RESEARCH ARTICLE

Audience Effects, but not Environmental Influences, Explain Variation in Gorilla Close Distance Vocalizations — A Test of the Acoustic Adaptation Hypothesis

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Close distance vocalizations are an integral part of primate vocal communication. They exhibit large acoustic variation which has been suggested to constitute flexible responses to the highly variable social setting of group living animals. However, a recent study suggested that acoustic variation in close distance calls of baboons may also arise from acoustic adaptations to environmental factors in order to counteract sound degradation. We tested whether the variation in calling rate and acoustic structure of gorilla close distance vocalizations may serve to counteract distorting effects of vegetation during sound propagation. Using focal animal sampling we recorded the vocal behavior of 15 adult individuals living in two groups: one group of western lowland gorillas *Gorilla gorilla gorilla* and one group of mountain gorillas *Gorilla beringei beringei*. We considered the distance between the caller and its nearest neighbor as the minimum transmission distance of calls; while vegetation density was quantified through measures of visibility. Our analysis revealed vocal plasticity in gorilla close calls in relation to changes in visibility and nearest neighbor distance. However, the observed changes in fundamental frequency and calling rate are unlikely to counteract degrading effects of vegetation, but rather seem to reflect reactions to variation in spatial and visual separation from other group members, similar to the audience effects demonstrated in a range of other species. We propose that vocal plasticity to counteract distorting environmental effects may not be prevalent across taxa and perhaps confined to species living in heterogeneous habitats with highly variable transmission conditions. Am. J. Primatol. 77:1239–1252, 2015.   © 2015 Wiley Periodicals, Inc.

INTRODUCTION

The fundamental notion behind communication is that information contained in a signal is reliably transferred from a sender to a receiver. In vocal communication, this transfer can be impeded as sound experiences reverberation and absorption during propagation, leading to the attenuation, and distortion of the acoustic signal. The strength of such degrading effects depends on frequency-related and temporal features of vocalizations in relation to environmental characteristics and the distance the sound travels. Therefore, the acoustic adaptation hypothesis (AAH hereafter) predicts that the acoustic characteristics of vocal signals and calling rate should be adjusted to environmental features to enhance sound propagation, particularly if calls need to travel far distances [Morton, 1975; Waser & Brown, 1986, extended to call usage by Ey & Fischer, 2009]. Previous studies providing support for the AAH were mainly based on inter- or intra-specific

cross-site comparisons of long distance vocalizations used in populations living in densely vegetated (e.g., forest) and open habitats (e.g., grassland). However, a more recent study on baboons [Ey et al., 2009] suggested that environmental conditions also have an impact on the production of close distance vocalizations. In particular, their study indicated

that baboons exhibit a vocal plasticity that enables them to modify the acoustic structure of their grunts and calling rate when moving between forest and grassland areas within their home ranges. This is surprising because, given the generally short distances such calls need to travel, transmission conditions would not be expected to exhibit strong selective pressures on their production.

Close distance vocalizations are an integral part of primate vocal communication as they mediate the social interactions between individuals [e.g., Boinski, 1993; Boinski & Campbell, 1996; Cheney et al., 1995; Silk et al., 2000; Whitham et al., 2007]. They exhibit a large acoustic variation [e.g., Bouchet et al., 2012; Elowson & Snowdon, 1994; Lemasson & Hausberger, 2011; Sugiura, 2007] which has been suggested to constitute flexible responses to the highly variable social environment of group living animals [e.g., Bouchet et al., 2012; Snowdon et al., 1997]. While the acoustic variation within close distance calls can be driven by variability in underlying emotional states [e.g., Bayart, 1990; Rendall, 2003], they can encode information about the caller's identity [Rendall, 2003], group [Townsend, 2010], activity [Rendall, 1999; Radford & Ridley, 2008; Townsend, 2011], and social context [Rendall, 1999; Radford & Ridley, 2008]. Investigating to what extent the acoustic variation within close distance calls constitutes an adjustment to varying environmental conditions to counteract signal degradation will lead to a more comprehensive understanding of the functioning of close distance vocalizations.

Close distance vocalizations constitute a crucial aspect of gorilla vocal behavior [Fossey, 1972; Harcourt et al., 1986, 1993; Harcourt & Stewart, 1996, 2001; Schaller, 1963; Seyfarth et al., 1994; Stewart & Harcourt, 1994; Salmi et al., 2013]. These so called *close calls* are variable vocalizations ranging from short grunts to longer grumbles and hums which typically consist of one or more acoustic units [e.g., Harcourt et al., 1986, 1993; Harcourt & Stewart, 1996, 2001; Hedwig et al., 2014 Seyfarth et al., 1994; Salmi et al., 2013]. In a previous study we demonstrated that the gorilla close calls are built of five intergraded types of acoustic units (low pitched unit types: atonal grunt a1, tonal grunt t2, grumble t4; higher pitched unit types: short hum t1, long hum t3) which were flexibly, yet, non-randomly arranged into more than 150 combinations [Hedwig et al., 2014]. Acoustic, and particularly syntactic, variation within close calls, and calling rate appeared to correlate with the callers' activity, its role in vocal exchanges, that is whether calls were given as a reply, or spontaneously, as well as the proximity to other individuals [Harcourt et al., 1993; Hedwig et al., 2015; Seyfarth et al., 1994; Salmi et al., 2013]. Results of our previous study [Hedwig et al., 2015] suggest that parts of the syntactic variation within gorilla close calls may be adaptive in order to enhance signal transmission when communicating over large distances, by using combinations consisting of long unit types, which may increase signal detectability [Klump & Maier, 1990; Nemeth et al., 2006]. Gorillas are highly terrestrial, forest dwelling species that typically inhabit areas with dense ground vegetation [Bermejo, 1999; Nkurunungi et al., 2005; Tutin & Fernandez, 1984; Yamagiwa & Basabose, 2006]. Since absorption and reflection of sound is particularly strong when propagating close to the ground ["ground effect", Wiener & Keast, 1959] modifications of their close calls in response to such distorting environmental conditions are plausible.

Based on this, we investigated the influence of vegetation density and transmission distance on calling rate as well as duration and fundamental frequency of gorilla close calls, which we sampled from 15 adult individuals living in two groups: one group of western lowland gorillas *Gorilla gorilla gorilla* and one group of mountain gorillas *Gorilla beringei beringei*. We quantified vegetation density through measures of visibility and inferred the minimum transmission distance of calls from the distance to the caller's nearest neighbor. According to the acoustic adaptation hypothesis, we predicted that with increasing nearest neighbor distance and decreasing visibility the gorillas will: (i) emit more close calls since this will increase the likelihood of the signal to be detected by a recipient [Ey & Fischer, 2009]. Concerning the acoustic structure, we expected that increasing nearest neighbor distance and decreasing visibility the gorillas will lead to calls having a (ii) lower fundamental frequency since high frequencies are particularly affected by attenuating influences [Bradbury & Vehrencamp, 2011] and (iii) a longer duration, which increases transmission distance and the detectability of a signal [Klump & Maier, 1990; Nemeth et al., 2006]. In particular, since the importance of degrading environmental effects increases with increasing transmission distance, we expected an interaction between visibility and nearest neighbor distance. Alternatively, we may find correlations of calling rate and/or acoustic variation with visibility and/or nearest neighbor distance, which may reflect reactions to changes in visual and spatial separation to other group members similar to audience effects demonstrated in numerous other species [e.g., *Betta splendens*: Doutrelant et al., 2001; T*aeniopygia guttata*: Pollick et al., 2005; *Cebus paella*: Schel et al., 2013; *Pan troglodytes:* Vignal et al., 2004]. Given the syntactic structure of gorilla close calls [Hedwig et al., 2014], changes in their acoustic structure can happen on two levels. First, the gorillas may alter the unit type composition of their calls and hence use different combination types, and, secondly, the gorillas may

use the same combination types but modify the acoustic structure of the constituent unit types. In order to account for this we investigated the effects of visibility and nearest neighbor distance on the unit type composition of calls as well as the acoustic variation within calls with similar unit type composition (Table I).

METHODS

Study Sites and Subjects

We observed one group of mountain gorillas in Bwindi Impenetrable National Park (0°53–1°08N, 29°35–29°50E), Uganda. Data collection focused on 10 adult individuals (one silverback, five females, and four blackbacks) of the habituated "Kyagurilo" group [Robbins, 2008]. The study site consists of afromontane rainforest (altitude 1160–2600 m) which is characterized by a dense understory of herbaceous vegetation, interspersed with patches of closed-canopy forest. Due to regulations of the Uganda Wildlife Authority, observations were restricted to approximately four hours per day. Data collection was conducted usually in the mornings, on 312 days during a total of 12 months from October 2007 through October 2008.

One group of habituated western lowland gorillas was observed at the Bai Hokou study site (2°51N, 16°28E) which is located in the Dzanga–Ndoki National Park, Central African Republic (altitude 340–615 m). Data were collected on five adult individuals (one silverback, three females, and one blackback) of the "Makumba" group [Masi et al., 2009]. The habitat is a low altitude mixed-species semi-evergreen rainforest, interspersed with areas of *Gilbertiodendron dewevrei* (Caesalpiniaceae) closed-canopy forest and patches of open-canopy forest with dense terrestrial herbaceous vegetation. Data were collected in the mornings (7:00–12:00) and/or afternoons (12:00–17:00) on 124 days over a period of eight months from April to November 2009.

Data Collection

We used focal animal sampling [Altmann, 1974] during which we conducted continuous audio recordings of the focal animal's vocal behavior. For each vocalization the following contextual data were recorded: (i) the activity of the focal animal, which we categorized into resting (sleeping, sitting, grooming, nursing), and foraging (preparation and ingestion of food, locomotion between feeding spots), (ii) the distance of the focal animal to its nearest neighbor, which also included all non-adult individuals. We used this as a proxy for transmission distance. We thereby assumed that the nearest neighbor distance reflects the minimum distance the call had to travel in order to be received. It is possible that calls were directed to individuals further away than the nearest neighbor, which would result in an underestimation of the actual transmission distance, and an overestimation of acoustic adaptation given the nearest neighbor distances. To measure nearest neighbor distance we used the following categories: 0: physical contact, 1: > 0–2 m, 2: > 2–5 m, 3: > 5–10 m, 4: > 10–20 m, 5: > 20 m. (iii) We recorded whether the vocalization was given spontaneously or in reply to another individual's call. A reply was defined as any vocalization given within 3 sec after another individual's call [based on Seyfarth et al., 1994]. Our analyses focused on close calls given spontaneously by the focal animal excluding those given in reply to another individual's call. We did so for two reasons: first, our sample size did not allow us to statistically control for potential acoustic differences between calls given spontaneously and in reply, as known for gorilla double grunts [Seyfarth et al., 1994], and secondly, to prevent ambiguity in our measure of minimum transmission distance, as for reply calls we did not have enough measurements of the distance to the first caller. Additionally, we used instantaneous sampling [Altmann, 1974] to record the focal animal's activity and its nearest neighbor distance at 5 min intervals.

TABLE I. Overview of Predictions of the Acoustic Adaptation Hypothesis on Calling Rate and the Acoustic Structure of Gorilla Close Calls (See Figure 1 for Details on the Syntactic Structure)

	Calling rate	Acoustic structure	
		Call composition	Acoustic variation within combination types
With decreasing visibility and increasing nearest neighbor distance	Call more frequently	Combination types comprising long unit types (t4 and t3) and/or unit types of low fundamental frequency (t4 and t2) will be used more frequently	Constituent unit types will have a longer duration and/or a lower fundamental frequency

Given the syntactic structure of gorilla close calls, predictions concerning their acoustic structure were made on two levels: first, the unit type composition of calls and, secondly, the acoustic variation within calls with similar unit type composition (see methods section for details on how such combination types were defined).

Data on vegetation density were collected by measuring visibility every 10 min for the western gorillas and every 15 min for the mountain gorillas. We used different time intervals for the two study groups because the western gorillas changed their location more frequently compared to the mountain gorillas. To measure visibility, the first author kneeled down to a level that was approximately at the eye-height of a gorilla at roughly the location where the focal animal had been and estimated the farthest distance she could see using the following categories: 1: 0–5 m, 2: > 5–10m, 3: > 10–15 m, 4: > 15–20 m, 5: > 20 m. We validated these estimations by comparing them with actual measurements. We first estimated visibility as above and then subsequently moved with a bright orange cardboard sheet (measurements 26 × 17 cm) held waist-high in a straight line away from the observer. Once the sheet was no longer visible we measured its distance to the observer. Estimated and measured visibility records were strongly correlated (Spearman's rank correlation: $P = 0.83$, n = 201, $P < 0.0001$).

We used one category (category 5) for all calls with a nearest neighbor distance or visibility of > 20 m since distance estimations were likely to become inaccurate with increasing distance. To include visibility and nearest neighbor distance as quantitative rather than ordinal predictor variables into our analyses, we transformed them to interval scale by using the mid-point value of each category, as defined above, instead of the categories itself. Since mid-points cannot be derived for distance and visibility category 5 (> 20 m), we only analyzed calls given within up to 20 m of nearest neighbor distance and visibility, respectively.

Analysis

Call rate

We segmented each focal period into 5 min intervals according to the instantaneous sampling and calculated the number of calls given by the focal animal during each time interval (see supplementary material S1 for an overview of calling rates measured for the different study individuals). Visibility estimates for each time interval were obtained from each interval's temporarily closest visibility measurement.

We used a Generalized Linear Mixed Model with Poisson error structure and log link function for the analysis [GLMM; Baayen et al., 2008]. We have chosen GLMM for our statistical analysis as it enabled us to test the interacting influences of visibility and nearest neighbor distance on call rate while controlling for other possible factors influencing vocal production (e.g., Ey & Fischer, 2009). The GLMM additionally allows for taking random effects such as caller into account. In addition to visibility and nearest neighbor distance the model included

their interaction since the importance of degrading environmental effects increases with increasing transmission distance. Furthermore, we included the following control predictors as fixed effects (Table II): (i) activity (foraging/resting) because the behavioral context is known to correlate with the rate at which gorillas give close calls [e.g., Harcourt et al., 1986], (ii) group (western/mountain gorilla group) in order to control for differences in vocal behavior between the individuals of the two groups, potentially due to differences in social behavior [Gustison et al., 2012; Robbins, 2010; Salmi et al., 2013], (iii) time of day and a squared term of time of day to control for potential changes in calling rate throughout the day [e.g., Schneider et al., 2008], and finally, an autocorrelation term to account for temporal interdependence between data points (see supplementary material S2 for information on how the autocorrelation term was derived). Lastly, to control for pseudoreplication (i.e., data points from the same individual are statistically non-independent and hence specific individuals may drive an effect when in fact there is actually no effect), we incorporated "caller" as a random effect into the model [Bolker et al., 2009; Jaeger, 2008; Laird & Ware, 1982]. Following Schielzeth & Fortsmeier [2009] and Barr et al. [2013] we included random slopes for all fixed effects predictor variables except group, and the autocorrelation term to keep type I error rate at the nominal level of 5% (Table II). We could not account for the possibility of the random slopes being correlated with the random intercept since the respective models did not converge anymore. However, as shown by Barr et al. [2013] not accounting for such correlations does not severely affect type I error rate.

Acoustic structure

Analyses were conducted on a subset of calls used in a previous study in which we demonstrated the syntactic properties of gorilla close calls [Hedwig et al., 2014, Fig. 1]. We measured the mean fundamental frequency of calls semi-automatically with the custom-made software LMA developed by Kurt Hammerschmidt [Hammerschmidt, 1990; Schrader & Hammerschmidt, 1997] on spectrograms with a 4 Hz frequency and 4 ms temporal resolution. If the close calls consisted of multiple acoustic units the mean frequency of the call was calculated as the mean of the average frequencies calculated per unit. Atonal units (i.e., for which no fundamental frequency was detectable) were not included into the analysis since they were not recorded frequently enough to allow for a meaningful statistical analysis of their acoustic parameters. Call duration was measured manually on spectrograms with a 20 Hz frequency and 1 ms temporal resolution using Avisoft SASlab Pro (see supplementary material S1 for an overview of the fundamental frequency and duration of close

TABLE II. Overview of the different GLMMs used to investigate the Effects of Visibility and Nearest Neighbor Distance on Acoustic Parameters

Response variable	Test predictors	Control predictors	Random effects		Error	Sample size
			Intercept	Slope[d]		
Number of calls per 5 min interval	distance*visibility	activity + group + daytime^2 + autocorrelation term	Caller	Distance*visibility Distance Visibility Activity Daytime Daytime^2	Poisson	N = 1159 calls (11–220 per caller) N = 4469 intervals (258–361 per caller)
Mean fundamental frequency	w.dist*w.vis+ bw.dist*bw.vis	activity + group + age-sex + autocorrelation term	Caller Combination type	W.dist*w.vis[a] W.dist[a] W.vis[a]	Gaussian	N = 511 (6–78 per caller, 10–192 per combination type)
Duration	w.dist*w.vis+ bw.dist*bw.vis	activity + group + autocorrelation term		Bw.dist*bw.vis[b] Bw.dist[b] Bw.vis[b] Activity[b] Group[c]		

Sample sizes are given as overall numbers of calls and in brackets the range across the 15 individuals and the 10 combination types. Combination types are calls with similar unit type composition. Bw.dist and bw.vis represent the average distance and visibility per combination type. W.dist and w.vis represent the differences between each calls' distance and visibility and its combination type's average distance and visibility, respectively. If the average distance or average visibility per combination type (bw.dist and bw.vis) have a significant effect on the mean fundamental frequency or duration this suggests that distance or visibility, respectively, lead to changes in the unit type composition of calls and hence the use of different combination types. If variation in distance or visibility within combination types (w.dist and w.vis) reveal significance this suggests that the respective contextual variable lead to changes in the fundamental frequencies or durations within the constituent unit types. "*" Denotes an interaction and the respective main effect.

[a]Random slopes within random effects of caller and combination type.
[b]Random slopes within random effect of caller only.
[c]Random slopes within random effect of combination type only.
[d]Random slopes components were the same in the two models with mean fundamental frequency and duration, respectively, as the response.
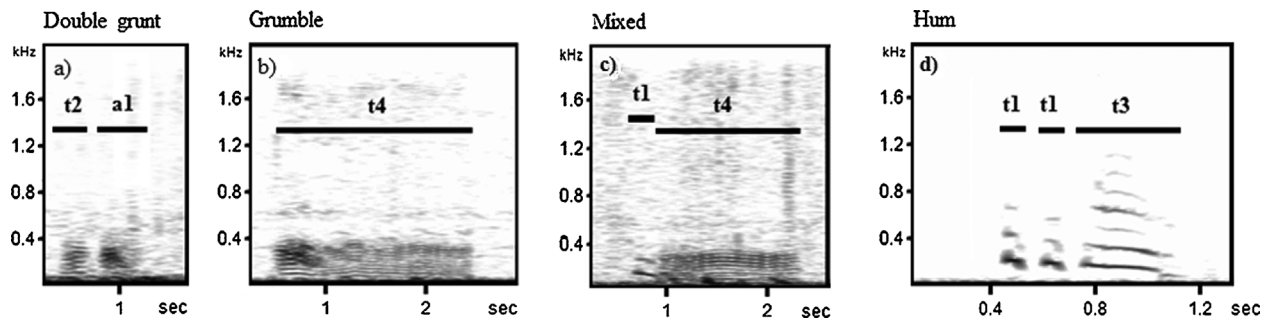
Fig. 1. Spectrograms illustrating typical examples of gorilla close calls, their syntactic structure, and classification according to previous studies [Harcourt et al., 1993, Hedwig et al., 2014]. Close calls usually consist of one or a series of acoustic units separated by periods of silence of at most two seconds (**a**, **d**). These units in turn often can be subdivided into subunits based on abrupt changes in the distribution of energy across frequencies (**c**). Based on temporal and frequency-related characteristics these units can be classified into five unit types, which can be arranged into combinations, defined as unique sequences of unit types. Grunts and grumbles usually consist of unit types of low fundamental frequency: atonal grunt a1, tonal grunt t2, or grumble t4 (**a**, **b**); hums consist of unit types of high fundamental frequency: short hum t1 and long hum t3 (**d**), while mixed calls consist of unit types of both high and low fundamental frequency (**c**) [Hedwig et al., 2014].

calls measured for the different study individuals). In order to account for the fact that gorillas may adjust the fundamental frequency or duration of calls to nearest neighbor distance and/or visibility through altering the unit type composition of their calls and/or, modifying the acoustic structure of the constituent unit types we categorized combinations into "combination types" based on their unit type composition. Specifically, we defined combination types such that they were invariant with regard to the relative proportion of unit types they comprised. For instance, all combinations comprising two particular types (e.g., *t1* and *t3*) with the same relative frequencies of occurrence were considered to be of the same combination type. To avoid problems resulting from small sample sizes per combination type we restricted our analysis to combination types with more than ten observations, resulting in a total of ten combination types (Table III).

We used General Linear Mixed Models with Gaussian error structure and identity link [GLMM; Baayen et al., 2008] for analyses. In addition to controlling for possible other factors influencing vocal production and taking into account random effects such as caller, the GLMM allowed us to test the interacting influences of visibility and nearest neighbor distance on unit type composition of calls as well as the acoustic structure of unit types simultaneously. With regard to the fixed and random effects these models were largely identical to that used for call rate (see above), but lacked the control variable daytime. To investigate whether the gorillas modify the unit type composition of calls and/or adjust the acoustic structure of unit types in response to changes in visibility and nearest neighbor distance we represented both nearest neighbor distance and visibility by two fixed effects using "within-subjects centering" [van de Pol & Wright, 2009]. First, we included the average distance and visibility per each combination type ("bw.dist", "bw.vis") to represent their variation

between combination types. Secondly, we included the differences between each calls' nearest neighbor distance and visibility and its combination type's average distance and visibility, respectively, in order to represent their variation within combination types ("w.dist", "w.vis"). If the average distance or average visibility of combination types have a significant effect on the mean fundamental frequency or duration of calls this suggests that the contextual variable (distance or visibility, respectively) lead to changes in the unit type composition of calls and hence the use of different combination types. If distance variation or visibility variation within combination types reveal significance this suggests that the respective contextual variable leads to changes in the fundamental frequencies or durations within the constituent unit types. Since the importance of degrading environmental effects increases with increasing transmission distance, we included the interaction between average distance and average visibility as well as distance variation and visibility variation within combination types.

In the model to investigate the influence of visibility and nearest neighbor distance on the fundamental frequency we included as control variables: age-sex class since age- and sex-related morphological variation is known to correlate with frequency-related acoustic characteristics [e.g., Ey et al., 2007], as well as activity because the behavioral context is known to correlate with the acoustic structure of vocalizations [e.g., Hauser & Marler, 1993; Morton, 1977; Owren et al., 1997]. We also included the control variable group (western/ mountain gorilla group) in order to control for differences in acoustic structure between the individuals of the two groups, potentially due to differences in body size [Bergmann, 1847; Ey et al., 2007; Taylor, 1997], social behavior [Gustison et al., 2012; Robbins, 2010; Salmi et al., 2013] or different habitat characteristics [Doran & McNeilage, 1998;

TABLE III. Acoustic Characteristics and Sample Sizes for the Combination Types investigated in this Study as well as their Classification according to Previous Studies (e.g., Harcourt et al., 1993; Hedwig et al., 2014)

	Grunts and grumbles			Hums				Mixed calls		
Combination type	t4	t2	t2_t4	t3	t1	t1_t3	t1_t3_t4	t1_t4	t2_t3	t3_t4
F0mean	29.6	40.0	32.4	160.4	164.2	203.2	115.7	91.8	73.8	87.1
Minimum	15	20	17	60	74	128	82.7	49	51	62
Maximum	62	78	57.5	436.7	312	354	140.3	148	101.5	116.5
Duration	1.8	0.5	1.4	1.6	0.7	1.6	2.1	1.4	1.2	1.9
Minimum	0.4	0.1	0.6	0.4	0.1	0.9	1.3	0.6	0.6	1.2
Maximum	6.2	1.2	6.5	5.8	1.3	2.7	4.0	2.1	2.4	4.1
# calls	192	120	63	46	17	10	20	20	10	13
Combinations	a1_a1_t4_t4	a1_t2	t2_t4	a1_t3	a1_t1	t1_a1_t3	t1_t4_t3	t1_t4	t2_t3	t3_t4
	a1_t4	t2_a1_a1	t2_t4_t2_t4	t3	t1_a1	t1_t3	t3_t4_t1			t4_t3
	t4_a1_a1_t4_t4	t2_a1		t3_t3	t1_a1_t1	t3_t1	t4_t1_t3			
	t4_a1	t2		t3_t3_t3	t1	t3_t1_t1_t3				
	t4	t2_t2		t3_t3_t3_t3	t1_t1					
	t4_t4				t1_t1_t1					
					t1_t1_t1_t1					
					t1_t1_t1_t1_t1					

Note that atonal units (i.e., for which no fundamental frequency was detectable, a1) were not included into the analysis since they were not recorded frequently enough to allow for a meaningful statistical analysis of their acoustic parameters.

Linsksens et al., 1976]. In addition to "caller" we also included "combination type" as a random effects variable into the model and random slopes for both (Table II). The model to investigate the influence of visibility and nearest neighbor distance on call duration was largely identical to the one we used for the mean fundamental frequency, but lacked the control variable age-sex class (Table II). We excluded this predictor because close call duration is unlikely to be correlated with body size (e.g., Ey et al., 2007).

Implementation

Models were fitted using the functions "glmer" (call rate) or "lmer" (fundamental frequency and call duration) provided by the lme4 package [Bates et al., 2013] in the statistical software environment R, version 3.0.2 [R Core Team, 2013]. To fulfil the assumptions of the Gaussian models (fundamental frequency and call duration) of normally distributed and homogeneous residuals, we visually inspected histograms of the quantitative predictors and responses as well as QQ-plots of the residuals plotted against fitted values. In order to achieve these assumptions being fulfilled we log-transformed mean fundamental frequency and square root transformed call duration, visibility and nearest neighbor distance. For the Poisson model investigating calling rate overdispersion was not an issue (dispersion parameter $D = 1.19$). For all models we tested for collinearity among the predictor variables by calculating Variance Inflation Factors [VIF, Field, 2005] using the function "vif" of the R package "car" [Fox and Weisberg, 2011] in combination with a standard linear model excluding the random effects, interactions and day time squared (R function "lm"). A maximum $VIF = 2.1$ across all models and predictors indicated that collinearity was not an issue and that calculated estimates reflect the independent effects of the predictors [Field, 2005].

To rule out significant effects of our test variables due to multiple testing, we first tested their overall significance by comparing the full model with all predictor variables, to a null model only including the control variables and the random intercepts and slopes [Forstmeier & Schielzeth, 2011], using a likelihood ratio test [Dobson, 2002] and the R function "anova". In case the interactions did not reveal significance, we excluded them to obtain easier interpretable *P*-values for the respective main effects [Schielzeth, 2010]. We derived *P*-values for the effects of the predictors in the Gaussian models by comparing the full model including all predictor variables to a reduced model without the predictor of interest using likelihood ratio tests [Barr et al., 2013; Dobson, 2002].

To check model stability we reran each model while excluding subjects, as well as combination types for the fundamental frequency and call duration models, one at a time and compared the obtained coefficients with those derived from the model based

on all data. Differences between coefficients were minimal for the calling rate model, so we concluded that our data set contained no influential subjects. Regarding the fundamental frequency model we found no indications for instabilities in the significant effects of visibility and nearest neighbor distance. However, the effect of activity and age-sex class on the fundamental frequency appeared to strongly depend on which subjects and combination types were included into the analysis. We found instabilities in the non-significant call duration model since the effect of the mean visibility per combination types (bw.vis) strongly depended on which combination types were included into the analysis.

Ethics Statement

This research complies with the American Society of Primatologists principles for the ethical treatment of animals as well as the ethical guidelines of the Department of Primatology of the Max Planck Institute for Evolutionary Anthropology and was conducted in accordance with the animal care regulations and national laws of Uganda, Central African Republic and Germany.

RESULTS
Call Rate

Visibility and nearest neighbor distance had a significant effect on calling rate (likelihood ratio test, $\chi^2 = 14.09$, df $= 3$, $P = 0.003$). More specifically, we found a significant interaction between the effects of visibility and distance to the nearest neighbor on the calling rate (Table IV). However, in contrast to the predictions of the AAH, individuals appeared to call at the highest rates when visibility and nearest neighbor distance where both at large but also at low values (Fig. 2).

Acoustic Structure

Visibility and nearest neighbor distance had a significant effect on the mean fundamental frequency of close calls ($\chi^2 = 22.67$, df $= 6$, $P < 0.001$), however, the effects were contrary to what we expected according to the AAH. First, the average visibility and distance of combination types (bw.vis and bw. dist) had a significant effect on the fundamental frequency of calls indicating that visibility and nearest neighbor distance lead to changes in the unit type composition of calls and hence the use of different combination types. After removal of the marginally non-significant interaction between average visibility (bw.vis) and average distance per combination type (bw.dist) (estimate $= -0.102 \pm$ SE 0.095, $P = 0.07$), it appeared that combination types consisting of the high pitched unit types t1 and t3 were

TABLE IV. Summary of the GLMM for Effects on Calling Rate

	Number of close calls per 5 min		
	Estimate	SE	P-value
Intercept	−2.010	0.153	[d]
Distance	−0.177	0.063	[a]
Visibility	0.068	0.048	[a]
Distance*Visibility	0.105	0.039	0.007
Activity[b]	< 0.001	0.065	0.997
Group[c]	0.883	0.250	< 0.001
Daytime	0.012	0.066	0.854
Daytime[2]	0.033	0.066	0.612
Autocorrelation term	0.298	0.016	< 0.001

Distance, visibility and daytime were Z-transformed, "*" denotes interaction between predictors.
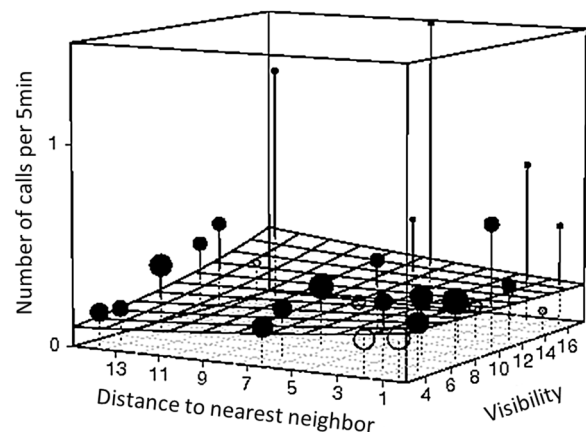[a]Not shown because of having no meaningful interpretation in the presence of a significant interaction.
[b]0 = foraging, 1 = resting.
[c]0 = mountain gorilla; 1 = western gorilla.
[d]Not shown because of having no meaningful interpretation.

more frequent when the nearest neighbor was far as well as when visibility was low (Figs. 3, 4; Table V). Secondly, the variation of visibility and distance to the nearest neighbor within combination types (w.dist. and w.vis) had a significant effect on the fundamental frequency, indicating that visibility and distance to the nearest neighbor also affected the fundamental frequency of the unit types constituting their calls (Table V). In particular, the fundamental frequency increased both with decreasing visibility when the nearest neighbor was close and with increasing

Fig. 2. Influence of visibility and distance to the nearest neighbor on the number of close calls given per 5 min. The surface represents the fitted values derived from the model. The elevation of the circles represents the mean number of calls per cell of the surface (filled circles depict mean values that exceed the fitted values; open circles represent mean values that fall below the fitted values). The volume of the circles indicates the number of data points per cell. Note that the gorilla produced most calls when both nearest neighbor distance and visibility were at large values, but also when the nearest neighbor and visibility were both at low values.
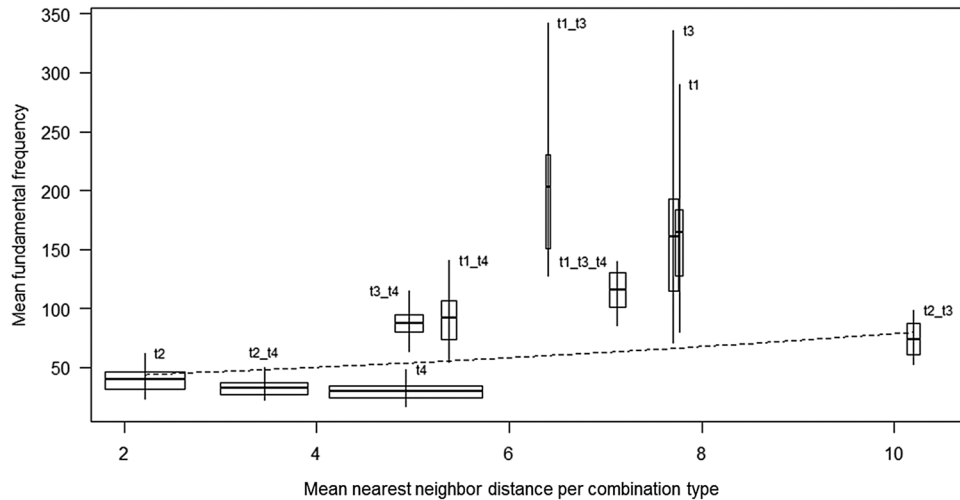
Fig. 3. Effect of nearest neighbor distance on the variation in fundamental frequency between combination types. Combination types given at higher nearest neighbor distances frequently included the unit types t1 and t3, which are of high fundamental frequency. The positions of the vertical lines along the x-axis indicate the average nearest neighbor distance per combination type. Horizontal lines indicate the median fundamental frequency and boxes the quartiles. The lower and upper end of the vertical lines indicate the 2.5 and the 97.5 percentile. The area of the boxes indicates the number of calls per combination type, and the dashed line indicates the fitted model.

distance to the nearest neighbor when visibility was high (Fig. 5). Moreover, the control predictor activity appeared to explain variation in fundamental frequency: when resting the gorillas used calls with lower fundamental frequency as compared to foraging (Table V). Finally, we found that western gorilla close calls were of lower fundamental frequency compared to those of the mountain gorilla individuals (Table V).

Overall, visibility and nearest neighbor distance had no significant effect on call duration ($\chi^2 = 7.263$, df $= 6$, $P = 0.297$). However, the control predictor activity appeared to explain variation in call

duration: when resting compared to foraging the gorillas used calls with shorter overall duration (Table VI).

DISCUSSION

Contrary to what we predicted, we found no modifications of calling rate, or the acoustic structure of gorilla close calls that could counteract degrading effects of vegetation during sound propagation. Our results are therefore in contrast to a previous study demonstrating acoustic adaptations to environmental changes in baboon grunts [Ey et al., 2009].
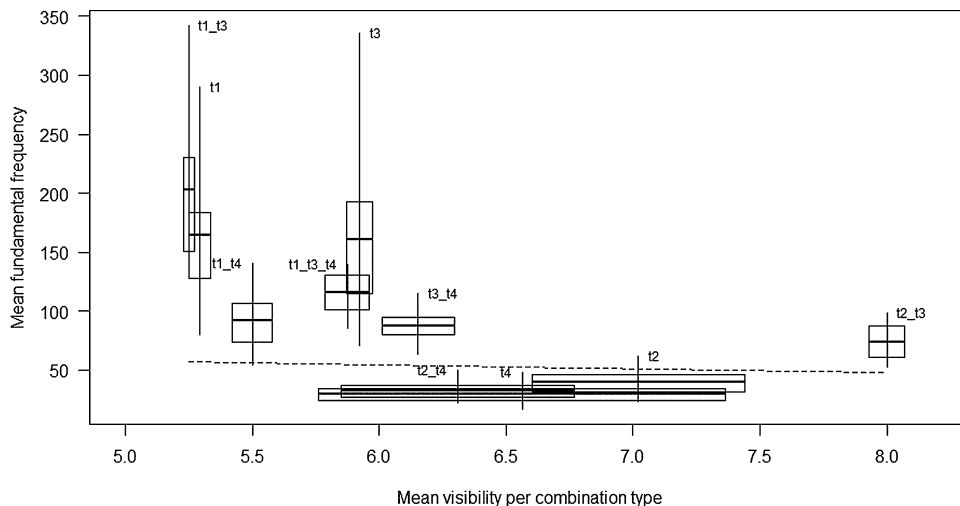

Fig. 4. Effect of visibility on the variation in fundamental frequency between combination types. Combination types given at low visibility frequently included the unit types t1 and t3, which are of high fundamental frequency. The positions of the vertical lines along the x-axis indicate the average visibility per combination type. Horizontal lines indicate the median fundamental frequency and boxes the quartiles. The lower and upper end of the vertical lines indicate the 2.5 and the 97.5 percentile. The area of the boxes indicates the number of calls per combination type, and the dashed line indicates the fitted model.

TABLE V. Summary of the GLMM for Effects on the Mean Fundamental Frequency of Gorilla Close Calls after Removal of Non-Significant Interactions

	Mean fundamental frequency		
	Estimate	SE	P-value
Intercept	4.096	0.124	[d]
Bw.dist	0.373	0.094	<0.001
Bw.vis	−0.209	0.070	<0.001
W.dist	0.022	0.015	[a]
W.vis	0.002	0.020	[a]
W.dist*W.vis	0.035	0.013	0.024
Age-sex class SB vs BB	0.038	0.079	0.001
Age-sex class BB vs AF	−0.088	0.056	<0.001
Age-sex class SB vs AF	−0.050	0.072	<0.001
Activity[b]	−0.005	0.022	<0.001
Group[c]	−0.227	0.054	0.001
Autocorrelation term	0.008	0.009	<0.001

Bw.dist and bw.vis are the average distance and visibility per combination type. W.dist and w.vis are the differences between each calls' distance and visibility and it's combination type's average distance and visibility. P-values were obtained using likelihood ratio tests."*" Denotes interaction between predictors.
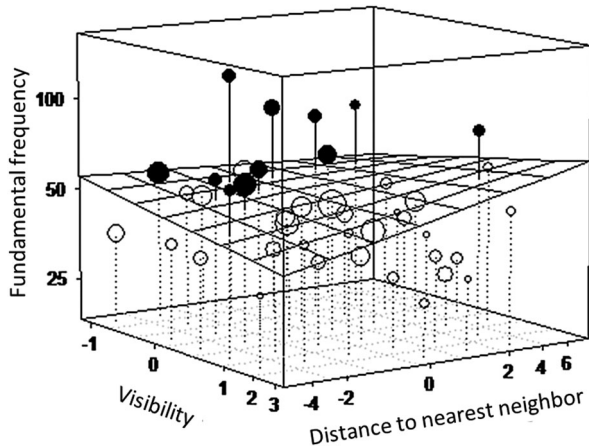[a]Not shown because of having no meaningful interpretation in the presence of a significant interaction.
[b]0 = foraging, 1 = resting.
[c]0 = mountain gorilla; 1 = western gorilla.
[d]not shown because of having no meaningful interpretation.

Instead, the observed effects of nearest neighbor distance and visibility on calling rate and acoustic structure may reflect responses to variation in spatial and visual separation from the nearest

Fig. 5. Influence of visibility and distance to the nearest neighbor on the fundamental frequency within combination types. Visibility and distance are indicated as the divergence-from the mean visibility and distance at which a given combination type was produced. The surface represents the fitted values obtained from the model. The elevation of the circles represents the mean fundamental frequency of calls per cell of the surface (filled circles depict mean values that exceed the fitted values; open circles represent mean values that fall below the fitted values). The volume of the circles indicates the number of data points per cell. Note that the fundamental frequency was lowest when visibility was high and the nearest neighbor close to the caller and increased both with decreasing visibility when the nearest neighbor was close and with increasing distance to the nearest neighbor when visibility was high.

TABLE VI. Results of the Final Model investigating the Effects of Visibility and Nearest Neighbor Distance on the Duration of Gorilla Close Calls after Removing the Non-Significant Interaction between Mean Visibility (bw.vis) and Mean Distance per Combination Type (bw.dist) (estimate = 0.07, SE = 0.055, P = 0.21) as well as the marginally Non-Significant Interaction between the Variation of Visibility and Nearest Neighbor Distance within Combination Types (w.vis and w.dist) (Estimate = 0.053, SE = 0.026, P = 0.052)

	Call duration		
	Estimate	SE	P-value
Intercept	1.095	0.078	[c]
Bw.dist	0.027	0.057	0.840
Bw.vis	−0.034	0.042	< 0.001
W.dist	−0.01	0.012	0.530
W.vis	0.022	0.024	0.476
Activity[a]	−0.08	0.035	0.026
Group[b]	0.128	0.088	0.160
Autocorrelation term	0.041	0.011	< 0.001

The significant main effect of the average visibility per combination type (bw.vis) might be due to multiple testing given the non-significant full-null model comparison (Forstmeier and Schielzeth, 2011). P-values were obtained using likelihood ratio tests.
[a]0 = foraging, 1 = resting.
[b]0 = mountain gorilla; 1 = western gorilla.
[c]Not shown because of having no meaningful interpretation.

neighbor. Individuals appeared to increase their calling rate when they were able to see their nearest neighbor being far away, but also when they were unable to see their nearest neighbor being close-by. Moreover, the gorillas appeared to alter the unit type composition of their calls, and hence used different combination types, but also adjusted the acoustic structure of unit types constituting their calls in relation to visibility and nearest neighbor distance. First, the gorillas were more likely to produce combinations consisting of unit types of high fundamental frequency, the short and long hum t1 and t3, when they were far from their nearest neighbor and when visibility was restricted. Secondly, within combination types, the fundamental frequency appeared to increase when the animals were able to see their nearest neighbor being far away, but also when they could not see their nearest neighbor close by.

Similar modifications of vocal (and other) behavior in reaction to the proximity of other individuals are widespread among social vertebrate species ["audience effects", Doutrelant et al., 2001; e.g., *Betta splendens*: Pollick et al., 2005; *Taeniopygia guttata*: Schel et al., 2013; *Cebus paella*: Vignal et al., 2004; *Pan troglodytes*: Zuberbühler, 2008] whereby most previous studies demonstrated audience effects on calling rate [e.g., Pollick et al., 2005; Townsend and Zuberbühler, 2009]. However, similar to audience effects on the vocal behavior of chimpanzees, our

results also suggest, first, an effect of the presence of other group members on the acoustic structure of vocalizations [Slocombe & Zuberbühler, 2007] and, secondly, that modifications of vocal behavior in relation to the distance to the nearest neighbor were conditional on what callers could see [Townsend & Zuberbühler, 2009].

As such, while pioneering studies on gorilla vocal behavior highlighted the prominent role of close calls in mediating the interactions between individuals within 5 m of each other [e.g., Harcourt et al., 1986, 1993], our results emphasize that spatial and visual separation from other group members also have an important influence on gorilla close calling behavior. Given that combinations including the higher pitched unit types t1 and t3 were particularly used in situations of restricted visibility and increased inter-individual distances, they may have some function in group coordination and maintaining group cohesion as proposed for some close calls by Harcourt et al. [1993]. This coordinative function of close calls was further suggested by an increased calling rate when individuals where able to see that their nearest neighbor was far away or unable to see their nearest neighbor close by. Our results suggest that the observed increase in calling rate was driven by the increased use of combinations containing high pitched unit types. While an increase in fundamental frequency may enhance signal detectability, since an increase in fundamental frequency corresponds to an increase of sound amplitude in a number of animal species [e.g., frogs: Cardoso & Atwell, 2011; dogs: Hsiao et al., 1994; humans: Liénard & Di Benedetto, 1999; birds: Lopez et al., 1988], changes in fundamental frequency are indicative of the caller's state of arousal across many primate species, including humans [e.g., Fichtel et al., 2001; Fischer et al., 2004; Murray & Arnot, 1993; Rendall, 2003]. Hence, the observed increased use of combination types comprising unit types of high fundamental frequency may reflect increased arousal and as such involuntary reactions in situations when group coordination is crucial. Similar arousal based mechanisms appear to drive syntactic variation in a number of other non-human primates' vocalizations, including the syntactic close call system of Diana monkeys *Cercopithecus diana* [Candiotti et al., 2012] or alarm call combinations that are given in alleviated alarm situations [*Saguinus oedipus*: Cleveland & Snowdon, 1982; *Cercopithecus diana*: Ouattara et al., 2009; Zuberbühler, 2002].

The lack of evidence for modifications of the acoustic structure of calls and call rate that could counteract degrading effects of the vegetation in this study is an important finding. An explanation could be that the gorilla close calls function sufficiently within their forest habitat given the relatively short distances they have to travel and their generally low pitch. Previous studies that demonstrated modifications in individual vocal behavior in relation to environmental conditions [e.g., Ey et al., 2009] were conducted on baboon species whose geographic as well as home ranges encompass a variety of habitat types from savanna-like grassland to lowland rainforest [Kingdon, 1997]. Hence, baboons seem to be exposed to a larger spectrum of different transmission conditions than gorillas, who reside entirely in forest habitats. This difference suggests that a vocal plasticity functioning to counteract distorting environmental effects may only be selected for in animal species living in highly heterogeneous habitats.

However, our results point to some potential differences in the vocal repertoire of western and mountain gorillas. Different habitats have specific frequency windows in which calls can function optimally and acoustic masking of ambient sound is avoided [e.g., Linskens et al., 1976; Nemeth and Brumm, 2009; Snowdon & Hodun, 1981; Schneider et al., 2008; Waser & Brown, 1984]. In line with this, one could argue that the average higher fundamental frequency in calls we found for the mountain gorilla compared to the western gorilla group might reflect adaptations to such different sound windows, because larger body size [Bergmann, 1847; but see Taylor, 1997] and the overall denser vegetation in the habitat of mountain gorillas [Nkurunungi et al., 2005] cannot explain their higher fundamental frequency compared to the western gorillas. Detailed measurements of ambient sound in the two groups' habitats would be necessary to explain the observed differences.

To conclude, our analysis revealed vocal plasticity in gorilla close calls in relation to changes in visibility and nearest neighbor distance. However, the modifications of acoustic structure, and calling rate we found are unlikely to counteract degrading effects of vegetation, but rather seem to reflect reactions to variation in spatial and visual separation from other group members, similar to the audience effects demonstrated in a range of other species [e.g., *Betta splendens*: Doutrelant et al., 2001; *Taeniopygia guttata*: Pollick et al., 2005; *Cebus paella*: Schel et al., 2013; *Pan troglodytes*: Vignal et al., 2004]. We hypothesize that habitat heterogeneity may be a driving force on the evolution of a vocal plasticity employed for counteracting distorting environmental effects. Further studies similar to the one presented here and by Ey et al. [2009] would facilitate a comparative analysis to test this hypothesis.

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