Large-brained, slowly developing, dependent offspring require long-surviving parents to reach maturity. A measure of this parental dependency effect is the differential survival of caretakers versus noncaretakers.

An orangutan mother with her offspring. Except for mothers and their offspring, orangutans lead a solitary existence. The burden of taking care of the slowly maturing offspring falls entirely on the mother. Birute Galdikas found that the average interbirth interval for orangutan mothers is eight years.

Big Brains and Parenting

by John M. Allman

Having a larger brain is linked to enhanced survival. This being the case, why don't more animals have large brains? The answer to this puzzle is that the costs of growing and maintaining a big brain are very high both for the individual and for its parents. In a newborn human the brain absorbs nearly two thirds of all the metabolic energy used by the entire body. This enormous burden results from the very large relative size of the brain in human infants and from the additional energy required for dendritic growth, synapse formation, and myelination, which is far greater even than the considerable energy required to maintain the adult brain. Because the brain requires nearly two thirds of the infant's energy supply, this constraint probably sets an upper limit in the evolution of brain size because the muscles and the other vital organs, the heart, the liver, the kidneys, the stomach, and intestines, must use energy as well.

Nurturing a large-brained baby imposes enormous energy costs on the mother because of the burden of lactation, which is far more costly than gestation. In small mammals lactation can triple the mother's food requirements. The nutritional constituents of breast milk are probably optimized for brain growth in particular species. In a carefully controlled study of children tested at age eight, those who had been bottle-fed human milk as babies had an average IQ 10 points higher than did the children who had been fed formula.

Not only are the energetic costs high, but development is slow in big-brained babies. George Sacher proposed that the brain serves as a pacemaker for the growth of embryos. In primate species, relative brain mass scales with the time after birth required to reach maturity, implying that the development of larger brains requires more time.

The additional time is needed for the postnatal growth of the brain, which in humans reaches its full adult size only by about the time of puberty. This postnatal growth includes the formation of myelin insulation around axons, which proceeds at different rates in different parts of the brain. Paul Flechsig showed that the axons of subcortical structures acquire their myelin insulation before

The myelinating pathways in a 7-week-old human infant, from the work of Paul Flechsig. This is a horizontal section through the forebrain and cerebellum; myelin is stained blue. Note that the myelinated pathways are already well developed in the cerebellum and the central parts of the brain at this stage, but there is relatively little myelin in the white matter associated with the neocortex. However, there is a U-shaped pathway (arrow) of myelinating fibers leading from the lateral geniculate nucleus of the thalamus to the primary visual cortex. Bands of fibers also lead to the primary somatosensory and motor cortical areas. The fiber connections of the higher cortical areas myelinate much later in development.

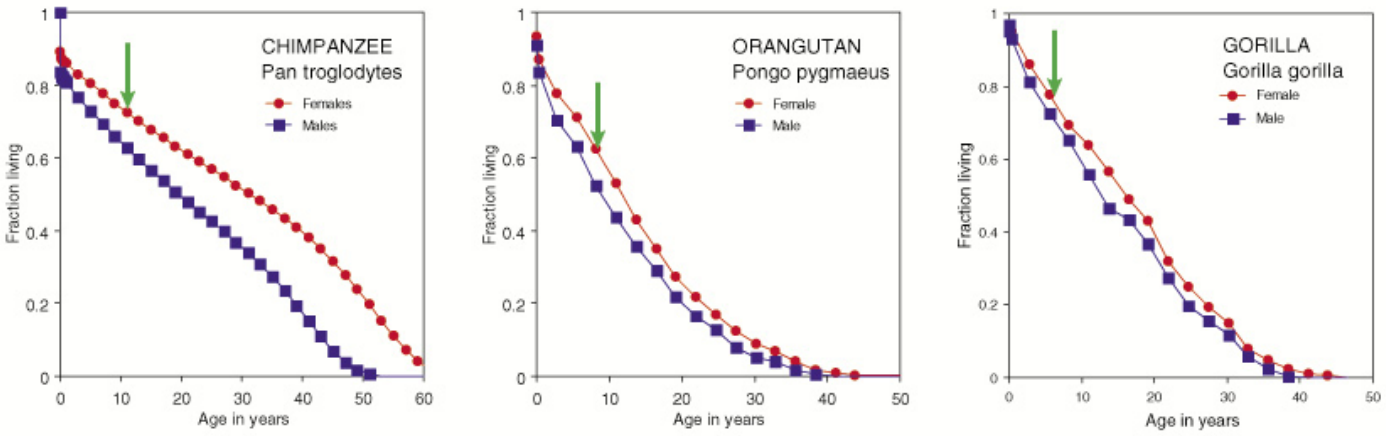
the cortex, and within the cortex the primary sensory areas are myelinated long before the higher cortical areas in the temporal, parietal, and frontal lobes.

The rate of synapse formation also varies among cortical areas. Peter Huttenlocher found that synapto-genesis is much slower in the frontal cortex than in primary visual cortex. Time is also required for the formation of experience-dependent connections essential for adult functioning. For example, as discussed in Chapter 6, the capacity to judge the size and distance of objects develops very slowly and is still quite immature in eight-year-old children. The gradual refinement of this capacity probably depends on countless interactions between the child and his or her spatial environment, which in turn influences synaptic changes in the visual cortex that continue quite late in childhood. Because the brain is unique among the organs of the body in requiring a great deal of feedback from experience to develop to its full capacities, brain maturation may serve as a rate-limiting factor that governs the maturation of the entire body. As Steven Quartz and Terrence Sejnowski have suggested, the animal's experience in interacting with its environment directs the growth of dendrites and the formation of synaptic connections. They propose that learning is a process that occurs in successive stages, each building on the earlier ones. Larger brains require a longer time to develop because more stages are involved.

Thus the rearing of large-brained babies requires parental support for commensurately long periods. Moreover, large-brained offspring are mostly single births and the interbirth intervals are long, which probably reflect the large costs of rearing these offspring. The parents must live long enough past their sexual maturity to sustain the serial production and maintenance of a sufficient number of offspring to replace themselves while allowing for the early death or infertility of their children. Therefore, I hypothesized that in large-brained species that have single births, the sex that bears the greater burden in the nurturing of offspring will tend to survive longer. If the caretaking parent dies, the offspring will probably die as well, but if the noncaretaking parent dies, this event will have little impact on the offspring's chances of survival. The death of a noncaretaking parent might even enhance the survival of its offspring by removing a competitor for scarce food and resources. Thus genes enhancing the survival of the caretaking parent will be favored by natural selection, since they will be more likely to be transmitted to the next generation than genes that might enhance the survival of the noncaretaking parent. Male primates are incapable of gestating infants and lactating; but in several species, fathers carry their offspring for long periods, and the young may stay close to the father even after they move independently. According to the caretaking theory, females should live longer than males in the species where the mother does most or all of the care of offspring; there should be no difference in survival between the sexes in species in which both parents participate about equally in infant care, and in those few species where the father does a greater amount of care than the mother, males should live longer. Roshan Kumar, Aaron Rosin, Andrea Hasenstaub, and I tested this hypothesis by constructing mortality tables similar to those used by the life insurance industry for male and female anthropoids (monkeys, apes, and humans) and comparing these data with the sexual division of care for offspring.

The great apes are our closest relatives. Chimpanzees, orangutans, and gorillas nearly always give birth to a single offspring, and the interval between births ranges from four to eight years. Female chimpanzees, orangutans, and gorillas have a large survival advantage in data obtained from captive populations.

For example, in captivity the average female chimpanzee lives 42 percent longer than the average male. In the case of chimpanzees there also are data available from populations living in nature. In a 22-year study of a population of 228 chimpanzees living in the Mahale Mountains near

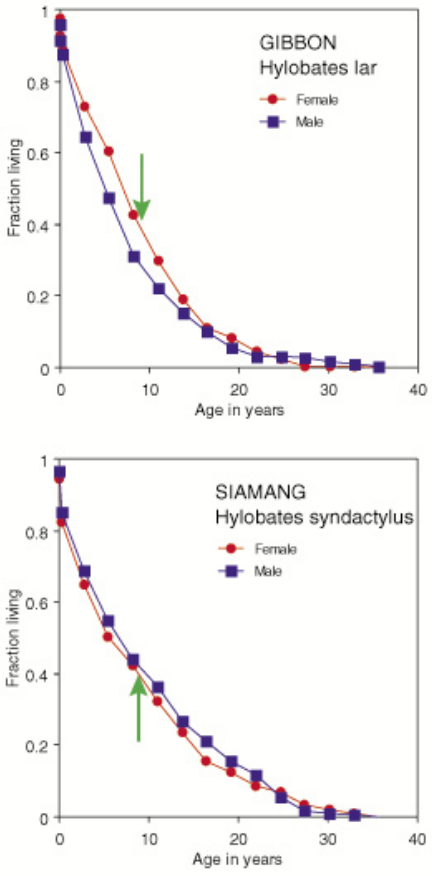


Differential survival between male and female apes. The chimpanzee data are from the work of Bennett Dyke and his colleagues; the orangutan and gorilla data were compiled from zoo records by Roshan Kumar, Aaron Rosin, Andrea Hasenstaub, and the author. (All the data in this chapter were published in the *Proceedings of the National Academy of Science*, Vol. 95, pages 6866-69, June 1998.) The arrow indicates the average age at which females give birth to their first offspring. The graphs show that at every age there are fewer surviving males than females.

A chimpanzee family studied by Jane Goodall at Gombe. The mother, Flo, was about 40 years old when this photograph was taken. Her infant, Flint, snuggles securely in her arms. Flo's adult daughter, Fifi, looks on, while the adolescent Figan grooms his mother. When Flo died a few years later, Flint, then 8 years old, died shortly thereafter, apparently unable to survive without her support. Maternal death is an important cause of death in young chimpanzees; maternal survival may even enhance the success of adult offspring. In her study at Gombe, Goodall noted that Flo's forceful personality contributed to the high status of her adult offspring. Male chimpanzees rarely care for their offspring. These factors would lead to natural selection favoring genes that would enhance female survival.

the shores of Lake Tanganyika, Toshisada Nishida and his colleagues found an equivalent number of male and female births but three times as many females as males in the adult population. This difference was not due to differential patterns of migration, and thus their observations indicate a strong female survival advantage for chimpanzees living in the wild. Chimpanzee mothers generally provide nearly all the care for their offspring, and females possess a very strong survival advantage. Although male care of infants is rare in chimpanzees, Pascal Gagneux and his colleagues have observed instances in which males have adopted orphaned infants and cared for them. Their observations indicate that the potential for male care is present in chimpanzees though rarely expressed. Orangutan mothers provide all the care for their offspring, which have very little contact with the solitary adult males. Gorilla mothers provide most of the care for their offspring, but the fathers protect and play with them. The female survival advantage in gorillas, while significant, is not so large as in chimpanzees or orangutans.

The lesser apes are our next closest relatives. Gibbons and siamangs live in pairs and have a single baby about once every three years. They maintain their pair bonds and defend their territories through spectacular vocalizations similar to the pair-bonding songs of birds. Gibbon mothers provide nearly all the care for their offspring, but David Chivers found that siamang males play a much larger parental role than do gibbon males. Siamang mothers carry their infants for the first year, but during the second year the male carries the growing infant. Siamang males are unique among apes in carrying their infants and in the closeness of their bonding with their offspring. Gibbon females have a survival advantage over males, but the situation is reversed in siamangs, where the males have a small advantage. Gibbon females on average live about 20 percent longer



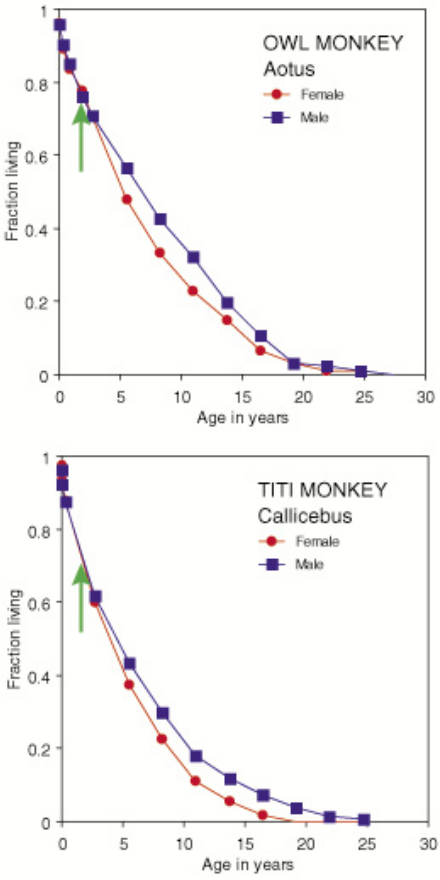
Differential survival patterns in gibbons and siamangs, closely related species living in the same habitat. Note that the female gibbons outlive males, but that male siamangs slightly outlive females. Siamang fathers are the only apes that carry their offspring on a regular basis. The data were compiled from zoo records by Roshan Kumar, Aaron Rosin, Andrea Hasenstaub, and the author.

than males, but siamang males live 9 percent *longer* than females. Siamang fathers are the only male apes that carry their infants and the only apes in which males outlive females.

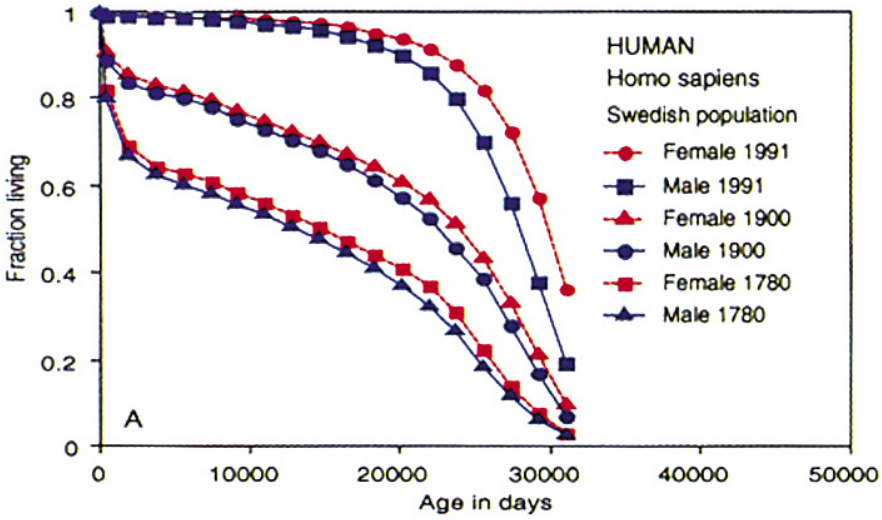
In Old World monkeys, females do most of the infant care, and several studies from natural populations show a female survival advantage. In New World monkeys, we found a significant survival advantage in captive spider monkeys, and John Robinson found a female survival advantage in the natural population of capuchin monkeys observed in Venezuela. In both spider and capuchin monkeys, mothers do virtually all the infant care. However the situation is dramatically reversed in two other New World primates, the owl monkeys and titi monkeys. These monkeys live in pairs like gibbons and siamangs, and also maintain their pair bonds and defend their territory through vocalizations. The fathers carry their infants from shortly after birth except for brief nursing periods on the mother and occasional rides on older siblings. I have observed in my colony of owl monkeys that if the father dies, the mother will not carry the infant, and thus the survival of the infant depends on the father. In both owl and titi monkeys, males and females die at the same rate until maturity, but after maturity the males have a survival advantage over females. Thus the timing of the male survival advantage corresponds to the period in their lives when they carry their offspring.

It is well known that women tend to live longer than men. It is often assumed that this is a modern phenomenon resulting from the greatly reduced risk of death in childbirth and other improvements in women's health practices. However, the female survival advantage is present in the oldest systematic records from a human population, which were collected in Sweden beginning in 1780, long before modern health practices were instituted. The female advantage is present at every age and for every Swedish census since 1780. In the Swedish population women live 5 to 8 percent longer than men. Similar female advantages were recorded in the earliest data from England and France in the 19th century and a female advantage has been present in most nations throughout the world in the 20th century. A female survival advantage has also been found for adults in the Aché, a well-studied hunter-gatherer population living in the forests of eastern Paraguay. These data strongly suggest that the survival advantage in human females has deep biological roots. However, it is smaller in relative terms than in gorillas, gibbons, orangutans, spider monkeys, and chimpanzees.

In most species there is a female advantage throughout life, but in all the anthropoids in which there are single births and the males carry their offspring, there is either no difference in survival between the sexes or there is a definite male survival advantage. These results run coun-



The adult male survival advantage in owl monkeys and titi monkeys, species in which the fathers carry their infants from shortly after their birth. The data were compiled from zoo records by Roshan Kumar, Aaron Rosin, Andrea Hasenstaub, and the author.



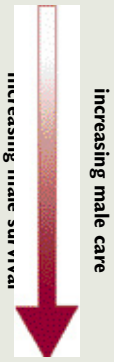
The human female survival advantage in the Swedish population in 1780, 1900, and 1991, plotted from data in the demographic study by Nathan Keyfitz and Wilhelm Fleiger and from the United Nations demographic database. (30,000 days is about 80 years.)

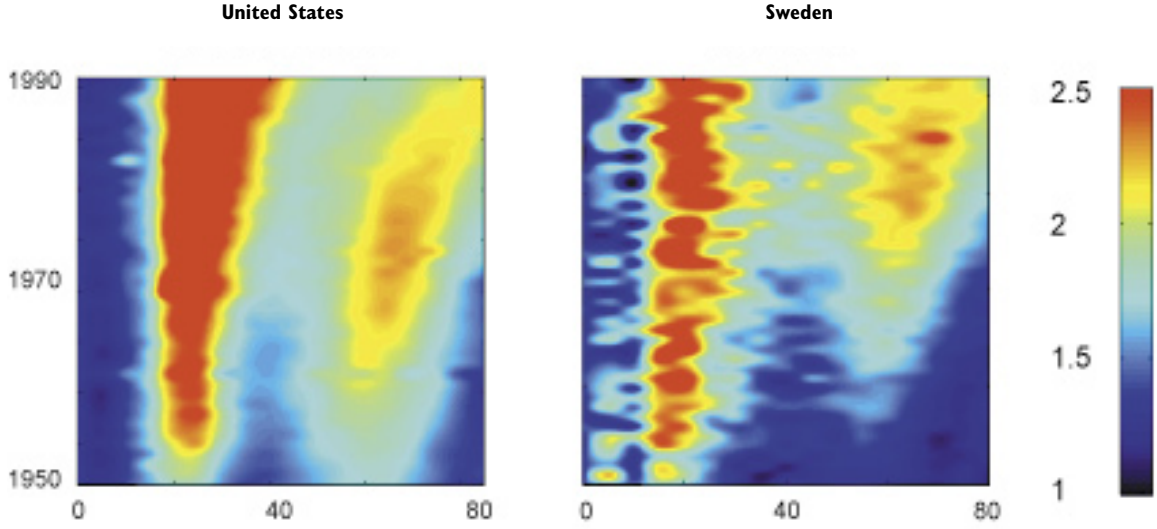
ter to the reasonable expectation that lugging a heavy squirming infant through the trees would increase the risk of falling or being eaten by predators. The magnitude of the difference in survival corresponds to the difference in the amount of care given to the offspring by each sex. Thus in the great apes where the mothers do virtually all the care, there is a large female advantage. Human males contribute significantly, but human females are the primary caregivers, and in humans there is a proportionally smaller, but still sizable, female advantage. In Goeldi's monkeys both sexes provide about the same amount of care and there is no difference in survival. In siamangs, both parents participate with the father taking over in the later stages of infant development, and siamang males have a small advantage. In owl monkeys and titi monkeys, males carry the babies most of the time from shortly after birth, and thus infant survival depends substantially on the male; in these monkeys there is a large male advantage.

Similar data have come from a nonprimate, big-brained species. Killer whales have very large brains. Their calves are born singly with an interbirth interval of 5 years, and they remain in close association with the mother throughout their lives. Males appear to have little direct role in parenting. A long-term demographic study of a natural population of killer whales in Puget Sound found that female life expectancy is more than 20 years longer than in males. The average female lives about 75 percent longer than the average male.

The differential mortality between caretakers and noncaretakers may be in part because the former are risk-averse and the latter tend to be risk-seeking. Caretakers tend to avoid risk because they risk not only themselves but also their offspring. This may be a conscious decision or the result of genetically determined instincts that would be favored by natural selection because they would lead to more surviving offspring. A second major factor may be a differential vulnerability to the damaging effects of stress. Natural selection would also favor the evolution of genes in caretakers that protect them against the damage induced by stress. The ratio between the rates at which males and females die varies during the course of life. In humans, the female survival advantage begins shortly after conception and continues throughout life with the largest advantage, in terms of the size of the ratio between male and female age-specific death rates, occurring at around age 25. In many countries, including the United States, Japan, and Sweden, there is evidence for a second smaller peak in the male to female death ratios later in life. Although smaller, these two peaks were present in the Swedish population in 1780. They also are present at about the same stages in the life cycle in some nonhuman primates such as gorillas and gibbons. The peak in early adulthood corresponds approximately to the period of greatest responsibility for childcare in women. The second peak appears to be related to a higher risk of heart disease and

PRIMATE	FEMALE/MALE SURVIVAL RATIO	MALE CARE
chimpanzee	1.418	rare
spider monkey	1.272	rare
orangutan	1.203	none
gibbon	1.199	pair-living, but little direct role
gorilla	1.125	protects, plays with offspring
human (Sweden, 1780–1991)	1.052–1.082	supports economically, some care
Goeldi's monkey	0.974	both parents carry infant
siamang	0.915	carries infant in second year
owl monkey	0.869	carries infant from birth
titi monkey	0.828	carries infant from birth





Excess male deaths as a function of age from 1950 to 1990 in the United States (left) and Sweden (right). Similar patterns are present in the data for Japan, Canada, and many other countries with well-developed health-care systems. The red pattern in the young-adult years indicates that more than twice as many men as women die at this stage of life. The pattern is smoother for the United States because of the much larger population size. The earlier Swedish data, going back to 1780, consistently show similar peaks in early and late adulthood, although the peaks are not as large as for modern data. This consistency suggests that biological factors are partially responsible. The second peak occurs after child rearing but reflects differential responses to stress earlier in life. The analysis was done by Andrea Hasenstaub and the author.

other afflictions in men. I believe that these two peaks represent two underlying mechanisms, one of which is mainly acting on the young and the other on the old. The first peak is largely due to differences between males and females in risk-taking behavior which results in higher rates resulting from accidents and violence in younger males. The second peak may result from increased male vulnerability to pathological conditions that develop without overt symptoms over a long period of time, such as high blood pressure and clogged arteries, which may be related to the cumulative effects of stress. By contrast, in owl monkeys and titi monkeys, the male survival advantage emerges shortly after maturity at the time when fathers begin to care for their offspring. This hypothesis would predict that their enhanced survival may be due to reduced risk-taking and vulnerability to stress.

In the contemporary United States population, women have lower risks than men of dying from the 13 most prevalent causes of death, indicating that the female survival advantage has an extremely broad base. A hormonal basis for this effect is evidenced by the observation by Francine Grodstein and her collaborators that post-menopausal women who currently receive estrogen replacement have a lower risk of death as compared to post-menopausal women who have never received supplemental estrogen. Estrogen enhances the actions of serotonin and thus may be responsible for reducing risk-taking behavior. Melanie Pecins-Thompson and her colleagues found in macaque monkeys that estrogen inhibits the expression of the gene that makes the transporter protein responsible for serotonin reuptake. Thus estrogen acts like drugs such as Prozac that inhibit the removal of serotonin at synapses and consequently increase the synaptic concentration of serotonin. Because of estrogen's effects on the serotonergic system it has been called nature's psychoprotectant.

Another possible basis for differential survival may be related to the stress hormones, the corticosteroids. The clearest evidence for this comes from a study by Robert Sapolsky who encountered and studied a group of vervets that had previously been subjected to chronic stress by overcrowded living conditions. Vervets are a type of monkey in which females do most of the care for offspring. Sapolsky found a substantial loss of neurons in a part of the cerebral cortex, the hippocampus, in males but not in females. The hippocampal neurons are richly supplied with receptors for the corticosteroid hormones, which are produced by the adrenal cortex to mobilize the body's defenses when subjected to stress. One role of the hippocampus is to regulate the pituitary's secretion of adrenocorticotropic hormone, which in turns signals the adrenal cortex to secrete the corticosteroid hormones into the bloodstream. The secretion of the corticosteroid hormones is the body's way of responding to severe, life-threatening emergencies, but the chronic secretion of these hormones can be very damaging. The hippocampal neurons are particularly vulnerable because they have many receptors for these hormones. Corticosteroids also suppress serotonin receptors in hippocampal neurons, which may diminish their stability and further increase their vulnerability. Because the serotonin reuptake mechanism is inhibited by estrogen, males may be more vulnerable than females in some species. The loss of the hippocampal neurons due to hyperexcitation means that the brakes on the secretion of the stress hormones are burned out, leading to escalating levels of damage and ultimately to death. Sapolsky's results indicate that male vervets are much more vulnerable to the destruction of the brain's system for regulating the stress response than are females. This may be the mechanism for male vulnerability in other species where females are the primary caregivers, and this theory predicts that the opposite would be true for those

species where males are the primary caregivers.

What is the biological role for the higher level of risk-taking in males in some species? In *The Descent of Man* in a section entitled the "Law of Battle," Darwin linked male aggression to competition among males for females. This has led to the widely accepted idea that aggressive males become socially dominant and because of their dominance enjoy greater sexual access to females and therefore greater reproductive success. However, there is evidence to suggest that other factors may be involved in male risk-taking.

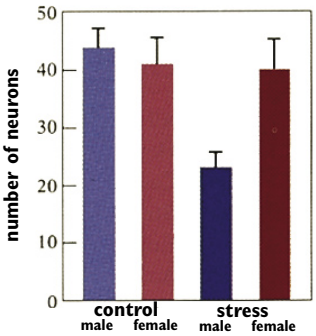
Let us begin by examining the first part of this relationship: does aggression lead to social dominance? In Chapter 2, I discussed the changes in social status in male vervet monkeys induced by experimentally manipulating serotonin levels. In this study, male status was invariably preceded by changes in affiliative behaviors with females in the social group such as grooming interactions. Increased affiliative behavior led to increased female support in dominance interactions with other males, which in turn led to rising status. Decreased affiliative behavior led to decreased female support, which in turn led to declining status. This investigation and many observational studies indicate that high status in primate groups is much more dependent on social skills and coalition building than on aggression.

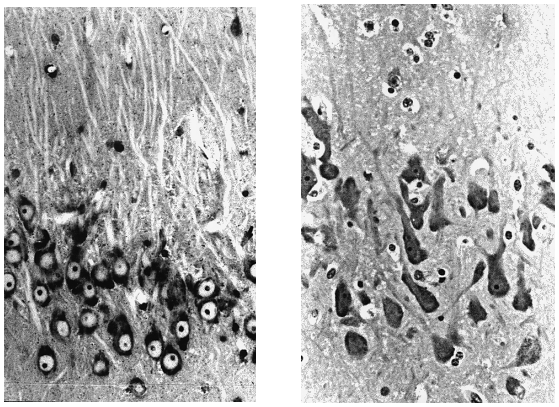
Now let us turn to the second part of the aggression-dominance-reproductive success theory: does the possession of high rank lead to reproductive success? Pascal Gagneux and his colleagues have conducted a long term study of the social structure of chimpanzees living in the Tai forest in the Ivory Coast. In order to measure male lineages, they extracted DNA from cells attached to hair samples for all the members of this group, and thus they were able to determine which chimpanzees had fathered which offspring. They found two surprising results. First, on the basis of the DNA patterns, they were able to rule out all the males in the group as possible fathers of half of the youngsters. Thus the females were covertly mating with males outside their social group; the status of those males within their own groups is unknown. Second, for the youngsters that were fathered by males within the social group, there was only a weak relationship between dominance and reproductive success. Brutus, the top ranking male for 10 years, and Macho, who was the alpha male for 1.5 years, sired no offspring during their periods of dominance, although each sired one after they declined in status. These results highlight the importance of actually determining male parentage through DNA studies, because it is only through such studies that male reproductive success can be determined, which is crucial for measuring the influences of different behaviors on the evolutionary process. Until there is a substantial body of genetically established data for a number of carefully observed primate species, the role of male dominance in reproductive success will remain undetermined. However, observations by Sapolsky in baboons does suggest that high male status does confer a different advantage. He found that the levels of cortisol, a corticosteroid hormone, are inversely related to social status. Therefore, high status males are less at risk to adverse consequences of this hormone. Important advantages of high status in males are reduced vulnerability to the deleterious effects of stress and better access to food resources.

There is strong evidence that high status does confer reproductive success in female chimpanzees, and it is clear that social competence plays an important role in determining the female dominance hierarchy. Goodall and her collaborators found that the offspring of high-status females are more likely to survive and that they mature at an earlier age. They also found evidence that the high-status females live longer than the low-status females. These effects may be the consequence of less stress and better access to food and other resources in the high-status females.

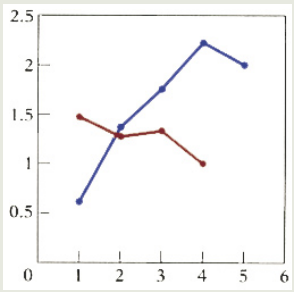
Social competence probably counts for more

The graph below shows the number of neurons in samples of hippocampal area CA4 in unstressed male and female controls and in stressed males and females. Robert Sapolsky and his colleagues also found similar neuronal losses in the other CA fields of the hippocampus of stressed males. In these monkeys, the stress resulted when they were captured by the Kenyan government at the request of farmers and housed under crowded conditions. The photomicrographs at right illustrate neuron loss in the hippocampus of stressed male monkeys. The left one is from the hippocampus of a control monkey; the right photomicrograph, from the same place in the hippocampus of a stressed male, shows a loss of neurons and dendritic atrophy in the remaining neurons.





Cooperative Male Care in Marmosets and Tamarins



The graph shows that infant survival in tamarins increases as a function of the number of caretaking males in the extended family groups; having more females results in a slight reduction in the number of surviving infants. (Blue represents surviving infants based on the number of adult males; red is surviving infants based on the number of adult females.) This graph, from the work of Paul Garber, is based on observations of 47 extended tamarin families living in nature.

Marmosets and tamarins, which are small New World monkeys, have many more offspring than other monkeys and have an unusual solution to providing care for their infants. Unlike other monkeys which have single births, marmosets and tamarins usually give birth to twins or sometimes triplets. Shortly after birth, females become sexually receptive and can conceive again. Thus marmosets and tamarin females can produce up to six babies per year. These primates have developed a different way to nurture their multiple, slowly developing, large-brained infants. Marmosets and tamarins live in extended families in which everyone and especially the males participate in infant care. Marc Van Roosmalen has even observed a male assisting in the birth process by cutting the umbilical cords and eating the afterbirth. Paul Garber found that the presence of up to 4 males in the family enhances the survival of the infants.

The males cooperate in caring for the infants in their group, and there is little aggression among males within the family. The males are very strongly attracted to the infants; they carry them whether or not they are actually their biological offspring, and they share food with them. I have even observed a male kidnapping the offspring of another family so as to carry it. Because of the cooperative care, offspring are less dependent on the survival of a particular caretaker. In our studies thus far we have found little difference in the survival of male and female marmosets and tamarins.

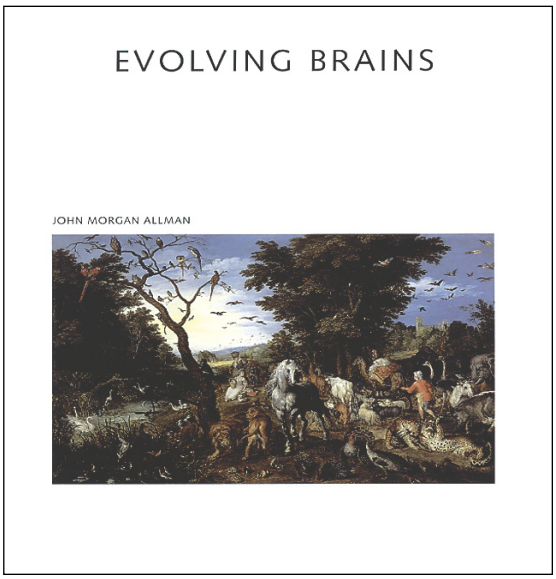
An extended marmoset family enjoys a quiet moment.

than aggression in achieving either high status or reproductive success in primates. Why then are the noncaretaking males aggressive and prone to risk-taking? Why would natural selection favor the evolution of behaviors that increase the risk of dying? I think the answer is that risk-takers constantly probe their world, seeking out new opportunities and detecting hazards in a constantly changing environment. Through their probing they generate new information that they communicate to close kin, thus enhancing their kin's survival and the propagation of their shared genes. Specific vocalizations for types of food and types of predators serve this communicative function. The risk-takers may also be crucial to colonizing new habitats during changing environmental conditions.

Both the evolution of large brains and the evolution of temperature homeostasis, as discussed in Chapter 5, required new developments in parenting behavior. Warm-blooded infants are dependent and cannot grow without parents to provide warmth and nutrition. Increasing brain size slows down postnatal development as measured by the ages at which different teeth erupt and by the age of sexual maturation. Large-brained, slowly developing, dependent offspring require long-surviving parents to reach maturity. A measure of

this parental dependency effect is the differential survival of caretakers versus noncaretakers. In primates, the caretaker effect has a large influence on the patterns of survival with as much as a 42 percent female advantage when males have little role in nurturing offspring versus as much as a 20 percent male advantage when males carry offspring from soon after birth. The male caretaking effect is not as large because only females provide nutrition for their slowly developing offspring through lactation. The mechanisms responsible for the survival differences between caretakers and noncaretakers may ultimately be related to neurochemical differences that favor risk-aversive behavior in caretakers and risk-seeking behavior in noncaretakers, as well as greater vulnerability to the damaging effects of stress in noncaretakers. □

John Allman has been working with owl monkeys since his graduate student days spent mapping the owl monkey's visual cortex. Much of his work since then has concerned how the brain is organized and how it processes and interprets visual information. In 1990 he received the Golden Brain Award from the Minerva Foundation for this body of work. Although known as a neurobiologist, all of Allman's degrees are in anthropology: BA, University of Virginia, 1965; and MA (1968) and PhD (1970), University of Chicago. He has been a member of the Caltech faculty since 1974 and professor of biology since 1984; he was named the Hixon Professor of Psychobiology in 1989. In the book from which this chapter is excerpted, he combines his neurobiological research with a life-long interest in evolution—and in behavior. And the owl monkey, whose relatively simple neocortex made it a good neurophysiological model, turns out to have interesting parenting behavior as well, as the father and child pictured on the cover illustrate.



John Allman's Evolving Brains *(A Scientific American Library volume) is available in bookstores, or it can be ordered directly from the publisher, W. H. Freeman and Company.*