AnthroQuest

The Newsletter of the L.S.B Leakey Foundation

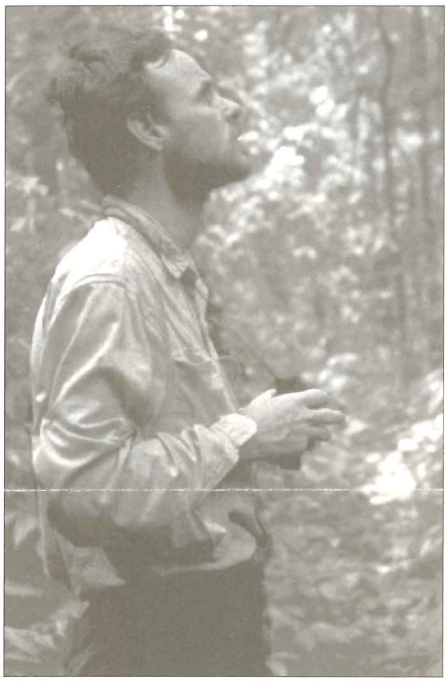
No. 5, Winter 1998

Apes and Our Ancestors: A Symposium at Stanford University

By Carel van Schaik

We have become so accustomed to spectacular discoveries of new hominid fossils that it is easy to forget that other activities, less spectacular, are also vitally important elements in our quest to understand human origins. On December 6, 1997, the Leakey Foundation organized a symposium at Stanford University to highlight recent developments in studies of primate behavioral ecology and cognition. Funding for the symposium was provided by the Ann and Gordon Getty Foundation.

Can studies of ape and monkey behavior teach us something about human evolution? For a long time, the general public accepted this proposition as an article of faith, while scientists dismissed it as unlikely. Scientists argued that because humans had branched off from the rest of the apes over 30 million years ago, the relationship was too distant for much to be learned from their behavior. Thus, human behavior was thought to be unique. However, recent molecular studies have drastically modified our family portrait. First, we now know that the last ancestor that we share with the chimpanzee species lived roughly 5-7 million years ago—in evolutionary terms, that is not very long. Many other primate species, such as baboons, have hardly changed over this same time span. Second, and highly relevant to the symposium's topic, these studies have shown that we are great apes, even African apes! Perhaps this discovery has the most impact when considered from the perspective of chimpanzees. Their closest relative is not the other black



van Schaik, Professor of Biological Anthropology and Anatomy at Duke University, serves as Sub-discipline Chair in Primatology for the Leakey Foundation's Scientific Executive Committee.

African ape, the gorilla, but instead it is humans!

It is therefore evident that what apes and monkeys do must be relevant to understanding the origins of human behavior. Less evident is how primate behavior helps to explain human behavior. The most obvious approach is to look for features shared by humans and great apes, and thus trace back their origins and study their functions in other species. Primatologists describe this approach as the use of the referential model. We call them *homolog-referential models* because we reason that these similar features (*homologies*) are inherited from a

Continued on page 3

Notes from the Field: On the Nature of Inter-community Aggression in Chimpanzees

By Marc Hauser and Richard Wrangham

In 1995, the Leakey Foundation pledged three years of support to this project, "A Long-term Study of Inter-community Aggression in Chimpanzees," through our Fellowship for Great Ape Research. The research goal is to enhance understanding of the evolution of social behavior among chimpanzees by focusing on problems that are central to issues of human evolution. Hauser and Wrangham's study concentrates on a series of experiments that test, for the first time, the effects of 'stranger' calls on resident chimpanzees in order to address several hypotheses accounting for aggression. The Foundation is proud to support this project which we hope will contribute to our knowledge of the nature and extent of chimpanzee aggressive behavior, a key issue in understanding how and why complex mental processes evolved within the primate order.

Marc Hauser is an Associate Professor at Harvard University in the departments of Anthropology and Psychology, and the Program in Neurosciences. Richard Wrangham has been a Professor of Biological Anthropology at Harvard University, specializing in primate behavior, since 1989.

Long-term studies of chimpanzees have revealed extensive territorial behavior by adult males, who frequently patrol the boundaries of their communities, and sometimes conduct raids into neighboring territories. Such lethal raiding has been implicated in the extinction of two communities in Tanzania and has been reported elsewhere. Understanding the high degree of cooperation shown by territorial chimpanzees may shed light on the evolution of human behavior, in

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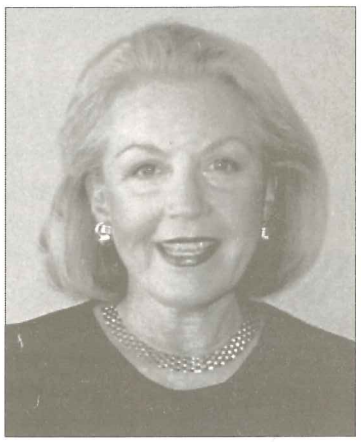
President's Message: Insights Primatology Offers

February 1998

Dear Members,



Louis Leakey was an innovator in his belief that the study of non-human primates offered another approach to understanding human origins. His interest in the early careers of the "Trimates," Jane Goodall, Dian Fossey, and Biruté Galdikas, helped change the direction of primatology. In 1957 while Jane worked with the Leakeys at Olduvai, Louis reflected on the idea that understanding primates in their social units might provide insight into the social behavior of early humans. Louis' initial vision later inspired Jane, Dian, and Biruté to study the richest model of early human behavior in modern existence—the great apes. Louis' hunch has more than held true; today, with the help of geneticists, biochemists, and other scientists, the theory that primates are our closest relatives has been established beyond a shadow of a doubt. As Jane once said several years after Louis' death, "it was real genius in Louis to think about doing this: to learn about early man through comparative studies of great apes. . . Louis was way ahead of his contemporary scientists in realizing the value of this kind of research."

After listening to the talks at the "Apes and Our Ancestors" symposium in December, I was reminded of Louis' foresight and again struck by how pleased he would be with the multidisciplinary aspect of primatology research today. The scientists who participated in the symposium held at Stanford University represent the broad scope of such studies. The ways in which they contribute to our understanding of these issues is highlighted in the summary article by Scientific Executive Committee member, Carel van Schaik.

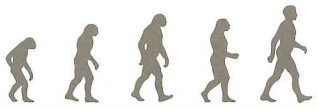
Historically, it has been difficult to find funding for long-term study sites. The majority of the Leakey Foundation's grants are at a lower range, $3,000 to 12,000, whereas long-term study sites often require upwards of $50,000 to 200,000 just to maintain basic operations. However, in the spirit of the unprecedented studies at long-term sites carried out by the Trimates, the Foundation strives to provide support to projects at long-term sites through our Fellowship for Great Ape Research, which is augmented by designated funds raised from individual donors. An update on one such important project supported by the Leakey Foundation is presented to us by Marc Hauser and Richard Wrangham in the "Notes from the Field" column.

The old adage that the more we learn, the more we know there is to learn, certainly rings true. The Leakey Foundation is proud of our role in helping to find answers to the most pressing questions about how we came to be human, yet there is still so much more to discover. An expansion of support will be required to maintain the viability of existing projects and to encourage new research efforts. We have set a goal to increase our endowment over the next decade to enable us to support more high quality, long-term projects. As always, I would like to extend my thanks to each of you, our members, for your support in this endeavor.

Sincerely,

Kay Woods

Kay Harrigan Woods
President



The Leakey Foundation

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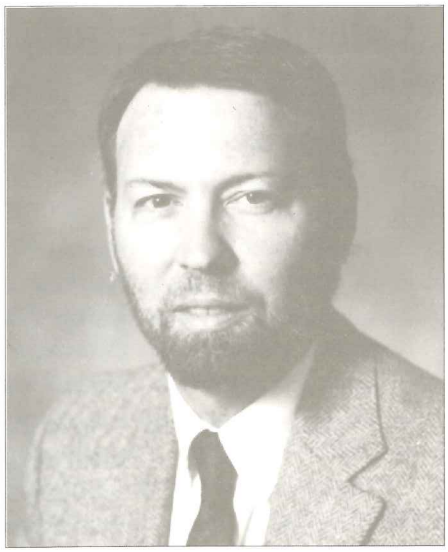
New website

Our web site is up and running so check us out!
www.leakeyfoundation.org

Apes *continued from page 1*

common ancestor shared by the species being compared. Sometimes identifying these features is easy: orangutans and chimpanzees use feeding tools in the wild; bonobos and gorillas can do so in captivity, and, if we study them longer, we may find that they too sometimes use tools in the wild. Thus, it is likely that our early ancestors, the hominids, had similar abilities. But many times pinpointing these relationships is more complex because our relatives send mixed signals: think of the bonobo/chimp contrast in male behavior, as highlighted by Richard Wrangham and Dale Peterson's book, Demonic Males. Chimp males have a violent streak that leads them to harass females and even unknown males; bonobo males show none of this behavior—instead they seem to solve their conflicts largely through sex. In cases like this we need additional approaches.

Another approach, called the *analog-referential model*, also relies on parallels to hominid behavior in a living species. However, in this model, we do not presume that we are studying the same behavior, in the evolutionary sense that different species inherited it from a common ancestor—but rather that the behavior represents a convergent, independently evolved, solution to the same problem. A classic example is the study of savanna baboons as a model for the way ecology and social life are affected by highly seasonal dry environments, or the study of cooperative hunting and food sharing in chimpanzees or social carnivores in order to examine how hunting and food sharing have affected social tendencies in humans.



Kevin D. Hunt. Hunt is the recipient of a 1986/87 grant in the amount of $4095 for his project, "Positional Behavior in Pan Troglodytes." His principal research interests are functional morphology, the evolution of the hominid face, and the evolution of human bipedalism, australopithecine, and ape ecology.

Yet analog-referential models have limitations. Dramatic variation in the lifestyles of animals does not only arise because they face very different problems, but also because, even when they face similar problems, they still tend to evolve different solutions. For instance, most primates have a life history that makes them much more vulnerable to

Continued on page 4

Notes *continued from page 1*

which cooperation within groups and competition between groups are both highly developed and closely related. Together with our graduate student, Michael Wilson, we have conducted field playback experiments to test the coordinated territorial behavior of chimpanzees in the Kanyawara community of Kibale National Park, Uganda. We have simulated intrusions into the Kanyawara range by playing back recordings of the long distance calls (pant hoots) of lone male 'strangers.'

Pant hoots are among the most common and conspicuous of chimpanzee calls. They are loud, traveling for 1-2 km through dense forest, and are produced in a variety of circumstances. Males give pant hoots when alone, apparently to see if any of their allies or associates are around, and may also give them during reunions, hunts, intergroup encounters, or upon arrival at bountiful fruit trees.

In each experiment, we played back the call of a single 'stranger' to Kanyawara chimpanzees, making it seem as if at least one intruder was encroaching on their territory. Our primary goal was to determine whether chimpanzees modify their response according to party size and composition. Previously, playback experiments on lions, a species that is also known to engage in intergroup violence, had shown that lionesses are more likely to approach 'intruders' if they outnumber the intruders. Male lions, however, always approached intruders, regardless of the odds. Do male chimpanzees, like male lions, always approach intruders, or do they, like female lions, approach only if they outnumber intruders? Under what circumstances, if any, do female chimpanzees approach intruders? In many species, territories are defended by individuals (as in red deer and orangutans) or mated pairs (as in gibbons). In such species, individuals generally respond to the calls of intruders with calls of their own. Do lone male chimpanzees risk calling to what appears to be a single intruder? Or do they only advertise their presence if they safely outnumber the intruder?

Experiments are still in progress, but to date we have conducted a total of 20 playbacks. When broadcast from a speaker, the 'stranger' pant hoot can be heard hundreds of meters from the speaker, and can be heard simultaneously by chimpanzees in widely separated parties; this method readily simulates a natural calling episode. Insofar as possible, observations of chimpanzees in all known parties are collected. Currently, we have observed the responses of individuals in 24 distinct parties over the course of 20 experiments.

Subjects responded to the playbacks in ways consistent with response to an intruder's call. In most cases, subjects stopped what they were doing,

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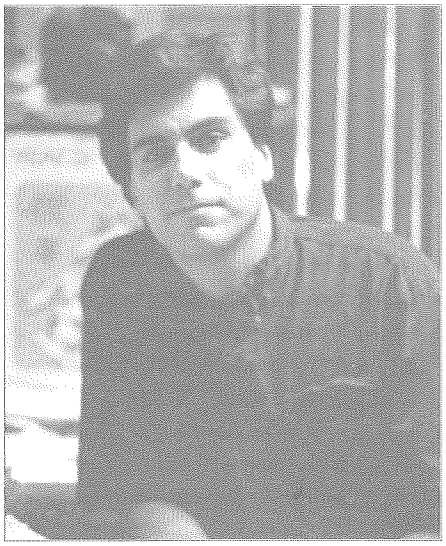
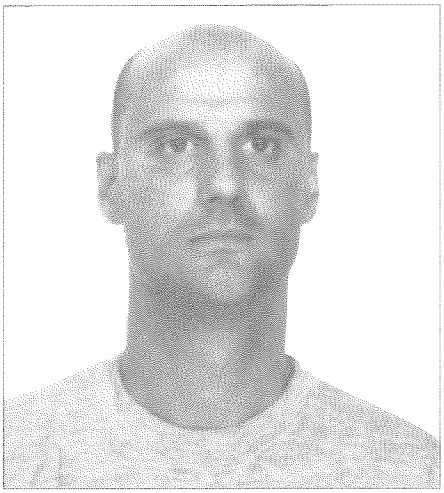


Craig Stanford. Stanford received a $6500 grant in 1990/91 for his project, "Behavioral Ecology of the Gombe Red Colobus: Effects of Chimpanzee Predation" and is the current recipient of a $5800 grant with Michelle Goldsmith for the project, "Behavioral Ecology of Sympatric Mountain Gorillas and Chimpanzees in the Bwindi-Impenetrable Forest Uganda."

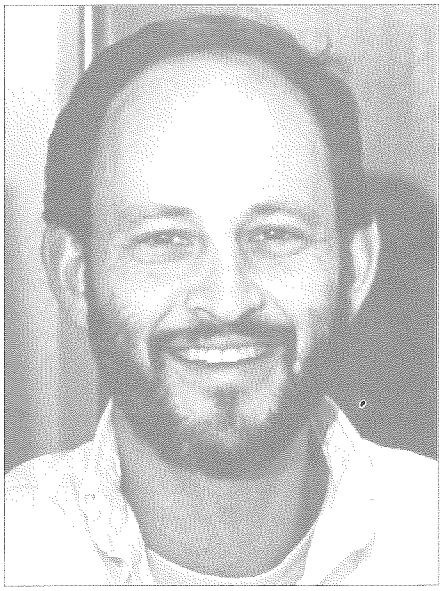
infanticide by males than most other mammals, but the social solution chosen by primates, year-round association between males and females, is different from the one picked by many carnivores faced with the same problem. For them, the price of association is too high, and females tend to avoid the areas visited by males or have come up with still other solutions. Since it is so difficult to predict the myriad ways in which external pressures mold behaviors in different taxa, it is usually safest to use closely related species as referential models. Hence, anthropologists focus on primates most of the time.

Most of our explanations seek to understand the function of behaviors by identifying the selective pressures that would have given rise to them. We try to develop ideas about how these same pressures would produce different behaviors in different animals due to the different biological background of each species. Consequently, our ideas should also be firmly grounded in evolutionary theory, and as the infanticide example makes clear, an exclusive focus on close relatives limits our understanding of a phenomenon. These more general models are called *strategic or conceptual models.* To test them, we need to study not just apes, but also monkeys, small nocturnal prosimians, and sometimes even non-primate animals.

I do not have the space to present detailed summaries of the fascinating papers presented at the symposium, but it may be useful to place the various talks into the framework offered by these models. The speakers at the symposium used a variety of approaches. Kevin Hunt's (Indiana University) work on the evolution of bipedalism comes most closely to using a homolog-referential model. Bipedalism is perhaps the most important defining characteristic of the australopithecines, which show a large range of morphological adaptations for this trait. But a careful study of the relatively rare instances of chimpanzee bipedalism showed that it largely serves "shuffle-feeding" on small fruits growing on bushes. Hunt argues that the ancestor of the australopithecines also used this positional behavior and that the expansion of habitats favoring shuffle-feeding has made possible the evolution of bipedalism as a locomotor adaptation.



Filippo Aureli. Aureli is Research Associate at the Yerkes Regional Primate Research Center and Visiting Assistant Professor in the Department of Psychology of Emory University. He has conducted primate research for over 10 years in both captivity and the field.



Marc Hauser. Hauser has received three grants from the Leakey Foundation: 1) a $3000 grant for "Conversations Among Kibale Chimpanzees" in 1987/88, 2) a $7500 grant for "Origins of Hemispheric Asymmetries Underlying Primate Vocal and Facial Expression" in 1993/94, and 3) the Fellowship for Great Ape Research with Richard Wrangham at $35,000 per year over three years for "Long-term Study of Inter-community Aggression in Chimpanzees" from 1995-98.

One of the most fascinating results of Craig Stanford's (University of Southern California) study of red colobus monkey hunting by chimpanzees is that the males are more likely to hunt when they are accompanied by estrous females, with whom they often share meat. This behavior can be viewed conservatively as an analog-referential model of hominid hunting and food sharing. But it can also be seen as a homolog-referential model. A recently proposed, radical reinterpretation of the function of large-game hunting in human hunter-gatherers suggests that it serves to increase mating opportunities for the successful hunter. Clearly, this interpretation is quite consistent with a homolog-referential model for this phenomenon, and suggests that hunting and sharing in chimps and humans are evolutionarily continuous.

Filippo Aureli (Yerkes Primate Center) discussed the various ways in which social animals deal with conflicts of interest and the real fights that inevitably ensue. Perhaps most surprising is

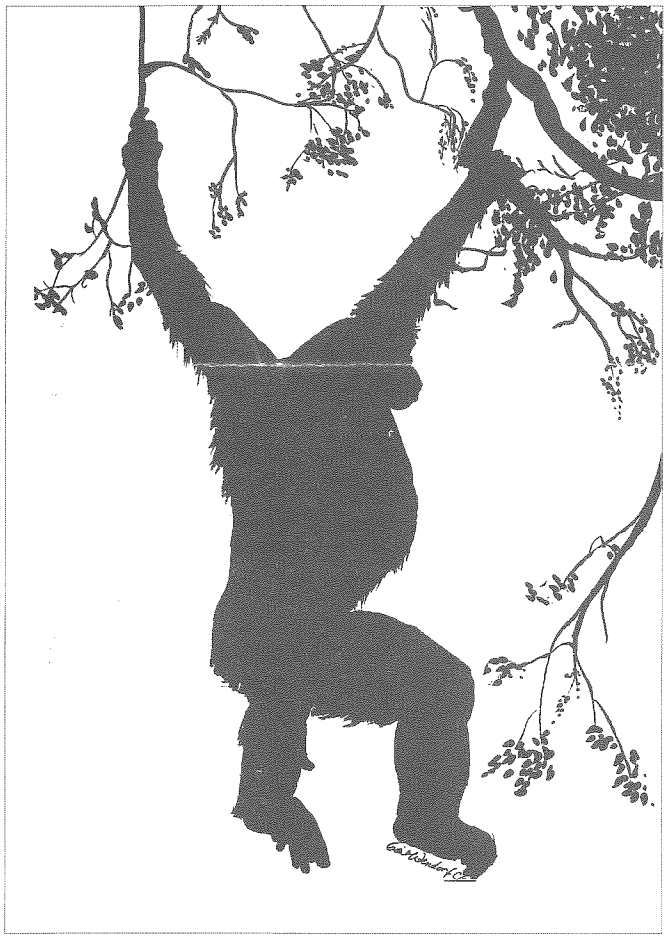
Continued on page 6

Notes *continued from page 3*

looked towards the speaker, climbed down from their trees, and either moved towards or away from the speaker, all within a few minutes of the playback. Individuals who didn't move or moved only a short distance (<20 m) in the 20 minutes after a playback were either in parties with few or no adult males (6 cases), mate guarding a female with a full sexual swelling (2 cases), or showing interest in hunting red colobus monkeys (1 case; in this case, 4 of 5 males did approach the speaker). In marked contrast to the response to 'stranger' pant hoots, subjects never gave any overt response to the control stimuli (crowned hawk eagle contact call and black and white colobus roar).

The presence of other parties within vocal range probably had some effect on response; separate parties were sometimes in vocal or visual contact in the hours before the experiment, and chimpanzees from separated parties sometimes joined together following the experiment. Nevertheless, being separated from allies by 50 meters or more also had an effect—the same adult females who traveled toward the speaker when in close company with adult males fled from the speaker in a later experiment, when they were out of sight but within vocal range of the same males. Adult males who counter-called in large parties failed to call when the same number of males were divided into separate parties. Focal parties were therefore treated as statistically independent entities in the following analyses.

Response to the playback differed strikingly between parties with different numbers of adult males. Counter-calling showed a statistically significant relation to whether a party had many (3 or more), few (1 to 2), or no adult males. Females never called unless in a party with adult males, and, in all but one case, parties with few males remained silent. Parties with many males counter-called immediately after the playback in every case. Travel response also depended mainly on the number of males in the party. Females never approached the speaker unless with adult males. Parties with few adult males sometimes approached the speaker. Parties with many males approached the speaker in 9 of 10 cases; in the one exception, chimpanzees moved about 50 m immediately after the playback, but according to the GPS readings, their path resulted in no net change in speaker-subject distance. Distance moved in the 20 minutes following the playback increased with the number of adult males in the party. Parties with no adult males moved a mean of 84 m away from the speaker, while parties with few or many adult males moved a mean of 155 m and 278 m towards the speaker, respectively. Neither speaker-subject distance nor range location had a significant effect on vocal or travel behavior.



Overall, it appears that while males in small parties were sometimes willing to approach an 'intruder,' they did so stealthily, without advertising their presence. Males in larger parties, on the other hand, call loudly upon hearing an 'intruder,' apparently because they outnumber the intruder. According to Jane Goodall, in all five lethal attacks observed at Gombe, one or two males immobilized the victim while the other(s) attacked. The risk of being attacked in such a manner probably underlies the reluctance of fewer than three males to announce their presence to an intruder, particularly when other as yet silent intruders may be present. To more precisely determine the relationship between party size and lethal inter-community attacks, future experiments will involve playbacks of stranger choruses, systematically manipulating the number of callers that appear to be challenging the territorial boundaries.

In summary, our research shows that when evaluating the threat of inter-community aggression, chimpanzees make calculated decisions about the relative power of their own party's current composition. Such decisions are not only affected by the actual structure of the party, but also by the relationships among individuals. To be effective, individuals must head off for attack in unison, and thus, each party member must trust the other. As such, the cluster of design features that characterizes chimpanzee warfare is remarkably similar to those that have been documented for humans engaging in war. Our aggressive nature is marked with the unambiguous imprints from our ape-like past. ■

Apes *continued from page 4*

that even though one might expect that primates involved in a fight would increase their distance for a while, many actually make up very soon after an altercation occurs. Numerous studies of such post-conflict behavior have led to the development of a conceptual or strategic model that is highly relevant to an understanding of conflict resolution in humans. But here too, phylogenetic constraints may be at work, because of all the species studied so far only chimpanzees show "consolation," where a third party not involved in the original conflict effectively comforts an animal who just lost a fight. One possibility is that only chimpanzees are smart enough to recognize the victim's anxiety and to understand that they can reduce it.

It is widely accepted that apes are in a league of their own when it comes to understanding the physical and social world they live in—making it easier to see how selective pressures on intelligent behavior (probably not unique among animals) could set off the spectacular cognitive evolution in the hominid lineage. Marc Hauser (Harvard University), however, threw cold water on this notion by arguing that several non-apes may also pass one of the most commonly used tests of self-awareness, mirror self-recognition (an ability thought to be limited to great apes). He also challenged this idea by contending that apes seem to fail some other obvious tests of advanced thinking. In other words, we need to go back to the drawing board and develop new models of cognitive evolution.

The study of human evolution is inherently multi-disciplinary, and as this symposium made abundantly clear, studies of the behavior, ecology, and psychology of primates and other mammals are critical elements of this grand endeavor. ■

Calendar of Events

1998	February 19	**Board of Trustees Meeting, San Francisco, CA**
	February 19	**Annual L.S.B. Leakey Lecture*** California Academy of Sciences, San Francisco, CA Dr. Bernard Wood, George Washington University
	April 23-25	**Board of Trustees Meeting, San Francisco, CA** Granting Session **Leakey Prize Award, San Francisco, CA** (Watch for an announcement of the recipient in the next issue of AnthroQuest!)
	May 24 - June 10	**Tour of Turkey** Istanbul, the Anatolian Plateau, and the Turkish Mediterranean
	August 15	**Fall General Grant Deadline**
	October 9 -10	**Board of Trustees Meeting, Washington, DC**
	December 4-5	**Board of Trustees Meeting** Granting Session (location to be determined)
1999	January 5	**Spring General Grant Deadline**
	February 18	**Board of Trustees Meeting, San Francisco, CA**
	February 18	**Annual L.S.B. Leakey Lecture*** California Academy of Sciences, San Francisco, CA (speaker to be determined)

*Open to all members

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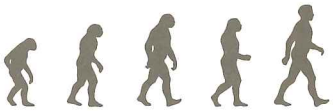

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