

# Final Report for the Leakey Foundation

---

In most primate species, one sex is socially dominant to the other sex and this dominance can lead to contest competition between the sexes and feeding priority for the dominant sex. Although very little attention has been given to the role of contest competition between sexes, it is expected to occur in chimpanzee for two reasons. First, male chimpanzees are all socially dominant to female chimpanzees, and even the lowest ranking male can supplant a female in feeding or social contexts (Wrangham 1980, Goodall 1986, Smuts 1987, Wrangham 2000). Second, chimpanzees feed mostly on ripe fruits in trees. These are a high quality food that are distributed in discrete patches (Wrangham 1977, 1986, Conklin-Brittain et al. 1998) and induce contest competition (Houle 2004).

The goal of this project was to assess the importance of inter-sexual contest competition (ISCC) between male and female chimpanzees. I conducted a 13 month field study at the Budongo Conservation Field Station (BCFS) in western Uganda. Using data from 1565 hours of field observation of which approximately 275 hours were in fruit trees, I tested three hypotheses regarding ISCC among these chimpanzees. First I examined whether female-directed aggression by males was significantly more likely in feeding contexts than in non-feeding contexts. I then tested the possibility that females were avoiding males in feeding contexts by looking at both the presence of females in feeding parties with and without males as well as their proximity to males in mixed sex feeding parties. I then tested if female feeding efficiency was reduced when feeding with males by examining the difference in relative feeding heights between males and females. Fruits located higher in the canopy of the tree are of

higher quality (Houle 2004) and therefore feeding sites higher in a tree are more desirable. For the hypotheses regarding female avoidance of males and feeding heights relative to males, I also tested the effects of individual female variation in the form of reproductive state, motherhood, and level of gregariousness on female feeding decisions. Data analyzed for this study come from both the BCFS long-term data from March 2006 to April 2007 as well as a dedicated study on female feeding efficiency which I conducted over the same time period.

Every morning, my field assistant (FA) and I entered the forest between 6:30 am and 7:00am to locate parties of chimpanzees. Once a party was located, an adult individual was selected as a focal individual and he or she was followed for as long as possible. Every 15 minutes, my FA recorded the identity and activity of individuals present in the party as well as the identity of the nearest neighbor to the focal individual and the location of the party relative to the 100m X 100m trail system. When a female was first encountered during the day, they were assigned a swelling grade of 0 to 4 based on the degree of swelling of the ano-genital tissue and any female with a swelling of 3 or 4 was said to be in estrous. All social interactions including copulations, grooming, and pant-grunts were recorded as they occurred.

In addition to using the long-term data, I also conducted a 13 month study at BCFS from March 2006 to April 2007. We always chose adult females as focals and when they entered fruit trees, we began recording a female tree focal observation (FTF). In each FTF, I recorded data on the identity of the focal individual and the score of her sexual swelling. Every 5 minutes, I recorded the identity of every other individual in the tree, their activity, their proximity to the focal and the feeding height of every individual in the tree crown. Feeding heights were visually

estimated and recorded as the distance in absolute values of meters from the bottom of the tree crown (the lowest fruit bearing branch) to the midpoint of an individual's body. If individuals were present in the party but were not in the tree, then I recorded their height as 0. Recording of an FTF stopped when the focal female left the tree or remained in a tree but did not feed for more than 30 minutes.

My results demonstrate that males had very little impact on the feeding decisions of female chimpanzees at Budongo. First, female-directed aggression by males was significantly more likely in non-feeding contexts compared to feeding contexts. In addition, females did not avoid males in feeding contexts. Females were equally likely to be in parties with males regardless of their activity. In mixed sex parties, estrous females were significantly more likely to have males as nearest neighbors compared to anestrus females while no other female characteristics (level of gregariousness or motherhood) had an effect on the likelihood of close proximity to males. Although dominant males fed higher in trees than subordinate males, neither males nor females were significantly more likely to feed higher than each other. However, there was a trend towards estrous females feeding higher in trees than males. Neither level of gregariousness of the female nor motherhood affected whether females or males fed higher in trees.

I conclude that although male chimpanzees are socially dominant to females, this dominance does not translate to feeding priority in this species at least with regard to feeding on fruit in trees. At this site, female-directed male aggression was not significantly more likely in feeding contexts suggesting that sexual coercion, status competition and/or policing of

female-female interactions are better explanations for this type of aggression at Budongo. Females also do not take male presence into account when they make feeding decisions regarding joining parties or their position relative to males in feeding trees. Females may have no choice but to feed in parties with males and since female-directed aggression is rare, they may not feel a threat by being in close proximity to males. In trees, there was no clear advantage for males of being the dominant sex with regards to the quality of the feeding sites in fruit trees. Estrous females did differ slightly from anestrus females but this most likely is a result of them being attractive to males at this time. I suggest that male dominance translates into feeding priority over subordinate males but not over females because male-male status competition is much more important to males than maintaining their dominance over females. Male dominance is secure over females and will not reverse and therefore males are motivated to assert dominance to each other in both feeding and non-feeding situations to maintain their rank.

This research provides a valuable methodological contribution to the study of chimpanzees in the wild. For this study, I used feeding heights as a proxy measure for the quality of the feeding site within a fruit tree. This method was based on research by Alain Houle and his colleagues (Houle 2004; Houle et al. 2007) who showed that the size, density, and quality of fruit was greater in the upper portion of tree crowns compared to lower in the crown. In a study conducted at Kibale National Park on frugivorous primates including chimpanzees and three monkey species, Houle (2004) demonstrated that in inter-specific interactions, dominant species (judged by the winners of agonistic encounters) fed higher than subordinate species when co-feeding in the same tree. Within the three monkey species, dominant

individuals also fed higher than subordinate individuals. Kahlenberg and Wrangham (Kahlenberg 2006; Kahlenberg & Wrangham 2005) then used feeding heights to study dominance and feeding competition at Kanyawara. They found that dominant individuals, both male and female, fed higher in trees than subordinate individuals. Interestingly, as previously mentioned in Chapter 4, Kahlenberg (2006) also found that males and females were equally likely to feed higher in trees at Kanyawara. Until this study, this method had not been tested outside of Kibale National Park. To validate this method, I showed that dominant males were more likely to feed higher than subordinate males. This result demonstrates that feeding heights are a valuable tool for field primatologists trying to understand contest competition between individuals.

My results also suggest an interesting methodological consideration for future studies of primate feeding ecology. Although my research indicates that males and females are equally likely to feed at sites of the same quality within fruit trees, previous research has demonstrated that males do maintain priority of access over females to certain types of valuable resources such as meat, honey or bananas (Goodall 1986; Parish 1994; Watts & Mitani 2002). While, this may suggest that the types of fruits eaten by chimpanzees at Budongo are not monopolizable, the fact that males contest with one another indicates that this is not the case. Instead, Marshall and Wrangham (2007) suggest that there are two kinds of preferred foods for primates. The first category includes preferred foods which are important and over-consumed relative to their abundance in the habitat (Leighton 1993; Marshall & Wrangham 2007). For chimpanzees, this includes ripe fruit. The second category of food involves those resources which are preferred but are less important because they are more rarely consumed. This may

be due to either increased risk or high costs involved in their procurement. For chimpanzees, this category would include meat, honey, insect prey as well as raided crops. My study demonstrates that patterns of intersexual contest competition differ with respect to these different kinds of preferred food among chimpanzees and future studies of feeding priority should distinguish between the importance of foods.

## References

- Conklin-Brittain, N. L., R. W. Wrangham, and K. D. Hunt. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. *International Journal of Primatology* **19**:971-998.
- Goodall, J. 1986. *The Chimpanzees of Gombe : Patterns of Behavior*. Belknap Press of Harvard University Press, Cambridge, Mass.
- Houle, A. 2004. Coexistence Mechanisms Among Frugivorous Canopy Primates in Kibale National Park, Uganda. *Universite du Quebec a Montreal*.
- Smuts, B. B. 1987. Gender, aggression, and influence. Pages 400-412 *in* B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker, editors. *Primate societies*. University of Chicago Press, Chicago.
- Wrangham, R. W. 1977. Feeding behavior of chimpanzees in Gombe National Park. Pages 248-258 *in* T. H. Clutton-Brock, editor. *Primate ecology : studies of feeding and ranging behaviour in lemurs, monkeys, and apes*. Academic Press, London ; New York.
- Wrangham, R. W. 1980. An Ecological Model of Female-Bonded Primate Groups. *Behaviour* **75**:262-300.
- Wrangham, R. W. 1986. Ecology and social evolution in two species of chimpanzees. Pages 352-378 *in* D. I. Rubenstein and R. W. Wrangham, editors. *Ecology and Social Evolution: Birds and Mammals*. Princeton University Press, Princeton.
- Wrangham, R. W. 2000. Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. Pages 248-258 *in* P. Kappeler, editor. *Male Primates*. Cambridge University Press, Cambridge, UK ; New York.