NOTES

Prologue

1. Huxley, 1989 (1894), p. 83.
2. Williams, 1988, p. 438.
3. Dewey, 1993 (1898), p. 98.

I. Darwinian Dilemmas

1. Dawkins, 1976, p. 3.
2. Gould, 1980, p. 261.
3. Dettwyler, 1991, p. 382.
4. Kurland, 1977, p. 81.
5. Midgley, 1991, p. 8.
6. Wilson, 1975, p. 562.
7. According to Kenneth Lux, opposition to welfare assistance (the so-called Poor Laws) was most evident in the second edition of Malthus' *Essay on the Principle of Population* and was expunged from subsequent editions: "A man who is born into a world . . . if he cannot get subsistence from his parents on whom he has a just demand and if the society does not want his labour, has no claim of right to the smallest portion of food, and, in fact, has no business to be where he is. At nature's mighty feast there is no vacant cover for him. She tells him to be gone,

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and will quickly execute her own orders, if he does not work upon the compassion of some of her guests. If these guests get up and make room for him, other intruders immediately appear demanding the same favour" (quoted in Lux, 1990, pp. 34-35).

8. Rockefeller quoted in Lux, 1990, p. 148.
9. History is not as simple as presented here. Charles Darwin, Alfred Russell Wallace, Thomas Henry Huxley, and Herbert Spencer each took a different position with regard to the (im)possibility of an evolved morality. Well-documented accounts of this early debate may be found in Richards (1987) and Cronin (1991). See also Nitecki and Nitecki (1993).
10. Yerkes and Yerkes, 1935, p. 1024.
11. Gene-centric sociobiologists often speak of "a gene for behavior *x*," regardless of what is known about the heritability of behavior *x* (usually, little or nothing). In reality, each gene acts in conjunction with hundreds of others. So every behavior is likely to depend on a wide range of genetic factors. Even if we grant gene-centric sociobiologists that their one-gene-one-behavior scheme is not to be taken literally—that it is a mere shorthand for discussion—it is advisable to balance it with another generalization, one that is at least as close to the truth: "Every character of an organism is affected by all genes and every gene affects all characters" (Mayr, 1963, p. 164).
12. Apparently Dawkins is not convinced that we are born selfish, in the vernacular sense. In response to Midgley (1979) he admits that selfish-gene rhetoric may well be out of touch with actual human motives: "To the extent that I know about human psychology (a rather small extent), I doubt if our emotional nature is, as a matter of fact, fundamentally selfish" (Dawkins, 1981, p. 558).

    This is a message to bear in mind, for it certainly is not evident in the author's writings. A general problem with pop sociobiology is that complex issues are compressed to such a degree that even if the author is fully aware of what is left out, the reader has no way of knowing. The simplifications are then perpetuated ad nauseam by less-informed writers until they haunt the field in general and must be countered as if they represented serious ideas (Kitcher, 1985).

    In *The Ethical Primate,* Midgley (1994, p. 17) has reiterated her views on the pitfalls and illusions of reductionist science, giving scathing attention to sociobiology's forays into the psychological domain: "Darwinism is often seen—and indeed is often presented—not as a wide-ranging set of useful suggestions about our mysterious history, but as a slick, reductive ideology, requiring us, in fact, to dismiss as illusions matters which our experience shows to be real and serious."
13. Hamilton, 1971, p. 83; Dawkins, 1976, p. 215.
14. Williams, 1989, p. 210.

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15. Williams, 1989, p. 210. One may wonder if Williams really meant to condemn Mother Nature as a wicked old witch. Perhaps, instead of *immoral,* he intended to say that nature is *amoral,* which is of course exactly what Huxley meant by "morally indifferent." However, Williams makes it quite clear that he sees a contrast between the biological and the physical order: "I would concede that moral indifference might aptly characterize the physical universe. For the biological world a stronger term is needed" (p. 180). When he distinguishes being struck by lightning (physical process) from being struck by a rattlesnake (animal action), Williams calls the behavior of the snake and other animals "grossly immoral." In normal usage this judgment would imply disapproval, yet he does not believe that an animal can be held accountable for its actions. But since there can be no morality without individual responsibility, Williams selected the wrong term: he does mean that nature is amoral, and his whole tirade unravels.
16. NSF Task Force, Newsletter of the Animal Behavior Society, vol. 36 (4).
17. Frank, 1988, p. 21.
18. The only similar report that I am aware of concerns captive dolphins. Two females showed interest in the labor of a third, remaining close to her until the fetus was expelled. The older of the two attending females and the mother then swam under the baby dolphin, one on each side. Had the infant not been able to reach the surface by itself, the two females most likely would have lifted it between their dorsal fins (McBride and Hebb, 1948).
19. Gould, 1988, title.
20. Kropotkin, 1972 (1902), pp. 18, 59.
21. To say, as Lorenz (1966) did, that animals rarely kill members of their own species because then the species would die out, assumes that animals care about the well-being of their group or species. Such naive group selectionism was dismissed by Williams (1966), who argued that variants pursuing this goal would rapidly lose out to variants placing private interests first. Natural selection favors individuals who procreate more successfully than others; the interests of groups or species are relevant only insofar as they overlap with those of individuals.

    Extreme sacrifices, however, such as human warriors endangering or giving their lives in combat, pose a serious challenge to this line of thought. Do these warriors not place the good of their group above private interests? To explain their behavior, it has been speculated that status and privilege accrue to surviving heroes, or to the families of those who actually lost their lives. If this is indeed the case, heroic acts on behalf of the community may increase the warrior's reproduction or the survival of his offspring, an argument attributed to R. A. Fisher by Alexander (1987, p. 170). Note, however, how this explanation injects moral mechanisms, such as approbation and gratitude, into a discussion

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about the origin of morality, creating a rather circular argument. Furthermore, it is hard to believe that, in practice, the families of fallen soldiers are better off than the families of soldiers who return alive from battle.

22. Pronouncements of the demise of group selection theory have been premature. Selection at the level of groups probably operates along with selection at the level of individuals and genes. Such "nested" selection models by no means introduce noncompetitive principles; rather, they transpose conflict up one level, from individual against individual to group against group (Wilson, 1983; Wilson and Sober, 1994).
23. Darwin, 1981 (1871), vol. 1, p. 166.
24. De Mandeville, 1966 (1714), pp. 18-24.
25. Smith, 1982 (1776), bk. 3, p. 423.
26. Smith, 1937 (1759), p. 9.
27. Ethologists distinguish sharply between proximate and ultimate causes. *Proximate causes* concern learning, experience, and the direct circumstances and motivations underlying behavior. *Ultimate causes* promoted a behavior in the course of evolution. If a behavior assists survival and reproduction, for example because it repels predators or attracts mates, this is the ultimate reason for its existence. Since evolution takes place on a timescale that escapes perception, only proximate causes exist in the minds of animals and most humans. Students of evolutionary biology are unique in that they care about ultimate causes.

    Unfortunately, proximate and ultimate levels are frequently confused, particularly when the function of a behavior seems so obvious that it is hard to imagine that the actors are oblivious to it. Popular nature documentaries contribute to the mixup by describing animal behavior in ultimate terms. They will explain that two male walruses fight over the right to impregnate a female, whereas these males neither know nor care about what happens in the female's womb after they have mated.
28. De Waal and van Roosmalen, 1979, p. 62.
29. Once, after I had explained these theories to a political scientist with antisociobiological sentiments, he commented with some *Schadenfreude*, "Oh, but then you are getting into exactly the same mess we are in." He meant that instead of having the neat, crisp, reductionist picture of human behavior advertised by the early sociobiologists, we are introducing so many layers and refinements that the complexity may begin to overwhelm us as does the hodgepodge of theories confronting the social sciences. The big difference, of course, is that biologists have a single core theory within which everything must somehow make sense, whereas the social sciences lack such an integrative framework.
30. The first use of the word "ethology" in its current meaning was a reaction against the laboratory-based biological science of the influential Baron Cuvier. Cuvier's most important adversary in the debates at the

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Academie des Sciences was Etienne Geoffroy-Saint-Hillaire, the father of Isidore, who proposed the ethology label. The term referred to the study of animals as living beings in nature, as opposed to the Cuvierian cadavers that smelled of formaldehyde. At approximately the same time, however, the renowned German evolutionist Ernst Haeckel coined *Okologie* (which became the English "ecology") for the relation between the organism and its environment. This term immediately overshadowed "ethology" and generated confusion about the exact meaning of the latter. Jaynes (1988) believes that the closeness in meaning, combined with the association of early French ethology with Lamarckism, prevented ethology from developing into a significant movement in the nineteenth century.

31. Age-specific symbol-learning sensitivity may extend to nonhuman primates. When Sue Savage-Rumbaugh tried to teach symbols to a fully adult bonobo, she met with little success. The ape, despite being cooperative and bright, learned only seven symbols; her two-and-a-half-year-old son, on the other hand, learned from just sitting in on the training sessions. Without instruction or reward, he picked up the use of many symbols and comprehended hundreds of spoken English words (Savage-Rumbaugh et al., 1986).

32. Special learning abilities or sensitivities involved in the acquisition of moral consciousness have also been discussed by Lewin (1977), Simon (1990), and Wilson (1993, pp. 148-152).

33. Well-known ethologists, such as Wolfgang Wickler, Irenaus Eibl-Eibesfeldt, and Konrad Lorenz, have extensively speculated in popular books about the biological roots of human ethics. It must have been increased awareness of the naturalistic fallacy that compelled Wickler (1981) to add a subtitle to the second edition of his best-seller, *Die Biologie der Zebn Gebote* (The biology of the Ten Commandments), which literally reads *Warum die Natur fiir uns kein Vorbild ist* (Why nature does not serve us as example). This literature was critically reviewed by the late German anthropologist and primatologist Christian Vogel (1985, 1988).

34. The fatal incident in the Arnhem colony was interpreted as political murder. It resulted from a collapse of the ruling coalition because of the leader's failure to grant sexual privileges to his ally. In the resulting power vacuum, another male suddenly rose to the top. He paid for this ten weeks later when the two frustrated former allies banded together at night to injure him so badly that his life could not be saved (de Waal, 1986a; 1989a, pp. 59-69).

    Since this was the very first report of such severe fighting within an established group, it may be tempting to dismiss it as a product of captivity. Recently, however, a similar event was described by Goodall (1992) for wild chimpanzees. The reigning alpha male fell from power after a gang attack that resulted in serious damage to his scrotum (the

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ensuing infection might have killed him had it not been for veterinary intervention). This intracommunity aggression was by far the most savage observed during thirty years at Gombe; such belligerence is more typical between communities (Goodall, 1986).

35. Lorenz, 1966 (1963), p. 167.
36. Hume, 1978 (1739), p. 469.
37. A wide range of views exists on biological constraints on morality. My personal opinion is that the evolutionary process provided us with the ability and the prerequisites for morality, as well as with a set of basic needs and desires that morality needs to take into account. The moral decisions themselves, however, are left to be negotiated among the members of society, hence are by no means specified by nature. Ruse (1986), in contrast, believes that "ought" feelings, such as a felt duty to assist others, have been put in place directly by natural selection: "We are talking of more than a mere feeling that we want to help others. It will be an *innately based sense of obligation* towards others" (p. 222; italics added). These differences of opinion need to be worked out within the framework of evolutionary ethics, the basic tenet of which is that the moral sense is not antithetical to but an integrated part of human nature (Ruse, 1988; Wilson, 1993).

2. Sympathy

1. Darwin,, 1981 (1871), vol. 1, pp. 71-72.
2. Wispe, 1991, p. 80.
3. On the basis of this incident, Porter (1977, p. 10) comments that he would not automatically discount the numerous reports of people who claim to have been saved by porpoises or some of the smaller whales. Accounts of Cetacea helping humans generally describe one of the following: (a) a drowning person is lifted to the surface; (b) a boat or ship is guided to safety (around submerged rocks, out of a storm); or (c) a swimmer is protected against sharks by a dolphin cordon. Reviews of both interspecific and intraspecific succorant behavior of Cetacea may be found in Caldwell and Caldwell (1966), Connor and Norris (1982), and Pilleri (1984).
4. Porter, 1977, pp. 10, 13.
5. Eibl-Eibesfeldt, 1990, p. 156.
6. Did Yeroen intentionally manipulate the other male's perception, or had he simply learned that limping reduces the risk of attack? The first possibility would have required him to imagine how he himself looked from the other's perspective; the second would have required little else than a rewarding experience during a period when he had been limping of necessity.

   Even if it is increasingly believed that great apes possess a capacity for

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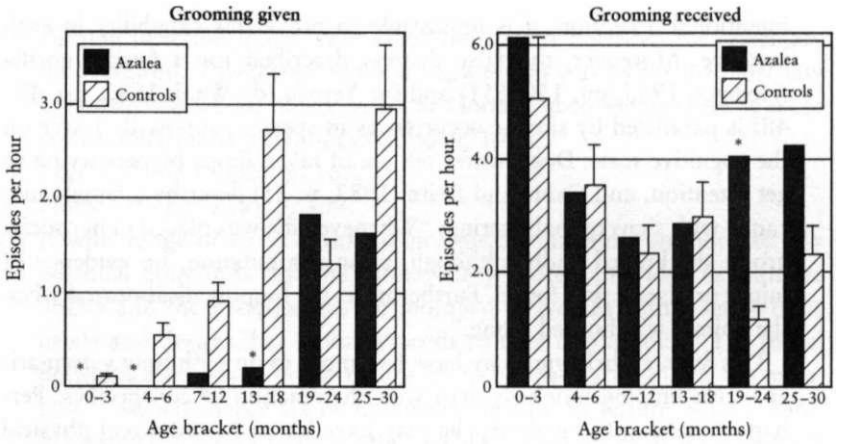
intentional deception, it is impossible to prove this capability in each instance. Moreover, the false distress described for a female gorilla (Hediger, 1955, pp. 150-151) and for Yeroen (de Waal, 1982, pp. 47-48) is paralleled by similar occurrences in species supposedly lower on the cognitive scale. Dog owners tell me of faked limps by pets trying to get attention, and Caine and Reite (1983, p. 25) describe a female macaque with signs of malingering: "Whenever she was placed in her social group she limped badly, although, upon examination, no evidence of injury or disease was found. Furthermore, the limping disappeared when the animal was housed alone."

This female's behavior may have had more to do with how veterinarians treat limping monkeys than with the reaction of conspecifics. Perhaps preferring to be alone, she may have learned from a real physical trauma in the past how to get people to remove her from the group. If so, Yeroen's deception differed from this monkey's, as well as from that of the gorilla and the dogs mentioned previously, in at least one aspect: it was intended to appeal to members of his own species.

7. Lieberman, 1991, p. 169.
8. Play inhibitions obviously are not limited to primates. As the owner of any large dog can testify, they are even more dramatic in animals such as carnivores that are equipped to do horrible damage in a fraction of a second. The acquisition of such inhibitions was observed in two female black bear cubs, Kit and Kate, raised by Ellis Bacon for a wildlife project in the Smoky Mountains. Bear cubs, although very appealing, can be quite aggressive in play and enter wrestling matches with an energy and force that totally overwhelm a human partner. Human skin being paper-thin compared to that of a bear, the legs and arms of the cubs' caretakers were covered with scratches, bites, and bruises. A dramatic, welcome change in play style occurred, however, when the cubs were approximately eight months old: "They acted as if they discovered he [Bacon] was different from a bear: there was a rapid decline of inadvertent scratching and biting, and they distinguished clothing (which was still fair game) from flesh. From then on, with the exception of occasional dominance testing, Ellis considered himself physically safe in their presence. In contrast, the cubs were still very rough with each other in play or fights" (Burghardt, 1992, p. 375).

   Moss (1988, p. 163) describes how the world's most formidable play partner, a bull elephant, learned to downsize in order to have fun: "Earlier in the year I had seen a large adult bull, Mark, lie down in an upright position in order to spar with another bull who was considerably smaller than he was. They had sparred playfully and briefly with both standing, but the young bull, MHO, turned away, and although Mark followed, M140 would not spar with him again. Then Mark sank down on his knees with his rear legs out behind him, and as soon as M140

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Total hourly grooming rates per age group for Azalea, a trisomic rhesus monkey, and the mean (plus standard error of mean, SEM) for twenty-three normal female peers of the same age (controls). Asterisks denote periods in which Azalea ranked at the extreme top or bottom of the distribution.

saw him he came straight over and started sparring. M140 was now the taller of the two."

9. After having devised this example, I heard from Sue Savage-Rumbaugh a striking story about an orangutan named Marie who had lost both arms early in life. Marie made precisely the kind of connection between her own body and that of another individual required for cognitive empathy. Savage-Rumbaugh, one of whose fingers is missing its tip, was grooming and talking to Marie, when the latter suddenly noticed the stumpy finger. She inspected it closely, holding Savage-Rumbaugh's hand with one of her feet. Marie then brought Sue's finger into contact with the stump of one of her own arms. She looked questioningly into her companion's eyes as if wondering if she saw the same connection.
10. As can be seen from the accompanying figure, Azalea's grooming activity was far below that of her peers until the age of 18 months. She received an average amount of grooming until this age, after which she began to receive substantially more than her peers. It is not clear whether these two developments were related. Data from de Waal et al. (1995).
11. Fedigan and Fedigan, 1977, p. 215.
12. In the sort of experiment that, in the words of Silk (1992a), makes one wonder about taxonomic bounds for compassion, Berkson experimentally blinded a number of young rhesus monkeys in a free-ranging population. These young monkeys, groping for roots as they went, had great difficulty in finding their way through the mangrove. Their mothers stopped often and waited for them, and the group as a whole was extra vigilant and alarmed if the blind infants were approached by human

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observers. "The blind babies were never left completely alone. . . . It is remarkable that there was always another animal in the group near them. In addition, two individuals who were unrelated to the mothers often stayed with the blind infants during this time" (Berkson, 1973, p. 585).

13. Scanlon, 1986, p. 107.
14. It is surprising how little we know about precisely which situations trigger succorance and which generate intolerance. Pavelka (1993, p. 92) describing free-ranging Japanese macaques, comments that incapacitated group members may meet with hostility. This was the reaction to staggering and stumbling individuals who were recovering from anesthesia after routine veterinary checkups. Even though the mothers would protect their drowsy infants, they sometimes bit and shook their offspring as if punishing them for inappropriate behavior. Over the years the monkeys became used to the sight of half-sedated group mates, and aggressivity toward them diminished.
15. Moss, 1988, p. 73.
16. Goodall, 1990, p. 196.
17. Flint was perhaps too old to be adopted by others. Younger orphans are frequently taken care of by female relatives, sometimes by unrelated females, and enjoy remarkable tolerance from adult males (Goodall, 1986, pp. 102-103; Nishida, 1979, p. 106). For a review of adoption in nonhuman primates see Thierry and Anderson (1986).

    In the Arnhem chimpanzee colony, Fons lost his mother when he was four. Soon afterward he was seen associating with adult males, particularly his presumed father, Luit, who became his mighty protector. Fons resembled Luit even at an early age (de Waal, 1982, p. 75), but he looks, acts, and sounds uncannily like the older male now that he is fully grown. Unfortunately, Luit died before the colony could be subjected to a paternity analysis.
18. Smuts, 1985, p. 23.
19. No agreed-upon explanation for human weeping exists. Outside the primate order, copious tear production is associated with marine habitats (probably because of the increased need for salt excretion). Thus, fresh-water crocodiles do not shed tears, whereas sea crocodiles do. Tears can also be observed in sea otters and seals. Because of this link with marine ecology, proponents of the "aquatic ape" theory view human tears as evidence that there must have been an aquatic phase during human evolution (Morgan, 1982).

    Accounts of tears in primates other than humans are extremely rare, and need to be considered with reservation. Most likely, people *expect* tears, hence project or imagine them. The only report by an experienced primatologist is in Fossey (1983). Despite my profound skepticism—could the "tears" have been due to excessive perspiration?—I present it

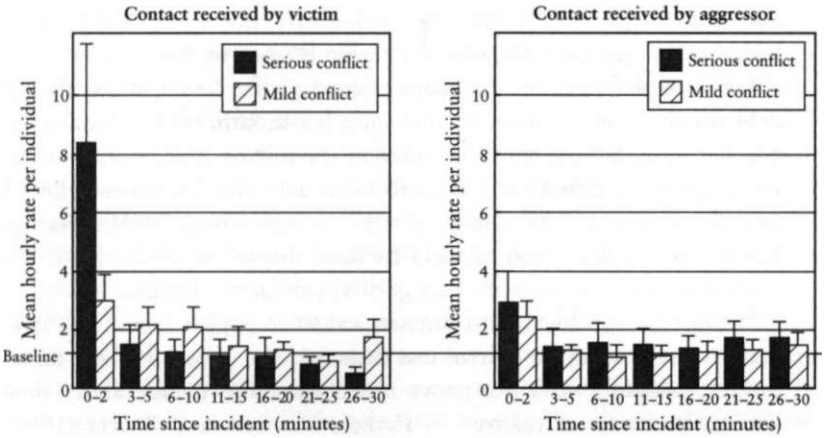
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here because Fossey was certainly aware of the extraordinary nature of her observation.

The account concerns Coco, a young mountain gorilla whose entire family had been wiped out by poachers. Following weeks of mistreatment and life in a tiny box, the young gorilla was claimed by Fossey and brought to her camp. There Coco for the first time saw her natural environment again. "Coco sat on my lap calmly for a few minutes before walking to a long bench below the window that overlooked nearby slopes of Visoke. With great difficulty she climbed onto the bench and gazed out at the mountain. Suddenly she began to sob and shed actual tears, something I have never seen a gorilla do before or since. When it finally grew dark she curled up in a nest of vegetation I had made for her and softly whimpered herself to sleep" (p. 110).

20. Yerkes and Yerkes, 1929, p. 297.
21. Temerlin, 1975, p. 165.
22. Boesch, 1992, p. 149.
23. The German naturalist Bernhard Grzimek was once attacked by an adult male chimpanzee, an event he was lucky to survive. When his rage had died down, the ape seemed very concerned about the outcome. He approached the professor and tried, with his fingers, to close and press together the edges of the worst wounds. Lorenz (1967, p. 215), who described this incident, adds that "it is highly characteristic of that dauntless scientist that he permitted the ape to do so."
24. The accompanying figure shows data from de Waal and Aureli (forthcoming) concerning 1,321 spontaneous aggressive incidents in an outdoor colony of twenty chimpanzees at the Yerkes Field Station. The graph demonstrates that immediately after fights (in the first two minutes) bystanders often make contact with participants in the conflict, particularly with the recipients of serious aggression.
25. Skinner (1990) saw both cognitive psychology and creationism as heavily influenced by religion. This element is obvious enough with regard to creationism, sometimes mislabeled creation science ("mislabeled" because creationists work with a single hypothesis, determined a priori to be true, whereas science tries to choose among alternative hypotheses). The effect of religion on cognitive psychology may be less evident—hidden as it is by centuries of sophisticated philosophizing, it is revealed in the persistent mind/body and human/animal dualisms. These dualisms lack a factual basis, and psychology would be much better off without them (Gibson, 1994).
26. Most readers would long ago have laid aside this book if I had limited myself to purely descriptive, technical language. There is a fine but important line between the use of anthropomorphism for communicatory purposes or as a heuristic device, and gratuitous anthropomorphism that projects human emotions and intentions onto animals without

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Mean (plus standard error of mean, SEM) hourly rates of affiliative contact (kissing, hugging, grooming, gentle touching) received from bystanders by individuals recently involved in fights. Contacts between former opponents (reconciliations) are excluded from the analysis. The thirty-minute window following each incident has been divided into blocks of two, three, and five minutes. Data are presented separately for incidents involving vocalizations and/or physical contact (serious conflicts) and mere silent threats and lunges (mild conflicts). The baseline shows the mean hourly contact rate received per individual.

justification, explication, or critical investigation. Strong opinions about the use and abuse of anthropomorphism can be found in Kennedy (1992), Marshall Thomas (1993), Masson and McCarthy (1995), and in Mitchell, Thompson, and Miles (forthcoming).

27. Burghardt, 1985, p. 917.
28. Diogenes Laertius, quoted in Menzel, 1986, p. 167.
29. Promises and problems of the cognitive approach to animal behavior have been extensively debated among ethologists. See Griffin (1976, 1984), Kummer (1982), Kummer, Dasser, and Hoyningen-Huene (1990), de Waal (1982, 1991a), and Cheney and Seyfarth (1990).
30. Carpenter, 1975, pp. 452-153.
31. This passage was translated from the Dutch by Kortlandt (1991, p. 11). Anton Portielje was a remarkable observer: he was also the first to notice enough difference between a chimpanzee and a bonobo to suggest, in 1916, that they might be different species. The distinction became official only in 1929 (de Waal, 1989, pp. 177-178).
32. Oddly enough, gorillas were long assumed incapable of passing Gallup's mirror-recognition test (reviewed by Povinelli, 1987). Since Westergaard, Hyatt, and Hopkins (1994) found that bonobos recognize themselves, the gorilla would have been the only anthropoid ape without self-recognition. Apart from not making much evolutionary sense (if the common

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ancestor of apes and humans had self-awareness, why should it have been lost in one species?), this conclusion is open to doubt.

A videotape featuring a language-trained gorilla, Koko, shows the ape deliberately using a mirror to stare into her mouth, tilt her head to get a better look, pick at her teeth aided by the mirror, and so on. A recent report confirms that Koko is able to make a connection between herself and the gorilla in the mirror (Patterson and Cohn, 1994). Perhaps Koko's special education brought forward this talent (Povinelli, 1994), yet it makes one wonder if other gorillas can lag far behind.

The familiar problem with negative evidence applies here. Even if we accept that passing the mirror-test demonstrates self-awareness, failing the test certainly does not prove its absence. For debate about these issues, the reader is referred to Parker, Mitchell, and Boccia (1994), volume 11(3) of *New Ideas in Psychology,* pp. 295-377 (1993), Heyes (1993), and Cenami Spada et al. (forthcoming). An experiment promising to turn the presumed gap between monkeys and apes into a gray zone was presented recently by Howell, Kinsey, and Novak (1994).

33. Hatfield, Cacioppo, and Rapson (1993, p. 96) define emotional contagion as "the tendency to automatically mimic and synchronize expressions, vocalizations, postures, and movements with those of another person and, consequently, to converge emotionally."

34. This correlation was reported by Johnson (1982) and Bischof-Kohler (1988). According to the latter study, the link between mirror self-recognition and the emergence of cognitive empathy holds up even after correction for age.

35. The main alternative to a cognitive explanation of the absence of consolation in macaques is the so-called social constraints hypothesis. It posits that macaques run serious risks in associating with an individual who has just been attacked. With their more tolerant and flexible relationships, chimpanzees may not be operating under the same constraints. We plan to conduct experiments to eliminate the risk of approaching a victim of aggression. If macaques still fail to contact distressed group members under these circumstances, the social constraints hypothesis would be weakened (de Waal and Aureli, forthcoming).

36. Certain birds weave leaves into their feathers, and hermit crabs tote around entire houses, replacing them as they grow with larger residences. These self-enhancements are identical in all members of the species and probably have nothing to do with self-awareness. The only nonprimates in which self-decoration might accompany awareness of its effect on others are dolphins and killer whales. Marine mammal trainers speak of their subjects' *jewelry,* meaning the bits of seaweed they string around their pectoral fins or flukes, or the dead fish they carry on their

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snouts (Pryor, 1975). Wild dolphins, too, tend to drag "stuff" around (Christine Johnson, personal communication).

If this is indeed self-decoration and not mere object play, it is intriguing in view of the highly developed succorant tendencies in the same mammals. Could the Cetacea, which after all have unusually large brains, be another group with increased awareness of the self? See some fascinating speculations by the neuroanatomist Harry Jerison (1986), and the first studies of dolphin self-recognition by Marten and Psarakos (1994) and Marino, Reiss, and Gallup (1994).

37. Even if apes are the most conspicuous behavioral copiers, they may not be the only ones. An intriguing monkey example comes from Breuggeman (1973, p. 196), who saw a juvenile rhesus monkey follow her mother while the mother carried a newborn. The daughter picked up a piece of coconut shell, carrying it ventrally in the same way that her mother held her new brother. When the mother lay down on her side, with one hand resting on the infant's back, the daugher did the same a few feet away, adopting the exact same posture while holding the shell.
38. Garner, 1896, p. 91.
39. Renewed experimentation on observational learning in monkeys and apes was pioneered by an Italian ethologist, Elisabetta Visalberghi, and an American developmental psychologist, Michael Tomasello. Thus far their findings have failed to support claims of full-blown imitation in nonhuman primates.

    Field-workers, such as Boesch (1991a, 1993) and McGrew (1992, pp. 82-87), are not convinced that absence of imitation in the laboratory implies absence in the natural habitat. Although not saying in so many words that captive chimpanzees are backward, they imply it when pointing out that one cannot expect individuals under impoverished conditions to be competent to perform complex tasks. This hypothesis is contradicted by the masterly tool use for which captive orangutans are known, whereas their wild counterparts rarely demonstrate anything close to this ability (Lethmate, 1977; McGrew, 1992). Furthermore, it has been argued that free time under captive conditions actually *promotes* innovation and social sophistication (Kummer and Goodall, 1985).

    Clearly, the real issue is not whether captive or wild primates are smarter, but whether the relevant variables have been controlled. The laboratory wins hands down on this count: observational learning covers a wide range of processes that cannot easily be disentangled in the field. For further discussion see Galef (1988), Visalberghi and Fragaszy (1990), Whiten and Ham (1992), Tomasello, Kruger, and Ratner (1993), and Byrne (1995).
40. Menzel, 1974, pp. 134-135.

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41. The ability to attribute knowledge, feelings, and intentions to others is now often phrased as the possession of a "theory of mind" about others. This expression derives from an experiment by Premack and Woodruff (1978) in which apes were challenged to infer the intentions of other individuals by watching their efforts on video. The apes seemed to have an idea of the mental states of others. Theory-of-mind research covers both child and nonhuman primate behavior (reviewed in Buttersworth et al., 1991; Whiten, 1991; Byrne, 1995).

    According to Cheney and Seyfarth (1991, p. 253), even the most compelling examples of attribution in monkeys and apes "can usually be explained in terms of learned behavioral contingencies, without recourse to higher-order intentionality. What little evidence there is suggests that apes, in particular, may have a theory of mind, but not one that allows them to differentiate clearly or easily among different theories or different minds." This passage was written, however, before Povinelli's experiments strengthened the case for attribution and perspective-taking in the chimpanzee (Povinelli et al., 1990, 1992).

    A serious problem with studies of the ape's theory of mind is the interpretation of negative results. The experimental subjects are sometimes presented with rather unusual situations, such as blindfolded persons or persons instructed to stare into the distance. Like us, apes are very sensitive to body language: an unresponsive human experimenter is likely to confuse and disturb them. In addition, the rules of eye contact are different in apes than in humans: rather than gazing directly at others—which they do under exceptional circumstances only, such as during a reconciliation—apes are masters at monitoring companions by means of peripheral vision and quick glances that are barely noticeable. Negative test results may therefore say more about the apes' expectations about normal social interaction and the species barrier in this regard than about their grasp of the connection between looking and seeing.

    The fairest comparison of apes tested by humans would be human children tested by apes; who knows how poorly children would do under such circumstances.

42. Example 1: de Waal, 1986b, p. 233; Example 2: de Waal, 1992d, p. 86; Example 3: de Waal, 1986b, p. 238; Example 4: de Waal, 1982, p. 49.
43. Menzel, 1988, p. 258.
44. Salk (1973) discovered the left-side cradling preference of human mothers, and Manning, Heaton, and Chamberlain (1994) report the same bias in gorillas and chimpanzees but not orangutans. See Hopkins and Morris (1993) for a review.
45. Mercer, 1972, p. 123.
46. Goodall, 1971, p. 221.
47. One notably different reaction to polio victims involved two adult males

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suspected to be siblings or nephews: Mr. McGregor (with paralyzed legs) and Humphrey (unafflicted). Humphrey stood by McGregor until the end, defending him against even the most dominant aggressors. After McGregor's death, Humphrey kept returning for nearly six months to the place where his possible relative had spent the last days of his life in great pain and misery (Goodall, 1971, pp. 222-224).

48. Nevertheless, members of one species are sometimes vicariously aroused by those of another species. Recently the entire chimpanzee colony at the Yerkes field station was intently following how animal care staff caught an escaped rhesus monkey in the forest around their enclosure. Attempts to lure the monkey back into his cage had failed. The situation became hairy when he climbed a tree. I heard one of the watching chimpanzees, a juvenile named Bjorn, suddenly utter whimpers while seeking reassurance from an ape next to him, reaching out to her. When I looked up, I saw that Bjorn's distressed reaction coincided with the monkey's clinging desperately to a lower branch of the tree; he had just been shot with a tranquilizer dart. People were waiting beneath the tree with a net. Although it was not a situation Bjorn himself had ever been in, he appeared to empathize with the monkey: he uttered another whimper when the escapee dropped into the net.
49. Turnbull, 1972, pp. 112, 230.
50. It is hard to imagine being delighted by the misery of others unless one has a bone to pick with them. Turnbull's (1972) observations have not gone unchallenged; one fascinating speculation has been that the anthropologist felt so isolated and frustrated living with the Ik that *he himself* began to derive joy from their misfortune (Heine, 1985).
51. Weiss et al., 1971, p. 1263.
52. In a careful review of the psychological literature, Batson (1990) compares the attitude of science toward human altruism to that of the Victorians toward sex: it is denied and explained away. All too often, caring for others is interpreted as caring about oneself.

    Experiments have failed to confirm this interpretation. Because there is no evidence for selfish motives behind *all* helping behavior, Batson concludes that people do possess a genuine caring capacity. Wispe (1991) supports this view, arguing that feelings of sympathy evaporate the moment self-interest enters as a conscious motive. This is not to deny an internal reward, but the reward seems specifically tied to the other's well-being. Alleviating another person's pain or burden gives a special satisfaction that is simply unavailable to those who base their help on hope for return favors, a desire for praise, or a wish to go to heaven. Such calculations may *mix* with sympathy, but they cannot replace it because "rewards are what sympathy is «or about.. . Even if one always derived pleasure from helping others, it would not follow that one helps others in order to feel pleasure" (Wispe, 1991, p. 81).

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Note that the issue of unselfishness is treated here from the perspective of motivation and conscious intent. Nothing is said about the possibility that acts of sympathy and cognitive altruism may, in the long run and perhaps quite circuitously, serve the actor's self-interest. Indeed, without such benefits the entire complex of empathy and helping behavior could never have evolved. The main point is that these benefits need not factor into the actor's conscious decision-making.

53. Wilson, 1993, p. 50.

3. Rank and Order

1. Hall, 1964, p. 56.
2. Example 1: author's translation of Trumler, 1974, pp. 52-53; Example 2: Lopez, 1978, p. 33; Example 3: Barbara Smuts, personal communication; Example 4: von Stephanitz, 1950, p. 814.
3. Modified from de Waal, 1991b, p. 336.
4. See de Waal (1982, p. 207). Nishida (1994, pp. 390-391) reports similar outraged reactions to violations of the social code. For example, he once saw a wild chimpanzee attack another from behind after a stealthy approach. This tactic is highly unusual: chimpanzees normally signal aggressive intentions in advance. Loudly screaming, the victim chased the attacker, who, although dominant, kept his distance. Speculating that the dominant did not fight back because he felt guilty about the sneak attack, Nishida concludes that "unusually fierce, prolonged retaliation on the part of a subordinate party and the corresponding reluctance to escalate the fight on the part of the dominant party may be one of the factors discriminating moralistic aggression from a conventional counterattack by a subdominant." This characterization of moralistic aggression may also apply to the extraordinary retaliation by Shade, a Japanese macaque, recounted in Chapter 4.
5. Hobbes, 1991 (1651), p. 70.
6. For decades the received view has been that animals engage in approach-retreat encounters, fights, and competitions that may *reveal* who dominates whom, but that the rank order itself is a mere construct of the human observer: animals neither classify themselves in terms of who dominates whom nor do they deliberately strive for better positions (Bernstein, 1981; Altmann, 1981; Mason, 1993).

   Less prominent in the textbooks, yet present at least since Maslow (1936), is the alternative that social dominance does exist in the minds of animals. For example, research on chimpanzees has produced evidence supporting what appear to be calculated, Machiavellian strategies to attain high status (de Waal, 1982). Theory formation tends to follow a pendulum pattern, and future students of animal behavior will no doubt revisit the issue of status striving. It is unclear at this point, for

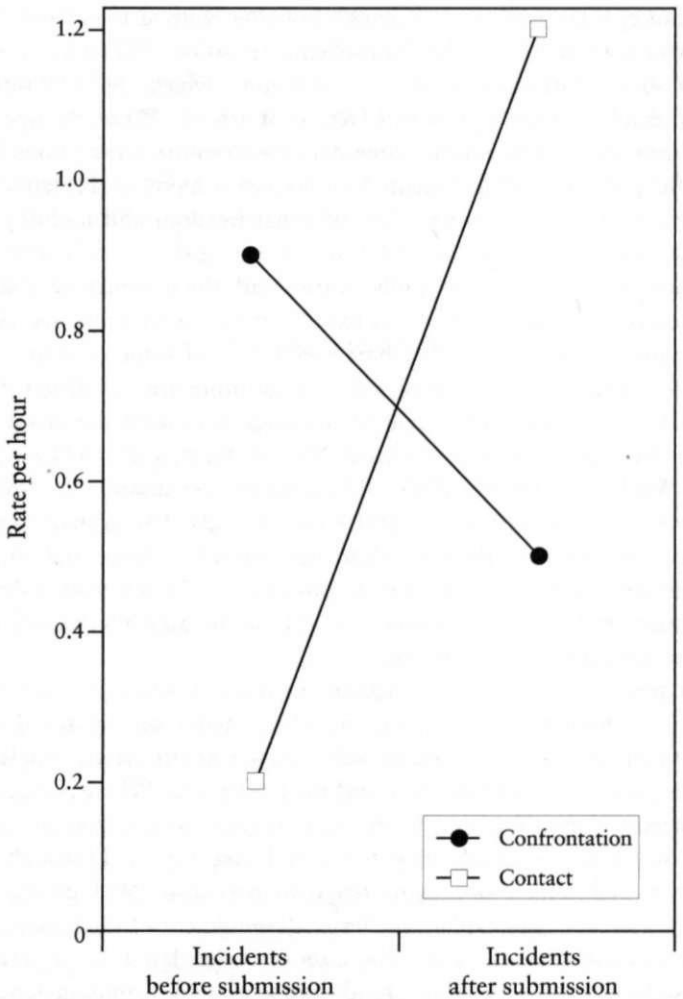
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instance, how much the "striving" position really differs from the following formulation of the "nonstriving" position: "The critical issue is not social status per se, but the extent to which the relationship is oppressive and the type of satisfactions it affords. When the oppressive constraints in a relationship consistently exceed the satisfactions for one of the participants, the potential for conflict is high. . . . Primates generally act so as to maximize their personal freedom and mobility under demanding circumstances" (Mason, 1993, p. 25).

7. Whereas the outcome of conflict varies with the presence or absence of allies, or the resource at stake, expressions of submission are virtually immune to such effects. The bared-teeth face of some macaque species or the chimpanzee's bobbing and pant-grunting are completely predictable: it is hard even to imagine a situation in which a dominant would give these signals to a subordinate (Noe, de Waal, and van Hooff, 1980; de Waal and Luttrell, 1985). The simplest explanation for the independence of context is a cognitive one, namely that primates know in which relationship they are dominant or subordinate and that they communicate these evaluations to one another. In this view, submissive gestures and facial expressions reveal how the animals *themselves* perceive dominance relationships.
8. My text speaks of male, not female, rivals because it is written with an eye on chimpanzees, a species in which males are by far the more hierarchical sex. Most male animals compete about mates; females compete over food for themselves and their offspring. Whereas male chimpanzees are no exception to this rule, female chimpanzees at the best-known field sites avoid competition by living dispersed throughout the forest, each female occupying her own core area (Wrangham, 1979). This tendency may explain the lesser development of the female hierarchy in these apes. Most monkeys, on the other hand, form permanent mixed-sex groups in which food competition is common: females of these species are as dominance oriented as males.

   Accounts of status competition in both male and female monkeys may be found in Bernstein (1969), Chance, Emory, and Payne (1977), de Waal (1977; 1989a, pp. 133-140), Leonard (1979), Walters (1980), and Small (1990).
9. Koestler, quoted in Barlow, 1991, p. 91.
10. The effect of submission on social relationships was investigated during three months of instability between two male chimpanzees, Yeroen and Luit, at the Arnhem Zoo (de Waal, 1986c). Over two hundred hours of observations were collected in order to document changes around the time of first submission. During the weeks prior to this moment, friendly contacts became increasingly rare, whereas aggressive confrontations and intimidation displays between the two males reached their peak. As usual during power struggles, the exchange of status signals ceased

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On March 16, 1978, Yeroen bowed and pant-grunted to Luit for the first time after three months of intense rivalry. Shown are mean hourly rates of aggressive confrontations and friendly contacts between the two males during seven observation days prior to and following Yeroen's first submission.

completely. The low level of contact occurred because the future dominant, Luit, walked away each time Yeroen approached.

Luit's attitude changed dramatically the day Yeroen uttered his first submissive pant-grunts: Luit suddenly became receptive to Yeroen's overtures. Aggression diminished and contact between the rivals increased over the next few days. Significantly, the longest grooming session of the entire period took place only a few hours after Yeroen's acknowledgment of Luit's status. This case study confirmed that peace-

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ful coexistence among male chimpanzees depends on a formal clarification of their dominance relationship.

11. Dog owners who believe in the efficacy of punishment after the fact may be right for the wrong reasons. Instead of having taught their pet to associate a bad habit with punishment, they may have taught them merely to avoid certain sights, smells, or locations associated with the transgression. For example, a dog learns to avoid a bedroom in which he was admonished for chewing a pair of shoes, hence stops the chewing inasmuch as he does not encounter the same shoes again (Vollmer, 1977).
12. The overly submissive macaques illustrate the advantage of attributional capacities found in humans, and perhaps in apes (Chapter 2). A chimpanzee confronted with similar behavior in a subordinate would probably suspect that something had been going on, in the same way that we guess from the absence of a happy greeting by a dog that a rule must have been broken. Because of this more complete understanding of what may lie behind an expression of emotion, chimpanzees and people need to be more careful: better lie-detecting abilities require more sophisticated lies. I have never seen subordinate male chimpanzees react in the same way as these macaques. Even when caught in the middle of a prohibited act, they tend first to try concealment of the evidence (such as dropping their hands over their penis) before responding with fear and submission.
13. Coe and Rosenblum, 1984, p. 51.
14. Davis, 1989, p. 88.
15. Scott, 1971, p. 81.
16. Darwin, 1965 (1872), p. 309.
17. Starting with Trivers' (1971) theory of reciprocal altruism, we now seem to have the first elements of a plausible scenario for the evolution of conscience. My discussion closely follows recent theorizing by Alexander (1987), Frank (1988), and Simon (1990) about susceptibility to social influence (Simon's *docility)* and emotional commitment (Frank). A central concept is reputation, or status, as defined by Alexander (1987, p. 95): "Systems of indirect reciprocity, and therefore moral systems, are social systems structured around the importance of status. The concept of status simply implies that an individual's privileges, or its access to resources, are controlled in part by how others collectively think of him as a result of past interactions."
18. A sharp distinction between the reason for the evolution of a behavior and its underlying motivation is assumed in discussions of evolutionary ethics by Frank (1988), Simon (1990), and myself (Chapter 1).

    Alexander (1987, 1993), in contrast, defends the position that, consciously or not, selfish motives guide all human behavior, including behavior that the actors themselves believe to be unselfish. Similarly,

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Badcock (1986) tries to reconcile our species' true nature—which he sees as literally selfish—with altruistic motives. To the rescue comes Freudian repression theory: the ego defends itself by presenting a distorted picture of internal processes. It hides selfish motives from our conscious self, presenting them in the most favorable light. In the view of Alexander and Badcock, then, the human mind expends a good deal of energy in concealing selfish agendas: we are sophisticated hypocrites.

In a review of Wright (1994), who adopts the same position, Steven Pinker (1994, p. 35), a cognitive neuroscientist, makes the by-now-familiar point (Chapter 1 notes 12 and 27) that this view confuses proximate and ultimate causation: "When a person's public stance is selfless but his private motives serve his interests, we can call it hypocrisy. However, when a person's public stance and private motives are both selfless but those motives came about because they once served the interests of his ancestors' genes, we have not uncovered hypocrisy; we have invoked a scientific explanation couched at a different level of analysis. . . . The evolutionary *causes* of our motives can't be judged as if they *are* our motives."

19. Lever, 1976, pp. 482, 483.
20. Gilligan, 1982, p. 104.
21. Gilligan has been accused of giving in to popular expectations about gender roles without careful research to back her position (Colby and Damon, 1983; Walker, 1984; Mednick, 1989; Smetana, Killen, and Turiel, 1991). Some believe that her ideas stand in the way of progress, a criticism leveled most harshly by Broughton (1983, p. 614): "Gilligan does not seem very concerned with societal transformation given her desire to imbed women even more deeply in the domestic and personal aspects of welfare in civil society."
22. Walker, 1984, p. 687.
23. Hoffman, 1978, p. 718.
24. Applying ethological methods of data collection in the field, Edwards (1993) found consistent sex differences across a dozen cultures in countries from Kenya to India, and from the Philippines to the United States. During middle childhood, boys spend more time away from the home than girls, and girls have more contact with and responsibility for infants. The latter difference probably reflects both girls' greater attraction to infants and socialization practices (mothers preferentially assigning child care to daughters).
25. Strier, 1992, p. 85.
26. The Finnish study is special in that it did not focus on open conflict only—which universally is most common in boys (Maccoby and Jacklin, 1974)—but included *indirect* conflict by asking children what they do when angry. A rather cruel picture of girls emerged: they said they could

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stay mad forever, whereas boys measured their anger in minutes (Lagerspetz, Bjorkqvist, and Peltonen, 1988).

A work of fiction detailing female-style conflict is Margaret Atwood's *Cat's Eye*. The author contrasts the torments to which girls subject one another with the more straightforward competition among boys. At one point, the principal female character complains: "I considered telling my [elder] brother, asking him for help. But tell what exactly? I have no black eyes, no bloody noses to report: Cordelia does nothing physical. If it was boys, chasing or teasing, he would know what to do, but I don't suffer from boys in this way. Against girls and their indirectness, their whisperings, he would be helpless" (Atwood, 1989, p. 166).

Unfortunately, sex differences in the domain of interpersonal conflict have been only poorly investigated. We are in the curious situation of knowing more about spontaneous aggression and reconciliation in nonhuman primates than in our own species (de Waal, 1989a).

27. Tannen, 1990, p. 150.

28. In well-established chimpanzee societies, males reconcile more readily after fights than females, and the male power structure is well defined and fiercely contested compared to the rather informal female hierarchy (Goodall, 1971, 1986; Bygott, 1979; de Waal, 1982, 1986c). As explained by Nishida (1989, p. 86), females decide dominance issues on the basis of seniority: "Unlike males, whose reproductive success depends on social status, female reproductive success may depend primarily upon acquiring a core area near the center of the unit-group's territory. Therefore, females who have acquired their own core areas have no pressing reason to strive for higher rank. Thus, a female's rank will be more or less fixed sometime after her immigration. Thereafter, her promotion in rank will be caused mainly by the death of senior high-ranking females and by the addition of younger low-ranking females to the hierarchy."

The rarity of overt conflict between female chimpanzees, and their relatively vague hierarchy, should not be interpreted as a lack of interest in competitive goals. Under particular circumstances, such as when wild females migrate into another community or when captive females are introduced to strangers, females do compete fiercely. In Arnhem, females did not give up their top positions willingly when adult males were introduced into the colony (de Waal, 1982); and when a new colony was established at the Detroit Zoo, females engaged in dominance strategies remarkably similar to those of males (Baker and Smuts, 1994).

Given the plasticity of the behavior of chimpanzees and other primates, researchers have moved away from deterministic explanations of sex differences. Discussions of these differences increasingly pay attention to potential, context dependency, social values, and payoff curves

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(Goldfoot and Neff, 1985; Smuts, 1987; de Waal, 1993b; Baker and Smuts, 1994).

29. The effect of social context on the nurturing abilities of rhesus monkeys was investigated by Judith Gibber and Robert Goy (Gibber, 1981, pp. 63-66). In one series of tests, individually-caged monkeys received an unfamiliar infant. Rhesus males normally pay little attention to young infants, but under these conditions they proved remarkably friendly. This response was not seen in the second test series, however, which involved pair-housed subjects. Males who individually had picked up and held infants failed to do so in the presence of a female companion: the female did most of the infant handling. Males apparently defer to the other sex when it comes to infant care.

30. Andries Vierlingh, translated by Schama, 1987, p. 43.

31. See Schama (1987, pp. 25-50) for a remarkable outsider account of Dutch history. That the tendencies noted are still part of the culture was demonstrated in 1995, when river levels in the Netherlands rose to the point that thousands of families had to be moved to higher land. In a show of solidarity, Queen Beatrix appeared in rubber boots at the threatened dikes.

32. These socioecological theories were developed by, among others, Wrangham (1980), Vehrencamp (1983), and van Schaik (1989). Another important variable, emphasized by van Schaik, is within-group competition. The energy invested in rank-related affairs obviously depends on the advantage of high rank. This advantage varies with the kind of food a species lives on: there is little point in trying to monopolize scattered low-energy foods, such as foliage; but it does pay to be dominant in the case of clumped high-energy foods such as fruits. A steep dominance hierarchy is therefore more likely under the latter condition. For a discussion of contrasting dominance styles in monkeys and apes see de Waal (1989b) and de Waal and Luttrell (1989).

    The idea that despotic dominance requires a closed exit door most likely applies to humans as well. For example, domestic abuse may persist especially when a victim's (perceived) options to quit the relationship are minimal. Conversely, a totalitarian regime may lose its grip once the national border has become porous. This happened when changes in neighboring countries created an opening for an exodus from East Germany. Erich Honecker's power evaporated as soon as people began voting with their feet.

33. For anthropological and evolutionary perspectives on despotism and egalitarianism see Woodburn (1982), Betzig (1986), Knauft (1991), Boehm (1993), and Erdal and Whiten (1994, in press). Boehm was the first to fully develop the idea that egalitarianism is not simply the absence of social stratification but the product of vigilance against excessive individual ambition.

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If hierarchical tendencies are counteracted in egalitarian societies, it is precisely because they have not disappeared. Thus, rather than fitting a naive, idealized picture of human nature, egalitarianism occurs in full recognition of the ubiquitous tendency of men to accumulate power and privilege. There is only one way to neutralize this tendency: alliances from below. Ridicule and social control are important in holding ambition in check, but cannot work without sanctions. And sanctions against the top ultimately require joint action by lower levels.

Alliances from below are also recognizable in the balance-of-power arrangements of chimpanzees (de Waal, 1982, 1984). Most likely, therefore, the common ancestor of humans and apes already had a dominance orientation *and* leveling tendencies. Knauft (1991) is no doubt correct, however, that humans took the leveling tendency a giant step further by means of cultural norms and institutions.

Inasmuch as democracy can be interpreted as a hierarchical arrangement achieved by egalitarian means, the evolution and history of leveling mechanisms is relevant in relation not only to small-scale human societies but also to state organization.

34. Erdal and Whiten, in press.
35. De Waal, 1982, p. 124.
36. Usually, the control role in primate groups is restricted to a single dominant male. Although female macaques without relatives have been known to perform control activities (Varley and Symmes, 1966; Reinhardt, Dodsworth, and Scanlan, 1986), and a female chimpanzee may stop a fight if she is the highest-ranking individual present (de Waal, 1982; Boehm, 1992), the strong commitment of female primates to close relatives—and perhaps by extension to close friends—hampers impartial arbitration.

    In the early years, the Arnhem chimpanzee colony was dominated by Mama, a female without offspring. Unfortunately, we have little information on her rule. We do know from veterinary records that after males took over, the number of serious injuries in the colony dropped sharply. One possible explanation is that males were more effective than Mama at controlling fights (de Waal, 1982).

    In a cohousing experiment at the Wisconsin Primate Center with juvenile rhesus and stump-tail monkeys (Chapter 5), one mixed-species group was dominated by a male stump-tail, the other by a female stump-tail. Only the male performed control interventions, a task overriding the typical own-species bias. He intervened far more often than any other monkey, usually protecting losers even if it meant favoring rhesus monkeys over stump-tails (as he did in 67 percent of forty-six interventions). All other stump-tails favored their own species. The dominant female in the other group intervened only seven times, five of which were in support of other stump-tails.

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For discussion of the control role see de Waal (1977, 1984), Ehardt and Bernstein (1992), and Boehm (1992, 1994).

37. Boehm, 1992, p. 147.
38. When Goblin, after having lost his top position in the Gombe community, tried to stage a comeback, he was defeated by a ferocious mass attack. The unusually hostile reception may have had something to do with the fact that Goblin had been a very tempestuous alpha male who frequently disrupted the group with his charging displays. "Possibly, his return would have roused a less dramatic response had he himself been a more peaceful and calm individual" (Goodall, 1992, p. 139).
39. The role of external threats, particularly from enemy groups of the same species, in the evolution of moral systems is a recurrent theme treated also in Chapters 1 and 5, and emphasized by both Darwin (1871) and Alexander (1987).

4. Quid pro Quo

1. Isaac, 1978, p. 107.
2. This rule cannot explain how altruistic exchanges started. A mere response tendency ("Do as the other did") does not suffice. According to computer simulations of tit-for-tat strategies, an initial cooperative attitude is necessary (Axelrod and Hamilton, 1981).
3. Indeed, this attitude is so unhumanlike that it may develop only under the most extreme circumstances. See Chapter 2 for Turnbull's (1972) claim that the Ik abandoned morality in the face of severe food shortages.
4. Milton, 1992, p. 39.
5. These ideas have been summarized by another anthropologist, Kristen Hawkes, who argues (1990) that men have an interest in providing food bonanzas that can feed many hungry mouths. Hunting success and generosity increase a male's attractiveness as a mate and help foster political ties. The meat distribution strategies of male chimpanzees discussed later on in this chapter seem entirely compatible with Hawkes's "showing off" hypothesis. See also note 20 to this chapter.
6. Lee, 1969, p. 62.
7. According to the French sociologist Claude Fischler, meat blurs the line between ourselves and what we eat. We both challenge and confirm our self-identity when consuming another being made of blood, bones, brains, secretions, and excretions. In this view, human flesh is the superlative meat; and Fischler (1990) indeed argues in *L'Homnivore* (a wordplay making a maneater out of an omnivore) that our obsession with animal foods ultimately derives from ancient practices of cannibalism and human sacrifice. A link with this past is also preserved in the Roman

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Catholic ritual of ingesting bread and wine as representations of Christ's flesh and blood.

8. Nishida et al., 1992, p. 169.
9. De Waal, 1982, p. 110.
10. According to Sahlins (1965), human reciprocity takes two forms: (a) "vice versa" movements of goods and services within dyadic relationships, and (b) centralized exchanges via a recognized authority who pools and redistributes resources. The latter function may be performed by a chief or, in modern society, the government.

    Centralized reciprocity is recognizable in both the food distribution strategies of top-ranking chimpanzees and their control role—their tendency to defend the weak against the strong (Chapter 3). In both cases a dominant individual dampens competition to the advantage of low-ranking members, in return receiving support and respect.

    Studies on aid giving and sharing in human children, too, fit this pattern. Apart from reciprocity at the dyadic level, they demonstrate increasing protectiveness and generosity with increasing status (Ginsburg and Miller, 1981; Birch and Billman, 1986; Grammer, 1992).
11. Detailed information about chimpanzee predation and meat sharing can be found in Teleki (1973b), Goodall (1986), Boesch and Boesch (1989), Boesch (1994ab), and Stanford et al. (1994a).

    Whether bonobos fit the predation hypothesis of the evolution of sharing is still ambiguous. Despite reports of meat sharing (Badrian and Malenky, 1984; Ihobe, 1992; Hohmann and Fruth, 1993), predation seems relatively insignificant. For example, bonobos have not been observed to hunt monkeys; on the contrary, their relations with monkeys seem rather friendly (Ihobe, 1990; Sabater Pi et al., 1993).

    Plant food sharing, in contrast, is common. At a provisioning site for bonobos in Zaire, sugarcane was widely shared (Kuroda, 1984), and bonobos have also been seen to divide large *Treculia* and *Anonidium* fruits, some weighing 30 kilograms apiece (Hohmann and Fruth, forthcoming). Perhaps consumption of these fruits helped promote sharing tendencies. It should be added, though, that my own captive studies suggest that the bonobo's food-related tolerance is no match for that of the chimpanzee (de Waal, 1992b; and note 16 to this chapter).
12. Sharing between mother and offspring occurs in most or all primates, including rhesus monkeys, as does cofeeding on a clumped yet abundant food source. When I speak of "nonsharing" species, I mean primates with a predominantly competitive mode of interaction around food, in which subordinates never remove food directly from the hands or mouth of unrelated dominants. Generally, these species also lack communication signals specific to the sharing context, such as gestures and vocalizations to solicit food.
13. Goodall, 1986, p. 357.

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14. D'Amato and Eisenstein, 1972, p. 8.

15. The main effect of food deprivation is to increase interest in food. But the same effect can be achieved by presenting favorite foods. I feel that there is so much to be discovered in this way that food deprivation is wholly unnecessary. The capuchins and chimpanzees in our tests receive foods that they particularly like but do not normally get, at least not in such abundance.

16. Feistner and McGrew (1989), who review primate patterns of food distribution, define sharing as the "transfer of a defensible food-item from one food-motivated individual to another, excluding theft" (p. 22).

Below is a classification of four methods of interindividual food transfer during interactions relative to plant food in chimpanzees at the Yerkes Primate Center (de Waal, 1989d), bonobos at the San Diego Zoo (de Waal, 1992b), and capuchins at the Wisconsin Primate Center (de Waal, Luttrell, and Canfield, 1993). All methods of transfer occurred in all species, but chimpanzees showed more tolerant transfers (cofeeding and relaxed taking) and bonobos more intolerant transfers (forced claims and theft).

Forced claim or theft: One individual supplants another at a food source, grabs food by force, or snatches a piece and runs. The first two patterns are typical of high-ranking individuals; the last, of subordinates and juveniles.

Relaxed taking: One individual, in full view of the possessor, removes food from his or her hands in a relaxed or playful manner without threat signals or use of force.

Cofeeding: An individual joins the possessor to feed peacefully on the same source, which both may hold. This category includes active food donations: 0.2 percent of all transfers in chimpanzees, 2.7 percent in bonobos, and 1.8 percent in capuchins.

Nearby collection: An individual waits for dropped pieces and scraps, which are collected from within arm's reach of the possessor.

	Chimpanzees	Bonobos	Capuchins
Number of transfers	2,377	598	931
Forced claim or theft	9.5%	44.5%	26.2%
Relaxed taking	37.1%	15.7%	26.5%
Cofeeding	35.9%	17.6%	9.2%
Nearby collection	17.6%	22.2%	38.0%

17. The effect of celebration was investigated through a variation in the method with which bundles of foliage were provided to the chimpanzees:

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Keeper delivery: A caretaker brought bundles from a distance, giving the colony one to two minutes for celebration before the bundles were thrown into the enclosure.

Self-delivery: Well before the trial, I concealed the bundles behind me on the observation platform. At an unexpected moment, I threw them into the enclosure, giving the colony no chance to prepare for the event.

Aggression at the moment that the food arrived was rare under either condition; most of it occurred when individuals tried to join existing feeding clusters, or begged from possessors. On average, self-delivery trials involved 1.5 times more aggressive incidents than keeper-delivery trials. This finding is consistent with the idea that celebration increases social tolerance. The ambiance seemed less explosive during sessions preceded by this flurry of body contact and rituals confirming the hierarchy (de Waal, 1992b).

18. Respect for possession was first investigated in relation to sexual partners in hamadryas baboons. Males of this species do not interfere with each other's bonds with females: even large, totally dominant males are inhibited from taking over the female of another male after having seen the two together for a couple of minutes (Kummer, Gotz, and Angst, 1974). Recently, Kummer and his coworkers conducted further experiments on possession and property rules, which showed similar inhibitions in relation to objects (Sigg and Falett, 1985; Kummer and Cords, 1991; Kummer, 1991).

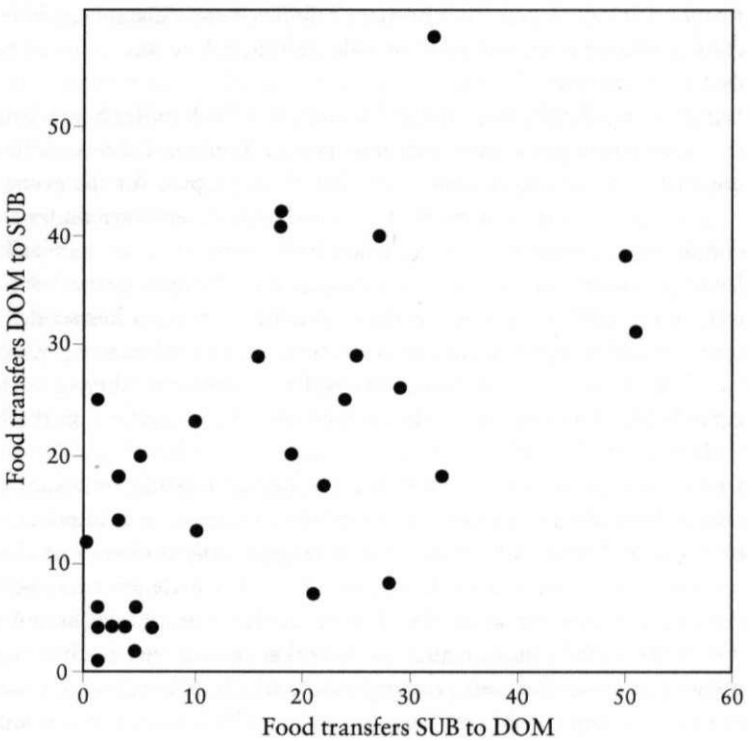
19. The accompanying graph (p. 246) illustrates that shared amounts are correlated and well balanced within pairs of dominant and subordinate chimpanzees. Since a few rank relationships were ambiguous, only thirty of the thirty-six pairings among the nine adults are included. Reciprocity, tested on the entire 9 x 9 matrix, resulted in a correlation of $r = 0.55$ ($P = 0.001$). See de Waal (1989d) for details.

20. Sex-for-food transactions have been documented by Kuroda (1984) for wild bonobos, and by de Waal (1987, 1989a) for captive bonobos. Such exchanges are less prominent but not absent in chimpanzees (Yerkes, 1941; Teleki, 1973b). Thus, the best predictor of hunting by male chimpanzees in Gombe National Park is the presence of estrous females in their traveling party. One motivation for hunting, then, may be to increase mating success through sharing with females (Stanford et al., 1994b).

21. Smuts, 1985, p. 223.

22. In our own economy, the value of various services is expressed in a common currency: money. The evolutionary equivalent of money, reproductive fitness, is hard to measure. A discussion of this issue by Seyfarth and Cheney, with reference to their own field data, is contained in a collection of papers on the current state of knowledge of reciprocal

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Scatter plot of food transfers from dominant to subordinate chimpanzees (**DOM** to **SUB**) against transfers in the opposite direction (**SUB** to **DOM**). Each dot represents one adult-adult partner combination.

altruism. See *Ethology and Sociobiology* 9 (1988, pp. 67-257). Reciprocity is also a central theme in Harcourt and de Waal's volume on alliance formation (1992).

23. For details see de Waal and Luttrell (1988). The same statistical elimination procedure was applied to food sharing, with identical outcome: a significant level of reciprocity remained after controlling for symmetrical relationship characteristics, such as kinship and association time (de Waal, 1989d).

24. Silk (1992b) challenges the claim that only chimpanzees have a system of direct revenge. The author reports reciprocal *contra* interventions among male bonnet monkeys. Because interventions against the established order were as uncommon in these monkeys as in other macaques, it remains to be seen how comparable their behavior is to that of chimpanzees, who retaliate regardless of the hierarchy (de Waal and Luttrell, 1988). For further data on revenge in monkeys and apes see de Waal (1982, 1989d), Aureli (1992), and Cheney and Seyfarth (1986, 1989).

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Discussions from an evolutionary perspective have been provided by Trivers (1971) and by Clutton-Brock and Parker (1995).

25. Jacoby, 1983, p. 13.
26. Chagnon, 1988, p. 990.
27. Huxley, 1989 (1894), p. 140.

5. Getting Along

1. Midgley, 1994, p. 119.
2. Lorenz, 1981, p. 45.
3. Ardrey (1967) called our species the Killer Ape, based on Dart's (1959) depiction of *Australopithecus* as a carnivore who loved to devour writhing flesh and slake its thirst with warm blood (a truly imaginative conclusion, given the limits of fossil data). Dart saw the lust to kill as humanity's "mark of Cain," a feature that sets us apart from our anthropoid relatives. This line of thinking led others to seek the origin of war in hunting, and to present aggressiveness as a prerequisite to progress (Cartmill, 1993).

   One of several problems with the Killer Ape myth is that it equates carnivorousness with violence against one's own kind. We need to distinguish aggression definitively from predation, as Lorenz (1966, p. ix) wisely did when he defined aggression as "the fighting instinct in beast and man which is directed against members of the same species." Thus, it is assumed that a leopard killing an antelope is motivated by hunger, whereas a leopard driving another leopard out of his territory is motivated by aggression. For one thing, members of the same species communicate extensively during confrontations. They have ritualizations and inhibitions to prevent bloodshed, whereas predators usually assail their prey without warning signals and without pulling any punches. The difference in form and purpose of the two kinds of attack is obvious if we compare a cat stalking a mouse with one bristling and hissing at a rival.

   In light of Lorenz's emphasis on this crucial distinction, the most preposterous cover under which his *On Aggression* ever appeared (undoubtedly selected for marketing purposes) was one featuring a dramatic painting of a lion sinking teeth and claws into a frightened horse.
4. Notable exceptions are developmental studies by Sackin and Thelen (1984), Hartup et al. (1988), and Killen and Turiel (1991). Consistent with the theoretical framework presented in this chapter, Killen and Turiel note that fights among children are not always destructive; they often have a social orientation. "Children's conflicts are not solely struggles about selfish desires or aggressive impulses. Children are responsive to others and engage in negotiations to resolve their conflicts" (p. 254).
5. Initially, this flexibility baffled field-workers. Did chimpanzees know

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stable groups at all? After years of documenting the composition of chimpanzee parties in the Mahale Mountains, Nishida (1968) was the first to crack the puzzle. He discovered that the ever-changing parties belong to an umbrella group, the members of which mix freely among themselves yet never with members of another such group. Nishida called this higher level of organization a "unit-group," yet the literature came to favor Jane Goodall's term "community" (mere "group" would hardly do, given the fission-fusion character of chimpanzee society).

6. The qualifier "best-known wild populations" is necessary, given the remarkable behavioral diversity—sometimes called cultural variation—of wild chimpanzees. Even populations in similar habitats in the same part of Africa differ in communication gestures and tool technology (Nishida, 1987; McGrew, 1992; Wrangham et al., 1994).

   Female-female relations are probably the most variable element of chimpanzee social organization (de Waal, 1994; Baker and Smuts, 1994). These relations range from close in all captive colonies known to me, to rather loose in wild populations at the Gombe and Mahale Mountains national parks in Tanzania (Nishida, 1979; Goodall, 1986) as well as in the Kibale Forest in Uganda (Wrangham, Clark, and Isabirye-Basuta, 1992).

   This variability may not represent an absolute difference between captive and wild conditions, however. Female bonding appears to exist in a small chimpanzee population "trapped" by agricultural encroachment in a forest of approximately 6 square kilometers on top of a mountain in Bossou, Guinea. Despite the substantial amount of available space, Sugiyama (1984, 1988) often saw the majority of individuals in this forest travel together in a single party, and measured relatively high rates of female-female grooming. Similarly, female chimpanzees seem more sociable in Tai Forest, Ivory Coast, than at other sites: they frequently associate, develop friendships, share food, and support one another. Boesch (1991b) attributes this sociability to cooperative defense against leopards.

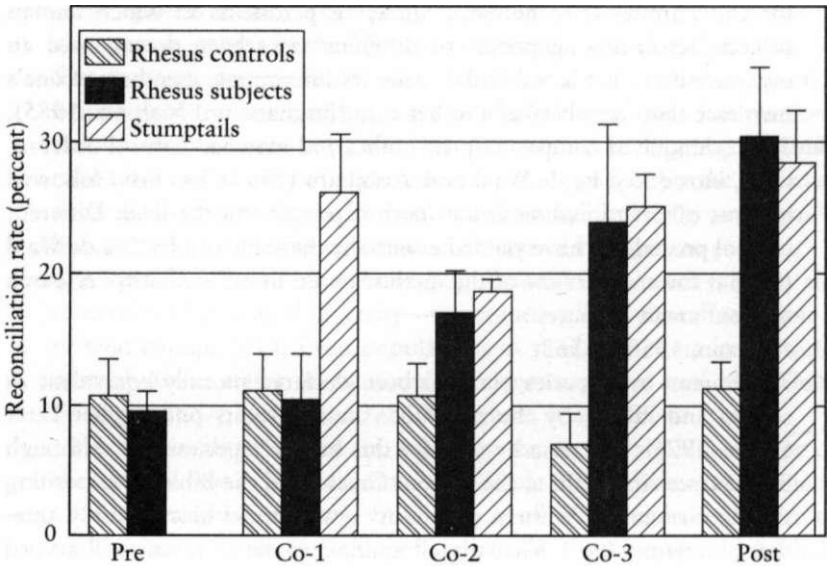
7. Masters, 1984, p. 209.
8. Van Schaik, 1983, p. 138.
9. Boinsky, 1991, p. 187.
10. Norris, 1991, p. 187.
11. Bowlby, 1981, p. 172.
12. Moss, 1988, p. 125.
13. Using portraits of familiar individuals of both species, Matsuzawa (1989, 1990) compared facial discrimination by chimpanzee and human subjects as measured by latency with finding the correct name (the chimpanzees had first learned to match faces with name-keys on a computer keyboard). He found that recognition of human faces is easier for humans than chimpanzees, and recognition of chimpanzee faces easier

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for chimpanzees than humans. Similar experiments in which human subjects select among people of different races have documented an own-race bias, that is, we find it easier to differentiate members of one's own race than members of another race (Brigham and Malpass, 1985).

14. The technique of comparing postconflict and matched-control observations, introduced by de Waal and Yoshihara (1983), has been followed in most observational studies in both captivity and the field. Different control procedures have yielded essentially the same results. See de Waal (1993a) for an overview of the methods used in reconciliation research on nonhuman primates.
15. Altmann, 1980, p. 163.
16. The human own-species bias has been declared morally equivalent to sexism and racism by the Australian animal-rights philosopher Peter Singer (1976). The term he uses for this bias is "speciesism." Although Singer traces its origin to the ancient Greeks and the Bible, thus positing that speciesism is a Western peculiarity, own-species bias certainly antedates humanity itself. Virtually all animals, given a choice, will accord their own kind the better treatment, and cross-species exploitation is absolutely rampant in nature (for instance, some ant species keep aphids as livestock, or force other ant species into labor; Holldobbler and Wilson, 1990).
17. As expected, stump-tails were characterized by high reconciliation rates (see figure, p. 250). Rhesus monkeys not exposed to stump-tails (rhesus controls) had low rates throughout the experiment. Rhesus living with stump-tails (rhesus subjects), in contrast, started out at the same level as the controls, but rose steadily during the cohousing phases (Co-1, 2, and 3), remaining high even after removal of the stump-tails in the post-phase (from de Waal and Johanowicz, 1993).
18. This insight is not limited to Japanese teachers. An early American student of child behavior, Helen Dawe (1934, p. 154), noted that "the mother or teacher who continually interferes is depriving the child of excellent opportunities to learn social adjustment." When Peter Verbeek, a graduate student, observed children at an outdoor playground in Florida, he found that approximately one-third of the fights were broken up by teachers. The teachers would tell the children to "make peace," yet only 8 percent of the combatants continued to associate after a forced reconciliation compared to 35 percent after an independently resolved dispute.
19. Gottman, 1994, p. 41.
20. Kurland (1977) was the first to report high rates of aggression between kin in free-ranging Japanese macaques. This paradoxical observation was confirmed for rhesus and stump-tail monkeys in outdoor enclosures by Bernstein and coworkers (Bernstein and Ehardt, 1986; Bernstein, Judge, and Ruehlmann, 1993) and de Waal and Luttrell (1989). Further-

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Conciliatory tendency increases in rhesus monkeys housed with stump-tails. Shown are individual means (plus standard error of means, SEM) of aggressive conflicts followed within three minutes by reconciliation. Before and after the experiment (pre- and post-phases), subjects were housed with members of their own species only (no pre-phase data are available on stump-tailed monkeys).

more, kinship ties are not the only bonds characterized by frequent aggression; the same applies to ties among nonkin (de Waal and Luttrell, 1986).

The number of fights among kin ceases to be exceptional if time spent together is taken into account. The high aggression rate is therefore partly a product of proximity. Yet the same is true of other kinds of interaction, so that a connection with proximity cannot be used to devalue high aggression rates among kin unless one is prepared to do the same for grooming and other affiliative behavior (Bernstein, Judge, and Ruehlmann, 1993).

There is no evidence that aggression among kin is relatively mild: injuries do occasionally result. How, then, does the matrilineal organization survive all this infighting? The key is that fights among kin and other close associates are relatively often reconciled (reviewed by Kappeler and van Schaik, 1992). A parallel report in human children finds friends preserving proximity despite high conflict rates (Hartup et al., 1988).

21. Obviously, juvenile chimpanzees do not vomit as a conscious threat; they simply get extremely frustrated and upset. My "investment" language is

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inspired by Trivers' (1974) provocative analysis of parent-offspring conflict as a genetic tug-of-war.

In this battle of wills mothers have weapons, too. Jane Goodall offered a striking example at a symposium entitled "The Great Apes Revisited" (Mexico, 1994). In Gombe National Park, chimpanzee Fifi had shown regular five-year interbirth intervals, almost like clockwork. Her last birth, however, occurred when her previous child, Faustino, was only three and a half years old. The abrupt drop in maternal attention caused Faustino to have incredible tantrums. More than a year too young for weaning, he must have found life definitely "unjust." Fifi did not completely wean him, though; she continued to allow him to sleep in her nest, even to nurse along with his new sibling.

One of Fifi's original answers to Faustino's tantrums was to climb high in a tree and throw him literally to the ground, at the last instant holding onto an ankle. The young male would hang upside down for fifteen seconds or more, screaming wildly, before his mother retrieved him. Fifi was seen to employ this scare tactic twice in a row, after which Faustino stopped having tantrums that day.

22. Charlesworth, 1991, p. 355.
23. Hearne, 1986, pp. 43-14.
24. This discussion is based on the work of Smuts and Watanabe (1990) and of Colmenares (1991). The study of baboon greetings has a much longer history, however, going back to Kummer's (1968) observations of so-called notification in hamadryas baboons. It seems a particularly promising area for research into nonverbal negotiation. Colmenares (1991, p. 59) summarizes the ingredients of negotiation as follows: (a) conflict of interest, (b) attempts to reach nonaggressive solutions, (c) assessing and influencing the other's intentions, and (d) accommodating one's initial goals to those of the other. For further thoughts on animal negotiation see Hinde (1985), Dunbar (1988, pp. 238-248), Noe (1992), and Chadwick-Jones (1992).
25. Smuts and Watanabe, 1990, p. 169.
26. Goodwin, quoted in Haglund, 1992, p. 140.
27. Quoted in *Washington Post,* February 28, 1992.
28. Ardrey, 1970, p. 62.
29. The reported homicide rates for the Netherlands and the United States come from the *World Health Statistics Annual* of 1987 and 1988. Homicide statistics per city were reported in the *New York Times* of August 5, 1990.
30. Thompson, 1976, p. 226.
31. The general public loves to hear about the biological roots of vice and depravity. Ever since de Mandeville (1714), authors have been more than willing to cater to this desire (Montagu, 1968). We first met this genre of literature in Chapter 1, in relation to the evolutionary process, but the

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aggression literature has, if possible, produced even more bad news about our species.

The standard trick is to present mean and selfish acts as proof of our true character, and to either overlook human kindness and sympathy, or demonstrate a hidden agenda behind it. Thus, in the same paradoxical way that the sexlessness of a dream can be taken as evidence for sexual repression, the manifest civility of most people can be explained as a facade hiding a brutish nature (Thompson, 1976).

32. Alexander and Roth, 1971, p. 82.

33. Perhaps the closest primate parallel to Calhoun's (1962) expanding rat population was a group of Japanese macaques in a corral of 0.8 hectare that grew from 107 to 192 individuals over a five-year period. Despite this increase of 79 percent in population density, the mean individual rate of aggressive acts per hour did not significantly vary over the years (Eaton, Modahl, and Johnson, 1980). For reviews of crowding research on nonhuman primates see Erwin (1979) and de Waal (1989c).

34. The table below summarizes the effect of a twentyfold area reduction on the Arnhem chimpanzee colony, based on data from Nieuwenhuijsen and de Waal (1982). Weighted individual rates of behavior during two summer periods (outdoors) are compared with those of three winter periods (indoors), resulting in factorial increases. Note that all measures except play were higher during the winters.

Measure	Outdoors	Indoors
Aggression	**1**	**1.7**
Proportion of severe aggression	1	**1.1**
Submissive greetings	**1**	**2.4**
Social grooming	**1**	**2.0**
Social Play	**1.4**	**1**

35. Given that macaques live in permanent groups in the wild, whereas chimpanzees form fission-fusion societies, it is entirely possible that the observed similarity in conciliatory tendency between captive and wild macaques does not generalize to captive and wild chimpanzees: distancing between adversaries ***is*** a realistic option for wild chimpanzees.

Even though chimpanzees on the Arnhem island have a great deal of space, they cannot get out of each other's way for more than a couple of hours. The observed similarity in conciliatory tendency during indoor and outdoor periods may be due, therefore, to the chimpanzees' having learned that it is better to reconcile right away than to run into an ill-willed opponent later on.

Some of the most spectacular reconciliations in Arnhem took place in the late afternoon, when the chimpanzees were being called into the building for their evening meal. If rival males had avoided each other

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following a confrontation, they might find themselves in the awkward and dangerous situation of having to spend the night unreconciled together in the same room. Under these circumstances, males were often seen circling each other outside, near the entrance door, testing preparedness to make up. These tense scenes usually ended with an outburst of screaming and embracing between the two—a highly emotional moment followed by grooming. Sometimes they groomed each other so long that the keeper proceeded to feed the rest of the colony while we waited until the two males had calmed down sufficiently to come in together. These reconciliations, clearly forced on the males by the anticipation of proximity, are oriented to the future. Accordingly, I have called them "truces" (de Waal, 1982, pp. 113-114).

36. For chimpanzees there is no such thing as "the" natural habitat. Environments in which these apes survive today range from relatively open, wooded savannas to dense rain forests. Moreover, most known chimpanzee populations have been affected by human activity, such as hunting or food provisioning. On the basis of her reading of the literature, Power (1991) has argued that provisioning at some field sites (such as Gombe's banana camp) turned the chimpanzees more violent and less egalitarian, and thus changed the "tone" of relationships both within and between communities. Power's analysis—which blends a serious reexamination of available data with nostalgia for the 1960s image of apes as noble savages—raises questions that will no doubt be settled by ongoing research on unprovisioned wild chimpanzees.

    The issue of provisioning is also relevant to this chapter's comparison of macaques under different conditions, because all populations (except the one studied in the field by Aureli, 1992) were provisioned. It is not well understood how the behavior of provisioned free-ranging monkeys compares to that of wild monkeys subsisting on dispersed natural foods. Asquith (1989) has reviewed the pros and cons of provisioning in the field.

37. Strier, 1992, p. 70.

38. In light of the current advances in genetic technology, a statement such as "We have to work within our biological endowment" is rapidly becoming outdated.

39. If monkeys sometimes reconcile "for" their matriline, the same mechanism might operate between groups. Intergroup relations were documented in a free-ranging population of rhesus monkeys at Morgan Island, South Carolina. The vast majority of intergroup encounters were hostile, but on eleven separate occasions adult females belonging to *different* groups were seen to assemble for grooming. Remarkably, these contacts involved alpha females of the respective groups, particularly of groups between which much fighting occurred. In a parallel with international diplomacy, several of these high-level contacts took place

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shortly after an intergroup fight, and may thus have served to reestablish peaceful relations (Judge and de Waal, 1994).

40. See de Waal (1989a, pp. 107-110) and Cheney and Seyfarth (1990, pp. 72-86) for further discussion of nonegocentric social knowledge.

41. Bodily harm to self is no doubt the first and foremost constraint on competition. According to Maynard Smith and Price (1973), the advantages of winning a fight are weighed against the cost of injury in case the adversary fights back. Van Rhijn and Vodegel (1980) refined this model by including the role of individual recognition.

    These early evolutionary models, however, considered physical damage only. Elsewhere I have discussed constraints on competition from the perspective of *social* damage. The social environment may be regarded as a set of resources (for example, cooperative relationships) the effective exploitation of which requires that energy be put into their preservation (de Waal, 1989b). Thus, Sigg and Falett (1985) speculated that the main function of tolerance in relation to food is that it permits high-ranking and low-ranking baboons to forage side by side, which in turn helps all of them to close ranks and defend themselves in times of danger.

6. Conclusion

1. Dewey, 1993 (1898), pp. 109-110.

2. The father of Japanese primatology, Kinji Imanishi, defined culture as "socially transmitted adjustable behavior" (Nishida, 1987, p. 462). Early data and concepts in the study of animal culture may be found in Kummer (1971), Menzel (1973), and Bonner (1980). Cultural transmission is usually contrasted with the acquisition of behavior through individual learning and/or genetic transmission: cultural transmission implies *learning from* others, and in its most effective form (perhaps limited to our species) *teaching by* others. Two recent books reviewing primate cultural phenomena are McGrew (1992) and Wrangham et al. (1994).

3. Proudhon, quoted in Hardin, 1982, p. 184.

4. For a balanced account of the controversy over the use of monkeys and apes in biomedical research, see Blum (1994). This science journalist's book ends with a description of the Yerkes Field Station as the sort of model facility that animal advocates should be able to accept. As a behavioral scientist working at this facility and a few others devoted to research, education, and conservation, I often feel caught in the middle of the controversy. I fully recognize the need to treat animals with respect and compassion, and I am a strong proponent of social housing for nonhuman primates (see, for instance, de Waal, 1992c). At the same time, I greatly appreciate the benefits derived from biomedical research, benefits that even the staunchest critics of such research are not prepared to decline.

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The strategy of both sides in this acrimonious debate has been to depict the other as inhumane or immoral. Ironically, a debate such as this one is precisely what defines us as moral beings. As with all true dilemmas, the majority of people feel torn between two undesirables: inflicting pain upon animals and forgoing the medical advances produced thereby.

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