Final report

The socioecological function of vocal communication in gorillas

Submitted by:

Daniela Hedwig

PhD candidate

Max Planck Institute for Evolutionary Anthropology, Germany

Contact: hedwig@eva.mpg.de

1. Research Goal

A species' vocal behavior is shaped by its social organization (Marler, 1965; 1976; Gautier & Gautier, 1977; Hauser, 1996; Blumstein & Armitage, 1997; McComb & Semple, 2005), which in turn is determined by environmental characteristics (Wrangham, 1980; Sterck et al., 1997; Isbell & Young, 2002). *Gorilla* is an excellent genus to investigate the socioecological forces that have shaped vocal contact systems because gorillas live in a diversity of habitats differing in the availability and distribution of food resources as well as visibility. To date little is understood about gorilla vocal communication and our knowledge largely derives from the small population of mountain gorillas, which live in an extreme high altitude habitat in the Virunga volcanoes.

The overall goal of this study is to explore how gorillas use vocal communication to socially adapt to their environment by testing hypotheses concerning the function of particular vocalizations while following a comparative approach. Therefore, I am comparing the behavior of mountain gorillas *Gorilla beringei beringei* (MGs) in Bwindi Impenetrable National Park, Uganda and western gorillas *Gorilla gorilla gorilla* (WGs) of Dzanga- Ndoki National Park, Central African Republic.

The funding provided by *The Leakey Foundation* has enabled the conduct of the first study providing directly comparable data of the social behavior of the well studied mountain gorilla and the elusive western gorilla. It helps us understand how primates use vocal communication to maintain their social relationships under different environmental conditions and contributes to our understanding of the evolution of sociality in primates and humans.

2. Data collection

I collected behavioral data on western gorillas during 11 months of field work at 'Bai Hokou' in Dzanga- Ndoki National Park, Central African Republic from January 2009 through December 2009. In brief, I conducted focal animal samples on all adults during

which I recorded all vocalizations as well as any affiliative or aggressive behaviors and measures of spatial proximity. Additionally, I took measurements of habitat visibility (see grant proposal for additional details).

3. Summary of publications

Over the course of the study we finalized one paper on how socioecological differences shape the use of the 'hoot-series' as a within-group long-distance contact call in MGs and WGs (Hedwig et al., submitted). Currently, I am working on a manuscript investigating the function of the 'double-grunt' and its use in WGs and MGs (Hedwig et al., in prep.). The next publications will focus on the function of the so called 'nonsyllabled' calls, as well as an analysis of the acoustic properties of the WGs and MGs vocal repertoire (two manuscripts by Hedwig et al., in prep.).

4. Summary of findings

4.1. The 'hoot-series'

In MGs the 'hoot-series' is primarily used by silverbacks as part of the chest-beat display given towards females and during intergroup encounters, so it is believed to play a role in male mating strategies to gain access to females (Robbins, 2009; Sicotte, 1994). However, recent reports suggest that WGs use this call also as a contact call (e.g. Masi et al., 2009), a type of vocalization that allow group members to maintain contact with one another while visually separated (for an overview see Cunha & Byrne, 2009). Based on the unexpected observation of a highly frequent use of this call in the WG compared to the MG study group, we set out to investigate the function of this call, which was not part of the proposal.

In particular, we investigated the impact of group dispersion and habitat visibility on the use of the 'hoot-series' in MGs and WGs in order to investigate its potential function as a within-group long-distance contact call.

WGs exhibited higher inter-individual distances compared to the MGs (Fig.1), which live in a habitat characterized by poorer visibility compared to WG (Fig.2). The WG silverback hooted ten times more frequently than the MG silverback. These differences may be due to differences in group dispersion, presumably dictated by differences in feeding ecology, as the spatial separation from other group members was likely the stimulus for his calling. He hooted at a significantly higher rate when alone compared when another individual was within ten meters of him (Fig.4). Adult females hooted only rarely, but replied with other vocalizations to 40% of the hoots given by the silverback, when they were at risk of separation themselves.

Our findings suggest that the 'hoot-series' without accompanying chest-beat serves as a within-group long-distance contact call. Differences in the frequency of calling between the two species are likely due to differences in group dispersion, potentially caused by differences in food availability in the two species' habitats. Our study suggests that group dispersion is an important factor explaining the variation in vocal communication systems across animal species. The male biased usage of the 'hoot-series' stands in contrast to the contact call systems of some Old World monkeys, but reflects the social system of gorillas and emphasizes the central role of the silverback within a group.

4.2. The 'double-grunt'

The 'double-grunt' is the vocalization most commonly emitted by MGs. As it is used in seemingly context unspecific way, a variety of functions have been proposed; ranging from signaling location, coordination of activities as well as mediating feeding competition or affiliative interactions (Harcourt et al., 1993; Harcourt & Stewart, 1996; Seyfarth et al., 1994; Stewart & Harcourt, 1994; Harcourt & Stewart, 2001. I am currently testing hypotheses concerning the function of the double grunt by investigating the influence of proximity to other group members, activity, patterns of social behavior, as well as habitat visibility on the use of the 'double-grunt' in MGs and WGs.

I found no difference in the frequency of usage of the ‘double-grunt’ between WGs and MGs. My preliminary analysis indicates that the ‘double-grunt’ is used by both study groups most frequently while resting, with decreasing proximity to other group members, while habitat visibility does not seem to influence its usage. While this is in line with previous suggestions that the gorilla close range calls function to modulate social interactions, instead of being contact calls, it rules out a function in mediating feeding competition and suggests a role in coordinating activities or affiliative social interactions. Further analysis is currently ongoing.

5. Upcoming studies

We will send a summary of additional results deriving from the project that was partially funded by the Leakey Foundation soon. There are three other manuscripts in preparation that will substantially expand our knowledge of the vocal communication of gorillas. In addition, the results will enable us to increase our comprehension of gorilla sociality as well as the socioecological driving forces behind vocal communication systems.

Figures

Fig. 1a.

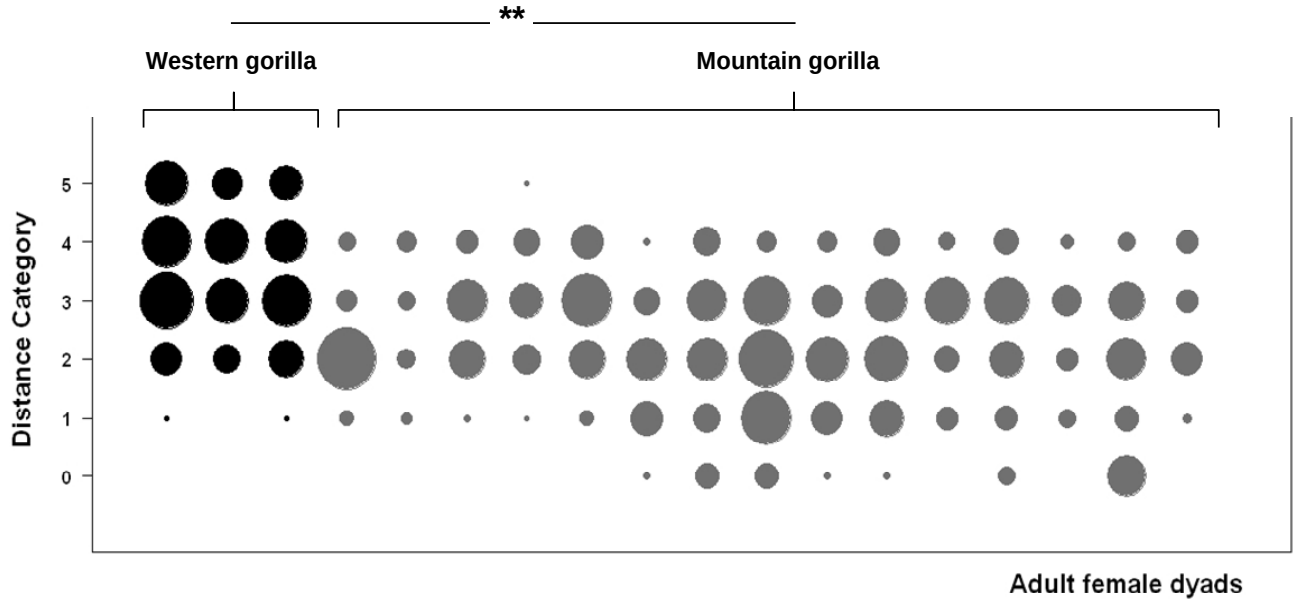

Fig. 1b.

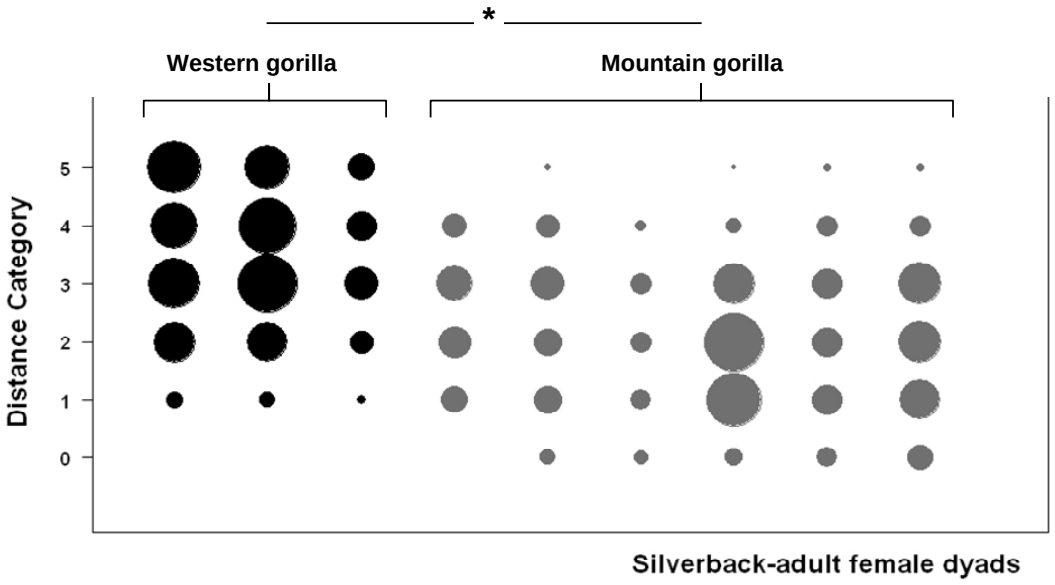

Fig. 1a, b. Time spent by each female-female dyad (2a) and silverback-female dyad (2b) in the respective distance categories. Each vertical row represents one dyad. The diameter

of the black dots indicates the number of scan samples that each distance category was scored. The color of the dots indicates the species: black- western gorilla, grey- mountain gorilla. Distance categories: 0: physical contact; 1: <2m; 2: >2-5m; 3: >5-10m; 4: >10-20m; 5: >20m. Asterisks indicate significant differences between the western and mountain gorillas ('*'- significant at the 0.05 probability level; '**'- significant at the 0.01 probability level). Statistical details: a) western gorilla: N = 3 dyads, median distance category = 4 (>10-20m), mountain gorilla: N = 15, median distance category = 2 (>2-5m); Mann Whitney U-test: U = 3.5, $p < 0.01$; b) western gorilla: N = 3 dyads, median distance category = 3 (>5-10m), mountain gorilla: N = 6 dyads, median distance category = 2 (>2-5m); U = 1, p = 0.04.

Fig. 2

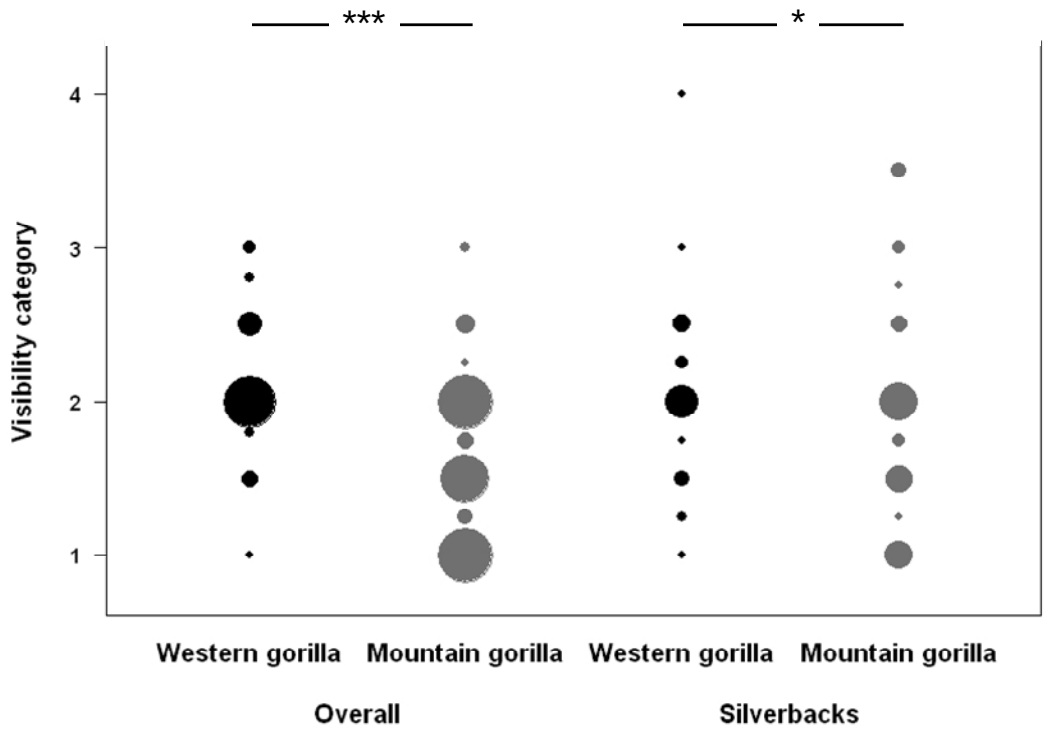

Fig. 2. Time spent by adult western and mountain gorillas, and silverbacks only, in areas characterized by the respective visibility category. The diameter of the black dots

indicates the number of observation days with the respective daily median visibility. The color of the dots indicates species: black- western gorilla, grey- mountain gorilla. Visibility categories: 1: 0-5m; 2: >5-10m; 3: >10-15m; 4: >15-20m; 5: >20m. Asterisks indicate significant differences between the western and mountain gorillas ('*'- significant at the 0.05 probability level; '***'- significant at the 0.001 probability level). Statistical details: overall visibility: mountain gorilla: N =174 days, median daily visibility = 1.5 (25% percentile = 1, 75% percentile = 2); western gorilla: N = 74 days, median daily visibility = 2 (25% percentile = 2, 75% percentile = 2); U = 10165, p < 0.0001; only silverbacks: mountain gorilla: N = 72 days, median daily visibility = 2 (25% percentile = 1.5, 75% percentile = 2); western gorilla: N = 40 days median daily visibility = 2 (25% percentile = 2, 75% percentile = 2.5): U = 1865.5, p = 0.015).

Fig. 3.

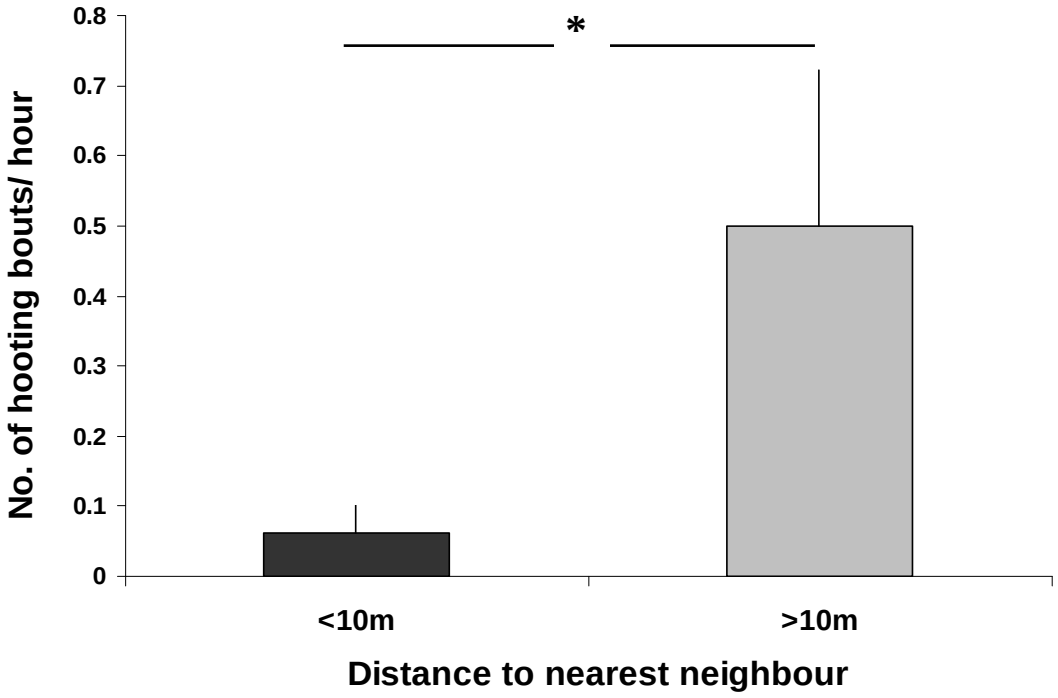

Fig. 3. Number of hooting bouts per hour given by the western gorilla silverback when his nearest neighbor was <10m distant compared to when his nearest neighbor was >10m

distant. Error bars indicate standard error. Asterisks indicate a significant difference between the hooting bout rates (‘**’- significant at the 0.01 probability level).

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