ANIMAL BEHAVIOUR, 2006, 72, 169–180
doi:10.1016/j.anbehav.2006.01.013

Available online at www.sciencedirect.com

SCIENCE DIRECT®

Ecological and social influences on the hunting behaviour of wild chimpanzees, *Pan troglodytes schweinfurthii*

IAN C. GILBY*, LYNN E. EBERLY†, LILIAN PINTEA* & ANNE E. PUSEY*

*The Jane Goodall Institute's Center for Primate Studies, Department of Ecology, Evolution and Behavior, University of Minnesota

†Division of Biostatistics, School of Public Health, University of Minnesota

(Received 29 September 2005; initial acceptance 2 November 2005; final acceptance 4 January 2006; published online 6 June 2006; MS. number: A10257)

There has been considerable discussion of the factors that influence the hunting behaviour of male chimpanzees. Explanations invoking social benefits hinge upon the potential for males to share meat with sexually receptive females in exchange for mating ('meat for sex'), or to share meat with other males in exchange for social support ('male social bonding'). Ecological factors may also affect hunting: chimpanzees may hunt more frequently (1) in response to food shortages ('nutrient shortfall'); (2) when energy reserves are high ('nutrient surplus'); (3) in habitat types with good visibility and increased prey vulnerability; and/or (4) when ecological factors favour cooperative hunting. We used 25 years of data on chimpanzees in Gombe National Park, Tanzania, to examine the relative importance of social and ecological factors in the decision to hunt red colobus monkeys, *Colobus badius*. The presence of sexually receptive females was associated with a significant decrease in hunting probability, suggesting that males face a trade-off between hunting and mating ('meat or sex' rather than 'meat for sex'). Hunting by specific males did not vary with adult male party size, providing evidence against the male social-bonding hypothesis. After controlling for the effects of party size, diet quality was not associated with the probability of hunting or hunting successfully. Hunts were more likely to occur and to succeed in woodland and semi-deciduous forest than in evergreen forest, emphasizing the importance of visibility and prey mobility. Finally, per capita meat availability decreased with adult male party size, suggesting that hunting was not cooperative. These results provide evidence against social explanations for hunting in favour of more simple ecological alternatives.

Capture of mobile prey provides nutritional benefits, but even for specialized carnivores, can be costly in terms of energy expenditure and risk of injury (Packer & Ruttan 1988). Studies of hunting in a variety of species show that animals weigh these benefits and costs in hunting decisions. Ecological factors, particularly pursuit costs, are central to hunting studies (Creel & Creel 1995; Creel 1997; Packer & Caro 1997). African lions, *Panthera leo*, hunt more in areas where prey are most vulnerable (Hopcraft et al. 2005), have better hunting success in long grass and on dark nights (Funston et al. 2001), and cooperate to capture large ungulates when the mutual benefits outweigh the costs (Grinnell et al. 1995). Similarly, wolves, *Canis lupis*, preferentially kill white-tailed deer, *Odocoileus virginianus*, in areas with increased stalking cover (Kunkel & Pletscher 2001). Wild chimpanzees have a diet composed chiefly of fruit and leaves, but they also capture and eat a variety of mammals, birds and other vertebrates (Wrangham 1977; Nishida et al. 1979; Goodall 1986), preying most frequently upon red colobus monkeys, *Colobus badius* (Uehara 1997; Mitani & Watts 2001). Recent studies of the factors that influence chimpanzee hunting decisions and success have emphasized the potential social benefits of hunting. Selective meat sharing may yield increased mating opportunities and/or aid in the maintenance of cooperative intrasexual relationships, thus providing added incentives for hunting. However, ecological factors are also likely to be

Correspondence and present address: I. C. Gilby, Department of Anthropology, Harvard University, 11 Divinity Ave, Cambridge, MA 02138, U.S.A. (email: gilby@fas.harvard.edu). L. E. Eberly is at the Division of Biostatistics, School of Public Health, University of Minnesota, Minneapolis, MN 55455, U.S.A. L. Pintea is now at The Jane Goodall Institute Africa Programs, 4245 N. Fairfax Drive, Arlington, VA 22203, U.S.A. A. E. Pusey is at the Jane Goodall Institute's Center for Primate Studies, Department of Ecology, Evolution and Behavior, University of Minnesota, St Paul, MN 55108, U.S.A.

0003–3472/06/$30.00/0

important determinants of hunting probability and success in chimpanzees, as they are in other predators.

In this study, we used 25 years of data from Gombe National Park, Tanzania to examine social and ecological explanations for male chimpanzee hunting behaviour. We used multivariate statistics to test several nonmutually exclusive hypotheses. This allowed us to examine the relative importance of a single variable while controlling for the potentially confounding effects of additional variables associated with alternative hypotheses.

Social Factors

Chimpanzees live in complex fission–fusion communities within which individuals travel in subgroups (parties) of changing composition (Nishida 1968; Wrangham & Smuts 1980; Goodall 1986). Males compete for dominance rank and may form reciprocal, cooperative social relationships or 'alliances' (de Waal 1989; Wrangham et al. 1992; Mitani et al. 2000). Females are considerably less social than males, except during periods of sexual receptivity (Goodall 1986; Mitani et al. 2002), when they develop a conspicuous anogenital swelling (Goodall 1986; Wallis 1997).

Male social bonding

The male social-bonding hypothesis proposes that the potential of using meat to foster intrasexual alliances provides a social incentive for hunting (Stanford et al. 1994b; Mitani & Watts 2001). This predicts that upon encountering a red colobus troop, a male chimpanzee will be more likely to hunt if there are many other adult males present, assuming that large parties are more likely to contain an ally (Mitani & Watts 2001). In support of this idea, several studies have reported that the probability of hunting (by at least one chimpanzee) increases with party size (Stanford et al. 1994b; Hosaka et al. 2001; Mitani & Watts 2001; R. W. Wrangham, personal communication). However, each male ultimately decides whether or not to hunt; therefore, it is more informative to conduct analyses at the level of the individual (i.e. the target of focal-animal sampling). No study to date has investigated the effect of party size on hunting by specific individuals.

Meat for sex

The 'meat-for-sex' hypothesis proposes that male chimpanzees hunt to obtain meat to entice swollen (sexually receptive) females to mate (Stanford et al. 1994b; Stanford 1998). This predicts that a male will be more likely to hunt in parties containing sexually receptive females, independently of the number of adult males. Using long-term data from Gombe, Stanford et al. (1994b) provided evidence consistent with the meat-for-sex hypothesis, reporting a positive correlation between the presence of swollen females and hunting frequency. In two communities in Kibale National Park, Uganda, however, there was no such correlation (Ngogo: Mitani & Watts 2001; Kanyawara: R. W. Wrangham, personal communication).

Ecological Factors

Nutrition

The availability of ripe fruit in chimpanzee habitat varies considerably over time, resulting in predictable and unpredictable nutrient shortfalls (Chapman et al. 1995; Wrangham et al. 1998). The 'nutrient shortfall' hypothesis proposes that hunting frequency will increase when fruit is scarce and chimpanzees need to supplement their diet with meat (Teleki 1973; Takahata et al. 1984; Stanford 1996, 1998). In support of this idea, two studies have reported that hunting frequency at Gombe was highest during the dry season (Stanford et al. 1994b; Gilby 2004), when body masses tend to be low (Pusey et al. 2005). However, it is unclear whether nutrition was responsible for this trend. An alternative, the 'nutrient surplus' hypothesis, proposes that a chimpanzee will be more likely to hunt when diet quality is high and it can more easily absorb the energetic costs of hunting (Mitani & Watts 2001). This idea is supported by data from Ngogo and Mahale Mountains National Park, Tanzania, where hunting frequencies were highest during times when ripe fruit was plentiful (Ngogo: Mitani & Watts 2001; Watts & Mitani 2002a, b; Mahale: Nishida et al. 1979; Takahata et al. 1984). However, these studies did not control for potentially confounding factors, such as party size, that are often correlated with fruit abundance and that affect hunting behaviour.

Vegetation type

Forest structure is likely to affect chimpanzee hunting behaviour. The habitat at Gombe is a mosaic of evergreen, semideciduous forest and deciduous woodland (Clutton-Brock & Gillett 1979). Hunting is arguably more costly in evergreen forest, where trees are tall, the canopy is thick and continuous, and the understory is dense, characteristics that reduce visibility and provide many escape routes for prey. Branches in the upper canopy are thin and flexible, increasing the risk of serious injury to chimpanzee hunters. In contrast, hunting costs should be lower in semideciduous forest and woodland, where the canopy is often broken and there is little or no vine cover or ground-layer vegetation. In the woodland habitat, trees reach only 12–15 m in height (Clutton-Brock & Gillett 1979). Thus, because of such contrasting characteristics, a male should be more likely to hunt (and succeed) in semideciduous forest or woodland than in evergreen forest. Several studies have supported this idea. Chimpanzees at Gombe and Ngogo were most likely to hunt and succeed in areas with broken canopy and/or secondary growth (Wrangham 1975; Stanford et al. 1994b; Watts & Mitani 2002b). Differences in hunting patterns between chimpanzees at Taï National Park, Côte d'Ivoire and Gombe may be due to consistent differences in forest structure (Boesch 1994).

Cooperation

Chimpanzees usually hunt red colobus monkeys in groups, but there is disagreement over the extent to which they hunt cooperatively. According to a well-known