



Disturbing Behaviors of the ORANGUTAN

By Anne Nacey Maggioncalda and Robert M. Sapolsky

The orangutan is one of humankind's closest relatives. One of the four great apes (the other three are gorillas, chimpanzees and bonobos), *Pongo pygmaeus* is exquisitely adapted for life in the forest canopies of the Southeast Asian islands of Borneo and Sumatra. With their long arms and hooklike hands, orangutans are adept at swinging from tree to tree in search of tropical fruits. They are among the most solitary of large primates and the only great apes found outside Africa. Orangutans are also notable for the striking size difference between males and females: the average weight of an adult male (about 90 kilograms, or 198 pounds) is more than twice that of an adult female.

An adult male orangutan is an impressive sight. The animal has a pair of wide cheek pads, called flanges, and a well-developed throat sac used for emitting loud cries known as long calls. The mature male also has long, brightly colored hair on its body and face. These are secondary sexual characteristics, the flamboyant signals that male orangutans flaunt to proclaim their fertility and fitness to the opposite sex. The features emerge during orangutan adolescence: males reach puberty at around seven to nine years of age, then spend a few years in a far-from-impressive "subadult" stage, during which they are

about the same size as mature females. The males reach their adult size and develop secondary sexual traits by ages 12 to 14. Or at least that's what primate researchers used to think.

As stable social groups of orangutans were established in zoos, however, it became clear that an adolescent male could remain a subadult, in a state of arrested development, until his late teens. In the 1970s studies of orangutans in the rain forests of Southeast Asia by Biruté M. F. Galdikas of Simon Fraser University in British Columbia and others produced the same finding: sometimes males were arrested adolescents for a decade or more, about half their potential reproductive lives. Variability of this magnitude is fascinating—it is like finding a species in which pregnancy could last anywhere from six months to five years.

Biologists are keenly interested in studying cases of arrested development because they often shed light on the processes of growth and maturation. In some instances, the cause of arrested development is a genetic disorder; for example, a mutation in the receptor for a growth factor in humans results in a form of dwarfism. Environmental factors can also slow or halt an organism's development. For instance, food shortages delay maturation in humans and many other animals. This response

Studies of these great apes show that some males pursue an unexpected and disquieting evolutionary strategy

Orangutan means "man of the forest" in the Malay language. These great apes typically feed, nest, socialize and mate in the jungle canopy.



is logical from an evolutionary standpoint—if it is unclear whether you will survive another week, it makes no sense to waste calories by adding bone mass or developing secondary sexual characteristics. Gymnasts and ballet dancers who exercise to extremes and anorexics who starve themselves sometimes experience delayed onset of puberty.

Among male orangutans, though, the cause of arrested development seems to lie in the animals' social environment. The presence of dominant adult males appears to delay the maturation of adolescent males that are in the same vicinity. Until recently, researchers believed that they were observing a stress-induced pathology—that is, the adolescent orangutans stopped developing because the adult males bullied and frightened them.

Over the past few years, however, we have conducted studies suggesting that arrested development among orangutans is not a pathology but an adaptive evolutionary strategy. The arrested adolescent males are capable of impregnating females, and by staying small and immature (in terms of secondary sexual features) they minimize the amount of food they need and lower the risk of serious conflict with adult males. But the strategy of these arrested adolescents has a disquieting aspect: they copulate forcibly with females. In other words, they rape.

Measuring Stress

The first investigations into this subject focused on groups of captive orangutans. Terry L. Maple, then at Zoo Atlanta, and other zoo biologists found that adolescent males remained developmentally arrested as long as there was a mature male in their enclosure. If the researchers removed that dominant male, the adolescents soon began to develop into adults. This kind of social regulation had been observed previously in other species. Among mandrill monkeys, for instance, socially dominant males develop dramatic secondary sexual characteristics, such as large testes and high testosterone levels, whereas subordinate males do not. In tree shrews and many rodent species, puberty is delayed in the subordinate animals. In another example, elephant poaching in certain areas of Africa has recently produced orphaned males that grew up in a fairly unsocialized manner. When in “musth”—a male elephant's mating period—these animals become quite aggressive and dangerous. Some zoologists have reported an effective solution: introducing older, more dominant males into the region, which results in social suppression of musth in the rogue males.

In all these cases, researchers have generally agreed that the stress of being subordinate accounts for the developmental arrest. During a typical period of stress for a mammal—say, a sprint across the savanna to escape a predator—energy is mobilized to power the muscles. As part of this process, a variety of long-term building projects in the body are inhibited, including growth, tissue repair and reproductive functions. It is the logic of triage: the animal concentrates on survival during



Hundreds of thousands of orangutans roamed throughout Southeast Asia about 10,000 years ago, but their range is now limited to parts of Borneo and Sumatra. Their number has dwindled to fewer than 20,000. Given the current rate of hunting and habitat destruction, researchers say, orangutans could disappear from the wild within two decades.

the emergency and resumes long-term tasks later, if there is a later. But when an animal undergoes chronic stress, such as that caused by social subordination, the triaging can have adverse consequences, such as decreased growth, lower levels of sex hormones, reduced fertility and delayed puberty. In humans, severe and prolonged psychological stress can cause growth to stop in children, a rare syndrome called psychogenic dwarfism.

At first glance, adolescent male orangutans also appear to be under chronic stress. Adult male orangutans are extremely aggressive to adolescents, particularly within the confines of a zoo. In the wild, orangutan males are dispersed and solitary, belligerently defending a large territory that encompasses several females' territories—sort of a scattered harem. But even there, adolescents are well aware of the threatening presence of a mature male. One signal is a musky odorant that adult males spread about their territories. In addition, mature male orangutans announce their presence by performing long calls; John C. Mitani of the University of Michigan has found that these resonant cries can travel for miles.

Researchers had made little effort, however, to test the hypothesis that the stress of being near a dominant male induces hormonal changes that arrest development in adolescents. In 1989 we began looking for a way to examine the hormones of arrested adolescent orangutans to determine whether these animals were indeed under chronic stress. Ide-

ally one would want to measure the levels of relevant hormones in the orangutans' blood, but this was impossible to do, for ethical and practical reasons. So we took advantage of the fact that the average levels of various hormones in the animals' blood are reflected in a fairly parallel fashion in their urine. Getting urine from wild animals would be immensely difficult, so we studied captive populations. Thanks to the generous help of zookeepers, curators and veterinarians at 13 zoos, we obtained more than 1,000 urine samples from 28 male orangutans, along with information on their developmental status (juvenile, arrested adolescent, developing adolescent or adult), housing, diet, medical history and growth records. In collaboration with Nancy M. Czekala of the Center for Reproduction of Endangered Species at the San Diego Zoo, we measured the levels of nine hormones, comparing animals in different developmental stages.

First we focused on growth hormone, which is crucial for normal maturation. Among the juveniles, arrested adolescents and adults, growth hormone levels in the urine were low and extremely similar, within 15 percent of one another. In contrast, adolescent males that were maturing into adults had growth hormone levels approximately three times as high. This result basically served as an internal control, showing that the external assessments of an animal's development stage closely matched the hormonal profile relevant to growth. In other words, adolescent males going through a developmental spurt in terms of appearance—growing larger, increasing the size of their cheek flanges, and so on—were experiencing hormonal changes as well.

We then considered hormones that respond to stress. Probably the best known is adrenaline (also called epinephrine), which plays a central role in energy mobilization. Epinephrine, unfortunately, cannot be measured accurately in urine. We could, however, determine levels of another key class of stress hormones called the glucocorticoids, which can suppress

growth, tissue repair and reproduction. In addition, we measured the levels of prolactin, a stress-indicative hormone that can inhibit reproduction.

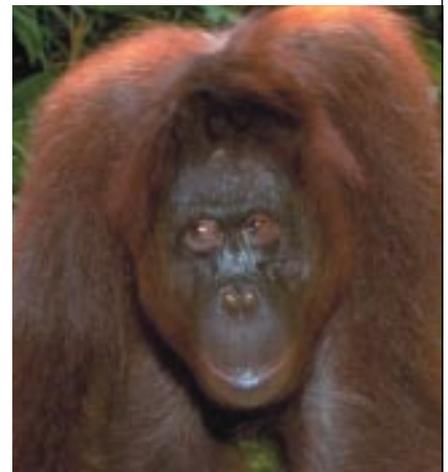
This is where we got a surprise. Glucocorticoid levels did not differ among juveniles, arrested adolescents and adults. Prolactin levels did not differ either. But adolescents going through the developmental spurt had glucocorticoid and prolactin levels roughly double those of the other groups. It wasn't the developmentally arrested adolescents who seemed to be stressed—it was the developing adolescents.

We got another surprise when we examined reproductive hormones in these animals. As expected, adolescent males who were developing secondary sexual characteristics had hormonal profiles implying an active gonadal system. Developing males had higher levels of testosterone and luteinizing hormone (which stimulates the release of testosterone) than did the arrested adolescents. But the levels of these hormones in arrested adolescents were equivalent to those seen in adults. Moreover, arrested males had levels of follicle-stimulating hormone (FSH), which stimulates sperm maturation in males, equal to those of developing adolescents or adult males. And other investigators have found that arrested adolescents have mature functional sperm and that their testes are the same size as those of developing adolescents.

Evolutionary Strategies

These findings overturned some long-held assumptions about orangutans. Apparently, arrested adolescents are neither stressed nor reproductively suppressed. What is going on? It turns out that there is more than one way for a male orangutan to improve his chances of reproducing.

A cornerstone of modern evolutionary theory is that animal behavior has evolved not for the good of the species or the social group but to maximize the number of gene copies passed on by an individual and its close relatives. For a long time, the



Secondary sexual characteristics distinguish the adult male orangutan (*left*) from the arrested adolescent male (*center*) and the adult female (*right*). Perhaps the most prominent of these features are the adult male's wide cheek pads, called flanges, and the well-developed throat sac used for emitting loud cries known as long calls. Also, the average weight of adult males is more than twice that of arrested males and adult females.

study of primates was dominated by simplistic models of how animals achieve this goal. According to these models, male behavior consists of virtually nothing but aggression and competition to gain access to females. If only one female is sexually receptive in a group with many males, this competition would result in the highest-ranking male mating with her; if two females are receptive, the males ranking first and second in the hierarchy would mate with them, and so on.

But this kind of behavior is rarely seen among social primates. Instead male primates can choose alternative strategies to maximize their reproductive success.

Why should there be alternatives? Because the seemingly logical strategy—developing powerful muscles and dramatic secondary sexual characteristics to excel at male-male competition—has some serious drawbacks. In many species, maintaining those secondary characteristics requires elevated testosterone levels, which have a variety of adverse effects on health. The aggression that comes with such a strategy is not great for health either.

Furthermore, increased body mass means greater metabolic demands and more pressure for successful food acquisition. During famines, the bigger primates are less likely to survive. For an arboreal species such as the orangutan, the heavier body of the mature male also limits which trees and branches can be accessed for food. And the development of secondary sexual characteristics makes a male more conspicuous, both to predators and to other males that view those characteristics as a challenge.

The competition between adult males and developing adolescents probably explains the elevated levels of stress hormones in the latter. In the eyes of an adult male orangutan, a developing male is soon to be a challenger, so naturally he becomes a prime target for aggression. The same pattern is seen among horses and various other social ungulates: it is not until the young males start developing secondary sexual characteristics that the unrelated dominant males begin to harass them into leaving the group. Another example comes from work by one of us (Sapolsky) with wild baboons. Some socially subordinate male baboons have much higher glucocorticoid levels

than do the dominant animals, primarily because these subordinates are actively challenging the high-ranking males.

In contrast, the key impression that a developmentally arrested male communicates to an adult male is a lack of threat or challenge, because the immature male looks like a kid. Arrested male orangutans are apparently inconspicuous enough to be spared a certain amount of social stress. What is more, the “low profile” of these animals may actually give them a competitive advantage when it comes to reproduction. In many primate species, the low-ranking males are doing a fair share of the mating. Genetic paternity testing of these primates has shown that the subordinate males are quite successful in passing on their genes. This finding extends to orangutans: studies of zoo populations have proved that arrested males mate and that these matings are fertile. More recently Sri Suci Utami Atmoko, then at Utrecht University in the Netherlands, showed that arrested adolescents fathered approximately half of the orangutan babies at her Sumatran study site.



Why are these low-ranking males taking part in so many matings? In some primate species, such as the savanna baboon, the females can decide with whom they will mate, and they frequently choose males who exhibit strong male-female affiliation and parental behavior rather than male-male competition. Even when dominant male baboons stand guard to prevent low-ranking males from mating, the females often initiate surreptitious matings—sometimes referred to as “stolen copulations”—with the subordinates. For low-ranking male baboons, the strategy of pursuing affiliative “friendships” with females is a viable one because it avoids the metabolic costs, injuries and stress of male-male competition.

But arrested male orangutans do not engage in long-term affiliative relationships with females, although an arrested male may sometimes accompany a female for several days as she roams through the forest. Furthermore, the great majority of adult female orangutans are sexually receptive only to mature males. So how do the arrested males mate? Observations

(The Authors)

ANNE NACEY MAGGIONCALDA and **ROBERT M. SAPOLSKY** have been studying the evolution of male orangutan reproductive strategies for more than a decade. Maggioncalda, who received a Ph.D. in biological anthropology and anatomy from Duke University in 1995, is a retired lecturer in the program in human biology at Stanford University and in the department of anatomy at the Stanford University School of Medicine. Sapolsky, who earned a Ph.D. in neuroendocrinology from the Rockefeller University in 1984, is professor of biological sciences and neurology at Stanford and a research associate at the National Museums of Kenya. His research interests include neuron death, gene therapy and the physiology of primates.

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Orangutans are among the most solitary of large primates, but they occasionally travel and feed in small bands. Three orangutans groom one another in a Borneo forest (opposite page). An adult female rests with her offspring in Borneo's Tanjung Puting National Park (above).

of orangutans both in the wild and in captive populations have indicated that the arrested males forcibly copulate with females. Rape is an apt term for these copulations: the adult females usually resist the arrested adolescents fiercely, biting the males whenever they can and emitting loud, guttural sounds (called rape grunts) that are heard only under these circumstances. Adult males sometimes rape, too, but not nearly as often as the arrested males. In a study conducted in Borneo during the early 1980s, Mitani and his field assistants observed 151 copulations by arrested males; 144 of the matings were forced.

Thus, two reproductive strategies appear to have evolved for adolescent male orangutans. If no fully mature males are nearby, the adolescent will most likely develop quickly in the hopes of attracting female attention. When adult males are present, however, a strategy of arrested development has its advantages. If the social environment changes—say, if the nearby adult males die off or migrate—the arrested males will rapidly develop secondary sexual features and change their behav-

ior patterns. Researchers are now trying to determine exactly how the presence or absence of adult males triggers hormonal changes in the adolescents.

Unpleasant Findings

What are the lessons we can learn from the male orangutan? First, a situation that seems stressful from a human's perspective may not necessarily be so. Second, the existence of alternative reproductive strategies shows that the optimal approach can vary dramatically in different social and ecological settings. There is no single blueprint for understanding the evolution of behavior. Third, although the recognition of alternative strategies built around female choice has generally met with a receptive audience among scientists, the rape-oriented strategy of arrested male orangutans is not so pleasing. But the study of primates has demonstrated time and again that the behavior of these animals is far from Disney-esque. Just consider the strategic infanticide of langur monkeys or the organized aggression—sometimes called genocide—between groups of chimpanzee males.

One must be cautious, however, in trying to gain insights into human behavior by extrapolating from animal studies. There is a temptation to leap to a wrongheaded conclusion: because forcible copulation occurs in orangutans and something similar occurs in humans, rape has a natural basis and is therefore unstoppable. This argument ignores the fact that the orangutan is the only nonhuman primate to engage in forcible copulation as a routine means of siring offspring. Furthermore, close observations of orangutan rape show that it is very different from human rape: for example, researchers have never seen a male orangutan injure a female during copulation in an apparently intentional manner. Most important, the orangutan's physiology, life history and social structure are completely unlike those of any other primate. Orangutans have evolved a unique set of adaptations to survive in their environment, and hence it would be the height of absurdity to draw simpleminded parallels between their behaviors and those of humans. **M**

(Further Reading)

- ◆ **Reflections of Eden: My Years with the Orangutans of Borneo.** Biruté M. F. Galdikas. Back Bay Books, 1996.
- ◆ **Reproductive Hormone Profiles in Captive Male Orangutans: Implications for Understanding Developmental Arrest.** Anne Nacey Maggioncalda, Robert M. Sapolsky and Nancy M. Czekala in *American Journal of Physical Anthropology*, Vol. 109, No. 1, pages 19–32; May 1999.
- ◆ **Orangutans: Wizards of the Forest.** Anne E. Russon. Firefly Books, 2000.
- ◆ **Male Orangutan Subadulthood: A New Twist on the Relationship between Chronic Stress and Developmental Arrest.** Anne Nacey Maggioncalda, Nancy M. Czekala and Robert M. Sapolsky in *American Journal of Physical Anthropology*, Vol. 118, No. 1, pages 25–32; May 2002.
- ◆ More information on orangutans is available at the Web sites of the Orangutan Foundation International (www.orangutan.org) and the Orangutan Conservancy (www.orangutan.net).

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