

Environmental Factors and Aggression in Nonhuman Primates

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INTRODUCTION

Our primate relatives provide excellent models for understanding human aggression. Like us, most other primates are long-lived relatively brainy animals that live in complex societies in which aggression plays important roles. Unlike the favorite laboratory animals, rats and mice, which live in a nocturnal, underground world, primates are generally diurnal and readily observable in the wild. A few hours spent watching a troop of baboons or rhesus macaques should reward even the casual observer with examples of various aggressive interactions, from mild threats to squabbles and chases and perhaps even sustained attacks. Severe aggression, though rarely observed, marks many individuals with scars, disfiguring gashes, and open wounds. Our closest living relatives, chimpanzees, resemble humans in that they defend group territories and sometimes kill members of neighboring communities.

Many early studies of primates focused on aggression (e.g. Hall, 1964; Holloway, 1974; Zuckerman, 1932), and aggression remains a central topic of primate studies today. A search of Zoological Abstracts (1990–1998) found 1666 articles on nonhuman primate behavior, of which more than a quarter (446) concerned aggression (Howell, 1999). I will not attempt to review this entire literature here. Instead, I will focus on a few of the most important adaptive goals of primate aggression, reviewing some of the extensive literature on how primates use aggression strategically in response to environmental factors.

Definitions of Aggression

Aggression has been defined in numerous ways with some definitions including seemingly mild forms such as verbal aggression (*see* reviews in Eibl-Eibesfeldt, 1979; Volavaka, 1995). Here, I will attempt to focus on the least ambiguous cases. I will pay particular attention to the small fraction of aggressive interactions that result in killing, which is an unambiguous outcome that provides a particularly clear assay on factors responsible for aggression (Daly and Wilson, 1996). As an additional consideration, killing is the outcome of aggression that most concerns researchers interested in understanding and preventing human violence such as child abuse, homicide, deadly ethnic riots, genocide, and warfare.

From: *Neurobiology of Aggression: Understanding and Preventing Violence*
Edited by: M. Mattson © Humana Press Inc., Totowa, NJ

Kinds of Explanation

Many studies, including many chapters in this volume, focus on physiological mechanisms underlying aggression, such as brain structures and endocrine systems. Understanding physiological mechanisms is crucial, of course, but we now know that many of these mechanisms vary with environmental factors. Testosterone levels in male chimpanzees, for example, respond to social factors such as the number of fertile females available (Muller, 2002). A full understanding of any biological trait, including aggression, requires finding answers to four distinct kinds of explanation: ultimate (function), proximate (mechanism), development (ontogeny), and evolutionary history (phylogeny) (Daly and Wilson, 1983; Tinbergen, 1963).

Consider, for example, a male baboon about to start a fight. The male is a young adult who recently joined the troop, and his opponent is the troop's aging alpha male, recently weakened by disease. A functional explanation would focus on how the fight will affect the newcomer's reproductive success. By attacking the alpha male, the newcomer may gain alpha rank himself, enabling him to increase his share of matings with the troop's females. Proximate explanations might focus on the young male's neuroendocrine system, such as changes in serotonin and testosterone levels. Proximate explanations could also focus on the newcomer's assessment of the costs and benefits of fighting: in this case, the costs are unusually low, because the alpha male is weakened, and the potential benefits (gaining alpha rank) are enormous. Development also plays a role, especially life stage: the newcomer is now in his physical prime. A year or two ago he would have been too weak to challenge the alpha male, and in another few years his own physical powers will start to decline. The newcomer's current physiology may depend on many other factors in his development. Was his growth interrupted by harsh seasons of drought? Was his mother high ranking enough to compete successfully for food for herself and her offspring? Considering evolutionary history, male baboon psychology has been shaped by the costs and benefits of aggression over many generations. Over the years, it has paid for males to emigrate from the troop of their birth, join a new troop of strangers, and fight to attain high rank while still in their physical prime. Had he been born a male chimpanzee instead, he would have stayed in his natal group instead of seeking his fortunes elsewhere.

Keeping in mind that a complete understanding of aggression requires all four kinds of explanation, here I focus on the functional goals and economics of aggression. I briefly examine five potential goals of aggression: mates, food, land, killing of adults, and killing of infants. Aggression may serve various additional functions, such as defense of self and offspring from predators, but limited space prohibits an exhaustive survey. For each goal, I discuss potential benefits and costs involved in attaining that goal. I then describe how those costs and benefits might vary depending on environmental factors.

Costs and Benefits of Aggression

In a recent review of primates as models of human aggression, Kalin (1999) observed that "all forms of aggression in rhesus monkeys appear to be modulated by environmental factors." This observation applies equally to other primates and indeed most animals. Like any other product of natural selection, aggressive behavior should be designed to benefit the aggressor's "inclusive fitness," which is evolutionary jargon for the reproductive success of an individual (and the individual's kin, insofar as they

are affected) (Daly and Wilson, 1983). Because the costs and benefits of aggression vary according to circumstances, individuals should not perform aggressive acts blindly or automatically, but should, instead, modulate their aggression according to relevant environmental factors.

Modern behavioral biology thus views aggression as a strategic option to be used when assessment of the odds indicates that the fitness benefits will outweigh the costs (for excellent reviews, *see* Archer, 1988; Huntingford and Turner, 1987). Important benefits of aggression include access to resources essential for reproductive success, especially mates, food, and territory. Costs of aggression include energy expenditure, the risk of injury or death, and opportunity costs, in that time spent fighting could be spent looking for food or mates instead. The relative balance of costs to benefits varies with environmental factors. For example, theoretical considerations suggest that animals should avoid fighting opponents that are larger, better armed, or more numerous than themselves (Parker, 1974). Animals also should be more likely to fight over valuable resources, such as fertile females or rich food sources (Parker, 1974). Such assessment of environmental factors has been demonstrated experimentally in diverse species including spiders (Leimar et al., 1991), toads (Davies and Halliday, 1978), and lions (McComb et al., 1994).

In practice, the actual costs and benefits involved are usually difficult to measure, especially in the wild, where many factors vary simultaneously and interact in complicated ways. Fortunately, our understanding of aggression in wild primates now benefits both from technological advances and from the maturation of long-term observational studies. Molecular technology enables field workers to collect genetic and endocrine data from hair, feces, and urine without harming or even directly contacting the study subjects. Using these methods, we can now test whether types of aggression, such as infanticide, yield reproductive benefits (Borries et al., 1999) and how environmental factors influence hormone levels (Muller, 2002). Studies of intergroup aggression now rely on playback experiments, using portable speakers and high-quality recordings to simulate intruders (Kitchen, 2000; Mitani, 1990; Wilson et al., 2001). Maturing long-term studies of many species and multiple populations of the same species enable rich comparative tests of how and why aggression varies over space and time. Computerizing long-term data on ranging and other behavior enables quantitative tests, such as the specific benefits obtained by territorial expansion (Williams, 2000; Williams and Pusey, submitted).

Aggression Controversies: Function Vs Dysfunction

Explanations of aggression in terms of inclusive fitness calculations continue to provoke controversy, especially when applied to lethal aggression, and even more so when applied to humans (Lewontin, 1999; Sommer, 2000; Sussman, 1999; Wrangham, 1999). Much of this controversy stems from enduring hostility toward any biological explanation of human behavior (reviewed in Niehoff, 1999; Sommer, 2000; Tooby and Cosmides, 1992). The controversy also has roots in the attempt by early ethologists, such as Konrad Lorenz, to counter the Victorian view that nature is “red in tooth and claw.” Lorenz regarded aggression as an adaptation, but he asserted that animals do not intentionally kill one another in the wild owing to a supposed inhibition against killing members of their own species (1966).

Early field studies supported Lorenz's view. Most animals are peaceful most of the time; long studies are needed to observe severe fights among long-lived slow-reproducing animals in the wild. Schaller, for example, emphasized that during the year he spent observing gorillas in the wild, they appeared to be gentle giants (Schaller, 1964). Longer field studies, however, found that male gorillas can fight fiercely and inflict severe wounds (Fossey, 1983). Male gorilla skulls frequently show evidence of healed bite wounds (Jurmain, 1997), including canines embedded in the skull (Fossey, 1983). Moreover, both male and female gorillas sometimes kill the infants of other gorillas, and such infanticidal attacks account for up to 37% of infant mortality (Fossey, 1984; Watts, 1989).

Despite the continued popularity of the view that animals are "naturally pacifists" (Lorenz, 1966; Montagu, 1976; Power, 1991), accumulating evidence permits us to discard this hypothesis. The consensus in animal behavior studies is that aggression, including deadly aggression, is simply part of ongoing competition in a world of limited resources (Archer, 1988; Huntingford and Turner, 1987).

Despite the growing consensus in behavioral biology, studies of human aggression rarely examine fitness costs and benefits (for notable exceptions, *see* Daly and Wilson, 1988; Wilson and Daly, 1998). Instead, many discussions of environmental influences view aggression as a dysfunctional response to factors such as overcrowding (Ostfeld and D'Atri, 1975), poverty (Pagani et al., 1999), too much television (Johnson et al., 2002), or abusive parents (Barnow et al., 2001). Although such factors clearly have important effects on aggression in humans, we should be cautious of the implicit assumption that aggression is bad, and that a bad environment leads to bad behavior. Focusing on variables perceived as "bad" can distract attention from factors with a more direct causal link to aggression.

For example, a widespread view is that high levels of aggression result from high population densities. Although, in general, individually measured rates of aggression do increase with population density, many studies have found only a weak effect or an inverse relation (Judge and de Waal, 1997; Moore, 1999). From an evolutionary perspective, there is no reason to suppose that animals should require an ideal population density to behave adaptively. Indeed, population density varies greatly among populations in the wild and, by definition, should be highest in habitats most suitable for the species in question. Focusing on population density obscures the influence of variables more likely to have a direct influence on aggression, such as intruder pressure, population age structure, and the abundance and distribution of food (Janson and van Schaik, 2000; Moore, 1999). In general, examining the functional goals and related costs and benefits of aggression should result in sharpened evolutionarily relevant hypotheses.

MATES

Benefits

In any sexual species, reproductive success obviously requires mating success. The benefits of competing for mates, however, differ between the sexes. Mating among mammals involves a highly asymmetric bargain (Trivers, 1972). Females provide an egg and a commitment to gestate, lactate, and raise the young. Males provide sperm and usually little else. Because females invest so much in each pregnancy, they tend to be choosy

about their mates. Because males stand to gain so much from each mating, males tend to mate with as many females as possible, and compete intensely with other males for mating opportunities. Numerous exceptions exist to the general trend of coy choosy females and promiscuous caddish males. Female chimpanzees, for example, are far from coy; instead, they often attempt to mate with every male in their community, probably as an anti-infanticide strategy (Wrangham, 2002). Male tamarin monkeys help feed and carry their young (Goldizen, 1988), and males in many species defend their young from predators (van Schaik and Hörstermann, 1994) and potentially infanticidal rival males (van Schaik, 2000b). Nevertheless, even in the exceptional cases, females invest far more in their offspring than males. Because of this asymmetry, males are much more likely to fight for a mate than females, and fights between males are much more likely to lead to injury or death.

Costs

Aggressors face high potential costs when competing for mates, including energy expenditure and risk of injury or death from fighting. Competing for mates also can incur more subtle costs. For example, male baboons often “mate guard” by traveling closely with a fertile female, mating with her, and repelling rival males. While mate guarding, males reduce their daily travel distance to match that of the females they guard, reducing their food intake (Alberts et al., 1996). In species with intense contest competition for mates, males face the additional cost of growing the large body size, muscle mass, and canine weaponry needed to compete successfully. Male gorillas, for example, grow to twice the size of female gorillas. In most mammals, the only environmental limitation on growth to full adult size is sufficient nutrition. Among orangutans, however, male growth depends on the social environment (*see* Operational Sex Ratio).

Environmental Factors

When competing for mates, males fight most intensely when the net benefits appear to be highest. The primary environmental factor favoring aggressive competition for mates is, of course, the presence of fertile females. The intensity of male competition also depends on two additional factors: the operational sex ratio and the ratio of young males to older males in the population.

Fertile Females

The frequency of male aggression varies closely with the number of mating opportunities. In seasonally breeding species, such as rhesus macaques, males injure one another most often during the mating season. For example, in the colony of free-ranging rhesus macaques on Cayo Santiago, Puerto Rico, 87% of male deaths occurred during the mating season (Wilson and Boelkins, 1970). Male rhesus macaques exhibit seasonal changes in sexual behavior, testes mass, and scrotal color. Experiments with ovariectomized females artificially brought into estrus (with estradiol benzoate) revealed that the presence of an estrus female is sufficient to induce all of these physiological changes in sexually quiescent males (Vandenbergh, 1969)

In species that breed year round, aggression varies depending on the cycles of potentially fertile females. Among chimpanzees, males modulate their fighting effort according to the likelihood of conception. Cues that indicate likelihood of conception include

sexual swellings and individual reproductive history. Female chimpanzees advertise their fertility with a large, bright pink anogenital swelling, and may provide other (perhaps olfactory) cues to the timing of ovulation (Wrangham, 2002). Females who have had at least one offspring (parous) are more likely to conceive than females who have never given birth (nulliparous). Males therefore compete intensely for access to parous females with sexual swellings, but do not fight over (and may even ignore) fully swollen nulliparous females. Male aggression also varies within each female's cycle. Early in a female's cycle, before she is likely to conceive, she often mates with all available males. As probability of conception increases, however, tensions rise. Muller (2002) found that when parous females were maximally swollen, males had higher testosterone levels, and aggression was more frequent and more severe. High-ranking males may guard the female, threatening or fighting any male who approaches her. Males may even team up with one or more partners in coalitionary mate guarding (Watts, 1998).

Operational Sex Ratio

Male mating opportunities depend not only on the number of females in the population, but how often those females are fertile, which in turn depends on interbirth intervals. A statistic designed to capture this information is the operational sex ratio, which is defined as the number of breeding females that will be available to each male each year (Emlen and Oring, 1977; Mitani, 1990). If the operational sex ratio is particularly low, intense fighting can result. A horrific unintended experiment in extremely low operational sex ratios occurred in the 1920s, when zookeepers at the London zoo formed a group of 100 hamadryas baboons that contained only six females (de Waal, 1989; Zuckerman, 1932). In the wild, hamadryas baboons live in multilevel societies based on "one male units," which are groups of females fiercely defended by a single male (Kummer, 1968). At the London zoo, the males fought brutally with one another and herded the females mercilessly. Fighting continued even after 30 additional females were added. "Six and a half years later, the few surviving females were removed. Sixty-two males and thirty-two females, over two-thirds of the original population, had died of stress and injuries" (de Waal, 1989). Although such a bloodbath has never been recorded from the wild, skewed sex ratios can lead to fatal fighting. In Budongo Forest, Uganda, male chimpanzees ganged up on and killed a male of their own community during a time of particularly intense mating competition (Fawcett and Muhumuza, 2000).

Over evolutionary time, low operational sex ratio favors the evolution of large male body size (Mitani et al., 1996). In rare cases, development of large male body size depends on the social environment. Orangutan males, for example, occur in two morphs: big males and small males (Maggioncalda et al., 1999; Rodman and Mitani, 1987). Big males are nearly twice the weight of females, with conspicuous fibrous pads (flanges) on the sides of their face. Small males are about the same size as adult females and lack flanges and other secondary sexual traits. Small size also may serve as a sort of sexual mimicry, in that big males tolerate small males, but challenge other big males who enter their range (Mitani, 1985). Body size also relates to strategies for aggression: whereas big males fight other big males, small males adopt a "sneaking" strategy, mating with females (often coercively), but avoiding fights with other males.

These two morphs appear to be the result of developmental flexibility rather than fixed genetic differences. Small males can stay small for many years, but then grow big

when circumstances are more favorable. Male orangutans thus delay the costs of growing to large body size until social circumstances suggest the investment in growth will pay off.

Relative Number of Young Males

While most primate studies focus on the number of adult males in a population, the age structure of the male population may also affect rates of aggression. This factor appears relatively neglected in primate studies, but has been addressed in several human studies. Human males, like other primates, are most aggressive as young adults (e.g., 15–30 yr old). In the United States, regions that had unusually large numbers of young males, such as the western frontier, experienced high crime rates (Courtwright, 1996). Mesquida and Wiener (1996) argue that, in humans, male coalitionary aggression is best understood as a “reproductive-fitness-enhancing social behavior” and that such aggression should be most frequent when a society contains a relatively large number of young males. Analysis of collective aggression in a wide variety of modern states found that societies with relatively many young males had more conflict-related deaths (Mesquida and Wiener, 1996). A large ratio of young to old males is a feature of rapidly growing populations. This finding suggests that intense male–male aggression should be a widespread trait of rapidly growing populations.

FOOD

Benefits

Primates in the wild spend much of their time either feeding or looking for food. Food is, of course, essential for both males and females, but is particularly important for females who gestate, nurse, and carry their offspring. Therefore, food is a crucial limiting factor for female reproductive success (Trivers, 1972). Food quality and distribution can affect grouping patterns and intergroup relations and have figured prominently in discussions of primate social evolution (Isbell, 1991; van Schaik, 1989; Wrangham, 1980).

Costs

Fights over food are generally less severe than fights over mates. Although food is essential for survival and reproduction, a given piece of fruit or leaf is usually low in value compared to the risk of injury from fighting. Overt aggression, therefore, should be limited to cases in which the contested item is particularly rare and valuable (e.g., Stevens and Stephens, 2002).

Environmental Factors

In general, animals are more likely to fight over food that is high quality and defensible. Chimpanzees, for example, mainly eat fruit and other plant parts, but sometimes hunt monkeys and other vertebrates. Meat obtained in such hunts elicits considerable excitement, feeding competition, and begging from chimpanzees (Goodall, 1986). Clumps of abundant food may influence aggression in at least three ways: (i) they serve as a focus for competition; (ii) they provide energy for fighting; and (iii) in species with fission–fusion societies, such as chimpanzees, abundant food brings together large parties, which may then be more likely to visit borders with neighboring groups.

Focus for Competition

Although natural foods, such as meat, can elicit aggression, an especially pronounced effect occurs with the introduction of human foods. In many early studies, researchers provisioned primates with cultivated foods to facilitate observations. Such provisioning provided exactly the sort of food distribution most likely to lead to increased aggression. For example, at Gombe, rates of aggression, including wounding, were higher during the early 1960s, when provisioning was intense, than in the late 1960s and 1970s, when provisioning was reduced (Wrangham, 1974). Other human sources of food, such as garbage pits, may produce similar effects on wild primate populations (Altmann and Muruthi, 1988). A study of rhesus monkeys found that rates of aggression were highest in captivity and in provisioned sites, such as farms and temples, with aggression occurring much less frequently in forest sites (Southwick, 1969). Although Southwick attributed the variation in rates of aggression to population density, food distribution may have been a more salient factor, given that the high-density populations all received food from humans.

Energy for Fighting

In general, aggression intensifies when resources are scarce or limited. Among wedge-capped capuchins, for example, fighting in large groups increases when food is scarce (Miller, 1996). Nonetheless, extremely limited food supplies can actually reduce aggression, as individuals lack the energy to waste on fighting. Southwick (1969) found that imposing food shortages on captive rhesus monkeys led to reduced rates of agonistic behavior. Abundant food can also free up energy for high-risk high-gain activities, such as hunting. For example, in contrast to the expectation that chimpanzees hunt animals when plant foods are scarce, chimpanzees in Kibale National Park, Uganda, hunt more often when fruit is more abundant (Watts and Mitani, 2002).

Food for Coalitionary Power

In chimpanzees, success in intergroup encounters depends on relative party size. Abundant food sources could increase the likelihood of border patrols, both by providing energy for long-distance travel and by bringing together the many males needed for safe patrolling. Testing this hypothesis is one goal of the current analyses of long-term data records of the chimpanzees of Gombe National Park, Tanzania.

STATUS

Benefits

In addition to fighting over specific resources, such as food and mates, primates frequently compete over status. In most primate species, individuals of one or both sexes can be ordered in a linear dominance hierarchy. Individuals generally appear keenly aware of their own place in the hierarchy. Chimpanzees, for example, give a specific call, the “pant-grunt,” when approaching higher ranking individuals. High rank generally provides priority of access to food, mates, and other resources. Recent analyses of DNA from wild populations supported the prediction of observational studies that high-ranking males father more offspring in baboons (Altmann et al., 1996), chimpanzees (Constable et al., 2001), and pygmy chimpanzees or bonobos (Gerloff et al., 1999).

High rank may also provide some protection from stress, depending on the stability of the hierarchy (Virgin and Sapolsky, 1997).

Even when rank is difficult for human observers to assess, it can have important fitness consequences. For example, dominance interactions between female chimpanzees are subtle, and for many years, researchers assumed social status did not have great importance for them. In contrast to this assumption, analysis of long-term records from Gombe National Park, Tanzania, found important effects (Pusey et al., 1997). Higher-ranking females had “higher infant survival, faster maturing daughters, and more rapid production of young.” High-ranking females appeared able to acquire better home ranges within the community’s territory and, thus, had access to a better food supply.

Costs

Status provides a cue to the cost of attacking a given individual. High-status individuals are dangerous to attack, either because they are big and strong or because they have many powerful allies. Loss of status can be especially costly. Falling from top rank can lead to a rapid and irreversible decline. With such high stakes, fights for alpha status can be especially fierce and are sometimes fatal (Kitopeni et al., 1995; Nishida, 1996). During times of intense competition for ranks, high-ranking individuals may suffer from increased stress (Alberts et al., 1992).

Environmental Factors

Status depends to some extent on individual traits, such as age, fighting ability, and political skills. Status also depends on factors in the individual’s environment, particularly the number of kin and the number and quality of rivals.

Kin

Many species of *Cercopithecines*, the group that includes baboons, rhesus macaques, and vervet monkeys, live in groups in which most females are related to one another, and most males are unrelated immigrants (reviewed in Dunbar, 1988). Female status depends largely on the number and rank of her kin. Large matriline generally outrank small matriline. Younger daughters rank higher than their older sisters, because the younger ones are born with more kin. Individuals with more kin win more fights and may be more likely to initiate fights with members of rival matriline.

Among chimpanzees and bonobos, males stay in their natal group and females usually emigrate at adolescence (Pusey, 1979; Gerloff et al., 1999). Because males stay in their natal group, average relatedness among males may be on the order of half-siblings (Morin et al., 1994), facilitating within-group cooperation. Male chimpanzees may sometimes form coalitions with brothers, but because of long birth intervals, chimpanzees rarely have brothers close enough in age to form useful coalition partners. Mitochondrial DNA studies show that in chimpanzees many coalition partners are not maternal siblings (Goldberg and Wrangham, 1997; Mitani et al., 2000). Among bonobos, male rank and reproductive success may depend on support from their mothers (Gerloff et al., 1999).

Number and Quality of Rivals

Dominance hierarchies are most stable when the top-ranking individual is clearly more powerful than any rivals. In chimpanzees, a powerful alpha male can maintain his rank

for many years. In Mahale National Park, Tanzania, the male Ntologi maintained his alpha status for 16 yr before being deposed and killed by his rivals (Kitopeni et al., 1995; Nishida, 1996). Status striving is much more intense when many equally matched contenders are jostling for rank (Maynard Smith, 1982).

LAND

Benefits

Many primate species defend territories, warning outsiders with loud calls and attacking intruders. Either or both sexes may participate in territory defense. For females, the primary benefits of a territory are food for self and offspring. Males may benefit both by defending a feeding territory for self, females, and offspring, and by defending females (Fashing, 2001).

Costs

Territory defense is energetically expensive and can result in costly fights with rival groups. The loud calls primates commonly produce to advertise territory ownership can also attract the attention of unintended audiences such as predators (Wilson et al., in review; Zuberbuhler et al., 1997).

Environmental Factors

Primates defend territories when it is economically feasible to do so (Mitani and Rodman, 1979; Lowen and Dunbar, 1994). Mitani and Rodman (1979) proposed an “index of defendability (D), which is the ratio of observed daily path length (d) to an area equal to the diameter (d') of a circle with area equal to home range area of the animal.” Species with an index of $D = 1.0$ or greater, thus had day ranges that were long compared to the size of their territory. Mitani and Rodman found that all territorial species and few nonterritorial species had an index of $D = 1.0$ or greater. Lowen and Dunbar (1994) developed a refined version of this model that generally supported Mitani and Rodman’s earlier findings. Although these models focused on comparisons among species, territory defense varies within species as well. For example, chimpanzees defend territories in forest sites, but the enormous home ranges occupied in drier savanna sites are probably not economical to defend.

Territorial behavior may vary among members of a group, depending on an individual’s stakes in defending the territory. For example, if high-ranking males gain a disproportionate share of matings, low-ranking males may have little incentive to join in intergroup fights (Nunn, 2000).

In forest habitats, male chimpanzees patrol the boundaries of their territories and show hostility toward any members of other communities except for estrous females without offspring (Goodall, 1986; Williams and Pusey, submitted). Chimpanzee intergroup relations include fatal attacks, which will be discussed more in the following section.

KILLING ADULTS

Perhaps the most widespread concern underlying studies of aggression is the question, “Why do people kill one another?” Enormous attention has focused on questions

such as whether such killing is uniquely human, and if other animals do kill conspecifics, why they do so. Despite early assertions to the contrary, intraspecific killing is not uniquely human. Animals sometimes kill both infants and adults of their own species. Because the risks involved and underlying evolutionary logic differ depending on the age of the victim, I discuss infanticide in the next section and focus on killing of adults here.

Lethal fighting is readily observed in small animals such as arthropods, including many species of ants (Holldobler and Wilson, 1990), fig wasps (West et al., 2001), and spiders (Leimar et al., 1991). Among larger animals, intraspecific killing occurs infrequently, but can account for a large fraction of adult mortality (reviewed in Gat, 1999; Wrangham, 1999). For example, despite Montagu's assertion that wolves "do not attack other wolves" (Montagu, 1979), field observations reveal that intraspecific fighting accounts for 39–65% of adult wolf mortality (Mech et al., 1998).

Intraspecific killing has been reported for at least eight primate species. Most attention has focused on intergroup "wars" in our closest relatives, chimpanzees (Manson and Wrangham, 1991). Killing also occurs occasionally in other apes, including orangutans (Knott, 1998) and gibbons (Palombit, 1993). In addition to the apes, fights sometimes result in fatal injuries in several monkey species, including baboons (Starin, 1994) and rhesus monkeys (Lindburg, 1971; Westergarrd et al., 1999). In red colobus monkeys, coalitions of male and female residents have killed potentially infanticidal male intruders (Starin, 1994). Recent observations have revealed fatal fighting in two species of capuchin monkeys (Miller, 1998; Perry, Manson, and Gros-Louis, unpublished data). Reports of intraspecific killing in other species will likely emerge as additional long-term studies mature.

Benefits

Killing is widely regarded as the result of accidental or unusual circumstances, rather than the goal of aggression. Lorenz, for example, described numerous cases of killing among fishes in captivity, but attributed these deaths to the inability of the victims to escape in confined quarters (Lorenz, 1966). In support of this view, many deaths in the wild do result from wounds that become infected rather than from a concerted effort by the attacker to ensure his rival's death (e.g., Drews, 1996).

Nevertheless, attackers may obtain at least four benefits from killing their rivals. First, attackers may gain immediate nutritional benefits by eating their rival. Such predatory attacks are widespread among fish and arthropods, but are rare among mammals (Polis, 1981). Chimpanzees, for example, often eat victims of infanticide, but rarely if ever eat adult victims (Watts and Mitani, 2000). Second, killing rivals directly eliminates competitors for status or for resources, such as food and mates. Third, killing unrelated rivals reduces the genetic contribution of rivals to the population. A fourth benefit applies to species that defend group territories. In general, larger groups tend to defeat smaller groups in territorial fights. By killing rivals, attackers reduce the numerical strength of rival coalitions, thereby increasing their chances of success in future territorial contests (Wrangham, 1999).

In some cases, the unintended death of the victim may even cost the attacker. For example, Sapolsky describes a case in which a female baboon died following infection of a bite wound inflicted by a male of her troop (Sapolsky, 2001). It seems unlikely that this male benefited from killing a potential mate.

Costs

The apparent inhibition against killing conspecifics results not from an urge to preserve one's species, but from the fact that killing rivals is usually difficult and dangerous. The costs of killing can be reduced dramatically, however, in species with coalitionary bonds (Manson and Wrangham, 1991). In a discussion of the costs of killing, Wrangham (1999) distinguished three categories of species. In the first category, which includes most species, killing occurs infrequently if at all. The second category includes a smaller number of species in which fights are dyadic, but frequently result in death. For example, 12% of male pronghorn antelope and 5–10% of male musk oxen may die from fighting during the annual mating season (Byers, 1997; Wilkinson and Shank, 1976). For such species, individuals compete over such high stakes (such as access to many fertile females) that even costly fights may pay off (Enquist and Leimar, 1990). The third category consists of species in which killing is frequent, but involves coalitions or "gang attacks." If members of one coalition greatly outnumber their rival, they can kill the rival without much risk of injury for themselves. Wrangham (1999) included two primate species in this category: humans and chimpanzees (with western red colobus a potential candidate).

Manson and Wrangham (1991) argue that gang attacks should occur most frequently in species with fission–fusion social organization, in which group members travel in subgroups (parties) of variable size and composition. Many primates, such as baboons and rhesus monkeys, live in stable troops in which opportunities for gang attacks rarely occur. Coalitionary killing has been reported, however, for some populations of baboons (Popp, 1978), rhesus macaques (Lindburg, 1971), and white-faced capuchins (Perry, Manson, and Gros-Louis, unpublished data).

Environmental Factors

Dyads

In species with only dyadic fights, killing should be rare except when the potential benefits are unusually high. Among primates, such fights appear most common during competition for mates and when males attempt to join a new group (Wilson and Boelkins, 1970; Brain, 1992).

Coalitions

Among species with coalitionary fighting, factors likely to influence the frequency of gang attacks include the following: (i) numerical imbalances; (ii) distribution and availability of food; and (iii) estrous females.

NUMERICAL IMBALANCES

Observations and field experiments show that chimpanzees assess numerical imbalances before approaching intruders (Watts and Mitani, 2001; Wilson et al., 2001). Watts and Mitani found that chimpanzees were more likely to approach the calls of neighboring groups when in parties with many males. In these observations, however, the party composition of neighboring groups was generally unknown. Wilson and colleagues conducted a series of playback experiments for a more controlled test (Wilson et al., 2001). Playback experiments found that chimpanzees were more willing to call to and approach a simulated intruder the more they outnumbered the intruder (Wilson et al., 2001).

Parties with one or two males remained quiet, approached in only half the cases, and approached more slowly when they did approach. In contrast, parties with three or more males gave a loud vocal response and rapidly approached the speaker. Chimpanzees are more likely to visit borders when in larger parties (Bauer, 1980; Wilson, 2001) and boundary patrols tend to contain large numbers of males (Watts and Mitani, 2001).

Playback experiments with howler monkeys also show evidence of numerical assessment (Kitchen, 2000). Kitchen played recordings of the howls of one or three male intruders to defenders in groups with one, two, or three males. Alpha males gave a weaker howling and approach response when played the howls of larger groups. Low-ranking males only howled and approached if their group outnumbered the simulated intruders.

Gang attacks should be more likely in cases in which a large group neighbors a small group. Although party size should vary for both groups, the larger group has a greater maximum party size and, therefore, has better odds of meeting the neighbors with an overwhelming numerical advantage. At Gombe, the main study community (Kasakela) now greatly outnumbers its two neighboring communities. In recent years, the Kasakela males have expanded their range considerably and have brutally attacked members of both neighboring communities (Wilson et al., submitted).

Even in cases where neighboring groups are of similar size, males in large groups may visit borders more often than males in small groups. The largest chimpanzee community studied to date, the Ngogo community of Kibale National Park, Uganda, contains at least 144 chimpanzees (Watts and Mitani, 2001). Ngogo chimpanzees patrol their boundaries at an unusually high rate. Only one of the communities neighboring Ngogo, the Kanyanchu community, has been habituated. Kanyanchu appears to be a very large community and may be similar in size to Ngogo.

In captive situations, management practices can create opportunities for gang attacks. For example, rhesus monkeys live in troops composed of one or more female kin groups (matrilines). Related females frequently join in fights against members of rival matriline. Such fights rarely lead to severe injuries under normal circumstances. In captive groups, however, members of matriline are frequently separated for management purposes. Under such circumstances, members of rival matriline may attack and kill a female separated from her kin (Westergarrd et al., 1999).

FOOD AVAILABILITY AND DISTRIBUTION

In fission–fusion societies, party size depends largely on food availability. When more food is available, larger parties form. Chimpanzees depend on ripe fruit, and the availability of ripe fruit can vary greatly over short distances. The possibility exists that one community could enjoy a bumper crop of fruit while their neighbors suffer through a lean season. The community with more fruit would travel in larger parties and would have an increased chance of meeting their neighbors with overwhelming numerical superiority.

Food availability also affects opportunities for killing, if it enables group members to travel in more stable parties. Among bonobos and some populations of chimpanzees, the costs of grouping appear to be reduced by the availability of high-quality herbaceous plants that enable individuals to continue feeding when traveling between fruit trees (Wrangham et al., 1996). Increased stability of parties may be responsible for the lack of observed coalitionary killing in both bonobos and chimpanzees of Tai National

Park, Côte d'Ivoire, despite hostile intergroup relations in both populations (Wrangham, 1999).

ESTROUS FEMALES

In chimpanzees, party size also varies with the number of estrous females. Estrous females attract many males, even when fruit supplies are poor. One intergroup killing at Kibale occurred when many males traveled with an estrous female into border regions (Kibale Chimpanzee Project, unpublished data).

KILLING INFANTS

In many primate species, infants face a serious risk of being killed by conspecific adults. Sociobiological explanations of infanticide have generated a large and contentious literature, with controversy continuing today (Bartlett et al., 1993; Curtin and Dolhinow, 1978; Hausfater and Hrdy, 1984; Hrdy, 1974; Schubert, 1982; Sussman, 1997; Sommer, 2000). Infanticide has been directly observed in the wild in 17 primate species and is known or strongly suspected to occur in a total of 39 primate species (van Schaik, 2000a). Infanticide also occurs in many other mammals, mainly carnivores and rodents, but also dolphins, horses, and hippos (van Schaik, 2000a). Infanticide rates vary among species and populations, but can account for a large portion of infant mortality. At least 30–40% of infant mortality results from infanticide in mountain gorillas (Watts, 1989), chacma baboons (Palombit et al., 2000), and howler monkeys (Clarke and Glander, 1984). In most cases, the infant killers are male, though in chimpanzees, gorillas, and others, including some rodents, females may commit infanticide (Goodall, 1977; Digby, 2000).

Benefits

Both nonadaptive and adaptive hypotheses have been proposed for infanticide. The two major nonadaptive hypothesis are that infanticide is (*i*) a social pathology caused by some disturbance, such as unusually high population density (Curtin and Dolhinow, 1978) or (*ii*) an accidental byproduct of generalized aggression (Bartlett et al., 1993; Sussman et al., 1995). Neither of the nonadaptive hypotheses explains the species distribution of infanticide or its occurrence in undisturbed environments (e.g., Enstam et al., 2002). While disturbance or pathology may account for some cases, current evidence supports the view that, in general, infanticide is a behavioral strategy that provides fitness benefits to infant killers (Palombit, 1999; van Schaik, 2000b). The particular benefits obtained may differ between the sexes and among species with different social organization.

The most prominent adaptive hypotheses for infanticide is the sexual selection hypothesis (Hrdy, 1974). This hypothesis proposes that males kill the infants sired by rival males to bring the infant's mother into reproductive status faster. Such killings usually take place after the infanticidal male has taken over a troop (e.g., hanuman langurs) (Hrdy, 1977) or entered a new troop (e.g., baboons) (Palombit, 1999). The sexual selection hypothesis now enjoys strong support (van Schaik, 2000c). Genetic testing has shown that male hanuman langurs selectively killed unrelated infants and were the most likely father of the mother's next infant (Borries et al., 1999). A similar hypothesized benefit

is that infant killing may induce females to join the attacker's group, as the attacker has demonstrated the inability of the female's current male to defend her (e.g., gorillas) (Fossey, 1983; Watts, 1989; Wrangham and Peterson, 1996).

The sexual selection hypothesis does not explain all cases of infanticide. Among chimpanzees, for example, many infanticides occur during intercommunity conflict, with little evidence that infant-deprived mothers later mate with the infant's killers. In addition to increased opportunities for mating, killing infants may provide at least four additional benefits to attackers, comparable to the benefits of killing adults (Hrdy, 1977; van Schaik, 2000c). First, attackers may gain immediate nutritional benefits by eating their rival. Among chimpanzees, for example, attackers often do eat infant victims (Watts and Mitani, 2000), but such cannibalism is rare among other primates and, even in chimpanzees, does not appear to be the primary motive for infanticide. Second, killing unrelated infants eliminates future competitors for resources such as food and mates. Third, killing unrelated infants reduces the genetic contribution of rivals to the population. Fourth, in species that defend group territories, killing infants of rival groups can reduce the rival group's coalitionary strength. Among chimpanzees, infanticide may depend on some combination of these factors (Arcadi and Wrangham, 1999; Watts and Mitani, 2000).

Costs

The primary cost to infanticide is that mothers, potential fathers, and others may defend infants. Among baboons, for example, female baboons form "friendships" with males who defend them against attack by potentially infanticidal male immigrants (Palombit, 1999). Another potential cost of infant killing is that in cases of uncertain paternity, males could kill their own offspring. Male chimpanzees of M-group in Mahale National Park, Tanzania, killed the infant of a female who had been absent from the group for several months prior to birth (Takahata, 1985). Takahata believed the infant was sired by M-group males, raising the possibility that a father mistakenly killed his infant. Though such mistakes may well happen, the possibility exists that, in this case, the chimpanzees evaluated paternity more accurately than the researchers. In the great majority of cases in which observers can estimate paternity with confidence, the killers are in fact unrelated to their infant victims (van Schaik, 2000c).

Environmental Factors

Environmental factors proposed to affect infanticide rates include population density, intruder pressure, the number of males in groups, and female dispersal patterns.

Population Density

A popular explanation holds that infanticide (along with other forms of aggression) is a pathological response to high population density (Bartlett et al., 1993; Curtin and Dolhinow, 1978; Judge and de Waal, 1997; Moore, 1999). Population density, however, is a poor predictor of infanticide frequency (Moore, 1999; van Schaik, 2000c). Infanticide occurs in populations with low density, such as patas monkeys (Enstam et al., 2002) and some langur populations (Newton, 1986). Among blue monkeys, comparison of high- and low-density populations found that infanticide rates were actually higher at low population density (Butynski, 1990).

Intruder Pressure

In most cases, male intruders represent the greatest threat of infanticide. Rates of infanticide should therefore vary with the rate at which lone males attempt to join or take over troops (Moore, 1999; Janson and van Schaik, 2000). In a comparative study of 16 primate species, Janson and van Schaik (2000) found that one measure of intruder pressure, the “relative rate of male replacement,” was the most important factor affecting infanticide rate.

Number of Males in Groups

In general, infanticide rate declines with increasing number of males per group (Janson and van Schaik, 2000). This result depends on two factors. First, males in multi-male groups may cooperate to defend against intruder males. Second, multi-male groups present a less attractive target to lone intruders, because, if they joined such a group, they would have to share matings with the group’s current males. In contrast, intruders joining one-male groups often expel the former resident male (Janson and van Schaik, 2000).

Female Dispersal Patterns

At Gombe, the mother–daughter pair of Passion and Pom were observed to kill three infants and were suspected of killing up to six more during a 4-yr period (Goodall, 1990). Goodall initially interpreted these killings as aberrant behavior resulting from Passion’s strange personality and poor mothering skills. In recent years, however, observers have witnessed additional attempts by females to kill newborns (Pusey et al., 1997). These observations suggest that Passion and Pom’s behavior was not the result of social pathology, but, instead, simply be an extreme example of ordinary female–female competition. All observed female infanticide attempts have involved pairs of females (usually mother–daughter) attacking lone mothers. This suggests that female infanticide at Gombe depends not on individual pathology, but on the numerical advantage gained by females with grown daughters or other close allies.

At most study sites, female chimpanzees leave their natal group at adolescence, thereby avoiding the risk of inbreeding (Pusey, 1979). At Gombe, roughly half of females stay in their natal community or return there to have infants. This unusually high percentage likely results from the few choices available to females. The park contains only two groups besides the main study group, and destruction of forest outside the park has severed connections to any other chimpanzee communities. A number of Gombe females benefit from the unusual advantage of having an adult daughter in her group, which is a natural ally during fights with other females. In all observed female infanticide attempts, the attackers worked in pairs, and all but one pair involved a mother–daughter team.

CONCLUSIONS

Studies of primates have explored many ways in which aggression varies with environmental factors. Though our understanding of primate aggression is far from complete, current studies support the view that primates, like other animals, use aggression strategically. Primates assess various environmental factors, such as the relative fighting ability of their opponents and the value of the resource in question, to determine whether aggression is likely to pay.

Early observers of primate aggression, especially infanticide, cannibalism, and intergroup killing, regarded these behaviors as pathological or dysfunctional behaviors. Though some critics persist in this view, current evidence indicates that in most cases aggression follows evolutionary logic. Animals attack other animals when the costs of attacking are low or when the benefits are likely to be high. In a complicated world, animals may not always correctly calculate the odds of success, and cases of individual pathology surely occur. Moreover, pathologies do occur, and some behaviors that proved adaptive in ancestral environments may prove unsuitable to novel environments. Nevertheless, the evidence from field and laboratory studies supports the view that aggression occurs when it is likely to benefit the reproductive success of the aggressor and/or the aggressor's kin.

The focus on pathology and dysfunction includes a long history of searching for some single biological trait intrinsic to criminals and other aggressors, such as head shape, body type, XYY genotype (reviewed in Niehoff, 1999). Recent studies have focused on physiological traits such as serotonergic function (Wallman, 1999). Evolutionary considerations suggest that any such single trait is likely to provide, at best, a partial explanation.

In nature, individuals must contend with frequent changes in their environment and in themselves. Evolutionary considerations suggest that individuals should be designed to use aggression strategically. Rather than predicting individual fate, physiological mechanisms may provide a means for tracking the environment and motivating the individual to use aggression appropriately under particular circumstances. The studies reviewed above provide some examples of how physiology depends on environmental factors, such as the intensity of competition for mates. Our understanding of the relation between physiological mechanisms and functional goals should continue to improve with advances in technology for physiological assays of free-ranging animals.

Current evidence indicates that humans use aggression much as other primates do, to obtain fitness-enhancing resources such as mates, food, status, and territory (Chagnon, 1988; Daly and Wilson, 1988). For example, just as male rhesus monkeys, baboons, and chimpanzees are more likely than females to kill conspecifics, men commit murder far more often than women. Male sexual jealousy may account for 30–50% of all homicides (Daly and Wilson, 1988). Just as infant gorillas and langur monkeys risk being killed by new males, human children are up to 100 times more likely to be killed if living with a step-parent (Daly and Wilson, 1988). Intergroup conflict, from street gangs to world wars, involves territorial disputes. Members of street gangs mark territorial boundaries with graffiti (Alonso, 1999), and gangland homicides are frequently described as battles over “turf” (Decker and van Winkle, 1996). Just as howler monkeys and chimpanzees assess the odds of winning before joining an intergroup fight, people around the world participate in deadly ethnic riots when they perceive that the costs of attacking their enemies will be low (Horowitz, 2001).

Human violence does not result from the release of a built-up aggression drive, but neither does violence among other primates. Like other primates, we are sensitive to environmental factors that affect the likely payoffs of aggression. Moreover, unlike any other primate, we have some hope of learning lessons from history and science. Human societies show enormous variation in rates of aggression across space and time. Regions,

such as Western Europe and Japan, once plagued with war, are now among the most peaceful in the world. Rates of violent crime and warfare respond quickly to changes in demography and other environmental factors. A better understanding of how human violence responds to changes in costs and benefits should provide us with better tools to make our own societies safer from violence. Any hope of such solutions will require answers to all four of Tinbergen's questions of function, mechanism, ontogeny, and phylogeny.

ACKNOWLEDGMENTS

I thank Mark Mattson for the invitation to contribute this chapter. For helpful critiques, I am grateful to Seth Blackshaw, Bob Montgomery, Anne Pusey, Jeff Stevens, and Becky Sun. Dawn Kitchen and Julie Gros-Louis generously provided access to unpublished material.

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