

[4]. On the other hand, at low contrast, the sole basis for distinguishing visual signal from random noise is the signal's regularity across space and time. In this case, preserving redundancy becomes critical, and spatial pooling and temporal summation are desired.

Supplemental Data

Supplemental data are available at <http://www.current-biology.com/cgi/content/full/18/19/R904/DC1>

Acknowledgments

ARS was supported by NSF (BCS-0549036) and NIH (R21 EY017737), PKP was supported by NIH (R01-DC02852), NSF (IIS-0205271 and SBE-0354378) and ONR (N00014-01-1-0624). CCP was supported by CIHR (MOP-79352).

References

1. Sclar, G., Maunsell, J.H., and Lennie, P. (1990). Coding of image contrast in central visual pathways of the macaque monkey. *Vision Res.* 30, 1–10.
2. Shapley, R. (1990). Visual sensitivity and parallel retinocortical channels. *Annu. Rev. Psychol.* 41, 635–658.
3. Shapley, R.M., and Victor, J.D. (1978). The effect of contrast on the transfer properties of cat retinal ganglion cells. *J. Physiol.* 285, 275–298.
4. Pack, C.C., Hunter, J.N., and Born, R.T. (2005). Contrast dependence of suppressive influences in cortical area MT of alert macaque. *J. Neurophysiol.* 93, 1809–1815.
5. Livingstone, M.S., and Conway, B.R. (2007). Contrast affects speed tuning, space-time slant, and receptive-field organization of simple cells in macaque V1. *J. Neurophysiol.* 97, 849–857.
6. Peterson, M.R., Li, B., and Freeman, R.D. (2006). Direction selectivity of neurons in the striate cortex increases as stimulus contrast is decreased. *J. Neurophysiol.* 95, 2705–2712.
7. Polat, U., Mizobe, K., Pettet, M.W., Kasamatsu, T., and Norcia, A.M. (1998). Collinear stimuli regulate visual responses depending on cell's contrast threshold. *Nature* 391, 580–584.
8. Sceniak, M.P., Ringach, D.L., Hawken, M.J., and Shapley, R. (1999). Contrast's effect on spatial summation by macaque V1 neurons. *Nat. Neurosci.* 2, 733–739.
9. Krekelberg, B., van Wezel, R.J., and Albright, T.D. (2006). Adaptation in macaque MT reduces perceived speed and improves speed discrimination. *J. Neurophysiol.* 95, 255–270.
10. Stone, L.S., and Thompson, P. (1992). Human speed perception is contrast dependent. *Vision Res.* 32, 1535–1549.
11. Tadin, D., Lappin, J.S., Gilroy, L.A., and Blake, R. (2003). Perceptual consequences of centre-surround antagonism in visual motion processing. *Nature* 424, 312–315.
12. van Hateren, J.H. (1992). Real and optimal neural images in early vision. *Nature* 360, 68–70.

¹Department of Psychology, University of California, Riverside, Riverside, California 92521, USA. ²Department of Psychology, Boston University, Boston, Massachusetts 02215, USA. ³Department of Cognitive and Neural Systems, Boston University, Boston, Massachusetts 02215, USA. ⁴Montreal Neurological Institute, McGill University School of Medicine, Montreal, Quebec, Canada H3A 2B4.
E-mail: aseitz@ucr.edu, christopher.pack@mcgill.ca

Primate hunting by bonobos at LuiKotale, Salonga National Park

Martin Surbeck and
Gottfried Hohmann*

Chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*) hunt and consume the meat of various mammals. While chimpanzees frequently hunt in groups for arboreal, group-living monkey species [1,2], bonobos are thought to focus on medium-sized terrestrial prey, such as forest antelopes, squirrels and other rodents, which are caught opportunistically by single individuals [3]. The absence of monkey hunting by bonobos is often used to illustrate the divergent evolution of the two *Pan* species [4]. Here, we present the first information on hunting of diurnal, arboreal and group living primates by wild bonobos.

Monkey hunting in chimpanzees is related to social aspects, such as bonding between males and mating effort [1,2]. The lack of monkey hunting in bonobos has been linked to a lack of male bonding and reduced levels of aggression [4,5], implying the behavior is driven not by nutritional benefits but by reproductive advantages.

We observed bonobos hunting at LuiKotale (Figure 1) in the Salonga National Park, Democratic Republic of Congo. Records on monkey hunting were obtained from members of one habituated community consisting of nine reproductive males, 12 reproductive females and 12 immatures. There were three cases of successful hunting when bonobos captured and ate monkeys and two cases in which hunting attempts did not succeed (Table 1). In all successful cases, bonobos obtained immature monkeys.

Bonobos changed their travel direction and silently approached their prey after detecting them through auditory and visual cues. When bonobos were underneath the monkey group, they stopped and several individuals took position at the bases of different trees directing their visual attention towards the

monkeys. Twice bonobos were seen to capture prey in a sudden pursuit into the trees while some individuals remained on the ground. In the third case, the actual hunt was not observed. In all cases, the monkey group had moved arboreally at a relatively low elevation (10–20 m). While the bonobos were silent during hunts, they vocalized during meat eating. Individuals who initially possessed the prey maintained control over the carcass, despite being the subject of close attention by other members of the party. As with meat-sharing in chimpanzees [1,2], individuals who possessed the carcass both actively transferred pieces of meat to other party members in response to begging gestures, and tolerated co-feeding by others on the same carcass.

It has been suggested bonobos do not hunt monkeys because aggression was selected against when ecological conditions favored female gregariousness and alliance formation [4]. An alternative view is that insufficient data from multiple bonobo populations, incomplete habituation, and effects of human interference precluded observation of monkey hunting [6]. While more data are required before conclusions can be drawn about the relationship between social traits and hunting behavior, our data raise other questions: Do the observed cases present a novel behavior? What are the environmental and social factors promoting hunting and meat eating at LuiKotale?

So far, evidence for hunting and meat eating by bonobos has largely been based on fresh fecal samples [3]. Only one sample contained the digit of a black mangabey, *Cercocebus aterrhimus*, but it was not entirely clear if bonobos had

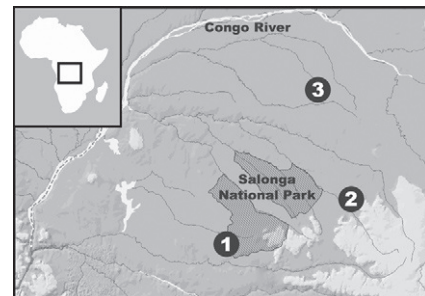


Figure 1. Field sites mentioned in the text. 1: LuiKotale, 2: Lilungu, 3: Wamba.

Table 1. Bonobo monkey hunts at LuiKotale.

Date	Bonobo hunting party size and composition	Composition of monkey group	Prey species	Age and sex of first possessor	Begging by other individuals	Age/sex of meat recipients	Duration of meat eating (minutes)
15.04.	3 adult females, 1 adolescent female, 1 adolescent male	Redtail	Redtail	Adult female	All	2 adult females	61
25.04.	2 adult males, 1 adult female, 2 adolescent females	Black mangabey, Wolf's guenon	Wolf's guenon	Adult male	1 adult male, 2 adolescent females	no sharing	>40*
01.05.	1 adult male, 1 adolescent male, 4 adult females, 1 adolescent female	Black mangabey, Wolf's guenon	Wolf's guenon	Adult female	All	Adolescent male	115
27.04.	2 adult male, 3 adolescent males, 3 adult females	<i>Black mangabey, Wolf's guenon</i>					
27.04.	2 adult males 3 adult females 1 adolescent female	<i>Red colobus</i>					

Information on successful and unsuccessful (italic) hunts on monkeys by LuiKotale bonobos. Recipients are those party members who received meat from the possessor of the carcass. Duration refers to the time period between capture of prey and termination of meat consumption.

*in this case, the acquisition of meat was not seen and therefore, we were not able to measure the exact time period of meat consumption.

hunted the mangabey themselves, or whether they had taken it from another predator. In both *Pan* species, hunting of mammalian prey is relatively rare and its detection requires frequent, close-range observations. Field studies in the Taï Forest (Ivory Coast) have accumulated one of the largest data sets on monkey hunting by chimpanzees, but it took years before researchers were able to directly observe monkey killing [1]. We tend to believe that improved habituation made our observations possible (rather than the behavior being novel).

The study site of LuiKotale is close to the Lokoro river and *terra firma* forest accounts for just a small proportion of habitat. Synchrony of fruit production is low and periods with low rainfall last longer than at other sites [7]. Local patterns of food abundance are therefore perhaps more variable. While it is unclear which environmental parameters enhance hunting of arboreal prey at LuiKotale, reports on other bonobo populations suggest the mere ability to obtain potential prey does not necessarily result in carnivory: at the Lilungu site (Figure 1), bonobos catch guenons and colobus monkeys but do not eat them [8], and at Wamba (Figure 1), bonobos and red colobus monkeys have been seen to engage in mutual grooming [9]. Without data on diet composition and energy supply, explanations of the differences in faunivory across

sites are speculative. At present, we cannot exclude the possibility that inter-site variation in hunting behavior, like inter-site variation in tool use and other behaviors of both *Pan* species, reflects variation in local, socially transmitted traditions [10].

At LuiKotale, both sexes were active in pursuing and hunting monkeys which confirms the active role of adult females in prey acquisition and meat sharing (Table 1). It is tempting to relate this to social patterns such as alliance formation and cooperation among adult females. Future work on bonobos at LuiKotale offers the possibility to explore the social and ecological conditions that promote monkey hunting by bonobos; this will contribute to a better understanding of the evolutionary significance and proximate causation of aggression, hunting and meat eating in hominoid primates.

Acknowledgments

We thank the Institut Congolaise pour la Conservation de la Nature (ICCN) for granting permission to conduct research at Salonga National Park. Fieldwork at LuiKotale is supported by the Max-Planck-Society, the L.S.B. Leakey Foundation, National Geographic Society, the Volkswagen Foundation, and private donors. The methods used to collect observational data in the field are in compliance with the requirements and guidelines of the ICCN, and adhere to the legal requirements of the host country, the Democratic Republic of Congo. We thank Kevin Langergraber and three reviewers

for helpful comments, and Matthew Chmielewski and Barbara Decrossac for their help in the field.

References

- Boesch, C., and Boesch-Achermann, H. (2000). *The Chimpanzees of the Taï Forest. Behavioural Ecology and Evolution* (Oxford: Oxford University Press).
- Mitani, J.C., and Watts, D.P. (1999). Demographic influences on the hunting behavior of chimpanzees. *Am J. Phys. Anthro.* 109, 439–454.
- Hohmann, G., and Fruth, B. (2008). New records on prey capture and meat eating by bonobos at Lui Kotale, Salonga National Park, Democratic Republic of Congo. *Folia Primatol.* 79, 103–110.
- Wrangham, R.W. (1999). Evolution of coalitionary killing: the imbalance-of-power hypothesis. *Yrbk. Phys. Anthro.* 42, 1–30.
- Wrangham, R.W., and Peterson, D. (1996). *Demonic Males. Apes and the Origins of Human Violence* (New York: Houghton Mifflin).
- Stanford, C. (1998). The social behavior of chimpanzees and bonobos - empirical evidence and shifting assumptions. *Curr. Anthropol.* 39, 399–420.
- Hohmann, G., Fowler, A., Sommer, V. and Ortmann, S. (2006). Frugivory and gregariousness of Salonga bonobos and Gashaka chimpanzees: the abundance and nutritional quality of fruit. In *Feeding Ecology in Apes and other Primates*, G., Hohmann, M., Robbins, C., Boesch, eds. (Cambridge: Cambridge University Press), pp. 123–159.
- Sabater Pi, J., Bermejo, M., Illera, G., Vea, J.J. (1993). Behaviour of bonobos (*Pan paniscus*) following their capture of monkeys in Zaire. *Int. J. Primatol.* 14, 797–804.
- Ihobe, H. (1990). Interspecific interactions between wild pygmy chimpanzees (*Pan paniscus*) and red colobus monkeys (*Colobus badius*). *Primates* 31, 109–112.
- McGrew, W. (2004). *The Cultured Chimpanzee. Reflections on Cultural Primatology* (Cambridge: Cambridge University Press).

Department of Primatology, Max-Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103 Leipzig, Germany.

*E-mail: hohmann@eva.mpg.de