote significance where $P < 0.05$.



correlation between the percentage of social looks and the number of aggressive behaviors subjects directed at others ($r_s = -0.77$, $n = 9$, $P < 0.014$) (Fig. 12).

Males and females did not differ significantly in the number of looks directed at females (Mann Whitney U $P = .806$) or males (Mann Whitney U $P = .806$). Likewise, males and females did not differ significantly in the number of looks received from females (Mann Whitney U $P = .624$) or males (Mann Whitney U $P = 1.0$).

Figure 12. Number of aggressive behaviors directed at others for nine brown capuchin monkeys relative to the percentage of looks given that were socially directed.



DISCUSSION

Dominance Rank

Not unexpectedly, this group did not display a discernable linear rank order. Clearly, though, social dominance status was identifiable in this study, and individuals could be categorized as generally dominant or subordinate, or somewhere in between.

The dominance groupings we found in this study were significantly related to age, but not to body weight or to sex. Interestingly, the dominant tier included the animals of middle age, the middle tier included the youngest individuals, and the subordinate tier included the oldest animals. Two of the middle tier juveniles were the offspring of the subordinate tier females. It is unknown whether the father of the juveniles was the dominant male or the subordinate male. It is unclear why the oldest individuals were the most subordinate in this group. In contrast, observers of wild populations of brown capuchins have reported that the oldest individuals are the dominant individuals (Izawa, 1980). As social relationships in this group were already established prior to our study, we have no information about the factors causing the present social dynamics to develop. Differences in individual experiences, personalities and motivational levels likely operate to determine individual social status. Propensity toward aggression is likely an important factor in this regard (van Honk et al, 2000).

Aggressive Behavior

There were no significant differences between males and females in the number of aggressive behaviors towards either males or towards females. Thus we found no effect of sex as neither females nor males were more likely to receive aggression.

Aggressive behavior by dominants reported in this study was likely related to feeding competition. Aggressive behaviors were the most violent and occurred most

frequently during feeding sessions when the animals were provisioned with preferred foods (fruits, cereal, peanut butter, apple sauce). Janson (1985, 1990) reported that feeding is a major source of competition in brown capuchin groups. In fact, competition for food resources is regarded as a critical factor influencing brown capuchin social dynamics (Janson, 1985; Phillips, 1995). Dominant individuals in wild groups are known to aggressively displace others from food sources, engaging in kleptoparasitism (DiBitetti and Janson, 2001). Dominant individuals typically occupy central spatial positions in the group that afford them the greatest opportunity to exploit food sources discovered by others (DiBitetti and Janson, 2001).

In the present study, dominant individuals caused subordinates to occupy peripheral positions within their enclosure through periodic aggressive episodes and threats, both during and between feeding sessions. Subordinates often stayed in constant motion in their attempts to avoid dominants, enabling dominants to occupy preferential positions, on elevated perches and near food sources (boxes, cardboard tubes, plastic jugs and other enrichment items containing preferred foods designed to promote foraging behavior). Aggressive behavior by dominants thus likely allows dominants to maintain spatial superiority over subordinates so that dominants have preferential access to food when food is available. Even outside of feeding sessions in this study, the animals had access to monkey chow and water ad libitum, which could have been a continuing source of competition causing aggressive behaviors.

Social Monitoring

We found that the dominant tier individuals received significantly more looks than other tiers in the group, and gave significantly less. We also found that subordinates

received significantly less looks than the other tiers and gave significantly more. Middle tier individuals received significantly more looks than subordinate tier individuals, and gave more looks than dominant tier individuals although the difference was not significant. The results confirm a relationship between social status and social monitoring, both in the amount of looking behavior in which individuals engage and in the frequency with which individuals are being observed.

Our results show that this relationship is related to the directionality of aggressive behaviors within the group. We found a significant negative correlation between the number of looks given and the number of aggressive behaviors directed at others. That is, dominant tier individuals looked at others the least but attacked others the most. Furthermore, we found a significant positive correlation between the number of looks received and the number of aggressive behaviors directed at others: individuals that received the most looks behaved the most aggressively. The significant positive correlation between the number of looks given and the number of aggressive behaviors received from others shows that individuals that looked at others the most were also attacked the most.

These results suggest that social monitoring behavior is related to social status and functions as within-group vigilance to prevent attacks. Dominant individuals received the most social monitoring and gave the most attacks, especially to subordinates. Dominants, however, gave other individuals little attention, likely because the other individuals posed no threat. Dominant tier individuals never received aggressive behaviors. In contrast, subordinate individuals engaged in the most social monitoring and received the most attacks, indicating subordinate individuals monitor conspecifics frequently as a form of vigilance. By constantly looking at dominant individuals,

subordinates may have been attempting to avoid spatial proximity to dominants to maintain a safe distance. Likewise, subordinates received the least social monitoring because they offered no threat to other individuals in the group. Confirming this conclusion, subordinate tier individuals in this study were never seen to attack other individuals.

A recent study of vigilance behavior in wild brown capuchins supports our conclusions that social monitoring functions to prevent attacks from conspecifics within the group. Hirsch (2002) found that as group size in two separate populations increased, individual vigilance increased as well. This result was somewhat surprising, because in studies of birds and non-primate mammals, individuals in larger groups exhibit lower vigilance. It is thought that larger groups enable individuals to reduce vigilance and spend more time engaged in other activities because of the benefit of increased predator detection with larger numbers (Roberts, 1996). However, non-human primate studies have found the reverse to be true, as did the Hirsch study. It has been theorized that non-human primate groups differ from other species because although larger group size reduces predator threat, conspecific threat increases. Because of the violent (and sometimes lethal, in the case of infanticide) nature of non-human primate attacks, social monitoring becomes necessary for individuals to avoid increased threats from conspecifics as group size increases (Treves, 2000).

If the function of social monitoring is within-group vigilance, then, we would expect subordinate animals to spend more time engaged in social monitoring than in non-social monitoring because of the priority to avoid attacks. Dominant individuals, in contrast, would spend less time engaged in social monitoring and more time engaged in non-social monitoring. Our data support this hypothesis as well. We found that of the

looks by dominant animals, only 12% to 25% were directed at a social target. In contrast, 50% to 80% of looks by subordinates were directed at a social target. Subordinate tier individuals thus directed more of their visual attention to other group members than dominant individuals. Dominant tier individuals in turn, directed the majority of their attention toward other activities, like grooming, resting, and feeding. Spending more time than subordinates engaged in such behaviors may be an important component of the maintenance of group social organization. Dominant animals spend time engaged in activities that enhance their dominance status, while subordinates are prevented from doing so because within-group vigilance demands their time and energy. Dominants are then able to secure their positions within the groups because they have resources (better nutrition, health) and social alliances (built through grooming) that subordinates do not have that help them maintain their dominant status.

Stress Response

Social organization is also likely maintained through the stress response associated with the visual channel. As discussed previously, visual stimuli, particularly threatening facial expressions, gestures, and stares operate as stressors. Such stressors cause activation of the body's stress response. Over time, on-going visual stressors cause a chronic stress response that can lead to physiologic dysfunction including reproductive and immune system suppression. Thus continuing aggressive gestures and threatening expressions can cause physiologic weakening of subordinates, which would also function to maintain social organization. Although the primate visual system has adapted to enable individuals to perceive the aggressive disposition and intent of others visually, without actually engaging in combat, the body still experiences physiologic responses to social conflict. The connection between visual communication, neuroendocrine response

and behavior is therefore an important component of the maintenance of social organization. Moreover, the behavior of subordinates itself is also a function of the subordinate's own stress response, as high cortisol levels are characteristic of submissive behaviors.

Behavior of Juveniles

The youngest individuals in this group both directed aggressive behaviors at others and received aggressive behaviors, occupying a middle position between dominants and subordinates. While juvenile social monitoring behavior may also be explainable in terms of vigilance behavior and the stress response, aggressive behaviors by juveniles may also be a function of age and the process of social learning. Juvenile capuchin monkeys have been shown to be highly attentive to the activities of others in the group, especially adults with primary focus of attention on the alpha male (Adams-Curtis and Fragazy, 1995). Especially between the ages of 6 to 12 months, juvenile brown capuchins increase social interactions with other group members, directing less attention toward their mothers and begin to imitate behaviors (Byrne and Suomi, 1995; but see Welker et al, 1992). It is thus possible that the aggressive behaviors and social monitoring by juveniles was related to social facilitation, or behavior learned from watching others display behavior patterns over time. Feeding behavior in brown capuchins is learned through social facilitation, (Visalberghi and Addessi, 2001; Custance et al, 1999), and aggressive behavior may be as well. The majority of aggressive behaviors by juveniles (53.7%) were directed at third-tier subordinates, while the remaining 46.3% were directed at each other. It is therefore possible that juveniles in this study were watching dominant tier individuals because of social learning and then imitating observed adult behaviors by attacking subordinates.

Absence of Predators

The absence of predators in this captive group may cause the results of this study to differ from a comparable study of social monitoring behavior in a wild brown capuchin group. In the wild, individuals visually monitor their surroundings to detect predators (Treves, 2000). Individuals may also watch group members for signs of alarm, taking advantage of group detection and leaving more time for foraging and other activities (Roberts, 1996; Treves, 2000; Hirsch, 2002). Because our study group was captive, there was no threat of predators and thus no need for outside vigilance. These factors may have caused individuals to direct more attention towards other group members instead of directing attention elsewhere. Also, captivity prevented subordinate individuals from leaving the group or remaining on the group periphery. Both of these factors may have contributed to heightened aggressive behavior and heightened within-group vigilance, disrupting natural social dynamics in this species. Therefore it would be interesting to compare this study with a similar study of social monitoring and dominance relations in a wild population where behaviors would be more ecologically relevant, to determine if the same behaviors were applicable.

CONCLUSIONS

In conclusion, we found the method of measuring visual gaze developed by McNelis and Boatright-Horowitz (1998) applicable to brown capuchin monkeys. Although brown capuchins shift their gaze rapidly and frequently, a 5-s audio cue combined with a focal animal sampling method allowed for sufficient sampling. Concurrence of two observers after 30-h of practice resulted in high levels of observer reliability.

We also determined that visual communication is clearly important in brown capuchin monkey social dynamics. The results of this study support the hypothesis that differential social monitoring is a mechanism by which brown capuchin monkeys maintain social order. The degree of social monitoring was significantly different between social dominance tiers. The most dominant animals received the most attention from the less dominant animals, and dominant animals gave little attention to subordinates. The clear relationship between aggressive behavior and social monitoring suggests that frequent social monitoring is a function of fear and anxiety, and the need to monitor the position and psychological state of dominants to avoid attacks. Frequent social monitoring by subordinates communicates fear, anxiety, and submissive psychological state and thus reinforces social dominance status. Conversely, infrequent social monitoring by dominants communicates inattention to subordinates, lack of fear, and dominant psychological state. Thus dominance relationships are reinforced visually, through aggressive threats by dominants or submissive gestures by subordinates.

Dominants maintain their role in the social group by capitalizing on the anxious behavior of subordinates. Dominants engage in fitness-enhancing activities, like grooming, resting, and feeding while subordinates spend time and energy engaged in

social monitoring resulting in less opportunity to form alliances, rest, and forage.

Through frequent social monitoring, subordinates also experience chronic stress, which results in physiological dysfunction. Visual stressors also cause neuroendocrine activity that is associated with submissive, fitness-reducing behaviors. In this way, the dominant and subordinate positions of individuals are maintained.

Social monitoring by juveniles facilitates social learning about social dominance relationships. Although juvenile behavior in this study may be explainable in terms of vigilance behavior and the stress response, it could also be related to social facilitation. Once juveniles become adults, their own differential social monitoring will likely be a function of learned experiences, and will continue to reinforce social structure.

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APPENDIX

VISUAL ATTENTION DATA

	Miro	Noel	Georgia	Carlos	Nina	Isabelle	Vincent	Sosa	Cruz	Total	0	Total
Miro		20	13	10	7	12	7	25	12	106	808	914
Noel	38		24	26	20	14	5	14	32	173	671	844
Georgia	39	36		10	18	18	11	36	16	184	756	940
Carlos	60	68	31		17	5	37	33	33	284	643	927
Nina	76	94	141	47		38	33	85	61	575	423	998
Isabelle	67	65	169	38	38		26	86	49	538	462	1000
Vincent	179	184	94	119	64	66		131	71	908	249	1157
Sosa	45	40	67	45	21	40	29		38	325	503	828
Cruz	39	28	46	29	11	9	10	89		261	576	837
	543	535	585	324	196	202	158	499	312	3354	5091	8445

Total number of looks
received

Index of visual attention (number of looks received -
number of looks given)

Miro	Noel	Georgia	Carlos	Nina	Isabelle	Vincent	Sosa	Cruz
437	362	401	40	-379	-336	-750	174	51



12 June 2003

TO: Pamela Pannozzo
Kimberley A. Phillips, Ph.D.

FROM: Greg K. Szulgit, Ph.D.
Chair, Animal Care and Use Committee

A handwritten signature in black ink, appearing to be "G. Szulgit", written over a horizontal line.

On 31 December 2001, the Hiram College Institutional Animal Care and Use Committee reviewed your proposal entitled 'The role of visual perception in the maintenance of hierarchical social orders in *Cebus apella*.' This proposal, now designated #2002-02, was approved for the dates 1/10/02 – 1/09/03.

Amendments to protocols involving animals (including a change in the number or a change in species) must be reviewed and approved by the IACUC before these changes can be implemented.

cc: Michael A. Grajek, Ph.D.