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Post-Conflict Social Events and Stress-Related
Behaviors in Japanese Macaques (*Macaca fuscata*)

by

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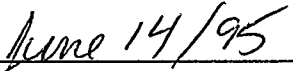
THE UNIVERSITY OF CALGARY
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The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies for acceptance; a thesis entitled "Post-Conflict Social Events and Stress-Related Behaviors in Japanese Macaques (*Macaca fuscata*)" submitted by Craig C. Lamarsh in partial fulfillment of the requirements for the degree of Master of Arts.


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ABSTRACT

Observations of free-ranging group of Japanese macaques were used to determine how individuals reacted to being the victims of aggression. The data were analyzed to determine if victims were involved in a number of social events which, hypothetically, may allow them to actively reduce the stress and uncertainty associated with the post-conflict period. Victims were shown to rarely reconcile their conflicts with their former opponents unless these animals were relatives or potential mates. Victims redirected aggression at third-parties significantly more after receiving aggression.

Stress levels of victims were measured through displacement activities to determine if victims became more anxious in the post-conflict period compared with control levels. Female victims showed significant signs of stress while males were less affected by aggression. Finally tests were done to determine if, as hypothesized, reconciliation and redirection were social events which reduced stress in victims of aggression. Reconciliation was effective in returning stress activities toward their baseline levels while redirection was less effective at reducing stress.

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DEDICATION

For my Mom and Dad who
by nature and nurture through
their love and support have
made everything a possibility
and
to Kathy who gives me the
strength and encouragement
to face all our challenges together.

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CHAPTER ONE
INTRODUCTION TO AGGRESSION
AND THE STUDY OF POST-CONFLICT
BEHAVIORS IN NONHUMAN PRIMATES

Historical Perspective

After World War II, there was an heightened interest in the study of hostility in social animals and scientists looked for a relationship between animal and human aggressiveness (Collinge, 1993). While primates were initially believed to be extremely hostile, field studies in the 1960's and 1970's gradually dispelled these early presumptions and emphasized a more peaceful image of monkey and ape societies. Interest in the study of aggression continues, however, there has been a recent shift from studying the factors which cause aggression towards investigating the behavioral mechanisms through which primates seek to limit the consequences of aggressive confrontations (de Waal, 1986b).

Calm and Conflict: Aggression vs. Group Living

Competition for valuable or limited resources (e.g. food, mates, space) is a consequence of gregarious living which inevitably leads to conflict between members of primate social groups (Aureli et al, 1993; van Schaik 1983, 1989). Although Bernstein and Ehardt (1985) report that aggression accounts for less than 5% and often less than 2% of the total social behavior found in nonhuman primates, aggression plays a conspicuous role in primate societies. Even the most social of primates possess the capacity for aggression and ability to inflict serious injury upon other group members. These disruptive forces seem in direct

contrast with the high sociability and cohesive behaviors most often characteristic of social primate taxa (Bernstein et al., 1983).

Victims of aggression usually remain in their social groups suggesting there are benefits to gregarious living. Aureli (1992) states that "an individual obtains a higher fitness within a group than it would gain through solitary living" (329). While the victim of aggression has the option of leaving the social group, temporarily or permanently, group living confers the adaptive advantages of lower risks of predation and enhanced protection of resources against conspecifics (de Waal 1986b; van Schaik 1983, 1989; Kappeler 1993; Kappeler & van Schaik 1992).

Conflict can, however, be especially harmful for the victim of an aggressive confrontation. The recipient of aggression can suffer the adverse effects of injury, loss of a resource and disturbance of a social relationship (Aureli, 1992). In addition, victims are prone to renewed attacks by the former opponent and alternate opponents (Aureli et al. 1989; Aureli & van Schaik 1991b) and are less tolerated around resources (Cords, 1992). The "uncertainty" of the victim about its social position after an aggressive encounter can be observed in elevated stress responses (e.g. scratching, body shaking and self grooming) interpreted as physiological preparedness for renewed agonism (Aureli & van Schaik 1991b).

Introduction to Post-Conflict Behaviors

The persistence of group living in many primate species suggests that gregarious behavior evolved colaterally with mechanisms to prevent conflicts and repair social relationships disturbed by aggression. These mechanisms, it is hypothesized, override the dispersive effects of aggression and help to maintain

overall group cohesiveness (de Waal, 1986a; Cords, 1988; Aureli, 1992; Kappeler & van Schaik, 1992; Aureli et al., 1993). Kappeler & van Schaik (1992) outline a number of interactions which could be used by primates to modulate relationships which have been stressed due to aggression. There are two immediate reactions available for an individual which is assaulted. First, an animal which is threatened or attacked may formally submit and/or yield access to resources to an aggressive or dominant individual. A second option is that the individual which is attacked may retaliate against the attacker with aggression of its own. These two possible reactions by the recipient of aggression, while important components of the social forces structuring primate groups (see de Waal, 1986a), are not of primary concern in this study. The first option, consisting of deferent or submissive behaviors on the part of the subordinate animal, act to circumvent the type of aggressive incident which is of interest to post-conflict study from occurring (i.e. low level threats and uncontested displacement of subordinate animal). Likewise, aggression with retaliation are not researched as these behaviors often lead to unsettled disputes where no clear aggressor/victim relationship can be assigned which is an imperative for post-conflict research.

There are five remaining post-conflict social interactions available to victims of aggression, as per Kappeler and van Schaik (1992), which are investigated in this study. The first of these is *reconciliation*, where former opponents may exchange affiliative behaviors with each other shortly after an aggressive encounter repairing the damage to their social relationship. A second interaction proposed to occur after an aggressive incident is where the victim of aggression may have affiliative interactions with a relative or ally other than the former aggressor. This behavior has been termed *consolation* and could, in

theory, have a calming effect on the victim. A more specific type of third-party affiliation has been proposed where victims may seek non-aggressive interactions with the aggressor's kin thereby indirectly normalizing the relationship with the aggressor. Called *substitute reconciliation*, this behavior could work if it reduces the probability that the victim will be reattacked. Finally, it is possible that the recipient of aggression could defer a conflict situation with aggression of its own. The victim could, theoretically, accomplish this by redirecting aggression against a third party which may divert the attention of the former aggressor and others away from itself. This behavior, called *redirection*, has been documented in a number of nonhuman primate and other animal species. A more specific theory which will be considered is *kin-biased redirection* where victims redirect aggression specifically at members of the aggressor's matriline. Such aggression may, indirectly, incur damages on the aggressor which cause it to cease hostilities directed towards the victim (see Walters & Seyfarth 1987; Aureli & van Schaik 1991a; Cheney and Seyfarth 1989; Judge 1991).

Post-Conflict Behaviors: A Closer Examination

RECONCILIATION

There are scattered references to reconciliation-type behaviors in earlier primate literature (Blurton-Jones & Trollope 1968; van Lawick-Goodall 1968; Seyfarth 1977; McKenna 1978), however, reconciliation was first labeled as such and systematically studied by de Waal and van Roosmalen in 1979. Reconciliation is generally defined as friendly, or non-aggressive, interaction between former opponents shortly after an aggressive conflict (de Waal, 1986b).

"It is a behavioral concept rather than a straight-forward element or category of behavior. Whether animals bite or move their ears can be observed directly; whether they reconcile requires systematic observation over a certain time period following aggression, and a comparison with control levels of interaction" (de Waal & Ren 1988; 130).

Many studies of reconciliation have found that the levels of post-conflict affiliation only exceed the control levels for a few minutes after the end of a conflict and if reconciliation is achieved it happens quickly after a cease in aggression (Aureli et al. 1989; Cords 1988; de Waal & Ren 1988; de Waal & Yoshihara 1983; Kappeler & van Schaik, 1992; Ren et al. 1991; York & Rowell, 1988).

Since de Waal & van Roosmalen's (1979) seminal investigation of chimpanzee post-conflict behaviors, reconciliation has been investigated in a wide variety of primate species: red-fronted and ringtail lemurs (Kappeler, 1993), rhesus macaques (de Waal & Yoshihara, 1983), stumptail macaques (de Waal & Ren, 1988), longtail macaques (Cords, 1988; Aureli et al., 1989; Aureli & van Schaik, 1991a; Aureli, 1992 [wild population]; Cords, 1992a, 1992b; Cords & Aureli, 1992; Cords, 1993; Cords & Thurnheer, 1993), pigtail macaques (Judge, 1991), Japanese macaques (Aureli et al., 1993; Chaffin et al., in press), Tonkean macaques (Thierry, 1986), patas monkeys (York & Rowell, 1988), vervet monkeys (Cheney & Seyfarth, 1989 [wild population]), golden monkeys (Ren et al., 1991), bonobos (de Waal, 1987) (also mountain gorilla (Watts), Hamadryas baboons (Gore) unpublished data referred to in Kappeler and van Schaik, 1992)). All of these species, with the exception of ringtailed lemurs (Kappeler, 1993), showed evidence of reconciliation behavior.

The tendency for former opponents to reconcile has displayed enormous variability between species and across studies with frequencies of reconciled

conflicts ranging from 0% to 56% (e.g. 0% in ringtailed lemurs, 16.8% in red-fronted lemurs, Kappeler (1993); 7% in vervets, Cheney & Seyfarth (1989); 20.7% in longtail macaques, Aureli et al. (1989); 22.8% in rhesus macaques, de Waal & Ren (1988); 31% in patas monkeys, York & Rowell (1988); 48% in bonobos, de Waal (1987); 56% in stumptail macaques, de Waal & Ren (1988) (figures from Judge, 1991; Kappeler & van Schaik 1992)). There are two studies which report evidence of reconciliation behaviors in Japanese macaques. Chaffin et al. (in press) discovered a relatively low conciliatory rate of (5.9%) while Aureli et al. (1993) reported significant levels of reconciliation but did not represent their findings in percentage form.

Different species show great behavioral variation in how reconciliation is achieved. For example, bonobos, chimpanzees and stumptail macaques display certain behaviors during reconciliation not commonly used outside of this context (de Waal & van Roosmalen 1979; ; de Waal & Ren 1988). Diagnostic of reconciliation in bonobos are a variety of heightened sociosexual behaviors which occur between former opponents of all age and sex classes (de Waal 1987). In chimpanzees a kiss is the most frequently observed conciliatory¹ gesture (de Waal & van Roosmalen, 1979) and for stumptail macaques a "hold-bottom ritual" is the most characteristic reassurance behavior of reconciliation. However, not all species appear to have behavior patterns specific to reconciliation and there is no evidence for specific conciliatory repertoires in, for example, Japanese macaques or patas monkeys (Aureli et al. 1993; York & Rowell 1988).

Kinship of the interactants is an important variable influencing the conciliatory patterns in different species. Most studies report higher rates of reconciliation amongst maternally related animals (e.g. rhesus macaques - de

¹conciliatory refers to affiliative behaviors germane to the process of reconciliation.

Waal & Yoshihara, 1983; patas monkeys - York & Rowell, 1988; vervet monkeys - Cheney & Seyfarth, 1989; pigtail macaques - Judge, 1991). An interesting exception to this comes from Cords (1988) study of juvenile male longtail macaques where she found that kin reconciled significantly less than non-kin. These results contrast, in part, with Aureli et al. (1989) which found higher kin-related reconciliation in a group of longtail macaques with varied age-sex classes. However, Aureli et al. (1989) could not, for comparative purposes, limit their investigation to focus on juveniles due to lack of representation of data from this class of animals.

Which of the opponents is likely to initiate post-conflict reconciliation is another variable dependent on the species being investigated. De Waal & van Roosmalen (1979) report for chimpanzees that there is no significant difference between the frequency of the aggressor or victim to initiate reconciliations. For patas monkeys (York & Rowell, 1988) and rhesus macaques (de Waal & Ren, 1988), the first-contact initiative is more frequently taken by the aggressor. Among stump-tail macaques (de Waal & Ren, 1988) and pigtailed macaques (Judge, 1991), it is the victim of aggression which statistically more often approached the aggressor. For juvenile male longtail macaques (Cords, 1988) the aggressor most often initiated reconciliation while Aureli et al. (1991a) reports from their study of a mixed age-sex group of longtail macaques that the victim tended to make first affiliative contacts with the aggressor.

A final variable which could affect rates of reconciliation is based on the value of the relationship between the former opponents. For example, individuals who will aid in aggressive encounters and ones from whom are tolerant of co-feeding at clumped resources could be deemed valuable partners. Cords & Thurnheer (1993) developed a novel experimental approach to

determine whether reconciliation rates were affected by the value of the social relationship between non-related female longtail macaques. First, the researchers created 7 test dyads and recorded their baseline levels of interaction. Next, they experimentally induced aggression and recorded the rates of reconciliation. The animals were then taught how to access morsels of food from a machine by performing a simple cooperative task. Finally the reconciliation rates for the dyads were tested again under the hypothesis that the value of the relationship had been increased through the cooperative requirements of the experiment. For 6 of the 7 dyads, the reconciliation rate more than tripled after training and Cords and Thurnheer (1993) believe their results show that animals with valuable relationships are more strongly motivated to normalize their relationships when disturbed by aggression.

Functions of Reconciliation.

Most studies of reconciliation have assumed that reconciliation functions to repair the social relationship between former rivals. Whether reconciliation performs this function has been tested in two studies. Aureli & van Schaik (1991b) reported that among captive longtail macaques, reconciliation functioned to reduce the victim's anxiety as measured by a decrease in stress or displacement behaviors after reconciliation had taken place (Aureli & van Schaik 1991b). In a separate study of longtail macaques, Cords (1993) showed that reconciliation in longtail macaques restored tolerance around resources more quickly than occurred between animals which did not reconcile.

Kappeler & van Schaik (1992) outline four major hypotheses for the evolution of reconciliation: (1) a minimum cognitive capacity is necessary for reconciliation and perhaps coincides with other relevant variables such as

relative brain size and/or social complexity. This hypothesis merely anticipates which species are capable of reconciling and not why this would confer adaptive advantages. (2) Since gregarious primates must contend with inter-individual competition they have developed conciliatory behaviors as a requisite for retaining the advantages which group living confers (social evolution hypothesis; de Waal 1989a). (3) De Waal's (1986) "reconciled hierarchy" model predicts that reconciliation is functionally related to groups with strongly attenuated dominance hierarchies. Under this model, dominant animals will grant reconciliation to subordinate animals if they recognize, through appropriate behaviors, the superior status of the dominant. In this case, aggression is purported to be a constructive element of social life. (4) Finally, the "Good Relationship" hypothesis predicts that reconciliation may be more prevalent between individuals who have adaptive reasons for maintaining good relationships; e.g. (a) relatives (b) alliance partners (c) potential mates, or (d) members of a group-level alliance against other groups (Kappeler & van Schaik, 1992, p 61). Most of the existing data support aspects of the "Good Relationship" hypothesis and Kappeler & van Schaik (1992) believe this is the most promising direction of future study to attain a better understanding of the variability of reconciliation behaviors now evidenced between primate species.

CONSOLATION

A second option a victim could, theoretically, seek to reduce stress and ease its uncertainty about the social situation after receiving aggression is reassurance from members of a social group other than the former opponent and its kin. De Waal & van Roosmalen (1979) labeled such behavior consolation believing that affiliation with kin and allies may act to pacify the victim. Indeed,

Schino et al. (1988) provide evidence that allogrooming can function as a tension-reduction mechanism in longtail macaques, however, this evidence was not produced in a post-conflict context.

No study which has specifically looked for consolation has discovered post-conflict affiliative interactions above control levels apart from reconciliatory tendencies between the victim and the former aggressor. For pigtail and longtail macaques, the victim was just as likely to be in contact with a relative after involvement in aggression as during baseline control observations (Judge, 1991; Aureli & van Schaik 1991a). In Japanese, Barbary and stump-tail macaques, the victim actually contacted kin members less after aggression than during control periods (Aureli et al., 1993; de Waal & Ren, 1988). Aureli and van Schaik (1991a) question the theory behind consolation writing:

"It is difficult to envision a functional basis for consolation. It cannot have a direct effect on the relationship between the victim and the former aggressor, making it unlikely that it could reduce either the risk of being attacked again or the uncertainty of the victim's social position" (p.97-98).

Based on the lack of empirical evidence or sound theoretical rationale, Aureli and van Schaik (1991a) believe the concept of consolation needs to be re-evaluated.

SUBSTITUTE RECONCILIATION

Substitute reconciliation predicts that if reconciliation is not achieved between the victim and aggressor, the victim's next best option may be to seek affiliative interaction with members of the aggressor's matrilineal kin. It is hypothesized that such affiliation may indirectly repair the relationship between the former opponents and reduce the chances of renewed aggression against the victim (Kappeler & van Schaik, 1992). There are reports of such behavior in patas monkeys (York & Rowell, 1988), vervet monkeys (Cheney & Seyfarth 1989) and

pigtail macaques (Judge 1991) however interpretation of results are made difficult by the fact that these studies did not distinguish between the role of aggressor and victim.

In studies where the victim/aggressor roles are considered there is scant evidence for substitute reconciliation. Aureli and van Schaik (1991a) report evidence of substitute reconciliation in longtail macaques when they limited their analysis to include only the juveniles in their study group. They believe that it may be difficult for juvenile victims to access unrelated adult aggressors and, therefore, they seek to lower their chances of being reattacked by affiliating with the younger kin of their aggressor (p. 98). Judge (1991) discovered an alternate trend in pigtailed macaques where the aggressor had higher rates of affiliation with the victim's kin after aggression, however the victim showed no such attraction to the aggressor's kin following a confrontation. In testing for substitute reconciliation in Japanese macaques, Aureli et al. (1993) found no evidence for elevated affiliative behaviors between the victim and the aggressor's kin in the post-conflict period.

REDIRECTION

Another post-conflict behavior which may aid in arousal reduction of the victim is the redirection of aggression. This behavior has long been reported to occur in a number of nonhuman primate species (Itani, 1963; see also Scucchi et al. 1988 for review of macaque species). A popular theory concerning the purposes of redirection predicts that by behaving aggressively towards a group member, apart from the former opponent, the victim diverts the attention of its attacker and other group members to a more recent target. Redirection, in accordance with this reasoning, would have the short-term functional

implications of reducing the chances of re-attack on the victim thereby reducing the uncertainty about its social position (Itani, 1963; Scucchi et al. 1988). Redirections have been reported to occur primarily against animals subordinate to the victim and it is believed that the "additional costs to redirect aggression against a subordinate animal can be considered to be somewhat low, relative to the potential benefits of diverting the attention of the original aggressor to a third animal" (Scucchi et al., 1988; 235). However, female Japanese macaques also attacked higher ranking animals more frequently during redirections than in initial aggressive incidents which Scucchi et al. (1988) believe is an indicator that females also use redirection as a long term behavioral strategy to achieve higher ranks.

Rather than diverting attention of potential aggressors, de Waal (1977) suggests the victim may redirect aggression in an attempt to enlist the support of its former aggressor. Aureli and van Schaik (1991b) provide evidence that victims which are redirecting aggression against a third-party may "showlook" at their former aggressors, a behavior they interpret as an invitation for cooperative action or, at least, indications that their aggressive behavior will be tolerated. Redirection under these circumstances would provide reassurance to the victim and may be functionally equivalent to reconciliation in normalizing the relationship between the former opponents and reducing the victim's anxiety (Scucchi et al., 1988; Aureli & van Schaik, 1991b).

Victims may also use redirection of aggression more intentionally, specifically aiming aggression at vulnerable relatives of the former aggressor to change the attitude of the aggressor towards themselves (Aureli & van Schaik 1991a). A victim redirecting aggression against the aggressor's lower ranking kin may indirectly damage the former aggressor and function to inhibit future

agonistic actions by the aggressor against the victim (*ibid.*; Kappeler & van Schaik, 1992). In support of this theory, Aureli and van Schaik (1991a) discovered that longtail macaque aggressors were more disposed to reconcile with their victims after those individuals had redirected against their kin. Reports which suggest kin-biased redirection have also been published for vervets (Cheney & Seyfarth, 1989), pigtail macaques (Judge, 1983), baboons (Smuts, 1985) and Japanese macaques (Aureli et al., 1992) though quantitative evidence remains limited.

A final theory about the occurrence of redirection is that these behaviors may, simply, represent emotional frustration on the part of the victim. Third-party aggression could be a way for victims to "displace" their aggressive tendencies on an individual lower ranking than itself. Redirection may provide an emotional release for the victim but not provide any functional reassurance about its relationship with the former aggressor or its emotional uncertainty about its social position (see Aureli & van Schaik, 1991b; Maestripietri et al., 1992).

TENSION-RELATED (DISPLACEMENT) ACTIVITIES AND FUNCTIONAL ASPECTS OF POST-CONFLICT BEHAVIORS

A nonhuman primate which is the victim of aggression often manifests behavior consistent with elevated levels of anxiety which can persist even after a cease in aggression by its attacker. This behavior is generally attributed to a state of internal conflict and the victims loss of control over its social situation (Maestripietri et al., 1992; Aureli & van Schaik 1991b). "[T]he internal conflict may refer to the presence of strong motivation for two incompatible activities, namely withdrawing, reflecting the fear of renewed attacks by the former aggressor, and approaching, in order to achieve reconciliation" (Aureli & van Schaik 1991b). The

disruption of the relationship with a dominant individual may also lead to uncertainty concerning the tolerance or support the victim may expect from the aggressor or other group members in response to this aggression (ibid.). Indeed, there are numerous reports which show that victims are more susceptible to renewed agonism from former aggressors and other opportunistic aggressors taking advantage of the victim's tenuous social and psychological state (ibid.; de Waal & Yoshihara 1983; York & Rowell 1988; Aureli et al. 1989; Kappeler & van Schaik 1992). Aureli and van Schaik (1991b) believe that post-conflict stress is an adaptation whereby, through its aroused state, the victim of a confrontation maintains its preparedness to react quickly if it should be reattacked.

After aggression has ceased, it might be predicted that the victim's emotional state and physiological responses would return to baseline. However, if the victim still perceives a threat, stress responses may persist (Aureli & van Schaik, 1991b). During periods of uncertainty a primate often displays behaviors referred to as displacement activities which consist mostly of body-care actions, such as body-scratching, body-shaking, self-grooming and yawning, which are performed in contexts seemingly irrelevant to its ongoing social situation (Schino et al., 1991; Maestripieri et al., 1992). Displacement activities have been reported in a wide number of primate species (for review see Maestripieri et al., 1992) and several recent studies have proposed that they are good indicators of the physiological changes associated with tension and anxiety. As an ethological tool, displacement activities provide a good behavioral measure of the emotional states in nonhuman primate subjects (Schino et al. 1988,1990; Aureli & van Schaik 1991b; Troisi et al., 1991; Maestripieri et al., 1992).

Displacement Activities and Post-Conflict Study

Despite their being among the most conspicuous of primate behaviors, displacement activities have been mostly ignored in contemporary studies (Maestripieri et al., 1992). Recently, some researchers have been testing whether post-conflict events function to reduce levels of stress in the victims of aggression as measured through displacement activities. It has been demonstrated in captive longtail macaques that reconciliation reduces the rates of scratching (Aureli et al. 1989), body-shake and self-grooming (Aureli & van Schaik 1991b) in victims of aggression. Redirection also has been shown to reduce rates of scratching but is less effective in reducing body-shake and self-grooming (Aureli & van Schaik 1991b). Hence, the post-conflict behaviors of reconciliation and redirection seem to function, at least partially, in the reduction of anxiety in former victims (Aureli et al. 1989; Aureli & van Schaik 1991b).

RESEARCH OBJECTIVES AND RELEVANCE OF STUDY

Studies of post-conflict behaviors in primates, particularly macaque species are plentiful. To date, published research has emphasized the great variation in how different species manifest post-conflict events and the host of variables such as age, sex, rank and kinship which influence these behaviors. However, post-conflict research is still a relatively new and broad subject of inquiry with many areas of these phenomena yet to be researched.

One noticeable element missing from the growing body of post-conflict research stems from the fact that the vast majority of studies have been carried out using captive primate study groups. There is a very real possibility that the restricted ranges available to captive animals may artificially inflate frequencies of post-conflict events (Aureli, 1989). However, there is only one published

study of the post-conflict behaviors of a feral macaque group to compare with the substantial amounts of captive research (longtail macaques - Aureli, 1992). A principle objective of this study is to provide information concerning the post-conflict events and activities of free-ranging primates to enhance a comparative base for these behaviors as they occur in different environmental conditions.

Specifically, this study will investigate five post-conflict social events (i.e. interactions with conspecifics) which are theoretically available to victims of aggressive attacks in a free-ranging Japanese macaque troop. The data will be examined to determine if there is evidence of behavior consistent with patterns outlined for reconciliation, consolation, substitute reconciliation, redirection and kin-biased redirection. In addition to investigating the existence of these post-conflict social patterns, a more indepth exploration of possible factors affecting these behavioral patterns is undertaken where it is germane and informative.

Although displacement activities have been a long recognized component of primate behavior they have been neglected, until recently, as a topic of study (Maestripieri et al., 1992; Scucchi et al., 1988). Displacement behaviors, as ethological measures of stress, provide an excellent tool for primatologists toward better understanding the emotional states of the animals being researched. Specifically for post-conflict studies, the use of displacement behaviors as indicators of anxiety gives primatologists the opportunity to test whether post-conflict social events actually perform the arousal reducing function generally ascribed to them. That is, we can now determine, by using measures of displacement activities if, for example, reconciliation actually reduces or terminates the stress response in the victim. Thus far only two studies of longtail macaques have utilized such measures (Aureli, 1989; Aureli & van Schaik, 1991b). Another major objective of this study is to add to the limited

research base which uses displacement activities to measure the emotional status of primates.

This research will examine the possible displacement behaviors of body scratching, body shaking, yawning, run/jump startles and selfgrooming after individuals receive aggression. Levels of these behaviors are measured and compared between post-conflict and control periods to ascertain if these behaviors reflect elevated stress in victims. Similarly, the time budgets of victims will be examined to determine if/how their general activity patterns are affected by aggression and, in particular, if there are costs associated with receiving aggression (e.g. Do victims invest more energy in locomotory behaviors and less time eating?). Also considered is whether victims of aggression are more prone to be reattacked as evidence of this behavior is of theoretical relevance toward explaining the anxiety and motivations of the victim in the post-conflict period. Analyses will include specific consideration of the variables of sex and the level of aggression to determine if/how these affect the performance displacement behaviors and time budget activities.

Finally, where evidence for post-conflict events (e.g. reconciliation, redirection) are discovered, measures of displacement activities will be compared before and after these events occur. From this analysis it can be determined if post-conflict events reduce the stress responses in the victims of aggression as measured by a reduction in the performance of displacement behaviors. Most post-conflict studies assume that post-conflict social events normalize the behaviors of the victim and its uncertainty about its social position but few provide evidence of this function. This study will supplement the theoretical framework which guides most post-conflict research with additional analysis concerning the functions of post-conflict events.

Overview of Thesis

This thesis explores how the Arashiyama West Japanese macaques react both behaviorally and socially when they are the victims of aggression. Chapter two outlines the methods utilized in this research including brief descriptions of the study species, the study group and information on aggression and mating behaviors of Japanese macaques. Also included in this chapter is a general overview of the data collection and data analysis techniques used in this study.

Chapter three contains a quantitative analysis of social interactions which have been hypothesized to occur after aggression. Specifically, tests will be done examining the phenomena of reconciliation, consolation, substitute reconciliation, redirection and kin-biased redirection to determine if these events occur and some of the factors affecting their exhibition.

Chapter four takes a closer look at how and why victims are behaviorally affected by aggression. Displacement behaviors and time budgets will be analyzed to determine if aggression causes stress in victims or changes in their general behavior patterns which may confer negative costs of conflict. In addition, this chapter will examine evidence that victims are more prone to reattack which is a popular theoretical explanation for their physiological and emotional arousal in the post-conflict period. Finally, levels of displacement behaviors will be compared before and after post-conflict social events to help elucidate the functions of these behavior patterns.

In chapter five, the data from the two previous results chapters will be compared and discussed in the broader framework of post-conflict research. Theoretical models will be evaluated in light of the results of this study and suggestions where additional research would be fruitful are noted.

CHAPTER TWO

METHODS

Introduction

Early post-conflict studies were prone to methodological experimentation which confounded attempts at relating discoveries and conclusions to other available data. Recently, methodological standardizations have been suggested which facilitate inter-study and inter-species comparability of post-conflict data (Kappeler & van Schaik 1992; Kappeler 1993; Cords, 1993). From operational definitions for post-conflict events through precise outlines for the collection of control data, these methodological enhancements will be implemented in this study to increase the reliability of the data that is collected and its comparability with other post-conflict research.

Study Species: Japanese macaques

Indigenous to the islands of Japan, the Japanese macaque is the most northerly ranging of the non-human primate species. Japanese macaques are medium-sized quadrupeds with moderate degrees of sexual dimorphism. Widely considered among the heartiest and most adaptable of primates, the Japanese monkey expresses versatility in the environment it exploits, the food which it eats and the seasonal weather variations it endures. Though primarily terrestrial, Japanese macaques often seek trees to acquire food, shelter or transportation.

Social Organization and Dominance Structures

Japanese macaques live in multimale/multifemale groups characterized by female philopatry and male dispersal. Females and their maternal kin form the enduring core of Japanese macaque troops, while males usually emigrate at adolescence to eventually join a different group. The troop is, in theory, spatially arranged in a hierarchy comprised of concentric circles (Bramblett, 1976). The innermost rings consist of the high ranking unrelated males and the dominant female matriline. The outer rings consist of gradually lower ranking and often younger individuals, predominantly male with the outermost ring consisting of the most solitary and low-ranking of males often in the process of leaving or joining the troop. Japanese macaque dominance hierarchies appear to be rigidly linear with a high degree of stability (e.g. Eaton, 1984; Thierry, 1990; Chaffin et al., in press) and the rank of offspring corresponds to a high degree with that of its mother (de Waal et al., 1976).

Mating Season and Aggression

The mating season for Japanese macaques generally begins sometime in September or early October and continues through late January or early February (Pavelka, 1993). Aggressive behaviors increase during mating season with higher rates of male-female attacks, inter-male fighting and aggressive wounding which correspond to higher levels of testosterone in males and the numbers of estrous females (Enomoto, 1981; Eaton, 1984). Chaffin et al. (in press.) report a low rate of agonistic threats from a captive group of Japanese macaques suggesting that there may be little warning given by dominant animals previous to their attacks on subordinates (see also Pavelka, 1993). Japanese macaques also

seem to have less frequent but more intense aggression compared with other macaque species (Chaffin et al., in press).

Study Group: Arashiyama West Japanese Macaques

In 1954, Japanese primatologists began to study a group of Japanese macaques in the Arashiyama mountains. Aided by provisioning, this group grew to number 163 animals before fissioning in 1966 into two daughter troops (A and B). Troop A moved down the mountain and became a nuisance to the local human populations (see Fedigan, 1992). In 1972 this troop was caught and relocated to the United States (Bramblett, 1976). After subsequent moves the Arashiyama West Japanese macaques now reside on a ranch near the town of Dilley, Texas where they have adapted remarkably well to an arid environment very unlike that of Japan.

Originally living within a 58 acre enclosure outside of Dilley, the Arashiyama West macaques are no longer contained by the fencing and, able to leave this area freely, are now free-ranging animals. They are provisioned daily with corn, milo and monkey chow but they supplement their diets by foraging for insects and locally available shoots, berries, grasses, fruits, and seeds when in season. A few times each month, a truckload of various produce is brought in for their consumption and yearly two fields are planted with grain crops to expand the accessibility of food. There are two ponds and a number of spigots which provide water for the monkeys ad libitum.

The Arashiyama West colony of Japanese macaques has grown from an original population of 150 animals in 1972 to over 600 animals in 1994. In 1989, the troop fissioned with a small "splinter troop" of approximately 40 animals breaking off from the "main troop" which still consisted of over 500 animals (for

details see Pavelka, 1993). While the splinter troop population is more comparable with indigenous feral populations in Japan, the main troop's size is not abnormal for a provisioned population (Pavelka, 1993). The Arashiyama monkeys have been studied since 1954 and troop and individual histories and genealogies are available to researchers. Most of the animals have leg and facial tattoos which aid in individual identification.

Data Collection

This study occurred over a 6 month period between August 1994 and January 1995. August and September 1994 were used as an orientation and reconnaissance period where animal identification and field techniques were practiced. Though none of this preliminary data was utilized in final analyses, practice observations and focal techniques aided in familiarization with the behavioral and ranging patterns of this troop and standardization of behavioral definitions to be used in this study.

Data utilized in this study were collected during the mating season between September 22, 1994 and January 24, 1995. Pavelka (1993) reports that mating behavior for this troop typically begins toward the end of September or early October and ends in February. During this mating season initial estrus behaviors were noted September 1, 1994 and large numbers of animals were observed in estrus by the end of this month². Estrus behaviors were still highly evident during the end of the study period in January, 1995.

²during this study the researcher was also involved in another project which required recording observable signs of estrus (e.g. consorting pairs, seminal plugs and reddening of the face and perianum.)

Subject Animals

Data for this study came from observations of the main troop of the Arashiyama West macaques (for description see Pavelka, 1993). At the time of study this troop consisted of over 500 individuals of all age/sex classes which were well habituated to human observers. The researcher was able to identify approximately 90 percent of the animals over 5 years of age in this troop with the aid of individual tattoos and other physical and behavioral characteristics. Genealogical information was available for these animals and relatedness was considered to a minimum factor of 0.125% (e.g. aunt/cousins) all other animals being considered unrelated (see Massey, 1977). Individuals under 5 years of age were dropped as focal animals due to difficulties of positive identification and low representative data from these younger age/sex categories. These animals were, however, included in observations when they interacted with focal animals whether they could be individually identified or merely scored by age and sex.

Aggressive Interactions

Although the main troop is unrestrained from ranging freely, except for the obvious convenience of provisioning, they spend the vast majority of their time in one of two areas: the trailer area and the main tank area (see Appendix A). In order to maintain consistency between observations, only aggression in these two areas were considered (i.e. excluding sporadic forays into the fields or surrounding brushlands). There were no data collected within 1 hour after daily provisioning.

The author was situated such that as many animals as possible were in sight at any given time to heighten opportunities to observe aggression. For an

aggressive interaction to be studied the researcher had to witness a majority of the incident in order to assign an intensity level and had to recognize both opponents involved in the interaction. 'Light aggression' was defined by the occurrence of facial threats, aggressive vocalizations, locomotion by the aggressor for at least two meters and may include light bodily contact for less than 2 seconds (e.g. slap or cuff) (see de Waal & Yoshihara; 1983). Aggression was labeled 'Heavy aggression' when the aggressor pinched, grabbed or bit the victim to the point of causing apparent pain. Only dyadic aggression, involving an aggressor and a victim, were observed for this study due to the unique properties and effects of third-party (or more) involvement in aggressive situations (see Kappeler & van Schaik, 1992).

Post-Conflict Observations '(PCs)'

After the last aggressive act had passed between the opponents a 15 minute focal sample (Altmann, 1974) was tape-recorded on the victim's behavior. If the conflict between opponents resumed within the first two minutes of the focal sample then it was considered that aggression had not yet ceased and a new focal sample was begun. If the focal animal was out of sight for more than 1 minute the sample was abandoned. Recorded behaviors were based on a modified version of Fedigan's (1976) ethogram for Japanese macaques (see Appendix B) and sub-grouping into time budget categories was based on Aureli's (1992) design.

State behaviors were divided into 5 higher level behavior categories:

- 1) Stationary: includes sit, lie, stand, bipedal: not including selfgroom.
- 2) Locomotion: includes travel, lope, climb (up/down), chase, follow (dir/rec).

- 3) Eat/Drink: includes forage³, drink.
- 4) Social: includes huddle, sit/lie in bodily contact, groom/groom solicit (direct/receive), mount (direct/receive), play, muzzle (direct/receive).
- 5) Self groom (see ethogram)

Event behaviors recorded during focal samples (all occurrences) were based on Schino et al. (1988).

- 1) Body Scratch- A repeated movement by the hands or feet during which the fingertips are drawn across the individual's fur. Body scratches which were separated by at least 5 seconds of another activity were scored as separate events.
- 2) Body Shake- A shaking movement of the entire body similar to a wet dog.
- 3) Yawning- A gaping movement of the mouth resembling a human yawn.
- 4) Run/Jump Startle- A sudden explosive movement of the body. A jump startle occurs with a jerking movement of the animal's body in place often caused when the animal is caught unaware, for example of the approach of another animal unnoticed until within close proximity. A run startle includes an explosive movement across space usually caused by the sighting of a fearful stimulus (Fedigan, 1976). These behaviors were pooled together due to their similar motivations.

Matched-Control Observations '(MCs)'

As with the majority of post-conflict research, this study follows de Waal and Yoshihara's (1986) methodology using control observations to acquire baseline behavioral measures for comparison with an focal individual's PC data. De Waal and Yoshihara (1986) suggest that matched-control samples should be collected for the same individual at the same time the following day (if weather

³ includes foraging on natural vegetation or provisioned goods.

conditions are similar) and for the same duration as the PC observations. An MC observation would be postponed if the focal individual was involved in an aggressive interaction in the minutes preceding a focal sample. For this study an MC was postponed for 30 minutes if the focal animal was involved in aggression within 3 minutes before an MC.

De Waal and Yoshihara's (1986) methodology was designed for captive studies where animals have more structured daily routines and all the study animals are continuously grouped together. In a free-ranging study, activity patterns are less structured and this required the relaxation of some control measures for the collection of MC data. First, free-ranging animals, especially in a large group such as this, are less likely to be in proximity to each other at the proposed time for an MC than in the PC period just after they have interacted. To ensure the former opponents had the *opportunity* to interact in the MC period a proximity control was used such that animals had to be within 15 meters of each other and have the ability to see each other before a MC could begin (see Kappeler & van Schaik, 1992). This distance was selected for its comparability with the boundaries of captive groups in most situations. Second, it was difficult to locate opponent animals in proximity at the precise time of day when PC data was collected. Therefore, in this study an MC was started if animals were found in suitable proximity within one hour of the time of day when the PC had started. Third, if the conditions of the MC period were not met the day after the PC then attempts to meet these requirements were made on subsequent days. If proper MC conditions could not be met within 7 days the PC was discarded (see Aureli et al., 1993).

Data Analysis

There were 125 matched-control observations (MCs) which satisfied control period criteria from the 210 post-conflict (PCs) observations gathered. Data analysis was performed on these 125 PC-MC pairs, 98.4% of which represented unique dyads of opponents. Data were collected on dyadic aggression on an *ad-libitum* basis and it is believed that a representative sample of main troop aggression was collected. Male aggression on females accounted for 65 of the PC/MC observations, while there were 18 samples with male on male aggression and 42 with female on female aggression. Female aggression directed at males were rare and those observed fell outside this study's control parameters (e.g. they were the result of a polyadic aggressive sequences).

A number of the analyses in the results chapter require methodological refinements which are explained when necessary. Unless otherwise stated, statistical significance levels are set at 95 percent ($p < 0.05$) and trends are reported up to 90 percent ($p < 0.1$). All statistical analysis is performed using the Statview 4.1 program on a Macintosh computer.

CHAPTER THREE

POST-CONFLICT SOCIAL EVENTS

Introduction

There are a number of suggested behavioral patterns characterizing how nonhuman primates may respond to aggression. Reconciliation, where opponents affiliate shortly after aggression, is the most commonly reported post-conflict social interaction and its occurrence has been documented in several species of monkeys and apes. Consolation, where the victim of aggression has social interaction with a group member other than the former aggressor, has been suggested as a potential post-conflict behavior, however, has never been documented in a study employing control observations. Redirection behaviors have been reported to occur in a number of primate as well as other animal species and a variety of suggestions have been proposed concerning their functions.

In this chapter, data collected from the Arashiyama West Japanese macaques will be tested for evidence of the post-conflict events of reconciliation, consolation and redirection. Reconciliation behavior will be examined using a standard methodology which includes affiliative contact as well as using a proximity measure for this event. The effects of sex, kinship, initiator and contexts will be further examined to understand the exact nature of conciliatory behaviors. Tests for consolation behavior will be done to determine if this event is part of the behavioral repertoire of Japanese macaques. Under consolation more specific analyses will be used to determine if there are specific third-party individuals which victims may preferentially affiliate with after receiving aggression. Specifically, it will be analyzed whether victims show increased

affiliation with relatives of the former aggressor, that is, do victims show evidence for substitute reconciliation. Finally, redirection behaviors will be examined, with specific analyses on temporal trends, the effects which sex has on these behaviors, and to determine if there is evidence for kin-biased redirection. Results obtained from this section will be placed in context with the findings from other studies of nonhuman primates for preliminary evaluation.

RECONCILIATION

Introduction

In this section the post-conflict behaviors of the Arashiyama West macaques will be examined to determine if former opponents engage in friendly interactions more frequently after being involved in aggression than when there had not been an altercation (i.e. reconciliation). Proximity measures as well as the more conventional contact scores for reconciliation will be considered in an attempt to understand all of the potential conciliatory gestures for this species. In addition, different variables (e.g. sex, kinship) will be analyzed to determine if/how they affect the interactions between former opponents.

Data Analysis and Methods

Reconciliation was examined according to the definition of de Waal and Yoshihara (1983). If former opponents made affiliative contact earlier in the PC than the MC or only in the PC then the pair was labeled as "attracted". If former opponents made contact later in the PC than the MC or only in the MC then the pair was labeled "dispersed". However, rather than using the terms "attracted" and "dispersed" as per de Waal and Yoshihara (1983), this study will use the terms "earlier" and "later" respectively which connote fewer presuppositions (see

Aureli, 1992). Affiliative contacts were considered to be the same as those labeled under "Social" state behaviors in the data collection section.

Reconciliation as Measured Through Affiliative Contact

Of the 125 PC/MC observations, 113 pairs of former opponents did not make contact at all in either the PC or the MC. Under the null hypothesis, that reconciliation did not occur, the remaining 12 PC/MC pairs would be divided equally between 'earlier' and 'later' pairs. Seven pairs were found to be 'earlier' and five were found to be 'later' with no significant difference discovered between these affiliative levels ($\chi^2 = 0.667$, $p > 0.05$). Hence, there was no evidence for elevated levels of contact between former opponents in this group.

Proximity: A Measure of Reconciliation ?

During this study there were several observations in which former opponents did not exchange friendly contacts but were seen to come into close proximity of each other after a conflict without generating renewed aggression. Proximity is not a commonly used measure for reconciliation (but see Cords, 1993) because it may artificially inflate reconciliation estimates, especially in captive groups (Kappeler & van Schaik, 1992). However, proximity may be a more common conciliatory gesture in species with strongly attenuated hierarchies where it could be risky for a subordinate to attempt contact with unrelated dominant animals (Chaffin et al., in press; de Waal & Yoshihara, 1983). Especially in a study situation where there is a large availability of space and other possible interactants, movement into close proximity between former opponents may suggest less overt attempts to reduce the damages to their relationship incurred by aggression.

Reconciliation Measured Through Contact and Proximity

In order to test proximity as a conciliatory mechanism, the behavioral criteria considered to be affiliative interactions between former opponents were expanded. In addition to affiliative contact between former opponents, proximity was also considered to be a form of reconciliation if the victim or aggressor moved to within 1.5 meters of the other for a duration of at least 30 seconds and without the exchange of aggressive signals. When proximity measures were pooled with contact scores 12.8 percent (n=16) of opponent pairs were considered to have interacted earlier/only in the PC, with 4.8 percent (n=5) interacted earlier/only in the MC. Pooled scores indicate that opponents were significantly more attracted to contact or come into close proximity with each other in post-conflict periods when compare with control periods ($\chi^2 = 11.524$, $p = 0.0007$). For the remaining analyses these 16 pairs, as measured through contact and proximity scores, are considered to be reconciled opponent dyads.

Selective Attraction

Reconciliation may simply be an artifact of a general increase in the affiliative tendencies of the victim rather than a selective attraction for the former opponent. To test for this possibility, the total number of individuals the victim contacted in an affiliative manner in the PCs and in the MCs were compared. The number of former opponents which the victim made contact or came into proximity with was expressed as a percentage of the total number of affiliative partners summed from the PC data and the MC data (see de Waal & Ren, 1988). Former aggressors represented 16 of 94 (17.02%) affiliative partners in the PCs and 5 of 88 (5.7%) affiliative partners in the MC period. Opponents were more

selectively attracted to come into contact or proximity of each other in the PCs than the MCs ($\chi^2 = 4.568$, $p = 0.0326$).

Initiative to Reconcile

Many studies of post-conflict behaviors in primates have reported that one opponent, either the aggressor or the victim, initiates reconciliation behaviors proportionately more often than the other. The initiative to reconcile was examined to discover if such a trend was apparent for this group of Japanese macaques. The sixteen 'earlier' PC/MC pairs which were considered to be reconciled by contact and proximity scores were used in this analysis. The initiator of reconciliation was considered to be the animal which: a) approached its opponent and initiated or solicited affiliative contact (e.g. groom solicit, tail-up sex display) or b) approached to within 1.5 meters of its opponent for no less than 30 seconds without the exchange of aggressive signals.

Limited sample sizes, especially from the MC period, restrict the use of statistical analysis but a simple comparison of the initiator of reconciliation between the PC and MC samples suggests that there is no discernible pattern. In the PC period the victim took the initiative to make contact or close distances between itself and its opponent in 56 percent ($n=9$) of reconciliations while the aggressor took the initiative in the remaining 44 percent ($n=7$). The victim took the initiative to approach the aggressor in 60 percent ($n=3$) of the MCs while the remaining MC dyads were in contact at the beginning of the MC period so initiative could not be scored. Aureli et al. (1993) found no evidence from their study on captive Japanese macaques that either victims or aggressors were more likely to take the initiative to reconcile and the results from this study do not appear to contradict this conclusion.

Sex and Reconciliation

A test was performed to determine whether the sex of the opponents affected the rates of reconciliation. Of the 125 PC/MC focal pair, 65 consisted of male/female aggression, 42 were female/female aggression and 18 were male/male aggression. Of the 16 reconciled pairs, 11 were male/female dyads, the remaining five consisted of female/female pairs and there were no examples of reconciliation between male/male opponents. The relative rates of reconciliation were compared with each other using chi-squared analysis. Statistically, there was no significant difference between the sexes of opponent dyads and the rates of reconciliation ($\chi^2 = 3.662$, $p\text{-value} = 0.16$).

A less specific analysis which considered only the sex of the victim did show evidence of difference in reconciliation rates between the sexes. There were 107 female victims 16 of which were involved in reconciliations and 18 male victims none of which were involved in reconciliations. Statistically, there is a trend suggesting that female victims are involved in reconciliations more often than males ($\chi^2 = 3.087$, $p\text{-value} = 0.0789$).

Kinship, Sex and Reconciliation

Was there a correlation between the relatedness of opponents and their attractiveness to reconcile with each other in the post-conflict period? Small sample sizes restricted the use of statistical analysis, however, with descriptive statistics kinship appears to be an important factor in reconciliation. From the 16 reconciled opponent dyads, 31.25 percent ($n=5$) were related suggesting that kinship is strongly tied to the frequency of reconciliation.

When the sexes of the 5 related pairs which reconciled are considered there is an interesting trend suggesting that female relatives are the opponent pairs most attracted to each. There were only 5 female/female dyads which reconciled, 4 (80%) of these were related (3 mother/daughter pairs, 1 sister/sister pair). Of the 11 male/female dyads which were reconciled only 1 (11%) of these pairs was related (aunt/nephew). The related females which reconciled all did so through affiliative contact whereas the male/female reconciliation was a less overt proximity score. These results may indicate stronger and more frequent affiliative measures are prevalent between related females which have been involved in an aggression.

The Mating Season and Reconciliation

Estrus behaviors appeared to play a very influential role on the patterns of reconciliation for the Arashiyama West macaques. Of the 11 male/female aggressive interactions which were reconciled, 72.7 percent (n=8) of these focal samples contained evidence of mating behaviors (e.g. consort behaviors, courtship displays and approaches). Three of these interactions were the result of the female victims trying to gain access to their male aggressors and 5 resulted from courtship displays and approaches made by male aggressors to their female victims. In addition to the reconciled pairs, 'later' pairs also provide evidence that mating season behaviors influence reconciliation patterns. There were 5 later pairs, one female/female dyad and 4 male/female dyads. All of these male/female opponent pairs were in consorts at the beginning of their MC focals which resulted in their being scored as later. Mating and courtship between male and female Japanese macaques appears to increase the affinity of former

opponent pairs in both the PC and MC pairs and has a strong affect on male/female conciliatory tendencies.

Reconciliation Summary

In this section, reconciliation behaviors were examined using conventional measurements of affiliative contact between former opponents and less commonly used proximity measures. Victims of aggression in the Arashiyama West macaques, being a free-ranging troop, are virtually unrestrained by the distances they can place between themselves and their opponents. The Arashiyama West troop contains over 500 animals giving the victims of aggression the opportunity to approach and interact with hundreds of alternate conspecifics. Under such conditions, rapprochement to within 1.5 meters between opponents was accepted as a conservative measure of selective attraction and such proximity was considered to be a more subtle form of reconciliation than those achieved through contact.

Given the conservative definition of reconciliation used in this study, there was no significant attraction between opponents to make affiliative contact and, therefore no evidence of reconciliation. For comparative purposes if all PC contact scores are counted as reconciliations, by a more liberal measure of reconciliation, then only 5.6 percent (i.e. 7 of 125 PC/MCs) of adult Japanese macaque opponents reconciled in this study. This is much less than the 51.3 percent reconciliation rate in stumptail macaques, 22.8 percent reported for rhesus macaques (de Waal & Ren, 1988) or 20.7% in longtail macaques (Aureli et al. 1989). The most liberal measure for reconciliation in the Arashiyama West troop would include the 16 reconciled pairs under the broad definition including

contact and proximity scores. The resulting 12.8 percent still remains a very low rate of reconciliation in comparison with other primate species. This troop of Japanese macaques does not exhibit high conciliatory tendencies.

When some of variables included in the reconciled pairs were examined there were some interesting results. Female victims were involved in all of the reconciliations and there were no reconciliations in dyads with male victims. For female/female opponent dyads, relatedness was discovered to be the strongest factor influencing the rate of reconciliation and closely related females comprised 80 percent of the reconciled female/female pairs. In addition, the related female/female pairs made up over 57 percent of the reconciliations scored by the stronger affiliative contact measures.

Relatedness was not discovered to be a significant variable when considering reconciliations between male/female opponent dyads. Instead, estrus behaviors were the most influential factor affecting selective attraction between female opponents and their male aggressors. Of the 11 male/female dyads considered to be reconciled, 72.7 percent ($n=8$) included unmistakable signs of estrus. In addition, 4 of the 5 later pairs (i.e. opponents affiliated or were in proximity earlier/only in the MC period) consisted of male/female dyads, all of which were involved in consort behaviors.

Discussion: Reconciliation in Japanese Macaques

Reports on reconciliation behaviors in Japanese macaques are scant and the results varied. Chaffin et al. (in press) discovered, from a sample of 116 PC/MC pairs, equal proportions of contact (11 earlier pairs; 11 later pairs) in a captive group of 36 Japanese macaques. Chaffin et al. gives results which show there is no greater attraction between opponents after aggression than in control

periods to come into affiliative contact, which are similar to the results of this study. Chaffin et al. also examined proximity scores as a broader definition for reconciliation. Using this method they did discover that former opponents were significantly more often attracted than dispersed. The conclusions from this study and Chaffin et al. both emphasize that even when proximity measures are considered, Japanese macaques still exhibit low rates of reconciliation.

However, Aureli et al. (1993) report that they did find significant levels of reconciliation in pooled data from two captive troops of Japanese macaques. Using only contact scores, Aureli et al. discovered 33 percent of their opponent dyads reconciled while only 7 percent were 'later' pairs. Contrary to the results discovered in this paper and Chaffin et al., Aureli et al. discovered a relatively high conciliatory rate in Japanese macaques.

CONSOLATION AND AFFILIATION WITH SPECIFIC PARTNERS

Introduction

De Waal and van Roosmalen (1979) suggested that victims of aggression may exchange affiliative interactions with individuals other than the former aggressor. They labeled this behavioral pattern consolation with the implication that such third-party affiliation may act to reduce the victim's levels of stress and anxiety. There have been a number of studies which have specifically looked for consolation using proper control methods, none of which discovered evidence for elevated levels of affiliation with third-party individuals compared with control observations (e.g. Aureli & van Schaik, 1991a; Aureli 1992 (wild population) - longtail macaques; Judge, 1991 - pigtailed macaques; Aureli et al., 1993 - Japanese macaques; Aureli et al.; 1994 - Barbary macaques.

In examining the possibility that consolation behaviors may be restricted to certain subsets of animals some studies have focused their inquiries. For example, a number of studies have specifically looked for significant levels of third-party affiliation between the victim and its kin which could be considered the individuals best able to calm the victim (de Waal & Ren, 1988; Aureli & van Schaik, 1991a; Judge, 1991; Aureli et al. 1993, 1994). There are also studies which have investigated the existence of affiliation between victims and the former aggressor's kin (i.e. substitute reconciliation) (Aureli & van Schaik 1991a; Judge, 1991; Aureli et al., 1993). The majority of studies which have considered kin-biased and substitute reconciliation report no evidence of these behaviors. One exception is Aureli and van Schaik (1991a) which does report finding substitute reconciliation as part of the behavioral repertoire of juvenile longtail macaques and they believe other studies may fail to demonstrate these behaviors due to lack of data from this age class of animals.

Method of Data Analysis

Analysis parameters are identical to those contained in the Chapter two and the data analysis section for Reconciliation. One proviso is that affiliation between victims and their infants was not considered to be consolation. Macaques aged under one year are still very dependent on their mothers making it difficult to determine if social behaviors between them are related to the aggressive incident or not.

Do Japanese Macaques Console Victims of Aggression?

General Tests for Consolation

A number of different strategies were employed to detect if Japanese macaque victims sought or received consolation from individuals other than the former aggressor. First, a general test was performed where the proportion of PCs in which at least one affiliative interaction between the victim and an individual other than the former aggressor was compared with the same proportion from the MCs. Of the 125 PC/MC pairs, there were 53 PCs in which victims made affiliative contact with third party individuals, whereas victims contacted third party affiliates in 67 of the MC periods. There was no significant difference between PC and MC levels of third party affiliation and this test provided no evidence of consolation behaviors ($\chi^2 = 3.141$, $p\text{-value} = 0.0763$). The Chi-square test actually indicates a trend towards lower levels of affiliation with third parties after aggression than in control periods.

A second analysis was performed to detect if victims interacted with partners other than the former aggressor earlier in the PC period than in the MC period. The methodology is the same as de Waal and Yoshihara (1983) outlined for reconciliation and the first instances of third party affiliation were compared between PCs and MCs to determine if they were 'earlier' or 'later' pairs. There were 35 earlier pairs (i.e. third party affiliation happened earlier/ only in the PC) and 50 later pairs (i.e. third party affiliation happened earlier/ only in the MC). There were 40 PC/MC pairs not used in this analysis because either third party affiliation had occurred in the same minute block in the PC and MC samples ($n=5$) or there was no such affiliation by the victim ($n=35$). A Chi-square test was used to compare the 85 PC/MC pairs with third-party affiliation and again this

analysis offered evidence contrary to behaviors expected for consolation. Victims affiliated with individuals other than the former aggressor significantly less often or with a greater latency to do so after receiving aggression than when they had not been involved in an aggressive incident ($\chi^2 = 5.294$, $p\text{-value} = 0.0214$).

Finally a Wilcoxon matched-pairs signed-rank test was used to compare rates of affiliation in each PC/MC pair to determine if victims were more likely to interact with third-party affiliates after receiving aggression or in control periods. There was no difference between the post-conflict and control periods in relation to victims affiliating with animals other than the former aggressor (Tied $z\text{-value} = -0.820$, Tied $p\text{-value} = 0.3859$).

Kin-Oriented Consolation

Though there was no evidence for consolation, the generality of the previous tests may have obscured the potential that third-party affiliation may be more prevalent in particular dyads of individuals. For example, a victim of aggression may preferentially seek members of its own matriline for affiliation. The victim's kin are, theoretically, the best candidates for consolation and the individuals most likely to be interested in calming the victim (Aureli et al., 1993).

An analysis was done to test whether victims interacted more often with family members than non-related animals. In the PCs, victims had affiliative interactions with a total of 33 relatives and 45 non-related animals. In the MCs, victims affiliated with 35 relatives and 50 unrelated animals⁴. There was no significant difference discovered between the PC and MC period in the proportion of affiliation with related and unrelated animals ($\chi^2 = 0.021$, $p\text{-value} = 0.8837$) and, therefore, there is no proof for kin-biased post-conflict affiliation.

⁴ Analyses excludes 2 affiliates which could not be identified in the PCs and 5 from the MCs. These do not affect the statistical outcome of these tests.

Substitute Reconciliation (Affiliation With Kin of the Former Aggressor)

It has been hypothesized that if a victim cannot make contact with the former aggressor, then a possible alternative method to amend their relationship is for the victim to affiliate with the aggressor's matrilineal kin (Kappeler & van Schaik, 1992). To test for the possibility of substitute reconciliation the proportion of PCs in which the victim associated with the aggressor's kin was compared with the same proportionate occurrence from the MCs. The analysis was limited to the 118 PC/MC pairs in which the former opponents were not related to avoid the confusion of having third party affiliates related to both the victim and the aggressor. The results show that the victim affiliated with the aggressor's kin in only 0.85% of the post-conflict periods (n=1) and in 4.2% of matched-control periods (n=5) providing no evidence of substitute reconciliation. Though limited, the data could suggest an opposite trend where victims may avoid affiliative contact with the relatives of the former aggressor during the post-conflict period.

Consolation Summary and Discussion

There have been a number of studies which have specifically looked for consolation in macaque species but no evidence for this behavior has been documented. This study also found no evidence of consolation and instead demonstrated that victims were less likely to associate with third-parties after receiving aggression than in control periods. Many researchers have focused their analyses to test whether victims may affiliate only with specific subsets of the population at higher rates after it received aggression (e.g. victim's kin, aggressor's kin - substitute reconciliation). Results from this study show that

victims have no bias towards affiliating with its own relatives or the relatives of the former aggressor after receiving aggression. There was no evidence for any type of consolation in the Arashiyama West macaques.

Comparable with the results of this study, studies on longtail and pigtail macaques found no evidence for increased levels of affiliation in the post-conflict period between the victim and its kin (Aureli & van Schaik, 1991a; Judge, 1991). A separate study of Japanese macaques and research from Barbary and stump-tail macaques suggest that victims may actually contact their kin less after receiving aggression than in control periods (de Waal & Ren, 1988; Aureli et al. 1993).

A number of studies have looked for substitute reconciliation, however, Aureli and van Schaik (1991a) provide the only positive report for this behavior in longtail macaques. These authors believe substitute reconciliation may be more prevalent amongst juvenile victims of aggression which may find it easier to contact the more accessible younger kin of the former aggressor than the aggressor. Though this study found no evidence for substitute reconciliation data was limited to adult animals and the possibility cannot be dismissed that younger animals may manifest these behaviors.

REDIRECTION

Introduction

Redirection behaviors have long been reported to occur in a variety of animal species including many nonhuman primates. It is only recently, however, that researchers have begun quantitative analyses to determine if the victims of aggression are, in turn, more likely to aggress against a third-party shortly after the initial aggressive incident. As a post-conflict event, redirection has been theorized to have a number of functions. For example, redirection may be a form

of diverting the attention of the original attacker away from the victim onto a third individual or, more constructively, the victim may be seeking cooperation from the aggressor in its redirection efforts such collaboration helping to ease the tension on their relationship. Another hypothesis is that the victim may show biased tendencies to aim redirections at the lower ranking relatives of the aggressor which could indirectly incur damages upon and discourage further aggressive actions by the aggressor.

Method of Data Analysis

In this section data will be examined for evidence of redirection behavior in Japanese macaques. Statistical analysis will follow the same guidelines set out in the Methods chapter and in the Reconciliation and Consolation sections above including the following amendments. Redirected aggression could take the form outlined for 'light' or 'heavy' aggression but need not include locomotion by the victim. Visual and vocal threats, cuff and pinches (see ethogram, Appendix B) which could be performed by the victim without locomotion on any animal not involved in the original altercation were considered to be redirections.

Do Japanese Macaques Redirect Aggression?

General Tests for Redirection

To test if the Arashiyama West macaques redirected aggression, the proportion of PCs in which victims threatened an animal other than the former aggressor were compared with the same proportion of third-party aggression by the victims in the matched-control periods. Victims were responsible for at least one instance of third-party aggression in 38.4% (n=48) of the PCs and in 26.4% (n=33) of the MCs. The difference between PCs and MCs is statistically

significant ($\chi^2 = 4.109$, $p\text{-value} = 0.0422$) and this test provides positive evidence for redirection as a post-conflict event.

Redirection was also examined using the PC/MC method developed by de Waal and Yoshihara (1983). The PC/MC pairs in which the victim threatened an animal other than the aggressor earlier or only in the PC focal were labeled 'earlier' pairs and those which occurred earlier or only in the MC focal were called 'later' pairs. In 67 of the PC/MC pairs the victim did not attack another individual ($n=65$) or attacks came in the same minute block in the PC and the MC samples ($n=2$). Of the remaining pairs ($n=58$), there were 38 which scored 'earlier' and 22 which were 'later'. A Chi-square test comparing the earlier PC/MC pairs with later pairs provided confirming evidence for redirection in this troop of macaques and victims were shown to threaten other individuals significantly more and/or with greater haste after they themselves had been attacked than during control periods ($\chi^2 = 8.533$, $p\text{-value} = 0.0035$).

Finally, a Wilcoxon matched-pairs signed-rank test was done comparing PC/MC data for redirection. This non-parametric test is more sensitive than Chi-square tests in that it does not rely on pooled data but uses precise measures from each PC/MC pair. Again the results of this test confirmed that victims were responsible for significantly more aggression in the post-conflict period than in control periods (Tied Z-value = -2.713, Tied $p\text{-value} = 0.0093$).

Time of Redirection

How long after being attacked does it take for the victim to redirect aggression? A number of studies of post-conflict behaviors report that higher levels of third party aggression by the victim are most prevalent in the first few minutes of the PC when compared with control levels. To test for this possibility,

the minute block in which the first aggressive act by the victim against a third party were charted for the PCs and the MCs. The minute-block distributions for each PC/MC pair were compared using the Kolmogorov-Smirnov test and it was found that the PC and MC distributions for third party attacks were significantly different ($D=0.311$, $\chi^2 = 7.547$, $p < 0.0460$). Redirection in this troop of Japanese macaques occurs significantly more in the first two minutes after a victim receives aggression .

Kin-biased Redirection

It has been hypothesized that the victim of aggression may in turn redirect aggression against the kin of the former aggressor. By targeting a lower ranking member of the opponent's matriline it is believed that a victim may reduce its chances of being reattacked by the former aggressor and/or hasten reconciliation between them (Aureli & van Schaik, 1991b). This possibility was tested through comparing the identity of all the third-party individuals aggressed against by the victim in the PC to see if they were related to the original aggressor. Only the PCs with redirection in which the opponents were unrelated and the aggressor had at least one relative were considered in this analysis (see Aureli, 1992). From the 42 PCs used in the analysis, there were 70 individuals which received redirected aggression from the victim. Of these 70, only 59 could be positively identified and none of these individuals were related to the aggressor from the original altercation. Results are inconclusive due to missing data, but from at least 81.3% of third party aggression collected in this study there was no evidence supporting the theory of kin-oriented redirection.

Sex and Redirection

Did both males and females redirect aggression? This question was answered by comparing the number of aggression directed separately by males and females toward third-parties in the post-conflict period against control levels. Wilcoxon matched-pairs signed rank tests were used to compare the amounts of aggression between the PC and MC pairs for males then females. Males did not show significantly greater evidence for third-party aggression in the post-conflict period, however, the data is highly suggestive of a trend for redirection behaviors (Tied Z-value = -1.814, Tied p-value = 0.0696). Females, however, were significantly more likely to be aggressive in the post-conflict period and showed positive evidence for redirection (Tied Z-value = -2.133, Tied p-value = 0.0329).

Do males and females direct aggression at third-party individuals at the same rates? Male victims directed aggression at third-party animals in 78 percent (n=14) of the PC periods and in 61 percent (n=11) of the MC periods. As shown in the preceeding analysis this highlights a trend that males are more aggressive in the post-conflict period. Females victims, as shown above, were significantly more aggressive towards third-parties in the post-conflict period, increasing to 31 percent of PC periods (n=33) from 21 percent (n=22) in the MC periods. A Mann-Whitney U test was used to compare if there were differences in the amounts of third-party aggression performed by males and females. It was found that males performed significantly more aggression against third-party animals than females in both the PC and MC period (Tied Z-value = -3.960, p-value < 0.001). In general, males are more aggressive than females though

female tendencies to redirect increase more than males in the post-conflict period.

Redirection Summary and Discussion

There are a number of theoretical explanations for the function of redirection, for example, it may change the focus of attention to another individual or enlist the support of the aggressor in a cooperative effort which may help to mend the relationship. For both of these considerations, the potential benefits of redirection may be lower than the costs of aggressing against a lower ranking animal. In the Arashiyama West Japanese macaques redirection behaviors were documented and victims of an aggressive incident were significantly more likely to aggress against third-parties in the post-conflict period compared with control periods. Scucchi et al. (1988) also report on the redirection behaviors of Japanese macaques and conclude that non-adult animals performed the greatest number of redirections. Therefore, though positive results for redirection were also found in this study of Japanese macaques, rates of these behaviors may have been underestimated due to a lack of non-adult focal animals.

There are a few studies of nonhuman primates which report results supporting kin-biased retaliation behaviors. Cheney and Seyfarth (1989) have shown that vervet monkeys are more likely to threaten the aggressor's kin if they or one of their relatives have been the recipients of aggression. Aureli et al. (1992), reports kin-biased redirection among a captive group of Japanese macaques showing that victims would more often redirect aggression against the younger and subordinate relatives of their opponents. However, in considering many methodological differences with this paper, Aureli et al. used hour-long

observations and found evidence that kin-biased redirections often came in special contexts such as during polyadic interactions. Though there was no evidence discovered for kin-biased redirection in the Arashiyama West macaques, it may be that these behaviors are prevalent outside the methodological confines of this research.

When the redirection behaviors of the Arashiyama West macaques were analyzed by sex, female victims showed clear evidence for redirection whereas there was a lesser trend toward redirection evident for male victims of aggression. In general, males were more aggressive against third-party animals in both PC and MC periods. When the temporal distribution of redirection behaviors were considered it was discovered that the most significant amount of redirected aggression occurred quickly, within the first two minutes, following the original aggressive incident.

CHAPTER FOUR

THE EFFECTS OF AGGRESSION ON BEHAVIOR: HOW AND WHY DO VICTIM'S REACT?

Overview

This chapter is divided into two sections. The first section investigates how the behaviors of victims change after they receive aggression, looking specifically at the performance of displacement behaviors and the victim's time budgets. The analysis of displacement behaviors, compares levels of body scratching, body shaking, yawning, startle behaviors and self-grooming between their post-conflict and control rates to determine if these activities indicate evidence of stress in victims of aggression. An analysis of time budgets is used to determine how the general activities of the victims change compared to control levels after they receive aggression to understand if there are costs associated with receiving aggression.

The second section in this chapter provides analyses oriented towards answering why victims behave differently after they are aggressed against. Attacks (or reattacks) by the original or alternate aggressors on the victim in the post-conflict period will be compared with control levels to discover if victims are more susceptible to renewed aggression. Finally, levels of displacement behaviors will be compared before and after from focal samples where reconciliation and redirection occurred to determine if these post-conflict events reduced the anxiety levels of the victims. Where possible, both sections include additional analyses to determine how the sex of the victim and the level of aggression affected the statistical results concerning the behaviors under scrutiny.

SECTION ONE

DISPLACEMENT ACTIVITIES AND TIME BUDGETS

A) DISPLACEMENT ACTIVITIES AS A MEASURE OF STRESS

Method of Analysis

There is sufficient support in the literature that displacement activities are good behavioral indicators of stress in nonhuman primates (see Chapter One). Therefore, in this study, stress (also anxiety, tension) will be defined by elevated occurrences of displacement behaviors in the post-conflict period compared with their matched-control levels.

Data were analyzed in a number of different ways. Descriptive statistics were used to highlight overall trends in data and where sample sizes were too small for more powerful statistical manipulation. Where larger samples permitted, and depending on the type of data being analyzed, either Chi-square tests or non-parametric tests were used for comparative analysis. The statistical level of significance was set at 5 percent (i.e. $p < 0.05$) but behavioral trends are also mentioned for significance levels up to 12.5 percent (i.e. $p < 0.125$) to give leeway where small sample sizes may obscure potentially important results. The displacement activities being investigated in this section are described in the Methods chapter and in the sections below.

Results

1) Body Scratching

Body scratching is an easily observable behavior and has been reported as a displacement activity in many primate species (for review see Maestripieri et al., 1992). In addition to behavioral reports, Schino et al. (1991) have provided

pharmacological evidence that scratching behaviors are positively correlated with stressful situations in long-tailed macaques. Body scratching was the most commonly observed of the reported displacement behaviors to occur in this study. In 92 percent of the PCs ($n=115$) and in 86.4 percent of the MCs ($n=108$) focal animals performed *at least one* body scratch. These figures merely highlight that body scratching is part of the normal body care pattern of Japanese macaques and, like other displacement activities, is not a behavior specific to excited states.

The effects of aggression are emphasized when one looks at the actual number of body scratches performed by the victims after they are attacked compared with control levels. In the PC focal samples, victims performed 538 body scratches while there were only 385 examples of this behavior recorded in the MC periods; an increase of almost 40 percent. A Wilcoxon matched-pairs signed-rank test confirms that there is a significant rise in body-scratching performed by victims in the 15 minute period after aggression (Tied Z-value = -3.601, Tied p-value = 0.0003).

Do males and females body scratch at different rates after aggression? Tests were first done for each sex separately to discover if there was a rise in body scratching after aggression. Wilcoxon matched-pairs signed-rank tests were performed comparing the numbers of body scratches between PCs and MCs for females and males. Female victims showed a significant increase in body scratching after receiving aggression (tied Z-value = -3.421, tied p-value = 0.0006) while there was no evidence of increased scratching performed by males in the PC period (tied Z-value = -1.183, tied p-value = 0.2370). Next, body scratching was compared between the sexes to determine if males and females scratched at differing rates. A Mann-Whitney U test showed that there was no

significant difference between male and female rates of body scratching in the MC or PC periods (MC: Tied Z-value = -0.053, p-value = 0.9577, PC: Tied Z-value = -0.153, Tied p-value = -0.8785). These tests show that while female rates of body scratching increased significantly after conflict, male rates did not change noticeably and remained at levels not significantly higher than female MC levels, nor significantly lower than female PC levels.

How did light and heavy aggression affect the victim's performance of body scratching behaviors? To answer this question the mean rates of body scratching were calculated and compared between PCs with light aggression and PCs with heavy aggression. Interestingly, it was discovered that victims scratched less after heavy aggression than light aggression. Even though light aggression accounted for only 45.6 percent (n=57) of the 125 PCs they accounted for 54.3 percent (n=292) of the total number of body scratches. Heavy aggression made up 54.4 percent (n=68) of the total PCs but they accounted for only 45.7 percent (n=246) of the total body scratch scores from the PC period. A Mann-Whitney U test confirms that victims performed significantly more body scratches after light aggression than after heavy aggression (tied Z-value = -2.692, tied p-value = 0.0071).

2) Body Shake

Body shaking has also been reported to occur in primates in tense situations and has been suggested as a good behavioral indicator of stress (Schino et al., 1988; Aureli & van Schaik, 1991b; Maestripieri et al., 1992). Very low rates of body shaking were observed in the Japanese macaques in this study, however, there was a 120 percent rise in the *total* amount of body shakes performed by victims after aggression (n=41) than in control periods (n=18). To

account for the possibility that single animals were responsible for disproportionately high numbers of body shakes, only the number of PCs (n=25) with *at least one* example of body shaking were compared with the same amount from the MCs (n=15). A Chi-square test determined that there was not a significant rise in the amount of PCs with body shaking ($\chi^2 = 3.676$, p-value = 0.0538). However, the low p-value and 67 percent rise in PCs with body shaking suggests a trend towards higher levels of body-shaking in the post-conflict period and provides indications of stress in victims of aggression.

Next, the rates of body shaking were compared between the sexes to determine if levels of this displacement behavior changed for both males and females after they received aggression. From the 18 focal pairs with male victims there was only one example of body shaking in the MCs (5.5%) and two in the PCs (11%). This sample size is too small for statistical analysis but suggests that: a) males body shake at very low rates and b) the amount which they body shake is not radically affected by stressful situations.

From the 107 focal samples recorded on female victims, there were 24 PCs with a sum total 39 body shakes and 14 MCs with a total of 17 body shakes. A Chi-square test was used to compare the number of PCs and MCs with *at least one* body shake by females and it was discovered that there were no significant differences between these periods ($\chi^2 = 2.647$, p-value = 0.1038). The 71.5 percent increase in PCs with body shakes and low p-value from the Chi-square analysis provides modest evidence of elevated anxiety in female Japanese macaques which have received aggression.

Were the rates of body shaking affected by the level of aggression received by the victim? A Mann-Whitney U test was used to compare the PC rates of body shaking between focals with light and heavy aggression. There was no

significant correlation discovered between body shaking behaviors and the level of aggression (tied Z-value = -0.715, tied p-value = 0.4546).

3) Yawning

Yawning has been frequently reported as a displacement activity in non-human primates (for review see Maestripieri, 1992) but has not often been the subject of quantitative analysis (but see Schino et al. 1988; Troisi et al. 1990). To date, only one published investigation compared yawning behaviors between control and post-conflict periods and discovered that the rate of yawning did not significantly increase after longtail macaque victims received aggression (Aureli & van Schaik 1991b). In certain species (e.g. baboons: Hall & Devore, 1965) yawning has been perceived to relay a meaning of threat, however, some feel that displacement yawning can be qualitatively separated from normal yawning in that there is a different display of the teeth and careful avoidance of eye contact with others where it is believed yawns may acquire a threat status (Bertrand, 1969; Maestripieri et al. 1992; Aureli & van Schaik 1991b). Other authors report that high-ranking individuals may yawn more often than low-ranking individuals (for review see Maestripieri, 1992) however Troisi et al. (1990) found no such correlation between rank and yawning frequency in Japanese macaques.

In this study, yawning occurred at very low frequencies with 39 yawns observed in 14 PCs and 17 yawns recorded in 7 MCs. To correct for certain focal individuals accounting for disproportionate amounts of yawning the analysis was limited to comparing only the number of PCs and MCs with *at least one* case of yawning. A chi-square test discovered that though there were twice as many PC periods as MC periods with yawning (i.e. 14 PCs vs. 7 MCs) there was no

significance difference discovered between these values ($\chi^2 = 2.547$, $p\text{-value} = 0.1105$). The 100 percent increase in post-conflict focals with yawning suggests that this behavior may be indicative of stress in victims of aggression. The low p -value from the Chi-square test also provides a weak indication that yawning behaviors may be a result of stress, and positive results may be masked due to the small sample size afforded to the analysis.

Are there differences in the rates of yawning between males and females confronted with aggressive situations? Wilcoxon matched-pair signed-rank tests were used to compare the amounts of yawning for males and females to determine the effects, if any, of aggression. It was discovered that neither males nor females evidenced a significant change in the amounts of yawning performed between the MC and PC periods (males: tied Z -value = -0.428, tied p -value = 0.6684; females: tied Z -value = -1.350, tied p -value = 0.1770) When considering the sex of the victim, yawning behaviors did not indicate higher levels of stress for either male or female Japanese macaque victims observed in this study.

The performance of yawning behaviors were also compared between focal samples with light and heavy aggression. A Mann-Whitney U test did not yield any significant results concerning a relationship between the level of aggression and yawning (tied Z -value = -0.906; tied p -value = 0.3649). Overall, yawning occurred at very low rates and the sample sizes for these behaviors were too small to be conclusive concerning whether yawning is indicative of stress in victims of aggression.

4) Selfgrooming

Selfgrooming differs from the other displacement activities discussed in this paper in that it is a state behavior (temporally measured) rather than event behavior (measured by individual occurrence). To investigate whether selfgrooming behaviors were affected by aggression the cumulative time spent selfgrooming in the MC period was compared with time spent selfgrooming in the PC period. In the MCs, animals invested 129.28 minutes (mean=62 seconds/focal) selfgrooming and 181.18 minutes (mean=87 seconds/focal) selfgrooming in the PCs. This constitutes a 40 percent rise in selfgrooming behaviors in individuals which have been victims of aggression. A Wilcoxon matched-pairs signed-rank test confirms that there was a significant increase in selfgrooming after animals received aggression (Tied Z-value = -1.985, Tied p-value = 0.0472).

To determine the affect which aggression had on the selfgrooming practices of males and females, the amount of time spent selfgrooming by each of the sexes was compared between the PC and MC periods. Males selfgroomed for a total of 10.23 minutes (mean=34.1 seconds/focal) in the summed MC periods and 30.2 minutes (mean=100.7 seconds/focal) in the summed PC periods. A Wilcoxon matched-pairs signed-rank test did not yield significant differences between the PC and MC period for male selfgrooming (tied Z-value = -1.655, tied p-value = 0.0980). A low p-value and an almost 200 percent increase in selfgrooming behaviors are, however, strongly suggestive of a trend toward increased post-conflict stress levels in males.

Females selfgroomed for a total of 66.8 minutes (mean = 32.1 secs/focal) in the MCs and 84.7 minutes (mean = 40.7 secs/focal) in the PCs. A Wilcoxon

matched-pairs signed-rank test was done comparing PC and MC levels of selfgrooming for females with no significant differences apparent between control levels and post-conflict levels (tied Z-value = -1.479, tied p-value = 0.1391). Though there was a 27 percent increase in the post-conflict period, selfgrooming was not a strong indicator of stress in female victims of aggression.

Rates of selfgrooming were compared to determine if the level of aggression (i.e. 'light' or 'heavy') influenced the selfgrooming behaviors of victims. A Mann-Whitney U test was used to compare victims of light aggression with those of heavy aggression but did not discover any significant results (tied Z-value = -0.661, tied p-value = 0.5089). There was no correlation found between the severity of aggression received by a victim and how much they selfgroomed.

5) Run and Jump Startle

Run and jump startles refer to explosive movements where the individual bursts forward over space (run startle) or jerks in its place (jump). These behaviors frequently result when animals hear unidentified noises nearby or gain sudden awareness of other previously unnoticed animals in close proximity. Both startle behaviors indicate preparedness for quick action or avoidance while the source of unknown stimuli or the motivations of another animal are determined. No reference was found to startle behaviors in any literature on displacement activities, however, it is plausible that run and jump startles could mirror a heightened awareness in victims of aggression due to the uncertainty of the situation in the post-conflict period (Aureli & van Schaik, 1991b).

Pooled data from the 125 MC samples shows that there were 27 individuals which accounted for 35 examples of run/jump startles. In the same

number of PCs, there were 57 victims which performed a total of 80 run/jump startles. This represents a 111 percent increase in individuals performing startle behaviors after receiving aggression. A Wilcoxon matched-pairs signed rank was used to compare run/jump startles between the PCs and the MCs. This test confirmed that there were significantly more instances of run/jump startles in the PC period than the MC period (Tied Z-value = -3.927, Tied p-value = <0.0001) and startle behaviors provide positive indications of elevated stress levels in victims of aggression.

Did males and females both perform run/jump startles at higher rates after aggression? An initial survey of the data shows that of the 18 focal samples with male victims there was evidence of run/jump startles in only 1 MC focal and only 4 PC focals. The startle behaviors performed by male victims are too limited to submit to statistical analysis but it appears that run/jump startles are not a prevalent behavior in male Japanese macaques. Due to the limited sample size it is difficult to ascertain whether the increase in the PC period is due to aggression.

Startle behaviors were more common amongst female Japanese macaques. Of the 107 focal pairs with female victims, there was an example of run/jump startle behavior in 24 percent (n=26) of the MC periods and 52 percent (n=56) of the PC periods. A Wilcoxon matched-pairs signed-rank test was performed to determine if there were different rates of run and jump startles between the PCs and MCs and it was discovered that females did show evidence of a significant increase in run/jump startles in the post-conflict period compared with matched-control periods (Tied Z-value = -3.912, Tied p-value < 0.001). Startle behaviors did indicate aroused levels of stress in female victims while data on males is inconclusive.

A final analysis was used to determine if the level of aggression had an effect on the numbers of startle behaviors performed by victims. A Mann-Whitney U test compared focals with light and heavy aggression to the rates of run/jump startles. The results indicate that victims were significantly more likely to run/jump startle in the post-conflict period after receiving heavy aggression (tied Z-value = -2.503, tied p-value = 0.0123).

Run and Jump Startles as Displacement Behaviors?

Maestriperi et al. (1992) define displacement activities as "behavior patterns (mostly body care activities) characterized by their apparent irrelevance to the situation in which they appear" (p 967). Run/jump startles are similar to the other displacement behaviors used in this study in that: a) they are part of the animal's normal behavioral repertoire (i.e. not unique to an aroused post-conflict state) and b) the frequency of startle behaviors increased significantly after aggression when the individual is in an excited state.

Aureli and van Schaik (1991b) believe, however, that an animal may maintain an excited state so it can react quickly if reattacked. In contrast with the definition for displacement behaviors above, the maintenance of an excited state may indicate the relevance of increased run/jump startle behaviors to the post-conflict period. Despite their potential relevance to post-conflict situations, this study determined that run and jump startles were positively correlated with a stressed emotional state of victims (especially among females) in the post-conflict periods and are a good behavioral measure of anxiety levels.

B) TIME BUDGETS

Method of Analysis

Included in the time budget analysis were the higher level categories outlined under "state behaviors" in the Methods chapter (except 'selfgroom' which was analyzed with displacement activities above). These categories (stationary, locomote, eat/drink and social) condense many specific behaviors into a few basic groupings which are used to understand, at a general level, how victims respond to aggression. Such analysis is important to determine if there are costs associated with aggression, such as reduced feeding or higher energy expenditures due to increased locomotion. Statistical methods are the same as those outlined for displacement behaviors at the beginning of this chapter.

Results

For initial analyses, Wilcoxon matched-pairs signed rank tests were used to determine if there were any differences between PC and MC values for the time budget categories. The only significant difference discovered, interestingly, was that individuals spent more time engaged in stationary behaviors after receiving aggression than during control sessions (Tied Z-value = -2.580, tied p-value = 0.0099). Though not statistically significant the data also show there was a 40 percent decrease in eat/drink behaviors (tied Z-value = -1.550, tied p-value = 0.1212) and a 30 percent drop in social behavior scores (tied Z-value = -1.597, tied p-value = 0.1102) after victims received aggression. The reduced rates of these latter activities and low p-values from statistical analysis could be indicative of the effects of aggression on the time budgets of victims.

Were time budget activity rates different for males and females after they received aggression? Mann-Whitney U tests were used to compare time budget behaviors between the sexes. There were no differences discovered for eat/drink, stationary or social behaviors but male victims did perform significantly more locomotory behaviors than females in the post-conflict period (tied Z-value = -2.479, tied p-value = 0.0132). However, males also performed significantly more locomotory behaviors in the control periods than did females (tied Z-value = -2.180, tied p-value = 0.0292) so it must be concluded that the sex of the victim was not a factor in the performance of time budget behaviors after aggression.

An final analysis of time budgets was used to determine what influence different levels of aggression (i.e. light or heavy) had on the general behavioral patterns of the victims. Mann-Whitney U tests were used to compare the time-budget behaviors after light and heavy aggression in the PC period. Two significant results obtained were that victims remained stationary more often (tied Z-value = -2.580, tied p-value = 0.0099) and ate and drank less (tied Z-value = -2.917, tied p-value = 0.0035) after heavy aggressive attacks.

SECTION TWO

REATTACK AND THE BEHAVIORAL CONSEQUENCES OF RECONCILIATION AND REDIRECTION

I) REATTACK

Introduction

A number of sources have reported that victims of aggression are more susceptible to renewed attacks from former opponents and alternate aggressors

(Aureli and van Schaik 1991b; de Waal & Yoshihara 1983; York & Rowell 1988; Aureli et al. 1989, 1993 (wild study); Kappeler & van Schaik 1992). An aroused state, such as are indicated through heightened displacement behaviors, may be an evolutionary adaptation to maintain the victim's preparedness to react quickly if it should be reattacked. Therefore, in this study, the amount of aggression received by the victim was compared to determine if they were more frequently attacked in the PCs than during control periods. If victims are more frequently attacked after already receiving aggression, this could provide an explanation for the behavioral changes in the post-conflict period discussed in the displacement and time-budget section above.

Methods of Analysis

A renewed attack was defined as any aggressive act (as per Redirection methods outlined in Chapter 3) made by the former aggressor (except within two minutes of the initial attack; see Chapter 2) or alternate individual against the victim in the post-conflict period. Data were analyzed in the same as outlined for displacement and time-budget activities in the above sections.

Results

Are Japanese macaque victims more susceptible to reattack? A Chi-square test was conducted to determine if the proportion of PCs where the victim was attacked at least once was significantly different from the proportion of MCs. From the 125 PC/MC pairs of focal data, there were 27 PCs where the victim was reattacked compared with 16 MCs where the victim was aggressed against. The chi-square test does not give evidence that victims of aggression are significantly more often targets of additional aggression ($\chi^2 = 3.398$, $p\text{-value} = 0.0653$).

However, the 59 percent increase in PC periods where victims were reattacked and low p-value from statistical analysis does suggest a strong trend that victims are more susceptible to attack after they have already received aggression.

Did the sex of the victim influence the probability that it would be reattacked? Of the 18 PC/MC pairs with male focal animals, there was only one example from the MC and two from the PC where focal males received aggression. The limited sample size makes it difficult to reach conclusions concerning the susceptibility of males to reattack, however, it can be said that the males in this study were exposed to low rates of aggression. Female focals received aggression in 15 of the MC periods and in 25 of the PC periods. A Chi-square test did not discover a significant increase in aggression received by female victims of aggression in the post-conflict period compared with control levels ($\chi^2 = 2.158$, p-value = 0.1319). There was, however, an almost 67 percent increase in aggression received by females in the PC period and the absence of statistical evidence for reattack may be an artifact of the limited sample sizes recorded in this study.

Did the level of aggression received by the victim influence the likelihood that it would be reattacked? Of the 27 PCs where the victim was attacked, 14 of the original aggression had been 'heavy' and 13 had been 'light'. A Chi-square test revealed that there was no significant correlation between the level of aggression and the probability that a victim would be the target of additional attacks ($\chi^2 = 0.074$, p-value = 0.7855).

II) RECONCILIATION, REDIRECTION AND THE PERFORMANCE OF DISPLACEMENT ACTIVITIES

Introduction

Analyses of data in this chapter thus far have indicated elevated stress behaviors in victims after they received aggression and provided a strong suggestion that victims are at higher risk of reattack. It is a popular hypothesis that post-conflict events, such as reconciliation and redirection, may function to lower the stress levels of victims by reducing the uncertainty about the social situation and lowering the chances of reattack (Aureli & van Schaik, 1991b). To test this hypothesis, the stress activities of victims were compared to determine if the focal samples with reconciliation and redirection discovered in this study helped to reduce the stress responses in victims of aggression.

Methods of Analysis

In this section the problem of a limited representation of displacement behaviors and the nature of the data precluded the use of sophisticated statistical tests and analyses are done using descriptive statistics. Stress was again defined by the elevated occurrences of displacement behaviors in the post-conflict period as compared to matched-control levels. The rates per minute of each displacement activity are calculated before and after the occurrence of reconciliation and redirection to determine if there is a reduction in behavioral stress responses due to these post-conflict events. Rates of displacement activities are calculated from pooled data accumulated from the 16 focal samples with reconciliation and the 48 focal samples with evidence of redirection.

Reconciliation and Displacement Activities

Did reconciliation lower the stress levels in victims of aggression as measured through displacement activities? Before reconciliation the mean rate of body scratching performed by victims was 0.399/min. After reconciliation the mean rate of body scratching fell 82.2 percent to 0.219/min. Likewise, rates of body shaking dropped 146 percent (0.101/min to 0.041/min), startle behaviors decreased 152 percent (0.083/min to 0.033/min) and selfgrooming fell almost 43 percent (8.543 sec/min to 5.980 sec/min) after reconciliation⁵. The decrease in the performance of all displacement behaviors strongly suggests that stress levels are reduced when there is friendly or at least non-agonistic rapprochement between former opponents.

Redirection and Displacement Activities

Was redirection of aggression as effective as reconciliation in reducing the anxiety in victims? Mean data from focal samples with redirection indicate that there was a 35 percent drop in the rate of body scratching (0.425/min to 0.314/min), a 300 percent drop in body shaking (0.052/min to 0.013/min) a 34 percent decline in startle behaviors (0.039/min to 0.029/min) and a decrease of less than 2 percent of selfgrooming activities (5.098 sec/min to 5.008 sec/min) performed by victims after redirection. Body scratching and selfgrooming were the activities most frequently displayed by animals and these, perhaps, provide the best indications of stress levels in the victims. While redirection does appear to alleviate some of the anxiety, when compared with reconciliation, it is not as effective in reducing the stress responses of victims.

⁵ Yawning behaviors were not used in this analysis due to the infrequency of their occurrence.

Summary of results

This chapter investigated how victims were affected by aggression in the Arashiyama West macaques. Specifically, behaviors which had been previously reported to have, or were suspected of having, a displacement function were analyzed. It was discovered that body scratching, body shaking, run/jump startles and selfgrooming were performed more frequently by focal animals in the post-conflict period compared with control levels and it is believed that these displacement activities are good behavioral indicators of stress in the victims of aggression. There was no significant change in the rates of yawning between PC and MC periods and this behavior did not indicate increased stress in the victims of aggression.

Rates of displacement behaviors were more closely examined to determine if there were differences between how males and females reacted to aggression. Body scratching, body shaking, and startle activities were good indicators of post-conflict stress in female victims, whereas selfgrooming was the only displacement activity that relayed evidence of elevated anxiety in male victims in the post-conflict period. Male victims, overall, appeared to be less affected by aggressive attack than female victims.

The effects of the level of aggression on the rates of displacement activities were also tested. For the most part, the severity of aggression received did not seem to relate to differential amounts of displacement behaviors performed by victims in the post-conflict period. It was discovered, however, that run/jump startle behaviors increased most significantly after heavy aggression presumably mirroring heightened awareness/stress of the victim concerning the social environment. It was also found, curiously, that after heavy

aggression body scratching was less frequent than after lighter aggression indicating lower stress levels in animals which had been more severely attacked.

Time budgets of focal animals were compared between the PC and MC periods to examine how aggression affected the general behavioral patterns of the victims. From statistical analysis done on time budget behaviors, the only significant difference discovered was that victims remained more stationary after receiving aggression, while there were lesser trends suggesting that victims eat/drink and socialize less in the post-conflict period. More sensitive analysis, comparing time budgets between the sexes and in terms of aggression levels, determined that increased post-conflict stationary behaviors were significantly more prevalent in female victims and occurred significantly more after heavy aggression. When aggression levels were specifically compared with time budget behaviors, the trend alluding that victims eat/drink less discovered in the general analysis of the PC/MC period, was realized to be a significant reduction in these behaviors for victims of heavy aggression.

The second section of this chapter investigated reattack and the function of the post-conflict events of reconciliation and redirection. Though, not statistically significant, the data provide strong suggestions that victims are more prone to reattack after receiving aggression than they are to being attacked when there has not been previous aggression. When reattacks were compared by the level of aggression received in the initial attack, victims of light or heavy aggression did not appear to be differentially targeted for reattack. An analysis on the sex of the victims and the likelihood of being reattacked were inconclusive with weak evidence alluding to a possibility that females may be more frequent targets of this type of aggression.

After being attacked, victims showed behavioral indications of increased anxiety. When samples with reconciliation were analyzed it was determined that there was a large reduction in the frequency of displacement activities performed by the victim suggesting that reconciliation provides a reassuring or calming effect. The redirection of aggression also showed signs of a reduction in stress behaviors in victims, but this behavior does not appear to be as effective in alleviating stress as reconciliation.

CHAPTER FIVE

DISCUSSION AND CONCLUSIONS

Introduction

Chapters three and four investigated a number of the behaviors associated with the post-conflict period in Japanese macaques. In this chapter, results will be examined in the broader theoretical framework of post-conflict study and compared with results from similar investigations. Where possible evaluations of post-conflict behaviors of Japanese macaques are made and suggestions for further research are included where conclusions are difficult or unwarranted given the available data.

Chapter Three: Post-Conflict Social Events

1) Reconciliation

Aggression is an inevitability of group-living in nonhuman primates as group members compete for access to resources and rank. To mediate the dispersive effects of aggression, it is believed that primates coevolved behavioral mechanisms to cope with conflict and maintain group integrity. De Waal and van Roosmalen (1979) noticed opponents exchanging affiliative interactions soon after confrontations in chimpanzees and labeled this behavior pattern reconciliation with the underlying assumption that such exchanges functioned to repair the opponent's relationship. Since that time, numerous studies of a variety of primate species have also documented these behavior patterns.

Most hypotheses concerning reconciliation consider it to be an evolved trait, however, there are different reasons given for how it is adaptive. De Waal's (1986b) "reconciled hierarchy" model predicts that reconciliation is functionally

linked to the formalization of dominance relationships. In this model, the victim has the "choice" forced upon it between acknowledging its subordinate status through appropriate communications or receiving continued aggression. It is predicted that without these mechanisms to structure the opposing forces of competition and affiliation in social life then aggression would have dispersive effects.

Kappeler and van Schaik (1992) suggest that existing evidence does not support the "reconciled hierarchy" model as a general explanation for the adaptiveness of reconciliation. By reasoning of this hypothesis, primate species with strict dominance hierarchies should exhibit higher rates of reconciliation. However, redfronted lemurs, patas monkeys and stumptail monkeys (de Waal & Luttrell, 1989) have limited formalized dominance relationships yet all of these species show that significant amounts of conflicts are reconciled. An opposite trend is apparent in ringtail lemurs (*Lemur catta*) and in Japanese macaques (*Macaca fuscata*) where both species exhibit more strict dominance hierarchies but show no evidence for significant increases in affiliative contact after aggression (Kappeler, 1990; Chaffin et al., in press; present study).

Overlapping with this hypothesis, de Waal's (1989a) "social evolution" hypothesis suggests that, rather than just at the level of interindividual dominance relationships, animals must have evolved conciliatory mechanisms as a necessary precondition for group-living to deal with the dispersive effects of aggression (see Kappeler & van Schaik 1992). This theory predicts that gregarious primate species would show significant levels of reconciliation, however, results from ringtail lemurs and Japanese macaques again provide contradictory evidence. Gregarious living, at least in some species, does not seem to be dependent on the conciliatory gestures between group members.

The "Good Relationship" hypothesis suggests that reconciliation will occur between individuals whose relationship confers adaptive advantages. For example, maintenance of positive relationships between kin is important to the fitness of an individual, for relatives are most likely to be supportive in conflict situations (e.g. Aureli et al. 1992). Further, kin are expected to reconcile conflicts to limit the physiological costs associated with aggression (Aureli, 1989). The same rationale may be applied to positive relationships between non-related animals. Individuals, perhaps especially in female-bonded species (see Kappeler & van Schaik, 1992), may be more predisposed to affiliate with non-related group members which aid in agonistic conflicts or add some other beneficial dimension to the quality of the relationship (Cords & Aureli, 1992). For example, Cords and Thurnheer (1993) provide evidence that by artificially increasing the "value" of the relationship in unrelated dyads of female longtail macaques (through cooperative food tasks) reconciliation rates were increased between these individuals. The "good-relationship" hypothesis also predicts that reconciliation rates could be higher between sexually attracted male-female dyads. There may be strong adaptive incentives (i.e. procreation and perpetuation of genes) which increase the value of relationships between males and females and their conciliatory tendencies. Of course, for seasonal breeders, this hypothesis would be dependent on the conditions of estrus and attractivity.

Results from this study, in terms of the above models for the evolution of reconciliation, are most in agreement with the "good relationship" hypothesis. Though the conciliatory tendencies of the Arashiyama West macaques were limited, even by liberal definitions (i.e. including contact and proximity scores), there were trends in the data suggesting that female kin-members and sexually attracted male/female dyads were more likely to affiliate with each other after

their relationships were damaged by aggression. To date, female opponents have been shown to reconcile at significant levels in all female-bonded species, except ringtail lemurs (Kappeler & van Schaik, 1992). However, it has only been hypothesized that the relationship between estrus females and males may increase rates of reconciliation and there is no empirical evidence, aside from the suggestive results of this paper, to test rates of reconciliation as a function of the "reproductive condition" (ibid.). Focusing on the conditions of the relationship between aggressive opponents remains a promising area for future research.

A final aspect of the "good relationship" hypothesis predicts, based on the degree of social tolerance at the *group*-level, which species are more or less likely to reconcile conflicts. Under this model, groups with a high degree of tolerance between individuals and a relaxed "dominance style", require mechanisms to quickly repair damage caused by conflict and normalize relationships if social cohesion is to be maintained (de Waal 1989b; de Waal and Luttrell, 1989, Chaffin et al., in press). Evidence from stump-tail and Tonkean macaques (Thierry 1985), chimpanzees and bonobos (see Kappeler & van Schaik, 1992), which can all be characterized as having tolerant dominance styles, show high rates of reconciliation which agrees with this hypothesis.

Conversely, group-level data from species with "intolerant" social styles are also in keeping with the predicted trends of the "good friends" hypothesis. Japanese macaques and rhesus macaques, which could be considered as very intolerant species with strictly enforced hierarchical relationships, both show limited evidence of reconciliation (de Waal 1989b; de Waal and Luttrell, 1989; Chaffin et al., in press). Chaffin et al. speculate that, in such despotic societies, conflict may be a means by which dominant animals reinforce the dominance hierarchy forcing victims to experience stress and the threat of reattack

associated with the post-conflict period. However, such explanation does not provide a mechanism by which aggression is counterbalanced and group cohesion maintained.

A main assumption of reconciliation research is that conciliatory mechanisms evolved to counter the dispersive effects of aggression. That is, without ways to normalize relationships disturbed by conflict there would not be group-living in primates. However, these peacemaking mechanisms appear to have a very small role in aggressive circumstances for Japanese and rhesus macaques (de Waal & Luttrell, 1989; Chaffin et al., in press; present study). If gregarious living is not, as it seems for more "despotic" primate societies, contingent on mechanisms which temper the dispersive effects of aggression, why do these primates live in groups?

There is limited speculation on why and how "despotic" primate societies are able to remain in social groups. It has been suggested, that rather than repairing damaged relationships, Japanese macaques may rely more on avoiding conflict situations (Chaffin et al., in press). Indeed, compared with rhesus and stump-tail macaques, Japanese macaque aggression were less frequent but were relatively more intense (ibid.). Therefore, the risks of attack may be more limited in Japanese macaque groups, especially when individuals are attentive to avoid potentially problematic social situations. Chaffin et al. posit, that while the avoidance of aggressive circumstances is not a mechanism for modulating social relationships it may be a preventative means for maintaining sociality.

The fact that Japanese macaques live in social groups despite the dispersive forces of aggression and lack of conciliatory measures for controlling them, means the benefits of sociality must outweigh the negative costs of conflict. Results from both this study and Chaffin et al. show that a large proportion of

Japanese macaque conflicts go unresolved. This study suggests that kinship and sexual relationships are important factors which structure and bond Japanese macaque groups. However, more information on the nature of the relationships at the dyadic level, it seems, are necessary to discover what factors cause aggression and reconciliation and what social bonds keep Japanese macaque societies together.

2) Consolation

No post-conflict study, including the present study, which has specifically looked for consolation has found evidence for this social phenomenon. Aureli and van Schaik (1991a) criticize the theory of consolation believing that third-party affiliation has no functional basis for repairing the relationship with the aggressor, or reducing the victim's uncertainty about its social position or chances of reattack. While this is true, consolation could, by different theoretical rationale, function to lower the stress levels of victims through allogrooming (Schino et al., 1988) and/or provide added protection against reattack through increased proximity to kin-members most likely to aid in aggressive situations (Aureli et al., 1992). However, evidence from this study and other studies on Japanese, Barbary, longtail and stumptail macaques suggest that victims come into affiliative contact with kin and other third-parties less and are more prone to reattack after conflict than in control periods (de Waal & Ren, 1988; Judge, 1991; Aureli & van Schaik, 1991a; Aureli et al., 1993). There are no empirical evidence supporting any theory for consolation.

Given the negative evidence for consolation, future possible research interests might focus on questions of why relatives of victims are contacted less after attack when there are potential benefits to such social behavior. A possible

explanation is, perhaps, that because the victim is susceptible to reattacks by the aggressor third-parties avoid associating with the victim in the post-conflict period. In macaque societies matrilineal relatives usually share adjacent ranks (Aureli et al., 1992) and the majority of aggression is directed from dominant to subordinate animals (Chaffin et al., in press). Therefore, aggressors are likely to be dominant to the victim and its kin members. Does the inability to protect their kin and themselves cause relatives to avoid victims of aggression (Aureli et al., 1994) or do victims avoid bringing potential conflict upon their relatives?

Consolation behaviors do not appear to be adaptive in the genus *Macaca* but what about other, for example, non-female bonded primate species. De Waal and van Roosmalen (1979) suggested that consolation behaviors may be part of the behavioral repertoire of chimpanzees, a species where intervention against dominant individuals in aggressive interactions happens more frequently than in macaque species (Aureli et al., 1994). The concept of consolation does not appear to be valid when considering macaque species but still may prove useful for studies of other species with different social structures from which comparative data is lacking.

3) Substitute Reconciliation

The theory of substitute reconciliation originated from limited reports of affiliation occurring after aggression between opponents and their counterpart's kin in vervets, patas monkeys and pigtail macaques, (Judge, 1983, 1992; York & Rowell, 1988; Cheney & Seyfarth, 1989). These studies, however, did not specify the roles of the opponents, that is, which animal had been the aggressor and which was the victim in the altercation, making it difficult to evaluate what type of third-party affiliation was occurring. For example, Judge (1991) discovered

that while the aggressor affiliated more with the victim's kin after aggression, the victim showed no such attraction for the aggressor's kin.

Substitute reconciliation predicts that if reconciliation with the former opponent is not possible then the victim may take alternative action to appease the aggressor by affiliating with one of the aggressor's relatives. Theoretically, Kappeler and van Shaik (1992) believe, that substitute reconciliation could be functional if it lowered the chances that the victim would be reattacked by the former opponent. Alternatively, Judge (1991) has argued that substitute reconciliation could reduce broader damages of aggression since dyadic conflicts in vervets and some macaques species have been reported to escalate into polyadic aggressive exchanges including members of matrilineal kin from both sides (Cheney & Seyfarth, 1989; Aureli et al., 1992).

There is very limited evidence available to support any theory of substitute reconciliation. Aureli and van Schaik (1991a) report finding limited evidence of substitute reconciliation in longtail macaques but only, however, when they focused their analysis on the juveniles in their study group. These authors believe that such behaviors may be more prevalent in younger animals which may find it easier to approach the younger kin of the aggressor than the aggressor itself. This study and another study of Japanese macaques (Aureli et al, 1993) which specifically looked for substitute reconciliation did not find evidence for such behaviors, but neither of these studies limited analysis to juvenile animals. Available data make judgments concerning substitute reconciliation inconclusive. Further studies are necessary to create a comparative base to analyze these behaviors including, perhaps, special attention given to the younger age/ sex categories of study groups.

4) Redirection

There are many anecdotal references to redirection in the literature as well as a number of more recent post-conflict studies which provide quantitative evidence for these behaviors. This study discovered that the rate of aggression against third-parties increased significantly after aggression for Japanese macaque victims and most especially in the first two minutes of the post-conflict period. This pattern is very similar to what has been found in other studies of macaque species (Aureli & van Schaik, 1991a; Aureli 1992; Aureli et al., 1993).

An interesting result was discovered concerning redirection behaviors of the Arashiyama West macaques. While males showed higher overall rates of aggression, only females showed a significant increase in third-party aggression after being attacked and, hence, only females showed evidence of redirecting aggression. Scucchi et al. (1988) discovered that female Japanese macaques attacked higher ranking females more often during redirections than during initial aggressive incidents. These authors believe that female Japanese macaques may use redirection as a long-term behavioral strategy through intra-female competition to excel and settle their positions in the dominance structure. Though rank was not a factor available in this study, this hypothesis may explain the increase in female aggressiveness in the post-conflict period.

Many believe that redirection behaviors function to remove the attention of the aggressor and other potential attackers from the victim to a more recent target. Aureli et al. (1991b) report that during redirections in longtail macaques, victims may "showlook" at their former aggressors which may indicate that the victim is seeking cooperation in its attack (Aureli et al., 1992) or, more simply, acknowledgment that its behaviors are being tolerated. In the Arashiyama West Japanese macaques there were no observations of victims of aggression making

efforts to engage their former aggressors through any noticeable behavioral gestures. Ad libitum observations also indicate that most often the aggressor and victim were no longer in proximity or visual range of each when redirections occurred. Observations of Japanese macaques in this study show that it is unlikely that redirection behaviors are performed by the victim to manipulate its relationship with the aggressor.

Kin-biased redirection, it is theorized, is a form of redirection where the victim specifically targets lower ranking relatives of the former aggressor in order to indirectly damage the aggressor and cause it to cease attacks upon the victim. Aureli et al. (1992) give cursory evidence that such a system of "retaliation" may be part of the behavioral repertoire of Japanese macaques. There was no evidence from the available data in this study that Japanese macaque victims were more likely to redirect against the opponent's kin, however, Aureli et al.'s methodology took into consideration a longer post-conflict period (e.g. up to 1 hour) and was more sensitive to polyadic aggressive circumstances.

Chapter Four: The Effects of Aggression on the Victim's Behavior

Displacement Activities and Time Budgets

Recently, it has been suggested that certain displacement behaviors may be good behavioral indicators of aroused emotional and physiological states in nonhuman primates. Indeed, the Arashiyama West macaques showed evidence of an increase in body-scratching, body-shaking, run/jump startles and selfgrooming in the post-conflict period. These behaviors seemed to indicate sympathetic activation in victims and were considered to be good measures of the internal state of focal animals. There was no evidence of an increase in

yawning, perhaps because yawning may function as a threat or intimidation display in other contexts (see Aureli et al., 1992).

When rates of displacement behaviors were compared between males and females it was determined that females showed a significant increase in most displacement behaviors in the post-conflict period while selfgrooming was the only behavior indicating increased stress in male victims. This evidence is contrary to Aureli and van Schaik's (1992) examination of post-conflict displacement behaviors in longtail macaques where all of their focal animals showed similar behavioral responses after receiving aggression. There are at least two ways which the data on male displacement can be interpreted. First, aggression did not cause males to become stressed about their social situation in the post-conflict period. Second, due to effects the mating season (or some other factor of this group's structure), males may overall have been more anxious about their social situation which masked indications of stress after aggression because these were already present.

With the evidence of this study and ad libitum observations it appears that male victims were, overall, less affected by aggression than females. First, no male victim was ever recorded reconciling with its (male) aggressor. This could indicate that victims did not perceive the conflict as damaging to their social relationship, which may be considered more as competitive than valuable, and were therefore not anxious to repair this relationship. Second, there was no significant increase in aggression by male victims in the post-conflict period. Redirected aggression is, theoretically, a method used by victims to regain control of its social situation. The lack of evidence for redirection in the males of this study may be indicative that male victims are not anxious about their social position after receiving aggression. Third, from observations obtained in this

study, males were the recipients of fewer aggression and received aggression infrequently from females which comprise the majority of the population. Given these factors, males were at less risk of reattack in the post-conflict period which may also account for the limited stress responses recorded in males. Data recorded on male victims in this study were, however, limited and additional observations and a comparative sample from the non-mating season would allow more substantial and conclusive scrutiny of the effects of aggression on males.

A curious result this study discovered was that after receiving heavy aggression victims body scratched significantly less which would indicate lower stress levels. Body scratching was the most frequently observed displacement behavior and perhaps the best indicator of elevated stress. However, it is not believed that reduction in scratching after heavy aggression indicated lower levels of anxiety for these victims. Significant increases in startle behaviors attest that victims of heavy aggression were still alert to their social environment and anxious about their social position. However, some property of heavy aggression affected, especially female, victims differentially than light aggression (see de Waal & Yoshihara, 1983). Ad libitum observations indicate that victims, often with visible wounding, remained very still after heavy aggression, perhaps due to pain or shock associated with the severity of attack. However, lower rates of body-scratching are misleading as victims were visibly affected by heavy aggression. Levels of body-scratching were the only displacement behaviors used to study stress in longtail macaques (Aureli et al. 1989; Aureli, 1992). This study indicates that methods more sensitive to a variety of stress-related behaviors and quality of the aggression may lead to more accurate results.

The analysis of time-budget behaviors also provided evidence of the differential effects of heavy aggression. Female victims were significantly more often involved in stationary behaviors and would eat/drink significantly less after heavy aggression. This may indicate that there were greater costs associated with heavy aggression, such that victims could not or were not motivated to locate nourishment.

Reattack and the Consequences of Reconciliation and Redirection

Reattack was investigated in this study because it is the primary reason given why victims of aggression display elevated levels of stress activities even after aggression have ceased. It is theorized that due to the threat of reattack by the aggressor and alternate animals, maintenance of an aroused emotional state is adaptive in that it allows victims to react quickly if it is in danger of additional aggression. Quantitative evidence for reattack has only been documented in a few post-conflict studies of longtail (Aureli, 1989; Aureli & van Schaik, 1991b) and rhesus macaques (de Waal & Yoshihara, 1983) and patas monkeys (York & Rowell, 1988). Analysis of the Arashiyama West macaques also indicated that there were greater chances that a victim would be reattacked in the post-conflict period than when there had been no previous aggression. Evidence from this study supports the theory that victims may maintain an aroused emotional state due to increased chances of reattack.

Displacement activities as indicators of stress and anxiety are important to post-conflict investigations because they provide a measure of the functions of various social events. Most studies have assumed that reconciliation and redirection function to reduce the victim's anxiety about its uncertain social situation, however, there is little direct evidence confirming this function (Aureli

et al. 1989; Aureli et al. 1991b). This study used five separate tension-related activities to record stress levels in victims which allowed an analysis of how effective post-conflict events were in reducing the anxiety of victims. Though small sample sizes made it impossible to perform sophisticated statistical analysis, descriptive statistics were informative. It was determined that after reconciliation there was a dramatic overall reduction in the performance of displacement activities and reconciliation, as theoretically predicted, causes a faster reduction in the victims anxiety.

Displacement behaviors also show decline after redirection though more moderate than that after reconciliation. Interestingly, like this study, Aureli and van Schaik (1991b) discovered that redirection reduced rates of body scratching but was not as effective in reducing rates of selfgrooming. Overall it appears that redirection may reduce some of the anxiety of victims but it remains unclear how it is effective in restoring its social relationships and control of its social circumstances. Redirection may, as is alternatively proposed, function as a "quick release" mechanism by which the victim can relieve its frustration on a lower ranking animal. Additional studies of the contexts and relationships between dyads involved in aggression and redirection are necessary before reasons can be applied explaining why redirection reduces the stress responses in primate victims.

Summary

The Arashiyama West Japanese macaques are not as conciliatory as other species of nonhuman primates but, though reconciliations are relatively infrequent, they appear to occur more regularly between related or sexually attracted dyads. Certain dyadic relationships may confer adaptive advantages to

opponents who are, therefore, more motivated and accessible to each other for conciliatory exchanges or, at least, non-agonistic rapprochement. Reconciliations do lower the stress levels in the victims of attack and appear to normalize the relationship between opponents and the victim's social uncertainty in the post-conflict period.

Redirection behaviors were the most significant post-conflict event manifested by Japanese macaques and victims, especially females, often responded to aggression by directing aggression of their own at third-party individuals. There was no evidence that these behaviors were directed specifically at the relatives of the aggressor (i.e. kin-biased redirection) though such "retaliations" may occur in special circumstances outside the scope of this study. Redirections were moderately effective in reducing stress levels in victims but the cause of this is not self-evident.

There was no evidence that the Arashiyama West macaques consoled victims of aggression and the data pointed towards an opposite trend of less affiliation by victims after aggression. This data confirms reports from a number of other studies and consolation behaviors need to be reconsidered as a post-conflict social event, at least in female-bonded species.

Female Japanese macaques were more affected by aggression than males as measured through an increase in stress-related displacement behaviors. As theorized, stress may be more prevalent in victims because they are significantly more prone to be reattacked in post-conflict period. Such post-conflict arousal might be adaptive to keep the victim prepared to react quickly to further aggressive gestures by the former or alternate opponents.

This study adds to the growing body of post-conflict literature with data on the post-conflict social events in Japanese macaques. This is only the second

study to consider these behaviors in a free-ranging population of primates. Displacement behaviors as measures of post-conflict stress have been used in very few previous studies and these proved to be very useful tools for understanding the motivations and functions of social behaviors and events in victims of aggression.

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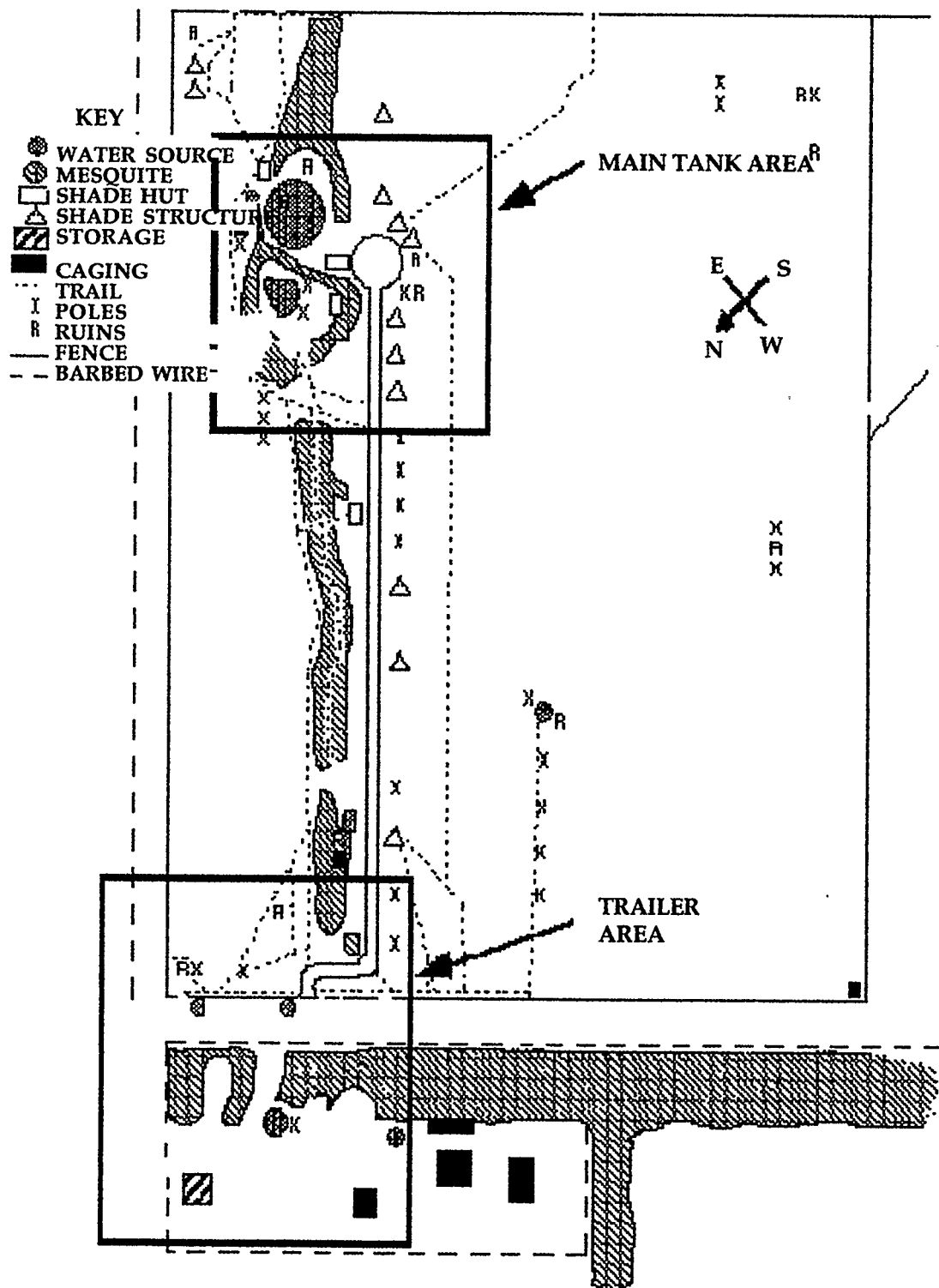
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APPENDIX A
S.T.P.O. ARASHIYAMA WEST SNOW MONKEY
SANCTUARY: BURNS RANCH SITE



APPENDIX B

ETHOGRAM

Adapted from Fedigan (1976).

- 1) Lie in bodily contact: with another monkey.
 - 2) Huddle: to sit in bodily contact with another monkey or monkeys. This occurs especially in cold weather, during courtship interactions and between mother and offspring.
 - 3) Approach (direct): a direct advance by one monkey towards another, almost always preliminary to a social interaction such as groom solicitation. An approaching monkey is usually dominant over the approached, or else signals friendly intentions as it approaches.
 - 4) Approach (receive)
 - 5) Groom solicitation (direct): a monkey presents a portion of its body (chest, back, etc.) to another monkey at very close range.
 - 6) Groom solicitation (receive)
 - 7) Groom (direct): one monkey inspects and cleans the fur of another. This is done with a gently rhythmical pattern of fur separation, scratching at the skin and stroking pulls of the fur, and for far longer periods than necessary for simple cleaning. Cleaning is an affiliative behavior.
 - 8) Groom (receive)
 - 9) Sex present (direct): a gesture of orienting the hindquarters toward another while sitting with the posterior raised slightly off the ground.
 - 10) Sex present (receive)
 - 11) Mount (direct): A stands up against the back of B, braces his feet on B's calves and his hands on B's back.
 - 12) Mount (receive)
 - 13) Initiate play (direct): one monkey closely and deliberately approaches another and causes a play interaction to begin usually by one of a group of fairly stereotyped behaviors: cuffing, pulling, mouthing or jumping on with accompanying play face expression.
 - 14) Initiate play (direct)
- see also: Wrestle, Brief grapple, Rough and tumble

- 15) Lip quiver: a rapid up and down movement of the lips over the teeth with the lips slightly pouted. It appears to be a reassurance signal used in social situations in which there might be some tension. Its most frequent use is by males in courtship interaction.
- 16) Fear grimace (direct): a submissive visual signal in which the lips are retracted from the teeth, with the teeth clenched.
- 17) Fear grimace (receive)
- 18) Chase (direct): to pursue another monkey with accompanying agonistic signals, indicating the intent is to do harm or drive away the chased individual.
- 19) Chase (receive).
- 20) Pinch or Grab: to take hold of another's body by the hand and squeeze to the point of causing pain.
- 21) Pinch (receive).
- 24) Bite (direct): to seize another with the teeth
- 25) Bite (receive).
- 26) Chase (direct): one monkey moves toward another who immediately moves out of the former's way. Frequently the displacer will sit down or stand in the exact location the displaced has just vacated. Although not as physically aggressive as some other agonistic gestures, 'displace' is usually a very clear indication of relative dominance status.
- 27) Lie: another inactive state differing from Sit only in the posture of the monkey. This behavior could also be recorded in proximity to or in contact with another monkey.
- 28) Stand: four-legged stance, usually a transitional behavior between sitting and traveling or other movement patterns. Occasionally a monkey may simply remain in this pose for some time.
- 29) Bipedal: to stand up on the two hind limbs and look around attentively. This is an attentive, locating behavior, performed predominantly during foraging trips. This stance is often the immediate reaction to an alarm call, or an unusual sound.
- 30) Climb (up): simple act of ascension by using the hands and feet. Climbing is used to obtain food from trees and bushes; to obtain a better view; and it is also a behavior which often follows a troop alarm.
- 31) Climb (down).
- 32) Jump startle: a sudden explosion movement of the body in place, occurring when a monkey is caught unaware, for example when another monkey is not heard and is suddenly observed at close range.
- 33) To cause a jump startle.
- 34) Run startle (alone): a sudden explosive movement across space, caused by sighting a fearful stimulus.
- 36) Run with troop: after an alarm, the majority of the troop runs in fright, usually all in the same direction towards trees or shelter.
- 37) Follow (direct): to travel direct behind in the path of another monkey.

- 38) Follow (receive).
- 39) Contact call: vocalizations commonly used as the troop moves through the brush, probably to locate specific troop members. Often a monkey will sit and call, apparently trying to locate or make contact with another individual.
- 40) Travel (alone): to move unaccompanied across the ground, at walking speed.
- 41) Travel (accompanied).
- 42) Lope: locomotor pattern of moving quickly in a swinging stride.
- 43) Forage: to eat natural vegetation; to eat provisioned food.
- 44) Drink: at two artificial ponds, out of water troughs or facets.
- 45) Muzzle (direct): one monkey places its mouth directly on another's mouth and sniffs intently, apparently in an effort to determine what the latter is eating.
- 46) Muzzle (receive).
- 47) Lunge or bluff charge: a plunge forwards towards an opponent in an agonistic encounter, followed by quick retreat.
- 48) Lunge (receive).
- 49) Slap (direct): the first monkey hits the second with the flat of its hand. An aggressive gesture occurring during agonistic encounters.
- 50) Slap (receive).
- 51) Visual and vocal threat (direct): consists of the following agonistic signal: stare, lid, gape, growl. The components are rapid and flexible in combination and in sequence, thus they are combined in the threat unit.
- 52) Threat (receive).
- 53) Displace (direct): one monkey moves toward another who immediately moves out of the former's way. Frequently the displacer will sit down or stand in the exact location the displaced has just vacated. Although not as physically aggressive as some other agonistic gestures, 'displace' is usually a very clear indication of relative dominance status.
- 54) Displace (receive).
- 55) Scream (direct): a loud, shrill vocalization indicating stress directed into the face of an opponent monkey. It also seems to function to inform the surrounding animals that an agonistic encounter is taking place and the screamer desires help. Thus it is not clearly an aggressive or submissive signal.
- 56) Scream (receive).
- 57) Avoid (direct): a monkey notices another in its path or coming in its direction and changes its movement pattern in order to avoid encountering the latter monkey.
- 58) Avoid (receive).
- 59) Seek aid: an individual in a dispute screams and looks repeatedly toward an uninvolved monkey for support, or else seeks to put this other individual between itself and the opponent.
- 60) Seek aid (receive).

- 61) Give aid: an individual responds to a seek aid by directing aggressive signals at the opponent monkey.
- 62) Receive aid.
- 63) Sex present (receive): a gesture of the hindquarters being oriented towards a monkey by another, while sitting with the posterior raised slightly off the ground.
- 64) Hip touch (direct): a gesture preliminary to a mount in which the actor pulls upward on the pelvis of the recipient. This is apparently an attempt to get the recipient into the proper position for mounting. Directed especially towards recalcitrant females.
- 65) Mount (direct): A stands up against the back of B, braces his feet on B's calves and his hands on B's back.
- 66) Mount (receive).
- 67) Thrust: forward-backward movement of the pelvis by the mounter. Performed both in the presence and absence of intromission.
- 68) Lip quiver: a rapid up and down movement of the lips over the teeth with the lips slightly pouted. It appears to be a reassurance signal used in social situations in which there might be some tension. Its most frequent use is by males in courtship interactions.
- 70) Estrus hack (receive): vocalization given by females in estrus. Some elements of sexual frustration or dissatisfaction are involved.
- 71) Courtship display (direct): during the mating season males approach estrus females in a relatively constant manner which consists of 'strutting' locomotion, pouted lips and raised tail. They often approach the female directly, push her, whirl around abruptly and either sit down next to her or assume a 'bird-dog' pose (the body is held rigid in a stands position while the male stares off at a distant point).
- 72) Body shake or shudder: a rapid, repeated twitching of the entire body which occurs when individuals are frustrated in their attempts at some type of social interaction. Body shakes are highly associated with weaning behaviors but are also given by courting males when females do not act receptive.
- 73) Fiddle: tinkering or fumbling with items in the environment to no observable purpose and for very short time periods.
- 74) Vigilance: an animal sits for a sustained period of time in an elevated position mainly facing away from the body of the troop although occasionally glancing back at it. The animal is obviously alert and monitoring the environment.