

## Can Early Hominid Behavioral Evolution Be Modeled on Chimpanzee Hunting Ecology?

### **Chimpanzee and Red Colobus. The Ecology of Predator and Prey**

By C.B. Stanford (1998) Cambridge: Harvard University Press. xvii + 296 p. \$35.00 (cloth). ISBN 0-674-11667-4.

### **The Hunting Apes. Meat Eating and the Origins of Human Behavior**

By C.B. Stanford (1999) Princeton: Princeton University Press. xi + 253 p. \$24.95 (cloth). ISBN 0-691-01160-5.

It has been hypothesized that predation is the major factor influencing group living in primates and other mammals, with group living conferring such antipredation benefits as reduced individual vigilance time and reduced probability of any single individual being killed (reviewed by Janson<sup>1</sup>). Some studies on primate group size have suggested that primate groups under predation pressure have larger mean groups. Data on other vertebrates demonstrate that when groups are under severe predation pressure life-history traits are skewed toward rapid reproduction at the expense of full development.<sup>2,3</sup> However, predation on primates is rarely observed, mainly because primatologists focus on primates and not their predators, but also because the presence of researchers typically dissuades predators from attacking. Accordingly, testing the predation hypothesis for group size and sociality is particularly difficult. This fact makes Stanford's *Chimpanzee and Red Colobus: The Ecology of Predator and Prey* quite an achievement because it is a synthesis of field data on a predator-prey system, one in which both the predator (chimpanzees) and the prey (red colobus) are habituated and observable. These data enable the evaluation of hypotheses regarding the effects of predation on life-history variables in a mammal species.

Male chimpanzees are major predators on red colobus monkeys at several sites in East Africa. Stanford worked at Gombe, a site with a long recorded history of chimpanzee observations, including hunting behavior. Stanford's data on Gombe red colobus groups demonstrate that the hunting of red colobus by male chimpanzees has important and predicted influences on red colobus life-history traits, such as larger mean group sizes, shorter gestation lengths, aseasonal breeding, and (possibly) shorter interbirth intervals. Reductions in gestation length and interbirth intervals are highly correlated with high predation pressure,<sup>2,3</sup> and larger mean group sizes are precisely what one would expect for primate groups under increased predation pressure. Following accepted life-history theory, Stanford's interpretation for red colobus is that these life-history trait changes allow reproducing red colobus females to replace lost infants, one of the preferred prey age classes at Gombe, in a short time without this loss significantly affecting the females' overall reproductive output. Considered in conjunction with other data emphasizing the importance of predation on increasing group sizes and the formation of polyspecific associations,<sup>4,5</sup> Stanford's red colobus life-history data support the hypothesis that primate sociality is strongly influenced by predation pressure, at least in some cercopithecoid species.

In contrast, the factors driving chimpanzees to hunt red colobus monkeys preferentially are much less clear. Although other vertebrate species are available for hunting, such as bush pigs, chimpanzees almost exclusively hunt red colobus monkeys. Stanford takes great pains to convince us that dietary deficiencies do not influence hunting. Chimpanzee hunting is seasonal, peaking at times during which Gombe chimps tend to lose body weight. Mesocarp nuts, a staple at Gombe, greatly outweigh monkey meat in number of calories and saturated fat and are available during the dry season. If chimpanzees at Gombe are under nutritional stress during the dry season, it is reasonable to expect

that nuts and seasonal fruit would be preferred over monkey meat, which is more costly in time and energy for males to procure. And yet Gombe males do hunt. However, at Gombe meat is parceled out by males among allies, along lines of kinship and dominance, and to females traveling with the hunting party. The presence of estrus females leads to larger party sizes and to increases in the frequency of hunting. Stanford considers the presence of females to be the best predictor of whether a party will decide to hunt. Based on these data, Stanford suggests that meat acquired by hunting has greater social than dietary value, and is instead used as a form of social currency. He hypothesizes that male hunting behavior is a mating tactic to exchange red colobus meat for sex with estrus females. He proposes that the cognitive requirements for the successful sharing of meat place high selective demands on social manipulation and politicking, the ultimate goal of which is to improve access to estrus females.

If the possession of meat allows greater access to estrus females, it is expected that males would exchange meat for copulations, which has indeed been observed. However, meat was exchanged for copulations in only 33% of all successful hunts in which estrus females were present. The number of actual unambiguous observations by Stanford of these exchanges was only five, three of which occurred on the same day during the same hunt. The rate of meat sharing with estrus females is comparable to that among Ngogo chimpanzees (Kibale, Uganda), where estrus females received meat about 29% of the time they were present.<sup>6</sup> Whether or not males received copulations in exchange is unknown. In addition, Watts and Mitani<sup>7</sup> found that both the number of hunts and number of kills per day significantly increased when more seasonally ripe fruit was available, which suggests that Ngogo chimpanzees and perhaps all chimps hunt when energy is more easily obtained. At Tai (Ivory Coast), chimpanzees distribute meat more cooperatively, rewarding hunters who participated in the hunt regardless of whether they were successful or not.<sup>8</sup>

The sharing of meat for sexual access to females may play a negligible role at Tai and other sites, with reciprocal meat sharing primarily among males perhaps being more important in maintaining alliances or dominance. There are no data to indicate that successful chimpanzee hunters, or at least the males that successfully control meat distribution, have a higher copulatory or reproductive success than others do, which would be expected if meat sharing among chimpanzees was a mating tactic. That there are so few undisputed observations of meat for sex at Gombe and other sites greatly weakens the hypothesis that meat for sex is a utilized reproductive tactic.

The causal mechanism driving male chimpanzee hunting behavior remains unclear. This is especially unfortunate because in *The Hunting Apes: Meat Eating and the Origins of Human Behavior* Stanford uses his hypothesis for male chimpanzee hunting behavior as the foundation of his model for early hominid cognitive and behavioral evolution. In this largely reworked version of Washburn and Lancaster's<sup>9</sup> "Man the Hunter" model, Stanford proposes that the origins of human intelligence are based not on cooperative big-game hunting but instead on the cognitive and strategic requirements involved in the harsh intragroup social politics surrounding meat-sharing. Because of the Machiavellian demands of forming intragroup alliances and coalitions, intelligence and cooperative behavior sufficiently evolved so that cooperative hunting became possible and replaced stealth and individualism, all based on the desire to control meat. In other words, "[s]ociality, better weapon manufacture, and larger brain size may thus be traits that arose in response to the need to find and capture prey." (*The Hunting Apes*, p. 105).

Although this model proposes some interesting ideas, there are several aspects that make it difficult to accept. Stanford suggests that modern hunter-gatherer men also use meat sharing as a political tool and mating tactic by displaying their hunting prowess to increase their sexual access to women. While it is true that among some hunter-gatherer groups, like the Aché, males who are more successful

hunters have much higher fertility,<sup>10</sup> the comparison to chimpanzee males may be too simplistic. Aché males do not and cannot monopolize their catch in the way that chimpanzee males do because the resources hunters acquire are monitored by the group with the expectation that the catch will be shared with less successful hunters.<sup>11</sup> At no time do Aché males have the control over resources, or the means to exploit this control, in the manner that Stanford has hypothesized is true for chimpanzee males. Another unanswered question left by this model is: If the control of meat by chimpanzee males is a mating tactic, why do they exchange meat for sex with females so rarely? The additional problem posed by the hunter-gatherer data used to formulate this model is that the informal phylogenetic bracketing of behavior of early hominids using chimpanzees and modern humans that Stanford proposed is questionable because numerous bracketing hominid and *Pan* taxa are extinct and their behavioral adaptations are unknown.<sup>12</sup> With the very limited comparative data available, it cannot be determined when the modern human behavioral pattern emerged. Lastly, this model does little to explain the evolution of the one adaptation, language, which is most intimately associated with greater cognitive ability.

The weaknesses of this or other previously proposed models of hominid origins<sup>9,13</sup> illustrate the inherent difficulties posed by constructing explanations for unique events, such as the origin of highly derived taxa with unique adaptations like language and complex sociality. As Cartmill has noted,<sup>14,15</sup> the problem of hominid origins is largely intractable because we lack the replicated comparative data (or homoplasies) on specific hominid adaptations with their associated causes. Without the natural, replicate data that made Stanford's investigations into red colobus life-history traits possible, or the origination of mammalian sociality possible, or an evolutionary explanation for the order Primates possible,<sup>15</sup> formulating an explanation for the origin of a unique and derived taxon is difficult, but not beyond the realm of investigation. Robust explanations that focus on the functional and ecological

contexts in which specific traits were likely to have arisen, using both biomechanical principles and resolved phylogenies, have been formulated with great success.<sup>16</sup> An integrative approach that synthesizes functional analyses of the fossils and the closest modern analogs, reconstruction of hominid paleoenvironments, and the determination of the underlying factors influencing the socioecology of extant apes is the one most likely to result in a satisfying explanation for the origin of hominids.

## REFERENCES

- 1 Janson CH. 2000. Primate socio-ecology: the end of a golden age. *Evol Anthropol* 9:73–86.
- 2 Reznick DN, Shaw FH, Rodd FH, Shaw RG. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science* 275:1934–1937.
- 3 Svensson E. 1997. The speed of life-history evolution. *Trends Ecol Evol* 12:380–381.
- 4 Bshary R, Noe R. 1997. Anti-predation behaviour of red colobus monkeys in the presence of chimpanzees. *Behav Ecol Sociobiol* 41:321–333.
- 5 Noe R, Bshary R. 1997. The formation of red colobus-diana monkey associations under predation pressure from chimpanzees. *Proc R Soc London B* 264:253–259.
- 6 Mitani JC, Watts DP. 1999. Demographic influences on the hunting behavior of chimpanzees. *Am J Phys Anthropol* 109:439–454.
- 7 Watts DP, Mitani JC. 2000. Chimpanzee predation on red colobus monkeys at Ngogo, Kibale National Park, Uganda. *Am J Phys Anthropol* 30:(Suppl) 315.
- 8 Boesch C. 1994. Cooperative hunting in wild chimpanzees. *Anim Behav* 48:653–667.
- 9 Washburn SL, Lancaster CS. 1968. The evolution of hunting. In: Lee RB, DeVore I, editors. *Man the hunter*. Chicago: Aldine de Gruyter p. 293–303.
- 10 Hill K, Hurtado AM. 1996. Ache life history: the ecology and demography of a foraging people. New York: Aldine de Gruyter.
- 11 Hawkes K, O'Connell JF, Rogers L. 1997. The behavioral ecology of modern hunter-gatherers and human evolution. *Trends Ecol Evol* 12:29–32.
- 12 Susman RL. 1998. Hand function and tool behavior in early hominids. *J Hum Evol* 35:23–46.
- 13 Lovejoy CO. 1981. The origin of man. *Science* 211:341–350.
- 14 Cartmill M. 1990. Human uniqueness and theoretical content in paleoanthropology. *Int J Primatol* 11:173–192.
- 15 Cartmill M. 1992. New views on primate origins. *Evol Anthropol* 3:105–111.
- 16 Ross C. 1996. Adaptive explanation for the origins of the Anthroidea (Primates). *Am J Primatol* 40:205–230.

Christopher P. Heesy  
Interdepartmental Doctoral Program in  
Anthropological Sciences  
Department of Anatomical Sciences  
Health Sciences Center, T-8  
State University of New York  
Stony Brook, New York 11794-8081  
© 2000 Wiley-Liss, Inc.