Primates—A Natural Heritage of Conflict Resolution

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The traditional notion of aggression as an antisocial instinct is being replaced by a framework that considers it a tool of competition and negotiation. When survival depends on mutual assistance, the expression of aggression is constrained by the need to maintain beneficial relationships. Moreover, evolution has produced ways of countering its disruptive consequences. For example, chimpanzees kiss and embrace after fights, and other nonhuman primates engage in similar "reconciliations." Theoretical developments in this field carry implications for human aggression research. From families to high schools, aggressive conflict is subject to the same constraints known of cooperative animal societies. It is only when social relationships are valued that one can expect the full complement of natural checks and balances.

With the early provocative description of *Australopithecus* as a lustful killer and the appearance of Konrad Lorenz's *On Aggression* in 1967, the origins of violence became a central theme in debates about human social evolution (*1, 2*). Popular authors spun the now familiar scenario according to which inborn aggressiveness, combined with male bonding in hunting and warfare, explains the human success story. The extraordinary appeal of this "killer ape" myth (*3*) has been attributed to the horrors of World War II. Confidence in human nature was at a low after the war, and the view that we are murderous psychopaths—or "a mentally unbalanced predator, threatening an otherwise harmonious natural realm" [(*4*), p. 14]—went down remarkably easily with scientists and the general public alike.

If we disregard this larger evolutionary debate and focus on the original research, it is obvious that aggressive behavior was studied as an individual rather than a social phenomenon. For example, Lorenz proposed his controversial drive concept according to which aggressive energy builds up endogenously, after which it seeks an outlet, whether in sports or warfare. He also emphasized genetic determinants, postulating an aggressive instinct (*1*). Psychologists, in contrast, developed their frustration-aggression hypothesis and studied the effects of role models and authorities (*5*). However different these outlooks, authors on both sides of the nature-nurture divide agreed on the antisocial character of aggressive behavior. According to ethologists, its main function was to cause dispersal, a view derived from territorial fish and birds in which threat displays do indeed serve to keep intruders at a distance. Psychologists, too, only saw negative consequences when a mouse was placed in a rat's cage to provoke an attack, when pain-induced aggression was incited among rats on an electric grid, or when human subjects were instructed to deliver high-voltage shocks to strangers (*6*). Focusing on aggression among individuals that did not know each other, students of both human and animal behavior thus laid the groundwork for what may be called the individual model [(*7*) and Fig. 1].

Inasmuch as the individual model is oblivious to social context, it fails to address how families or societies deal with the disruptive consequences of conflict. The model tells us how aggression starts, but not how it ends or is kept under control. In the real world, however, the vast majority of aggression involves familiar individuals, which means that aggressors and victims share a past and can be expected to share a future. A different model was needed, therefore, one that regards individuals as socially embedded. Inspired by gregarious study objects, primatologists were the first to move toward this more integrated paradigm.

Primate societies are characterized by cooperation. Some species, such as chimpanzees [*Pan troglodytes* (*8*)] and humans, show collective intercommunity violence. More often, however, alliances are formed within the group with two or more individuals banding together to defeat a third (*9*). As a result, high-ranking individuals are not necessarily the strongest, but the ones that can mobilize most support (*10*). The ubiquitous primate activity of grooming serves an important role in this political arena by fostering valuable partnerships (*11*). All members of a group are actively establishing and maintaining histories of interaction, known as social relationships. Studying monkeys and apes in cohesive groups, in both captivity and the field, primatologists increasingly made relationships, rather than individuals, the unit of analysis (*12*).

At the same time that these ideas arose, a simple observation changed the way we look at the social impact of conflict. Earlier research on nonhuman primates had emphasized appeasement and reassurance gestures (*13, 14*) and had hinted at relationship repair after fights (*15–17*). The latter phenomenon was named and empirically defined as the result of an incident in the world's largest chimpanzee colony at the Arnhem Zoo, in the Netherlands. When the alpha male fiercely attacked a female, other apes came to her defense, causing prolonged screaming and chasing in the group. After the chimpanzees had calmed down, a tense silence followed, broken when the entire colony burst out hooting. In the midst of this pandemonium, two chimpanzees kissed with their arms wrapped around each other (Fig. 2). These two chimpanzees turned out to be the same male and female central in the previous fight.

After reconciliation was defined as a friendly reunion between former opponents not long after an aggressive confrontation, data on hundreds of instances showed the pattern to be a regular, conspicuous part of social life in the Arnhem chimpanzee colony (*18*). Combined with other developments in the 1970s, this meant that a solid framework for the study of conflict resolution had come into place revolving around the following three elements: (i) indications of a calming function of grooming and other body contacts, (ii) recognition of long-term social relationships and their survival value, and (iii)

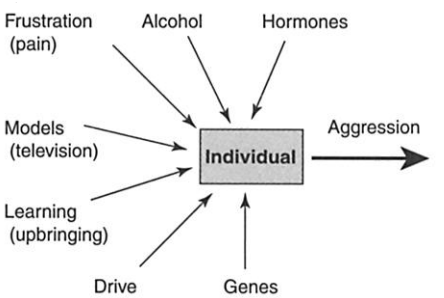

Fig. 1. The individual model of aggression. Many different influences, both external (e.g., role models) and internal (e.g., hormones), determine an individual's propensity to become aggressive. Because social consequences and feedback are not part of the model, it makes no predictions about conflict resolution.

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demonstration of a connection between aggressive conflict and subsequent interopponent reunions, called "reconciliations."

Primate Research

The reconciliation concept applies to animals a familiar human interpretation, which comes with connotations of rapprochement, conflict settlement, and even forgiveness (*19*). Reconciliation is best regarded as a heuristic concept capable of generating testable predictions regarding the problem of relationship maintenance (*20*). One central assumption is that a motivational state can be replaced relatively rapidly by its opposite: hostility and fear make way for a positive inclination. Another assumption is that this motivational shift serves the restoration of relationships. Since its introduction, more than 100 reports on 27 different primate species have been published, mostly in support of predictions derived from the reconciliation concept (*21*).

The first aim of research in this area has been to compare different expectations regarding the social consequences of aggression. The traditional notion that aggression serves a spacing function would predict decreased contact between individuals after open conflict. The reconciliation hypothesis, in contrast, predicts that individuals try to "undo" the social damage inflicted by aggression, hence, that they will actively seek contact, specifically with former opponents.

Testing these predictions requires a comparison with baseline data. The standard procedure is a controlled design known as the PC-MC method (*22*). One of the participants in a spontaneous fight is followed for a given time window (e.g., 10 min) to collect postconflict (PC) data, which is then compared with baseline information on the contact tendencies of the same individual in the absence of previous aggression (matched control or MC). These two sets of data allow for a division of opponent pairs into "attracted" pairs (i.e., contacting each other earlier in the PC than the MC) and "dispersed" pairs (i.e., contacting each other earlier in the MC than the PC). The conciliatory tendency (CT) after all observed fights can then be expressed as (*23*): CT = (attracted pairs – dispersed pairs)/(all pairs).

This measure has a built-in correction for normal contact rates, such that a CT of 0% means that the rate of friendly interaction between any two individuals is unaffected by previous aggression. Studies adopting this paradigm for primates have almost universally demonstrated positive CT values (for some species exceeding 50%), meaning that former opponents systematically contact each other more often than expected [(*23*) and Fig. 3]. Thus far, most studies have concerned captive primates. One comparative study found no difference in conciliatory tendency between a captive and wild population of the same species (*24*). That former opponents frequently engage in friendly interaction flies in the face of earlier assumptions about the dispersive impact of aggression, which should have resulted in negative CT values. Moreover, some species show behavioral specificity, that is, their PC reunions stand out by special gestures, vocalizations, or body contacts. Dependent on the species, postconflict reunions may include mouth-to-mouth kissing, embracing, sexual intercourse, clasping the other's hips, grooming, grunting, and holding hands.

With regard to the pacifying function implied by the reconciliation label, several studies have confirmed that the chance of renewed aggression is reduced and tolerance restored after PC reunion. For example, the probability of revival of a conflict is lower for reconciled than unreconciled conflicts (*25, 26*). When conflict was experimentally induced in pairs of monkeys, individuals permitted to reconcile were more tolerant of each other around a juice dispenser than individuals that had been prevented from reconciling, suggesting that reconciliation reduces aggression in the dominant and fear in the subordinate (*27*).

Displacement activities, such as self-scratching, may provide clues about arousal due to anxiety and social tension (*28*). Thus, self-directed behavior increases after anxiogenic drug treatment but decreases after anxiolytic drug treatment (*29*). Using self-scratching as a behavioral index, anxiety has been found to rise when an individual has just received aggression and to drop back to baseline more rapidly after reconciliation than without it (*30*). Reconciliation thus seems to have a calming effect. This is not to say that anxiety is restricted to the victims of aggression: the reconciliation concept, which revolves around social relationships, implies that not only losers but also winners have something to "worry" about. Behavioral signs of anxiety have indeed been measured in aggressors, especially after conflict in high-quality relationships. These findings fit the prediction that aggression-induced anxiety concerns the social tie and suggest an interesting emotional mechanism: Conflict in valuable relationships induces greater anxiety, which in turn creates a greater need for calming PC contact with the opponent (*31*).

Whereas all of these findings support the specific function suggested by the reconciliation label, which is to repair damaged relationships, it is hard to measure lasting effects. Could it be that the effects concern merely the immediate future (*32*)? This has been a point of debate, and careful data collection on long-term effects is needed. It has been argued, however, that because long-term social relationships are an emergent property of short-term interactions, a distinction between the two is artificial (*33*). Moreover, in virtually all primates studied, reconciliation is typical of partners with close ties even after controlling for their high level of interaction. Thus, in macaques, which form matrilineal societies with kin-based alliances, fights among kin are more often reconciled than those among nonkin [(*23*) and Fig. 4]. There are also the unifying group-hugs after rare aggression among male muriquis (*Brachyteles arachnoides*), a species in which males collectively defend a territory (*34*). Chimpanzee males, too, band together against neighbors and counter the disruptive effects of status competition within the group with a conciliatory tendency that far exceeds that of females (*35*). All of these cases support the prediction that long-term cooperative ar-

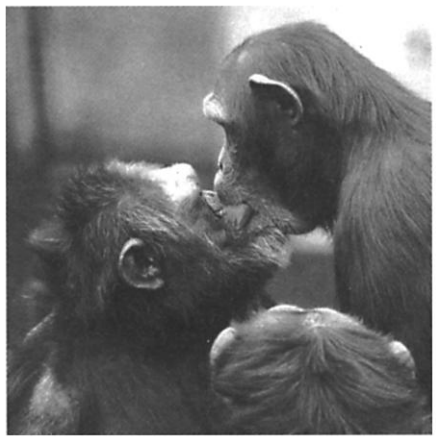

Fig. 2. Chimpanzees typically seal a postconflict reunion, or reconciliation, with a mouth-to-mouth kiss, as here by a female (right) to the dominant male. [Photograph by the author]

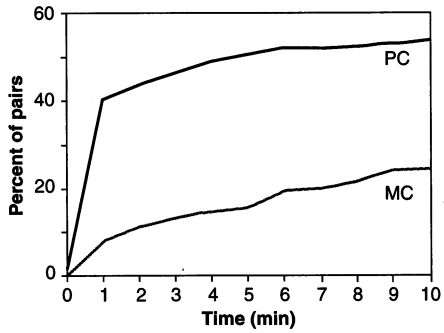

Fig. 3. Most primates show a dramatic increase in body contact between former opponents during postconflict (PC) as compared with matched-control (MC) observations. Earlier notions about aggression would have predicted the exact opposite, i.e., distancing between previous antagonists. The graph provides the cumulative percentage of opponent-pairs seeking friendly contact during a 10-min time window after 670 spontaneous aggressive incidents in a zoo group of stumptail macaques (*79*).

rangements are associated with frequent relationship repair.

As a testimony to the effectiveness of these mechanisms, aggression can become quite common in close relationships without endangering them. Thus, not only do macaque mothers, daughters, and sisters show high levels of grooming and mutual support, they also frequently fight; in fact, they do so more often than unrelated females (*36, 37*). This paradoxical finding can be explained by assuming that the more compatible or secure a relationship (*38*), the more the threshold for conflict can be lowered without posing a threat to that relationship. The same may apply to entire species, such as some conciliatory and tolerant macaques, which also exhibit high rates of mild aggression (*39, 40*). These high rates may reflect the reduced cost associated with aggression in a society in which reconciliation is easy.

One of the generalizations to come out of reconciliation research on nonhuman primates is the valuable relationship hypothesis (*41*), according to which reconciliation will occur especially after conflict between parties that represent a high social or reproductive value to each other. In other words, social relationships are commodities the deterioration of which needs to be prevented (*42, 43*). Apart from the above-mentioned observational data, experimental evidence comes from a study that manipulated the degree of cooperation among monkeys. Pairs of long-tail macaques (*Macaca fascicularis*) were trained to obtain rewards by acting in a coordinated fashion: The only way to obtain popcorn would be for two monkeys to sit side by side at a dispenser, a procedure that attached significant benefits to their relationship. After this training, subjects showed a three times greater tendency to reconcile after an induced fight than subjects that had not been trained to cooperate (*44*).

With these mechanisms in place, it is obvious that from a relationship perspective the central problem is not aggressive conflict per se, but the perceived value of the relationship and the way conflict is dealt with. In nonhuman primates, aggression is a well-integrated part of social life: it occurs in the best relationships, and its potentially negative impact is countered by a flurry of friendly social interaction. The individual model has therefore been replaced by a relational model, which places conflict in a social context (*7*). Instead of treating aggression as an instinct or an automatic response triggered by frustration, this model sees it as one of several options for the resolution of conflicts of interest. Other options are avoidance of the adversary (common in hierarchical and territorial species) and the sharing of resources (common in tolerant species). After having weighed the costs and benefits of each option, conflict may escalate to the point of aggression, after which there still is the option of undoing its damage by means of reconciliation, which option will be favored by parties with shared interests (Fig. 5).

The relational model thus allows for a cycling through conflict and reconciliation over time, representing negotiations that define or redefine the terms of the relationship. The prototypical example is the relationship between mother and offspring during weaning. A very intense, valuable relationship, which neither party can afford to break, is disturbed by rejections of nipple access mandated by the mother's future reproduction. The offspring's interests are quite different and would be served by continued nursing (*45*). A prolonged series of conflicts plays out between the two, sometimes involving aggression and often leading to temper tantrums, in which the offspring squirms and screams. After having cycled for months through daily confrontations and reconciliations, the new terms of the relationship may be reflected in a compromise: The offspring substitute-nurses by sucking on the mother's lower lip or by taking a skin fold close to her nipple into its mouth (Fig. 6). These outcomes show how conflict can shape relationships without permanently disturbing them.

The development of reconciliation in young primates has been little studied, but there is increasing evidence that we are dealing with a "skill" (i.e., a learned behavioral strategy) rather than hard-wired behavior (*38, 46*). This was demonstrated by an experiment that exploited interspecific variation in conciliatory tendency. Rhesus monkeys (*Macaca mulatta*)—a relatively aggressive, intolerant macaque with low levels of reconciliation—were exposed to a highly conciliatory close relative, the stumptail monkey (*M. arctoides*). Juveniles of both species were housed in mixed groups for 5 months. Following this, they were observed for 6 weeks with conspecifics only. This manipulation created a different social culture by producing rhesus monkeys with a three to four times higher conciliatory tendency than age mates that had never met the other species. Peacemaking tendencies rose gradually during cohousing with the gentle "tutor" species and remained high after its removal. This experiment demonstrated that reconciliation behavior of monkeys can be modified by social experience (*47*).

Cognitive prerequisites for reconciliation are minimal. It is essential that members of the species recognize each other individually and that participants in a fight remember their opponent's identity (*22*). In addition, as seen above, reconciliation probably involves evaluation of the benefits derived from relationships: Appreciation of relationship value will prevent risky overtures (any rapprochement carries the possibility of renewed conflict) for little gain. For most nonhuman primates, the above prerequisites are easily met. They are capable of much more, as reflected in the following examples of conflict resolution involving third parties.

Policing and pacification. High-ranking

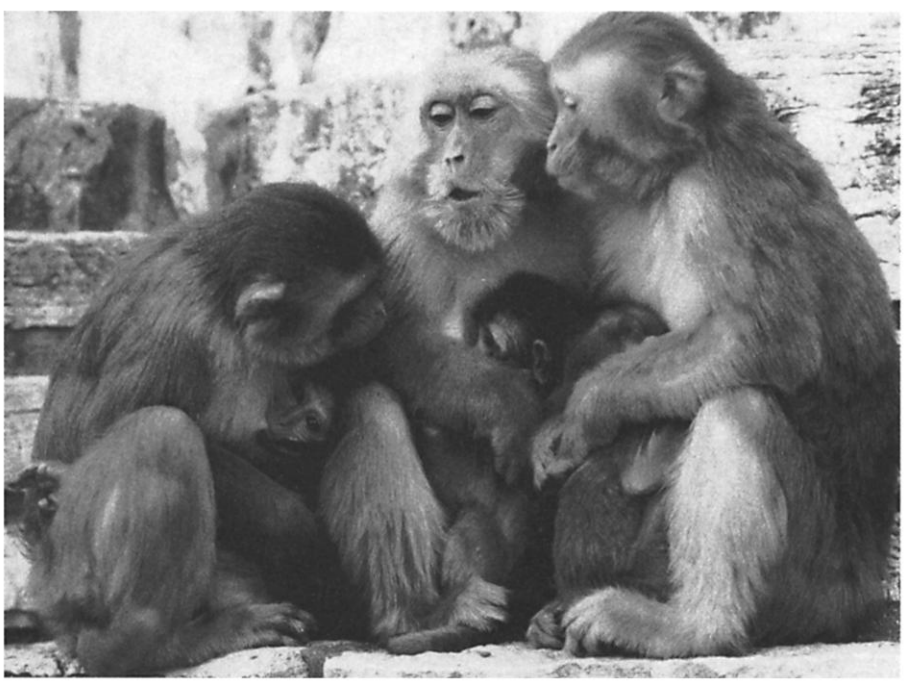

Fig. 4. Reconciliations allow rhesus monkeys to maintain tight kinship bonds despite frequent intrafamilial squabbles. Shortly after two adult sisters bit each other, they reunite sitting on the left and right of their mother, the alpha female of the troop, each female holding her own infant. The sisters smack their lips while the matriarch loudly grunts. [Photograph by the author]

individuals sometimes adopt a control role, breaking up fights or systematically protecting the weak against the strong (*48*). At other times they intervene peacefully or try to calm down one of the participants (*49, 50*). In species in which large males defend units of several females, such as Chinese golden monkeys (*Rhinopithecus roxellanae*), the leading male may maintain harmony by interposing himself between female contestants while holding their hands, and stroking or grooming both of them (*51*).

Triadic reconciliation. In macaques and vervets (*Cercopithecus aethiops*), relatives of the victim may seek contact with the opponent. For example, a mother may approach and groom the attacker of her daughter in what appears a reconciliation "on behalf" of her offspring. Such third-party contacts seem to serve the relations between entire matrilines (*52, 53*). Similarly, there exist field reports of intergroup reconciliations spearheaded by the alpha females of different monkey groups (*54*).

Third-party mediation. In perhaps the most complex pattern, thus far known of chimpanzees only, a female acts as catalyst by bringing male rivals together. After a fight between them, males may remain oriented toward each other, staying close, but without either one initiating an actual reunion. Females have been observed to break the deadlock by grooming one male, then the other, until she has brought the two of them together, after which she withdraws (*18*).

All of these tactics are elaborations on a basic behavioral mechanism that protects cooperative bonds. Many animals other than primates would stand to gain from such a mechanism and have the cognitive capacities to permit it. From the beginning, therefore, there have been calls to look beyond the primate order. Only very recently, however, has PC behavior become a topic of systematic research in such disparate mammals as spotted hyenas [*Crocuta crocuta* (*55*)], domestic goats [*Capra hircus* (*56*)], and bottlenose dolphins [*Tursiops* spp. (*57*)]. The results have been positive, suggesting that conflict resolution may be widespread indeed.

The evolutionary advantages of reconciliation are obvious for animals that survive through mutual aid: Reconciliation ensures the continuation of cooperation among parties with partially conflicting interests. At the same time, it should be realized that reconciliation was never predicted or even remotely considered by evolutionary theorists. Traditionally, cost-benefit analyses have started from the assumption that animals neither know nor need each other. Thus, the rarity of lethal aggression was attributed entirely to the physical deterrent posed by the opponent's fighting abilities (*58*). In many social animals, however, both parties stand to lose if escalated fighting damages relationships. The widespread occurrence of reconciliation, therefore, questions assumptions underlying earlier modeling and leads theorists to look at individuals as part of the larger benefit-benefit arrangements that we call societies.

Implications for Human Behavior

Ironically, research on how animals spontaneously make up after fights was for a long time ahead of how humans accomplish the same goals (*59*). This situation is rapidly changing, though, now that basic human research in this area is gathering steam, with some research shifting focus from aggression to conflict, negotiation, and compromise. For example, projects are under way in several countries to measure the development of conciliatory behavior in children.

The same ethological observation techniques developed for animals are applicable to children in the schoolyard or other settings of unstructured activity. Among preschoolers, two forms of conflict resolution have been noticed: peaceful associative outcomes, in which both opponents stay together and work things out on the spot (*60*), and friendly reunions between former opponents after temporary distancing (*61*). These two complementary forms of child reconciliation, expressed in play invitations, body contacts, verbal apologies, object offers, self-ridicule, and the like, have been found to reduce aggression, decrease stress-related agitation (such as jumping up and down), and increase tolerance (*62*). The striking similarity of these findings to those on nonhuman primates suggests causal, as well as functional, parallels. One of the single best predictors of peacemaking is positive contact between children before eruption of the conflict, suggesting a concern with the continuity and integrity of interactions with peers (*61, 63*).

Preference for integrative versus confrontational solutions to conflict is different for children from different cultural backgrounds (*64, 65*). For example, Kalmyk and Russian children hold hands after fights while reciting *mirilka*, or peacemaking rhymes such as, "Make peace, make peace, don't fight; if you fight, I'll bite, and we can't bite since we're friends" (*66*). Recent reviews of the literature on child conflict resolution stress the same themes as the primate literature, such as how friendship increases conciliatory tendency and how peacemaking skills are acquired through interaction with peers and siblings (*67, 68*). An impoverished social environment (as in the homeless) deprives children of this essential aspect of socialization (*68*), causing deficits in conflict management and moral development (*69, 70*). With the recent interest in conflict resolution at schools (*71*), there is a great need for basic information about how children behave

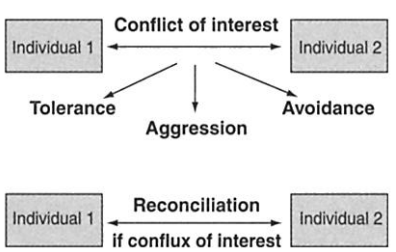

Fig. 5. According to the relational model, aggressive behavior is one of several ways in which conflicts of interest can be settled. Other possible ways are tolerance (e.g., sharing of resources), or avoidance of confrontation (e.g., by subordinates to dominants). If aggression does occur, it depends on the nature of the social relationship whether repair attempts will be made, or not. If there is a strong mutual interest in maintenance of the relationship, reconciliation is most likely. Parties negotiate the terms of their relationship by going through cycles of conflict and reconciliation.

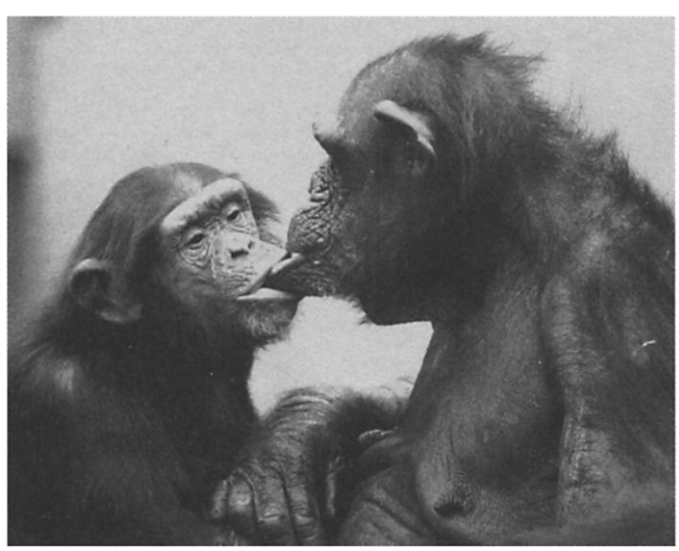

Fig. 6. A weaning compromise has been arrived at between a mother chimpanzee and her 4-year-old son. After repeated nursing conflicts, the son is permitted to suck on a part of the mother's body other than the nipple. [Photograph by the author]

among peers. Conflict resolution programs will need to be evaluated against behavioral change. This will require observational techniques not unlike those applied in the above primate studies complemented with attention to the unique role of language (*72, 73*).

In human adults, the topic of peacemaking is less well studied. The little systematic research that exists confirms that, rather than the rate and intensity of open conflict, it is the way conflict is being handled and resolved that matters most, for example, for marriage stability (*74*). There also exist cross-cultural comparisons that indicate how in human society reconciliation has been institutionalized, elaborated on, ritualized, and surrounded with a great many societal influences, such as the role of elders, conciliatory feasts, and compensatory payments (*75*). Peacemaking is a universal human preoccupation: some societies, such as the Malayan Semai, say that they fear a dispute more than they fear a tiger. No wonder that the Semai's *becharaa'*—an assembly of the disputants, their relatives, and the rest of the community—is opened by lengthy monologues in which the elders emphasize the mutual dependency within the community and the need to maintain harmony (*76*).

People everywhere seem to follow the relational model by taking overlapping interests into account when facing conflict, even at the international level. The European Community was founded on the premise that the best way to bring the parties together after World War II, and to ensure a peaceful future, was to promote economic ties, hence to raise the cost of damage to these relationships.

The conclusion from this growing area of research is that human aggressive conflict is best understood as an integral part of the social network. It operates within a set of constraints as old as the evolution of cooperation in the animal kingdom. Certain forms of aggression, such as warfare and random shootings, fall outside this framework, but the majority of aggression arises within the face-to-face group or family. It is this context that shaped human social psychology for millions of years, including both discordant and integrative social tendencies. And so, in a time when Lorenz's message about the dark side of human nature still finds an echo in popular writings about nonhuman primates (*77, 78*), other research is increasingly taking a perspective that includes the social impact of conflict, and how that impact is being buffered. Without denying the human heritage of aggression and violence, this research demonstrates an equally old heritage of countermeasures that protect cooperative arrangements against the undermining effects of competition.

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