Communication and Travel Coordination in Wild Bonobos

Isaac Schamberg

University of Pennsylvania, sisaac@sas.upenn.edu

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Abstract
Group movement is often governed by simple, decentralized rules. From swarming locusts to crowds of commuters, self-organization often eliminates the need for a more explicit form of coordination. Passive, local cues, however, cannot explain group movement in many circumstances, especially among populations exhibiting low spatial cohesion and highly differentiated social relationships. The research presented in this dissertation examines communication and travel patterns of wild bonobos (Pan paniscus), a species of great ape with a highly fluid ‘fission-fusion’ social structure, in which individuals from a single social group regularly divide into smaller subgroups (‘parties’). In Chapters 1 and 2, we investigate the long-distance vocalizations that bonobos use to communicate between separated parties. We find that call combinations, but not single call types alone, were associated with particular patterns of inter-party movement. Specifically, individuals who were highly motivated to approach and join another party produced ‘whistle-high hoot’ combinations, while individuals motivated to recruit others to their own party produced distinct ‘low hoot-high hoot’ combinations. In Chapter 3, we turn our focus to ‘branch drag’ displays, a form of within-party communication. Bonobos performed these displays before traveling to distant feeding trees, but not prior to shorter bouts of travel, thus potentially providing individuals with information about subsequent group movement. Results from all three chapters demonstrate that bonobos use particular signals to facilitate movement patterns that are typical of fission-fusion societies. Furthermore, we suggest that the unpredictable nature of such a social structure may have favored individuals who are able to flexibly produce signals related to movement in order decrease the uncertainty associated with fission-fusion dynamics, and thereby reduce the costs of group coordination.

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COMMUNICATION AND TRAVEL COORDINATION IN WILD BONOBOs

Isaac Schamberg

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in

Psychology

Presented to the Faculties of the University of Pennsylvania

in

Partial Fulfillment of the Requirements for the

Degree of Doctor of Philosophy

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Supervisor of Dissertation

Co-Supervisor of Dissertation

________________________

Robert M. Seyfarth

Professor of Psychology

Dorothy L. Cheney

Professor of Biology

Graduate Group Chairperson

________________________

Sara Jaffee, Professor of Psychology

Dissertation Committee

Daniel Swingley, Professor of Psychology

Elizabeth Lonsdorf, Professor of Psychology, Franklin and Marshall College
COMMUNICATION AND TRAVEL COORDINATION IN WILD BONOBS

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Dedicated to Lys, who this dissertation made a possibility
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Thank you to the village of Lompole for being tolerant of all the mindele stumbling around their forest and allowing us to follow the bonobos. Thank you to my parents for supporting me before and throughout this project. Thank you to Robert and Dorothy for showing me how to do research.
ABSTRACT

COMMUNICATION AND TRAVEL COORDINATION IN WILD BONOBOS

Isaac Schamberg
Robert M. Seyfarth
Dorothy L. Cheney

Group movement is often governed by simple, decentralized rules. From swarming locusts to crowds of commuters, self-organization often eliminates the need for a more explicit form of coordination. Passive, local cues, however, cannot explain group movement in many circumstances, especially among populations exhibiting low spatial cohesion and highly differentiated social relationships. The research presented in this dissertation examines communication and travel patterns of wild bonobos (Pan paniscus), a species of great ape with a highly fluid ‘fission-fusion’ social structure, in which individuals from a single social group regularly divide into smaller subgroups (‘parties’). In Chapters 1 and 2, we investigate the long-distance vocalizations that bonobos use to communicate between separated parties. We find that call combinations, but not single call types alone, were associated with particular patterns of inter-party movement. Specifically, individuals who were highly motivated to approach and join another party produced ‘whistle-high hoot’ combinations, while individuals motivated to recruit others to their own party produced distinct ‘low hoot-high hoot’ combinations. In Chapter 3, we turn our focus to ‘branch drag’ displays, a form of within-party communication. Bonobos performed these displays before traveling to distant feeding trees, but not prior to shorter bouts of travel, thus potentially providing individuals with information about subsequent group movement. Results from all three chapters demonstrate that bonobos use particular signals to facilitate movement patterns that are typical of fission-fusion societies. Furthermore, we suggest that the unpredictable nature of such a social structure may have favored individuals who are able to flexibly produce signals related to movement in order decrease the uncertainty associated with fission-fusion dynamics, and thereby reduce the costs of group coordination.
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This dissertation examines auditory and visual signals used by bonobos (*Pan paniscus*) to coordinate group movement. In Chapter 1, we focus on long-distance vocalizations used during inter-party communication and find that individuals who are highly motivated to approach and join another party produce ‘whistle-high hoot’ call combinations. In Chapter 2, we investigate a complementary form of inter-party communication, and find that callers who produce ‘low hoot-high hoot’ call combinations are likely to be approached by individuals from other parties. In both Chapters 1 and 2, we present evidence that call combinations better predict particular types of inter-party movement than single call types alone. Finally, in Chapter 3, we report on ‘branch drag’ displays, a form of intra-party communication, in which an individual runs along the ground while holding a branch in one hand. In many instances, branch drags function as dominance displays, but bonobos also use them in the context of travel. At locations where bonobos likely make decisions about group movement, individuals perform these displays before traveling long distances, but not prior to shorter bouts of travel.

The three studies that comprise this dissertation do not explicitly address the ‘meaning’ of these calls and displays produced by bonobos. Nevertheless, the research presented here can be viewed as part of the larger project of understanding the ‘meaning’ of animal signals—that is, an understanding of the information that animals have access to when they perceive a signal (Seyfarth and Cheney 2016). It is therefore useful, in this preface, to lay out the ways in which our research speaks to this broader topic. Here I omit discussion of the more particular matters relating to communication and travel coordination because I address these issues in the chapters that follow.

The meaning of any given signal is thought to derive both from the signal itself and the context in which it was produced (Marler 1961; Smith 1977). When there is a
predictable relationship between a signal and particular environmental or social features, the signal provides receivers with information about the presence of those features. In many cases, however, signals are associated with more general features of the environment, and receivers must incorporate contextual information to ‘correctly’ interpret the signal. For example, tufted capuchins (*Cebus apella nigritus*) produce ‘hiccup’ calls in response to terrestrial disturbances, including various types of predators. When an individual hears a ‘hiccup,’ it can infer the existence of an unspecified danger on the ground, but must incorporate additional contextual information—e.g., the behavior of group mates—to determine whether that threat is, say, a snake or a jaguar (Wheeler 2010).

While some consensus exists around the idea that signal and context combine to create meaning, significant questions remain regarding signaler flexibility, intentionality, and the nature of the information that receivers acquire. The three chapters presented here do not resolve any of these outstanding issues, but they do highlight several topics that can potentially inform our understanding of meaning in animal communication.

First, call combinations may represent a critical mechanism through which signalers can increase the different types of information they can convey with a fixed vocal repertoire. Chapters 1 and 2 provide evidence that by combining call types, bonobos are able to transfer information—through a reliable association between signal and behavior—that does not seem to be transferred through production of a single call type alone. How receivers interpret call combinations is still very much an open question (Schlenker et al. 2014), but the research presented here, along with a number of studies on monkey call sequences, suggests that call combinations may allow signalers to produce a wider range of messages than previously believed (Zuberbühler and Lemasson 2013).
Second, although signal and context combine to create meaning, the extent to which receivers rely on one or the other may depend on the extent to which signalers and receivers have a shared context. This point is illustrated by the distinction between the inter-party communication presented in Chapters 1 and 2, and the intra-party communication presented in Chapter 3. Across these two types of communication, the relative importance of the signal varied as a result of receivers’ access to information about the context in which the signal was produced. Seeing a branch drag display, with all its attendant cues, appears to strongly influence receivers’ interpretations, and permit them to distinguish between branch drags performed in agonistic contexts and those performed in travel contexts. By contrast, in instances of inter-party communication, receivers who hear calls from an out-of-sight party have only limited information about the context of the call. Consequently, interpretation of these distant calls relies heavily on the information contained in the signal itself. In such cases, call combinations may have been favored by natural selection because they allow signalers to transmit highly informative signals in the absence of contextual information.

The observation that a receiver who cannot see a signaler has very limited information about the context of the signal is somewhat tautological, but, may, nonetheless, be important in developing hypotheses about the evolution of complex signals. In situations where signalers and receivers do not share a context, signalers may be under selection pressure to produce more informative signals for receivers, who cannot depend upon contextual information. Researchers, therefore, may want to focus on such scenarios when investigating call modification, call combinations, or other forms of flexible signaling.

Finally, our investigation in Chapter 3 of the relationship between branch drags and subsequent travel distance raises the possibility that a signal may not only provide
information about a signaler’s current or imminent behavior. Just as social interactions have been shown to influence receivers’ future interpretations of signals (Wittig et al. 2007; Cheney et al. 2010), signals may also provide receivers with information about events likely to occur after the signal (such as feeding in a distant tree). Indeed, even if signals are produced in response to contemporaneous stimuli, receivers may be able to learn delayed associations between signals and behaviors. In light of the evidence that apes are capable of some form of planning (Mulcahy and Call 2006; van Schaik et al. 2013; Janmaat et al. 2014), researchers should be open to the hypothesis that receivers may be able to use signals to acquire information about the near-term future.

References


CHAPTER 1: Call combinations, vocal exchanges, and inter-party movement in wild bonobos

Abstract

The vocal repertoire of nonhuman primates is largely fixed. Individuals produce species-specific vocalizations from a young age, and do not acquire new call types over their lifetime. Yet despite these limitations, monkeys and apes are able to increase their vocal flexibility in several ways, including subtle acoustic modification, call combinations, turn-taking, and call persistence. Although primates have been observed to utilize these communicative features, the extent to which they integrate these abilities is not known. Here we show that certain long-distance calls produced by wild bonobos (Pan paniscus) assimilate several aspects of vocal flexibility in ways not previously documented in nonhuman primates. Communication between foraging parties exhibits context-specific call combinations relating to the movement of caller, call modifications that potentially target particular individuals, persistent call production, and call-and-answer exchanges in which the initial caller's behavior depends on the listener's reply. The selective pressure exerted by bonobos' fission-fusion social structure has likely favored the integration of these communicative capabilities.
Introduction

In recent years, field studies of monkeys and apes have drawn attention to the importance of call combinations in primate vocal communication. The extensive use of call combinations by certain species has led to some reconsideration of previous assumptions about the inflexible nature of primate vocal production. While the number of distinct call types a species can produce appears to be fixed, callers can increase their effective vocal repertoire through the use of call combinations (reviewed in Zuberbühler and Lemasson 2013).

Multiple species provide evidence that the information contained in call combinations differs from the sum of the information contained in the individual call types. Male Campbell’s monkeys (*Cercopithecus campbelli*), for example, use six different call types to produce non-random call sequences in response to predators and other environmental disturbances. Two features of their calling system have invited particular interest. First, ‘boom’ calls at the beginning of call sequences seem to alter the meaning of subsequent calls in the sequence. Males produce sequences of ‘krak-oo’ calls in response to the calls of leopards and crowned eagles, and after hearing other monkeys’ alarm calls towards those predators. In response to environmental disturbances such as falling branches, however, callers will produce a ‘boom’ call before uttering a sequence of ‘krak-oo’ calls. Heterospecific listeners react with predator avoidance behavior to ‘krak-oo’ sequences, but largely ignore ‘boom-krak-oo’ sequences (Zuberbühler 2002). Second, the composition of different call types correlates both with predator type (ground or aerial) and mode of detection (visual or auditory) (Ouattara et al. 2009a; 2009b).
Another example of call combinations comes from putty-nosed monkeys (Cercopithecus nictitans), which produce ‘pyow’ calls in response to general environmental disturbances as well as to leopards, and distinct ‘hack’ calls primarily in response to crowned eagles. When the two call types are produced sequentially in ‘pyow-hack’ sequences, however, the calls are associated with group movement that appear unrelated to leopards or eagles (Arnold and Zuberbühler 2006a; 2006b; 2008).

The use of call combinations is not limited to forest guenons. Gibbons (Hylobatidae), black-and-white colobus monkeys (Colobus polykomos and Colobus guereza), and titi monkeys (Callicebus nigrifrons) also produce call sequences in which the composition of call types corresponds to predator presence, predator type, and/or predator location (gibbons: Clarke et al. 2006; black-and-white colobus: Schel et al. 2009; titi monkeys: Cesar et al. 2013).

Call combinations also occur in non-predator contexts. Bonobos (Pan paniscus) produce call sequences containing five different call types when feeding near other individuals. The proportion of each call type in a sequence correlates with feeding preferences (or possibly food quality), and listeners can use this information to guide their own foraging behavior (Clay and Zuberbühler 2009; 2011). Chimpanzees (Pan troglodytes), too, appear to use call combinations extensively in social contexts such as feeding and traveling. Nearly 50% of their vocalizations are produced as part of a call combination, but the function these combinations remains ambiguous (Crockford and Boesch 2005). Similarly, female Diana monkeys (Cercopithecus Diana) use four call types to produce call combinations during social activities; again, however, the function of these call combinations is not yet known (Candiotti et al. 2012).
Taken together, these observations suggest that the information contained in call combinations may not derive, in a straightforward way, from the information contained in their constituent calls. How the informational content of call combinations arises (and differs) from individual call types is an active topic of research. It remains unclear whether any of the examples of call combinations are compositional, in that the ‘meaning’ of the combination is based on the ‘meanings’ of its constituent calls, or if the calls combine in a non-compositional manner to convey information unrelated to the informational content of the constituent calls (Schlenker et al. 2014; 2016).

In order to make progress toward understanding how primates combine call types, it is critical to collect data across populations and taxa. Comparison of different populations of Campbell’s monkeys has already led to new testable hypotheses about their alarm call system (Arnold et al. 2013; Schlenker et al. 2016), and reviews across taxa have generated new hypotheses about the evolution of language (Collier et al. 2014). Further comparative work has the potential to clarify the relationship between the selective pressures acting on a species’ communication systems and the call combinations exhibited by those same species.

Species exhibiting fission-fusion dynamics, in which members of a single social group regularly divide into smaller social units, may be of particular interest for investigations into call combinations. The demands placed on individuals living in fission-fusion societies may place selection pressures on individuals’ cognitive and communicative abilities because animals must maintain relationships with individuals whom they may encounter irregularly, and coordinate their behavior and movement with out-of-sight individuals. (Aureli et al. 2008). Several studies have documented the role of inter-party communication in fission-fusion societies. Bonobos and spider monkeys
(Ateles geoffroyi), for example, both use long-distance vocalizations facultatively to maintain contact and coordinate movement with out-of-sight individuals (bonobos: Hohmann and Fruth 1994; White et al. 2015; spider monkeys: Ramos-Fernandez 2005). Chimpanzees also use vocalizations to coordinate with out-of-sight individuals, and they appear to modify their call production based on knowledge of which individuals are nearby (Mitani and Nishida 1993; Kalan and Boesch 2015). Hyenas (Crocuta crocuta), in addition to exchanging long-distance vocalizations between out-of-site individuals, produce context-related call subtypes that facilitate mutually beneficial movement patterns between callers and receivers (Gersick et al. 2015).

While not all vocalizations exchanged between parties in fission-fusion societies involve call combinations, the uncertainty inherent in the movement patterns of fission-fusion societies—will Individual A approach B or vice versa?—may create situations in which contact calls that only provide information about identity and location are insufficient to facilitate effective group movement. Call combinations are one mechanism by which individuals can convey additional information about context or caller motivation to listeners and, thus, potentially, reduce the uncertainty involved in inter-party movement. Given the documented use of call combinations in chimpanzees and bonobos, call sequences likely play a role in inter-party communication in these two species.

Here we present data on the use of long-distance vocalizations by bonobos during inter-party movement. Bonobos produce several signals during the context of inter-party movement and combine these signals non-randomly. Here, we focus on two call types: the high hoot (HH) and the whistle-high hoot combination (W+HH). We report that wild bonobos produce the W+HH call combination when apparently highly motivated
to move from one foraging party to another. Callers are significantly more likely to move to a new party after producing a W+HH combination than after producing HHs alone, especially if the caller receives a response from the group it is about to join. Callers who do not receive a response are likely to call again, underscoring their motivation to receive a response before joining another party. Callers also modify the acoustic structure of their combined calls in a manner that distinguishes between those given spontaneously and those given in response to another call. We suggest that these four features have are adaptive because they coordinate activity with out-of-sight group-mates.

Methods

Data collection

Bonobos form long-term, stable communities, in which all members share a home range and form an exclusive reproductive unit (Kano 1992). Within a community, individuals form temporary subgroups, or ‘parties,’ that travel and forage separately from other parties. Parties are unpredictable in size (ranging from one individual to the entire community), duration (lasting from several minutes to several days), and composition (because animals do not always form a party with the same individuals).

For 13 months between July 2011 and March 2014, we sampled behavior and recorded vocalizations from 18 free-ranging adults (7 males and 11 females) at the LuiKotale field site in the Bandundu province of the Democratic Republic of Congo (Hohmann and Fruth 2003). Data collection included focal animal sampling, ad lib sampling, and scan sampling (Altmann 1974). Data on rates of vocalizations were
calculated from focal sampling; all other analyses use both focal and ad libitum sampling. We obtained 1224 hours of ad lib sampling and 117 hours 15-minute focal animal sampling. No subject was sampled within an hour of its last focal sample and effort was made to sample each subject in a party once before sampling any animal a second time. Focal samples included continuous data on vocal behavior and the occurrence of fissions or fusions in the focal animal’s party. Observers also collected data on affiliative, agonistic, and feeding behavior, as well as dominance interactions. Focal observations were supplemented by ad libitum observations of the same behaviors and vocalizations. Finally, every 15 minutes observers conducted a party composition scan, in which the identity of all bonobos visible was recorded. Party composition was defined as all individuals visible to observers or known to be within a radius of 50 meters of the focal animal (Lehmann and Boesch 2004). Observers visually scanned the surrounding area and conferred with other observers in order to identify all animals in the party. Scans also included currently out-of-sight bonobos that were known to be present based on observations in the previous 15 minutes. These fixed-time party composition scans provided the data for calculating baseline changes in party composition.

In addition to behavioral data, observers made continuous audio recordings of all directly observed vocalizations. Recordings were made using a PMD660 Marantz digital recorder and a Sennheiser ME66 microphone at sample rate of either 44.1 kHz or 48 kHz.

Spectrograms of audio files were created with WaveSurfer (version 1.88p) and RavenPro (version 1.5). Call types and call combinations were visually distinguishable in spectrograms (see Figures 1 and 3). Classification of call types followed descriptions of
the bonobo vocal repertoire in captivity (de Waal 1988) and in the wild (Bermejo and Omedes 1999).

When an individual produced a vocalization, observers noted the call type, the activity of the caller, the identity of individuals within 10 meters of the caller, immediate behavioral change after the call, and all vocalizations produced by the caller and by other individuals that preceded or followed the call. A caller was considered to have approached another party, if within 15 minutes after producing the call, it travelled more than 50 meters and encountered individuals that were not part of its most recent party. We chose 15 minutes as our time limit based on personal observations of typical travel time between parties and the length of focal animal samples.

Observers categorized each vocalization produced by subjects as a ‘spontaneous’ or ‘response’ call. ‘Spontaneous’ calls were those given in the absence of any calls by individuals outside the subject’s party during the 30 seconds prior to the focal animal’s call. ‘Response’ calls were those produced within 10 seconds of vocalizations from another party. Observers also noted whether each call received a ‘response’—that is, was followed within 10 seconds by vocalizations from bonobos outside the subject’s party. We chose 10 seconds as the window for response vocalizations because, based previous observations, bonobos occasionally take several seconds to respond to vocalizations. In most cases, however, responses were produced immediately after the spontaneous calls.

Due to the fragmented and unpredictable nature of bonobos’ parties, observers were unable to obtain simultaneous audio recording from both the spontaneous caller and the response caller during a single call exchange. That is, the observer either
recorded the initial, spontaneous calls and then heard the response from another party, or recorded the response calls just after hearing spontaneous calls from another party. Although observers could clearly hear vocalizations from other parties, only calls that were audio-recorded were used in analyses. Vocalizations produced by individuals in other parties were only used to classify audio-recorded vocalizations as either spontaneous or response calls.

Datasets

To answer our different questions, we used overlapping but non-identical datasets. To examine whether callers subsequently approached and joined another party, we used observations of 50 W+HH combinations (34 spontaneous calls and 16 response calls) recorded from 7 adult males and 7 adult females. We compared these W+HHs combinations to 75 observations of HHs alone (44 spontaneous calls and 31 response calls) recorded from 7 adult males and 8 adult females, for which the caller’s subsequent movement was definitively known. Some of these observations occurred as part of larger communicative events—i.e., callers had produced multiple bouts of HHs or W+HHs within a 10-minute window. In order to maintain independence between observations, we only included the final HHs or W+HHs given by a caller during a communicative event.

For the analysis on persistence in call production we included all observed W+HHs (72 spontaneous W+HHs and 16 response W+HHs) recorded from 7 adult males and 7 adult females. We also examined call persistence in all the HHs produced in the first five minutes of focal animal samples (31 spontaneous HHs and 23 response HHs) recorded from 7 adult males and 10 adult females.
For the acoustic analysis of whistle types, we included all W+HHs for which the audio recording was of a high enough quality to conduct the appropriate classification (56 spontaneous W+HHs and 13 response W+HHs) recorded from 6 adult males and 2 adult females.

Statistical analysis

To test whether certain calls and call combinations were followed by different behaviors by callers, listeners, or both, we used Generalized Mixed Models (‘glmer’ function in ‘lmerTest’ package’ in R version 3.1.2 GUI 1.65 Snow Leopard build (6833)). Because different individual callers contributed in different proportions to our pooled data, we entered caller ID as a random factor.

Ethical note

Subjects for this study were 18 free-ranging adult bonobos. Data collection consisted only of behavioral observations. The study was conducted in accordance with the current laws in the United States, Germany, and the Democratic Republic of the Congo. The research was approved by the Animal Care and Use Committee of the University of Pennsylvania (Protocol no. 804117).

Results

High hoots and Whistle-high hoot combinations

A common vocalization among bonobos is the high hoot (HH) (Fig. 1A), a loud, tonal call (de Waal 1988) given in a variety of non-aggressive contexts, and occurring in bouts consisting of 1-27 acoustic units (Hohmann and Fruth 1994), each with an
inverted-U shaped frequency contour. High hoots are audible for at least 700 meters in the forest (personal observation). They appear to be individually distinctive, and previous research suggests that they may facilitate the joining of separated parties (Hohmann and Fruth 1994; White et al. 2015). In our study, bonobos produced bouts composed exclusively of HHs at an overall mean ± SD rate of 1.09 ± 0.46 bouts per individual per hour (male rate=1.26 ± 0.35, female rate=0.98 ± 0.50).

High hoots are also produced in combination with long, tonal vocalizations, termed ‘whistles’ (Bermejo and Omedes 1999) (Fig. 1B). Whistles were almost always produced as the initial call of a call combination, either with high hoots or 'contest hoots', an agonistic vocalization (Genty et al. 2014). Individuals also occasionally produced whistles as a stand-alone call in the absence of either high hoots or contest hoots, corroborating previous research identifying the whistles as a distinct call type (Bermejo and Omedes 1999).

Whistle-high hoot combinations (W+HHs, Fig. 1C) consisted of one or two whistles and between one and 13 HH units. Whistles always preceded the HHs. Fourteen of 18 subjects produced at least one W+HH combination (S1). Males appeared to produce W+HHs more frequently than females. In our primary dataset, males produced 74% (37/50) of W+HHs. Furthermore, high-ranking males appeared to be less likely to produce W+HHs than mid- or low-ranking males. The two highest-ranking males produced 11% (4/37) of the W+HHs produced by males, while the other five males produced 89% (33/37) of the calls. Overall, subjects produced bouts containing W+HHs at an overall rate of 0.11 ± 0.25 bouts per individual per hour.
Fig. 1. Spectrograms of different call types: (a) high hoot bout containing four call units, (b) whistle, and (c) whistle-high hoot combination.

Effect of call type and call exchanges on post-call behavior

Our observations indicated that both HHs and W+HHs, were associated with inter-party movement. During 468 focal animal samples, subjects approached and joined another party in 8% (36/468) of samples. Of these approaches, 58% were preceded by
HHs; 11% were preceded by W+HHs; and 31% occurred in the absence of any long-distance calls (HHs or W+HHs). Thus the majority (69%) of inter-party movement events were preceded by long-distance vocalizations.

Whether or not a caller produced HHs in combination with a whistle appeared to be influenced both by the caller’s motivation to approach and join another party and by whether or not the caller’s vocalizations were part of a call exchange (Fig. 2). To examine the effects of call type and the occurrence of a response on callers’ approaching behavior, we ran a Generalized Linear Mixed Model (GLMM) with a logistic link function. We used a binomial outcome variable (approaching/not approaching another party) as the dependent measure, call type (HHs or W+HHs) and the presence or absence of a responding vocalization (with one exception, always a HH alone) as predictor variables, and caller ID as a random factor. We used likelihood ratio test to compare a full model that included all predictors against a null model that included only the random effects (Crawley 2014). The full model fit the data significantly better than the null model that included only ID as a random effect ($\chi^2 = 20.42, \text{df} = 2, P = 0.000$). Given this result, we ran a single model with two binomial predictors (whistle/no whistle, response/no response). Both predictors were significant (whistle/no whistle: $\beta = 2.6$, SE = 0.9, $z = 3.0$, $P = 0.003$; response/no response: $\beta = 2.0$, SE = 0.9, $z = 2.2$, $P = 0.025$).

In sum, callers were more likely to approach and join another party after producing W+HHs than HHs only, and more likely to approach after receiving a response. Callers were most likely to approach after both producing W+HHs and receiving a response (Fig. 2).
Fig. 2. The outcomes of observed (a) spontaneous W + HHs and (b) spontaneous HHs. Data on W+HHs were collected from 7 adult males and 7 adult females. Data on HHs alone were collected from 7 adult males and 8 adult females. Data are based on both focal and ad lib observations.

We also examined the relationship between receiving an apparent response and subsequent call production. Callers that produced spontaneous HHs alone produced additional HHs within 10 minutes of the initial call bouts in 20% (1/5) of cases when they received an apparent response, compared to 23% (6/26) of cases when they did not
receive an apparent response. Callers that produced spontaneous W+HHs produced additional W+HHs within 10 minutes of the initial call bout in 28% (5/19) of cases when they received an apparent response, compared to 49% (25/53) cases when they did not receive an apparent response.

To test the effects of receiving a response on the caller’s subsequent calling behavior, we created two GLMMs: one testing W+HHs and another testing HHs alone. Production of subsequent HHs was unrelated to whether a caller received a response ($\beta=0.1$, SE=1.5, $z=0.0$, $P=0.96$). For W+HHs, the correlation between receiving a response and subsequent call production was marginally significant ($\beta=-1.1$, SE=0.6, $z=-1.8$, $P=0.070$). Thus, callers tended to continue to call in the absence of an apparent response when producing W+HHs, but not HHs alone.

The preceding results were derived from instances in which the observer recorded vocalizations from the individual who initiated the calling bout, and then noted whether there was a vocal response from an (unidentified) caller in another party. There were also cases, however, when the observer recorded the responder’s calls after hearing spontaneous calls from an (unidentified) caller in another party. When we include these cases in our analysis of approach behavior, sample size increases from 44 HHs and 34 W+HHs to 75 HHs and 50 W+HHs and the correlation between producing W+HHs and approaching another party becomes stronger (likelihood ratio test: ($\chi^2=27.679$, df=2, $P=0.000$; GLMM: whistle/no whistle: $\beta=2.1$, SE=0.5, $z=4.4$, $P=0.000$, exchange/no exchange: $\beta=2.2$, SE=0.6, $z=3.6$, $P=0.000$).

Similarly, inclusion of response calls in the analysis on persistence strengthens the trend present in the data on spontaneous calls only. Specifically, callers who produced W+HHs that were part of a call exchange produced additional W+HHs in 22%
(8/35) of cases, whereas callers who produced W+HHs that were not part of a call exchange produced W+HHs again in 47% (25/53) of cases that were not part of a call exchange. ($\beta=-1.0$, SE=0.5, $z=-1.9$, $P=0.052$). There was no similar relation between persistence and the presence or absence of a call exchange for HHs ($\beta=0.5$, SE=0.6, $z=0.7$, $P=0.459$). In other words, when callers produced W+HHs that did not receive a response they tended to give additional W+HHs, whereas callers that produced HHs were equally likely to produce additional HHs whether they received a response or not.

**Effect of party composition and context on post-call behavior**

Social factors, such as party size and number of females in a party, were unrelated to callers’ behavior. The mean ± SD party size when caller’s subsequently approached another party was 6.1 ± 4.9 (n=13); party size when caller did not subsequently approach another party was 6.4 ± 3.2 (n=32). The number of females in the caller’s party when the caller subsequently approached another party was 3.9 ± 3.3 (n=13); the number of females in the caller’s party when the caller did not subsequently approach another party was 4.2 ± 2.1 (n=32). Neither party size nor number of females in the party was a significant predictor in a GLMM with approach/do not approach as the dependent measure and ID as a random factor (party size: $\beta=0.2$, SE=0.3, $z=0.2$, $P=0.822$; number of females in party: $\beta=-0.1$, SE=0.5, $z=-0.3$, $P=0.757$).

The different outcomes of HHs and W+HHs could have a byproduct of the different contexts in which bonobos produced these two call types. The context of production for HHs and W+HHs, however, were very similar. Of the 131 HH-only bouts produced by focal animals, 51% (67/131) were given during feeding, 29% (38/131) during periods of rest or grooming, and 20% (26/131) while travelling. Of the W+HH bouts with unambiguous contexts, 38% (14/37) were given during feeding, 43% (16/37)
during periods of rest, and 19% (7/37) while travelling. After approaching and joining another party, callers fed in 60% (12/20) of instances in which the context of unambiguous, travelled in 40% (6/20) of instances, and rested in 10% (2/20) of instances.

Production of W+HHs did not seem to differ according to the distance separating parties. We had precise measurements of the distance between the location of the call and the location of the subsequent fusion for 10 W+HH events. The mean ± SD distance was 207 ± 140m with a range of distances between 59m and 536m. Thus, W+HHs occurred at a wide range of inter-party distances, making it unlikely that there was a systematic difference between W+HHs and HHs according to this measure.

Acoustic analysis of HHs

Another potential explanation of the results is that HHs given as part of W+HH combinations were acoustically distinct from HHs given as part of HH-only bouts. If this were the case, the different information available to receivers when they heard W+HHs or HHs might have been due to differences in the acoustic structure of the HHs rather than the call combination. To test this hypothesis, we analyzed 20 HH-only bouts and 19 W+HH bouts from 5 different individuals. Each individual contributed between 3 and 6 HH bouts from both from HH-only bouts and W+HH combinations. We used 8 spectral measurements (Table S2) to construct two models: a discriminate function analysis (DFA) and a GLMM. The linear DFA with jackknifed prediction correctly classified 69% of HHs as being part of an HH-only bout or a W+HH combination. To test whether these proportions were significant, and to control for individual identity, we created a GLMM in which the 8 acoustic measurements served as predictor variables, individual identity and call bout ID were random effects, and call type (HH or W+HH) was the outcome
variable. The full model including all 8 acoustic measurements as predictor variables did not fit the data significantly better than the null model that included only the random effects ($\chi^2 = 10.22$, df=8, $P=0.25$). Thus, it appears that HHs given during HH-only bouts did not differ significantly in their acoustic features from HHs given during W+HH combinations.

*Call subtypes*

Callers appeared to systematically vary the acoustic structure of whistles depending on whether the call was produced spontaneously or in response. We recorded 56 spontaneous W+HHs and 13 W+HHs given in response that were suitable for acoustic analysis. Many whistles were flat, with a relatively stable frequency over the course of the call (Fig. 3A). Other whistles ('squiggles') showed much greater frequency modulation (Fig. 3B).
Figure 3. Spectrograms of (a) flat W+HHs and (b) squiggle W+HHs.

Almost all (91%; 51/56) spontaneous W+HHs contained flat whistles. By contrast, 85% (11/13) of W+HHs given in response contained a squiggle whistle. To test the association between whistle type and call order position (spontaneous/response), we performed a GLMM with call whistle type (flat/squiggle) as the dependent measure and call order position as a predictor variable. Call order position was a significant predictor of whistle type ($\beta=4.0$, SE=0.9, $z=4.5$, $P=0.000$). While the sample of observed squiggle whistles is small, all four individuals that produced at least two response W+HHs
produced squiggle whistles, suggesting that it is a feature of the bonobo vocal repertoire, not an idiosyncratic vocalization (Fig. 4). Only males were observed to produce squiggle whistles. There did not appear to be an effect of rank on the production of squiggle whistles.

Figure 4. Type of whistle (flat or squiggle) produced as part of spontaneous W+HHs and response W+HHs. The y-axis shows the percentage of flat whistles produced, calculated as (number of flat whistle/number of flat whistles+number of squiggle whistles). All whistles were either flat or squiggle. Data are shown for the four individuals who produced at least two spontaneous and response W+HHs.
In contrast to the two subtypes of ‘whistles’, there appeared to be no acoustic
differences between spontaneous and response HHs that were likely discernable to
listeners. Call unit duration and number of call units in a call bout were the acoustic
parameters that best predicted whether a call was given spontaneously or in response.
The mean ± SD duration of a spontaneous HH units was 0.192 ± 0.058 seconds; the
duration for a response HH unit was 0.154 ± 0.042 seconds (mean difference=0.038
seconds). The mean number of call units in spontaneous HHs was 5.25 ± 4.0; the mean
number of call units in response HHs was 4.6 ± 3.3 (mean difference=0.65 call units).
Using call unit duration as the sole predictor, a linear discriminate function (LDF)
analysis with jackknifed prediction classified 72 HH sequences as either spontaneous or
response calls with 68% accuracy. With number of call units as the sole predictor, calls
were classified with 67% accuracy. To test the significance of these predictions we ran a
GLMM with spontaneous/response as the dependent measure, call unit duration and
number of call units as predictor variables, and ID as a random factor. Unit duration was
a significant predictor of the outcome, whereas number of call units was not (call unit
duration: β =16.3, SE=6.1, z=2.7, P=0.007; number of call units: β=0.0, SE=0.1, z=0.9,
P=0.407). It is unclear, however, whether such a very small disparity in unit duration
(0.038 seconds) was perceptually significant to bonobos.

In sum, bonobos’ use of W+HHs both spontaneously and in response to another
caller potentially created an ambiguity for listeners. Callers appeared, however, to
systematically vary the acoustic structure of whistles, thereby potentially providing
listeners who had just called with the information that the call heard seconds after their
vocalization was indeed a response to the call they had just given.
Discussion

Bonobos use call combinations, persistent call production, call exchanges, and call subtypes to coordinate their movement between parties. Callers were significantly more likely to travel to a new party after producing W+HHs than after producing HHs alone. They were especially likely to move to another party if their initial vocalizations elicited an answer (i.e., were part of a vocal exchange). Persistence in production of W+HHs underscored callers' apparently high motivation to receive an answer from and travel to another party. Individuals also modified the acoustic structure of their call combinations in a manner that could have allowed listeners to distinguish between those given spontaneously and those given in response to another call.

These communicative abilities may have evolved in bonobos to solve a dilemma confronted by individuals living in fission-fusion societies: how to coordinate movement between individuals in separate parties. Many species use vocalizations to facilitate movement (e.g., Boinski 1993; Cheney et al. 1996), but the lack of cohesion in fission-fusion societies makes this coordination more difficult (Aureli et al. 2008). In addition, bonobos face—over long distances and with limited visibility—a problem common to all social interactions: whenever two individuals approach one another there is uncertainty about the outcome, since the best strategy for each depends on what the other is likely to do (Silk et al. 2000).

In response to these obstacles, bonobos appear to utilize four features of communication that, taken together, have not previously been documented in nonhuman primates: call combinations that accurately predict the caller’s imminent behavior; persistence in call production such that callers tend to produce W+HHs until they receive an apparent response; vocal exchanges in which the first caller’s subsequent behavior is
contingent upon the second caller’s response; and the selective use of acoustically distinct call subtypes, effectively marking a call combination as an apparent response to another immediately prior vocalization. These four phenomena have been separately observed in other primate species (context-specific call combinations reviewed in Zuberbühler and Lemasson 2013; persistence: Wich and de Vries 2006; Schel et al. 2013; exchange-dependent behavior: Digweed et al. 2007; acoustic modification in vocal responses: Sugiura 1998). However, the use of all four features in the same communicative event allows bonobos to coordinate movement between foraging parties despite an inherently unpredictable social structure.

Many of the features exhibited by W+HH exchanges are common in birds, both in male-male counter-singing and male-female duetting. Nightingales (Luscinia megarhynchos), for example, produce multi-element songs in which the presence one of the elements (the ‘trill’) signals a caller’s motivation to escalate aggression. Furthermore, whether or not the caller receives a response affects its subsequent behavior (Kunc et al. 2006; Schmidt et al. 2008; Sprau et al. 2010; Sprau et al. 2013). Such exchanges are widespread among passerines (e.g., Searcy et al. 2014), and, in some ways, W+HHS resemble these vocal interactions. Call persistence, however, appears to be an important aspect of W+HH exchanges that is not typically observed in birdsong. Nevertheless, the parallels between birdsong and W+HHS demonstrate that the use of call combinations, vocal exchanges, and call subtypes is not unique to bonobos, nor are the selective pressures associated with fission–fusion social structure necessary for the evolution of such communicative features.

Bonobos must frequently decide which social partners to associate with and which resources to exploit. These decisions depend on the behavior, location, and
motivation of other, out-of-sight individuals, creating an unstable—and potentially confusing—environment. Callers who can signal their imminent behavior, direct their calls at specific individuals, and adjust their behavior based on the occurrence of call exchanges may decrease the uncertainty associated with fission-fusion dynamics and reduce the costs of group coordination.

Although evidence suggests that the addition of whistles to a series of high hoots signals the caller’s motivation to join another party, the function of high hoots produced alone, in the absence of a whistle, remains to be determined. It seems possible that high hoots function to signal the caller’s identity and location, and that listeners’ responses to both call types depends in part on their relationship to the caller (e.g. baboons: Cheney et al. 1996). Playback experiments have the potential to elucidate these questions. As mentioned previously, whistles are almost always produced in combination with other call types – either with high hoots in the context of inter-party movement or with ‘contest hoots’ in the context of aggression (Genty et al. 2014). Another future direction would be to compare bouts of contest hoots that contain whistles and those that do not in order to identify features that differ systematically between ‘whistle-contests hoot’ combinations and ‘contest hoots’ alone. Such data might allow researchers to assess the impact of ‘whistles’ in the two different contexts and to draw tentative conclusions about the use of whistles more generally.

Conclusion

Bonobos use call combinations, persistent call production, call exchanges, and call subtypes to coordinate movement. Previous research has not documented the integration of these four features in nonhuman primate vocalizations. The ability to increase communicative complexity and efficacy by combining existing abilities may
have played an important role in the evolution of flexible communication across diverse taxa.

Acknowledgements

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References


Supplementary Tables

**Table S1.**

Summary of observed HHs and W+HHs and their outcomes.

<table>
<thead>
<tr>
<th>ID</th>
<th>W+H</th>
<th>W+HH</th>
<th>% APPROACH</th>
<th>HH ONLY</th>
<th>HH ONLY APPROACHES</th>
<th>% APPROACHES</th>
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<td>n/a</td>
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<td>WI (♀)</td>
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<td>100.00%</td>
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<td>NI (♀)</td>
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<td>33.33%</td>
<td>7</td>
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</tbody>
</table>
Table S2.
A list of the acoustic measurements used in acoustic analyses. Definitions are taken from the Raven Pro Users Manual (Revision 11).

<table>
<thead>
<tr>
<th>Acoustic measurement</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Duration</td>
<td>The length of time (s) that includes 90% of a call unit’s energy</td>
</tr>
<tr>
<td>Number of call units</td>
<td>The number of individual call units that comprise the call bout</td>
</tr>
<tr>
<td>5% Frequency</td>
<td>The frequency (Hz) that divides the selection into two frequency intervals containing 5% and 95% of the energy in the selection</td>
</tr>
<tr>
<td>1st Quartile Frequency</td>
<td>The frequency (Hz) that divides the selection into two frequency intervals containing 25% and 75% of the energy in the selection</td>
</tr>
<tr>
<td>Center Frequency</td>
<td>The frequency (Hz) that divides the selection into two frequency intervals containing 50% and 50% of the energy in the selection</td>
</tr>
<tr>
<td>3rd Quartile Frequency</td>
<td>The frequency (Hz) that divides the selection into two frequency intervals containing 75% and 25% of the energy in the selection</td>
</tr>
<tr>
<td>90% Frequency</td>
<td>The frequency (Hz) that divides the selection into two frequency intervals containing 95% and 5% of the energy in the selection</td>
</tr>
<tr>
<td>Minimum Frequency</td>
<td>The peak frequency contour’s lowest frequency (Hz)</td>
</tr>
</tbody>
</table>
CHAPTER 2: Bonobos use call combinations to facilitate inter-party travel recruitment

Abstract

Many primates produce vocalizations when motivated to initiate travel. These ‘travel calls’ are often acoustically similar to vocalizations that are unrelated to travel, and listeners appear to rely on a shared context with callers to correctly interpret the calls. When individuals use vocalizations to coordinate movement with out-of-sight group mates, however, such pragmatic cues are unavailable. Under these circumstances, effective communication may depend on more informative signals. Here we investigate travel-related vocalizations that occur when callers and listeners do not have a shared context: long-distance calls given by wild bonobos (*Pan paniscus*). We find that production of a single call type is not associated with any particular behavior, but production of a specific call combination is a) more likely than the single call type alone to be produced prior to travel, and b) more likely to result in inter-party recruitment—that is, individuals from other parties are more likely to approach the caller. These results suggest that use of call combinations allow bonobos to convey more specific information than in a single call type alone, and that this additional information allows for effective communication in the absence of a shared context between callers and listeners.
Introduction

Vocalizations often function to facilitate group travel in primate groups (review of New World primates: de Cuhna and Bryne 2009; review of Old World primates: Fischer and Zinner 2011). In many species, individuals signal their motivation to move by producing vocalizations prior to traveling. As more individuals begin to call, the likelihood that the group will begin to travel increases. For example, mountain gorillas (*Gorilla beringei beringei*) increase production of grunts before the initiation of travel, which may serve as a mechanism to assess collective motivation to move (Stewart and Harcourt 1994). Similarly, in chacma baboons (*Papio hamadryas ursinus*) the likelihood that a group will begin to travel increases as the number of individuals producing grunts increases (Fischer and Zinner 2011). Other mammalian species also produce calls prior to group movement. Among meerkats (*Suricata suricatta*), for example, individuals begin to travel once a threshold of approximately three calling individuals has been achieved (Bousquet et al. 2011).

In other species the vocalizations of particular individuals, rather than the total number of individuals who are vocalizing, appear to influence group travel. In white-faced capuchins (*Cebus capucinus*), for example, single individuals use trill vocalizations both to initiate travel and to change travel direction (Boinski 1993). Chimpanzees (*Pan troglodytes*) produce ‘travel hoos’ prior to bouts of travel; these vocalizations appear to be targeted at particular individuals and signal a caller’s motivation to travel jointly with closely bonded individuals (Gruber and Zuberbuhler 2013).

The travel vocalizations of these species differ in both the details of their production and their apparent cognitive underpinnings. One feature they share, however, is that vocalizations associated with travel are acoustically similar to calls produced in
other contexts. Baboons, for example, produce grunts both prior to travel and as signals of benign intent when approaching others. Playback experiments have demonstrated that while baboons distinguish between the two call subtypes, context also influences listeners’ responses (Rendall et al. 1999). Thus, while vocalizations appear to be important in initiating travel in many species, the vocalizations themselves may only be interpreted as ‘travel’ signals when listeners are able to integrate other contextual information, including the behavior of nearby animals.

If ‘travel’ vocalizations often rely on visual cues, how do animals coordinate travel with distant, out-of-sight group members? The problem is particularly acute for animals like chimpanzees and bonobos (*Pan paniscus*) that live in fission-fusion societies and may inhabit dense rainforest where visibility is limited. In these species, members of a single social group regularly divide into smaller subgroups (or ‘parties’) that forage out-of-sight of one another, but frequently reunite (Aureli et al. 2008). Have animals living in such societies evolved communicative strategies to overcome the obstacles of long-distance travel coordination?

Here we explore the use of long-distance calls that appear to coordinate group travel in wild bonobos. Individuals frequently move between subgroups, and such movement is often preceded by loud calls from one or both of the separated parties (Hohmann and Fruth 1994; White et al. 2015). When calling between separated subgroups, bonobos produce long-distance vocalizations termed ‘high hoots’ (HHs); under certain circumstances, bonobos also combine HHs with other call types, including ‘whistle’ (*W*) and ‘low hoot’ (*LH*) vocalizations.

In a previous paper, we examined the function of HHs, whistle-HH combinations (*W+HHs*), and call exchanges in a specific context: when a single individual appears to
be highly motivated to approach and join another party. We found that individuals who produced W+HHs were more likely to approach another party than individuals who produced HHs alone. Furthermore, callers who produced either HHs or W+HHs were more likely to approach another party if their vocalizations were part of a vocal exchange with an individual(s) in that party (Schamberg et al. submitted).

Here we present data on the use of HHs in combination with another call type, the ‘low hoot’ (LH), in the complementary, but distinct, context of inter-party recruitment. While our previous work investigated instances in which an individual approached and joined another party, here we focus on what could be thought of as the inverse situation: when a caller appears motivated to recruit other individuals to approach and join its own party.

Methods

Bonobos form long-term, stable communities, in which all members regularly associate with each other and share a home range (Kano 1992). Within a community, individuals form temporary subgroups, or ‘parties,’ that travel and forage separately from other parties. Parties are unpredictable in size (ranging from one individual to the entire community), duration (lasting from several minutes to several days), and composition.

For 13 months between July 2011 and March 2014, we sampled behavior and recorded vocalizations from 18 free-ranging adults (7 males and 11 females) at the LuiKotale field site in the Mai-Ndombe province of the Democratic Republic of Congo. The bonobos’ home range was located in dense rainforest with large patches of both terra firma and swamp forest (Hohmann and Fruth 2003). Data collection included focal
animal sampling, ad lib sampling, and scan sampling (Altmann 1974). Data on rates of vocalizations were calculated from focal sampling; other analyses used both focal and ad libitum sampling. We obtained 117 hours of 15-minute focal animal samples. No subject was sampled within an hour of its last focal sample and effort was made to sample each subject in a party once before sampling any animal a second time. Focal samples included continuous data on vocal behavior and changes in the composition of the focal animal’s party. Observers also collected data on affiliative, agonistic, and feeding behavior.

Focal observations were supplemented by 1224 hours of ad libitum observations of the same behaviors and vocalizations.

Finally, every 15 minutes observers conducted a party composition scan, in which the identities of all visible bonobos visible were recorded and the party’s primary activity was noted. Party composition was defined as all individuals visible to observers or known to be within a radius of 50 meters of the focal animal (Lehmann and Boesch 2004). Observers scanned the surrounding area and conferred with other observers in order to identify all animals in the party. Scans also included currently out-of-sight bonobos that were known to be present based on observations during the previous 15 minutes. These fixed-time party composition scans allowed us to calculate changes in party composition.

In addition to behavioral data, observers made continuous audio recordings of all vocalizations for which the caller and context could accurately be noted. Recordings were made using a PMD660 Marantz digital recorder and a Sennheiser ME66 microphone at sample rate of either 44.1 kHz or 48 kHz.
Spectrograms of audio files were created with WaveSurfer (version 1.88p) and RavenPro (version 1.5). Call types and call combinations were visually distinguishable in spectrograms. Classification of call types followed descriptions of bonobo vocalizations in captivity (de Waal 1988) and in the wild (Bermejo and Omedes 1999; Schamberg et al. submitted).

When an individual produced a vocalization, observers noted the call type, the context in which the call was produced, the activity of the caller, the identity of individuals within 10 meters of the caller, any behavioral change by the caller, vocalizations produced by the caller and by other individuals that preceded or followed the call, and the details of any subsequent changes in party activity, composition, and inter-party movement.

Observers categorized the context of each call based on the joint activity of the party at the time of a call: feeding, resting, travel, or ambiguous (when bonobos were engaged in more than one activity). Observers also noted if the context changed within five minutes after the production of a call.

In addition, observers noted whether the caller was on the periphery of the party. A caller was considered to be on the periphery of a party if, after having been engaged in a joint activity with members of its party, it increased its distance to 15-40 meters from the majority of the party. For example, an individual who exited a tree before other members of the party and then vocalized on the ground while the other members of the party remained in the tree was considered to be on the periphery of the party. Similarly, if a party began to travel after leaving a feeding tree, but one individual remained in the tree and vocalized as the other members of the party were moving away, the caller would be considered to be on the periphery of the party.
Observers also noted the following changes in the composition of the caller’s party within 15 minutes after the production of a call: 1) no change; 2) one or more individual(s) left the caller’s party; 3) the caller approached and joined another party that was stationary; 4) one or more individual(s) from another party approached the caller’s party while the caller’s party was stationary; and 5) the caller’s party and one or more individual(s) from another party met while both parties were traveling. In our analysis we termed the occurrence of (3) an ‘approach’ and the occurrence of either (4) or (5) a ‘recruitment.’

Observers categorized each vocalization produced by callers as a ‘spontaneous’ or ‘response’ call. Spontaneous calls were those given in the absence of any calls by individuals outside the caller’s party during the 30 seconds prior to the call. Response calls were those produced within 10 seconds of vocalizations from another party. Observers also noted whether each call received a response—that is, was followed within 10 seconds by vocalizations from bonobos outside the caller’s party. We chose 10 seconds as the window for response vocalizations because bonobos occasionally take several seconds to respond to vocalizations. In most cases, however, responses were produced immediately after the prior vocalization. A call was considered to be part of a ‘vocal exchange’ if it was a spontaneous call that received a response from another party, or if it was given in apparent response to call from another party.

Datasets

To answer our different questions, we used overlapping but non-identical datasets. To analyze the context of call production, we included 65 observed LH+HH combinations and 135 HHs for which the context of the call and context in the five minutes after the call were known.
To examine changes in party composition after a call, we used observations of 40 LHs+HHs and 75 HHs for which we had reliable data on post-call changes in party composition (including observations when there was no change). In some cases, callers produced multiple HHs or LHs+HHs during a single communicative event. However, almost all changes of party composition in our analyses (93%) occurred after the production of the final calls in such a series. For the purposes of statistical independence, our analysis of changes in party composition following the production of different call types includes only these final calls.

To test hypotheses about persistence in call production we included all 54 observed LH+HH combinations for which we had reliable data on subsequent call production and any changes in party composition.

**Statistical Analysis**

To examine whether certain calls and call combinations were followed by different behaviors by callers, listeners, or both, we used Generalized Mixed Models ('glmer' function in 'lmerTest' package in R version 3.1.2 GUI 1.65 Snow Leopard build (6833)). Because different individual callers contributed in different proportions to our pooled data, we entered caller ID as a random factor.

**Results**

1. **Call types**

A common vocalization among bonobos is the high hoot (HH) (Fig. 1A), a loud, tonal call given in a variety of non-aggressive contexts (de Waal 1988). HHs occur in bouts consisting of 1-27 acoustic units (Hohmann and Fruth 1994), each with an
inverted-U-shaped frequency contour. HHs are audible for at least 700 meters in the forest (personal observation). They appear to be individually distinctive, and previous research suggests that they may facilitate the reunion of separated parties (Hohmann and Fruth 1994; White et al. 2015; Schamberg et al. submitted). In our study, bonobos produced bouts composed exclusively of HHs at an overall mean ± SD rate of 1.09 ± 0.46 calls per individual per hour.

Bonobos also produce the ‘low hoot’ (LH), an acoustically noisy, low-pitched vocalization in which the caller produces sound through both inspirations and expirations (de Waal 1988; Bermejo and Omedes 1999) (Fig. 1B). Individuals most commonly produced LHs in combination with other call types (HHs and ‘whistles’) and non-vocal signals (buttress drums and branch drag displays), but also produced LHs independently (Table 1). In our study, bonobos produced signal combinations that contained LHs at an overall mean ± SD rate of 0.15 ± 0.19 calls per hour per individual. However, call production was highly skewed. The first-ranking male produced 20% (21/104) of all combinations containing LHs; and the second-ranking male produced 53% (55/104) of all such combinations. Despite this skewed distribution, all males (7/7) and 45% (5/11) of all females were observed to produce LHs.
Fig 1. Spectrograms of (a) high hoots and (b) a low hoot-high-high hoot combination.

Table 1 lists the number of different signal combinations that included LHs. Because LHs were most commonly combined only with HHs (63% of all observed combinations), and given the very small sample sizes for most of the other combination types, we examine only LH+HH combinations here.
Table 1. The number of observations for each type of LH combination. LH=low hoot, HH=high hoot, W=whistle, D=buttress drum, BD=branch drag.

<table>
<thead>
<tr>
<th>Signal</th>
<th>Observed cases</th>
</tr>
</thead>
<tbody>
<tr>
<td>LH alone</td>
<td>4</td>
</tr>
<tr>
<td>LH+HH</td>
<td>65</td>
</tr>
<tr>
<td>LH+D</td>
<td>7</td>
</tr>
<tr>
<td>LH+BD</td>
<td>6</td>
</tr>
<tr>
<td>LH+HH+D</td>
<td>8</td>
</tr>
<tr>
<td>W+LH+HH</td>
<td>9</td>
</tr>
</tbody>
</table>

2. Association between LH+HH and travel

LHs+HHs were more likely than HHs to be produced during travel: 32% (21/65) of LHs+HHs were given while traveling, compared with 18% (24/134) of HHs alone. Additionally, 44% (16/36) of LHs+HHs produced in stationary contexts (i.e., while feeding or resting) were followed by travel, compared to 22% (17/85) of HHs.

To examine the relationship between call type and subsequent travel, we used a Generalized Linear Mixed Model (GLMM) with a logistic link function, a binomial outcome variable (travel after calls/no travel after calls), and call type (HHs or LHs+HHs) as the predictor variable. Call type was significantly associated with subsequent travel ($\beta=1.1$, SE=0.4, z=3.6, p=0.009).

Bonobos also traveled significantly farther after, as compared with before, production of the first LHs+HHs. Based on 25 days when LHs+HHs were observed and GPS data were available, the mean ± SD rate of travel before the production of the first LH+HH combinations was 0.56 ± 0.29km/hour, compared to 0.69 ± 0.23km/hour afterwards (paired t-test: $t = -2.8$, p = 0.01).
3. Differences in post-call behavior associated with LHs+HHs and HHs

In addition to their association with subsequent travel, LHs+HHs were significantly more likely than HHs alone to be associated with subsequent recruitments (GLMM: $\beta=1.6$, SE=0.5, z=3.3, p=0.001). In contrast, callers were not more likely to approach another party after producing LHs+HHs than after producing HHs alone (GLMM: $\beta=-0.4$, SE=0.6, z=-0.6, p=0.577) (see Table 2 for data).

4. LHs+HHs and caller motivation

Two additional lines of evidence support the hypothesis that individuals who produced LHs+HHs were motivated to recruit others to join their party. First, callers who produced LHs+HHs were on the periphery of their party in 28% (18/65) of cases, compared to 10% (14/134) of cases for HHs alone (GLMM: $\beta=1.0$, SE=0.4, z=2.7, p=0.004). Second, when callers produced LHs+HHs that did not result in a recruitment, they produced additional LHs+HHs in 33% (13/39) of cases. In contrast, when callers produced LHs+HHs that did result a recruitment, they produced additional LHs+HHs in only 6% (1/16) of cases. There was a marginally significant association between LH+HH combinations that did not result in subsequent recruitments and callers producing additional calls (GLMM: $\beta=-2.0$, SE=1.1, z=-1.8, p=0.064).

5. Differences in post-call behavior associated with LHs+HHs and W+HHs

In a previous paper we showed that bonobos often produce high hoots in combination with a whistle (W+HHs) when apparently motivated to approach another party (Schamberg et al. submitted). In contrast, callers who produced LHs+HHs appeared to have been motivated to recruit others to join their own party (Table 2).
<table>
<thead>
<tr>
<th>Call type</th>
<th>Approaches</th>
<th>Recruitments</th>
<th>Total observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>HHs</td>
<td>16</td>
<td>9</td>
<td>75</td>
</tr>
<tr>
<td>LHs+HHs</td>
<td>5</td>
<td>16</td>
<td>40</td>
</tr>
<tr>
<td>W+HHs</td>
<td>30</td>
<td>5</td>
<td>50</td>
</tr>
</tbody>
</table>

*Table 2. Summary of post-call outcomes for HHs, LHs+HHs and W+HHs.*

To directly compare the behavior associated with these two types of call combinations, we examined whether W+HHs were more likely to result in approaches than were LHs+HHs and, conversely, whether LHs+HHs were more likely than W+HHs to result in recruitments. A GLMM with approach (yes/no) as the outcome variable, call type as the predictor showed that W+HHs were significantly more likely to result in an approach than LHs+HHs (β=2.3, SE=0.6, z=3.8, p=0.000). Conversely, LHs+HHs were significantly more likely than W+HHs to result in a recruitment (GLMM: β=-1.7, SE=0.6, z=-3.1, p=0.002).

Previous research on W+HHs also showed that post-call behavior partially depended on whether the call was part of a vocal exchange: callers who produced W+HH combinations that were part of a vocal exchange were more likely to approach and join another party than callers that produced the same calls in the absence of a vocal exchange (Schamberg et al. submitted). Based on this finding, we examined the effect that vocal exchanges had on the outcome of LHs+HHs. The association between vocal exchanges and subsequent recruitments was not significant (GLMM: β=0.1, SE=0.7, z=0.1, p=0.927). Thus, LHs+HHs that were part of a vocal exchange were equally likely to result in a recruitment as LHs+HHs that were not part of a vocal exchange.
6. Summary of outcomes for HHs, LHs+HHs, and W+HHs

In another effort to compare the effects of HHs, LH+HHs, and W+HHs on subsequent approaches and recruitments, we used odds ratios to express post-call outcomes (Table 3). Results indicated that each of the three call types—HHs, W+HHs, and LHs+HHs—was associated with a different outcome. Furthermore, being part of a vocal exchange strongly affected the outcome of W+HH but not of LH+HH combinations. Specifically, recruitments and approaches were approximately equally likely following HHs compared to baseline rates. Additionally, W+HHs rarely led to recruitments, but sharply increased the likelihood of approaches if they were part of a call exchange. Finally, LHs+HHs rarely led to approaches, but increased the likelihood of a recruitment regardless of whether or not they were part of a call exchange or not.

<table>
<thead>
<tr>
<th>Call type</th>
<th>Recruitment</th>
<th>Approach</th>
</tr>
</thead>
<tbody>
<tr>
<td>HH</td>
<td>2.6</td>
<td>3.4</td>
</tr>
<tr>
<td>W+HH (no call exchange)</td>
<td>2.2</td>
<td>8.2</td>
</tr>
<tr>
<td>W+HH (call exchange)</td>
<td>0.9</td>
<td>34</td>
</tr>
<tr>
<td>LH+HH (no call exchange)</td>
<td>11.9</td>
<td>0</td>
</tr>
<tr>
<td>LH+HH (call exchange)</td>
<td>12.7</td>
<td>3.1</td>
</tr>
</tbody>
</table>

Table 3. The likelihood of either ‘approaches’ or ‘recruitments’ after specific calls or call combinations, compared to baseline rates. The numbers in each cell represent the odds ratio, calculated as the odds of a specific outcome following a specific call type divided by the odds of that outcome during baseline observations (Tabachnick & Fiddell 2007:462). Baseline data were derived from focal animal samples. Data on W+HHs are taken from Schamberg et al. (submitted).

Discussion

Bonobos used LH+HH call combinations during inter-party travel recruitment. LHs+HHs were more likely than HHs to be given by callers that were traveling, and when produced while resting or feeding, LHs+HHs were more likely that HHs to signal
imminent travel. Bonobos also traveled more after the first observed LH+HH combination on a given day than before the production of LHs+HHs. All of these data support the view that LH+HH combinations were associated with group travel.

In addition to their general association with travel, LHs+HHs were likely to result in recruitments, involving the movement of other individual(s) from another party toward the caller’s party. In this respect LH+HH call combinations differed from another of the bonobos’ call combinations, W+HHs, which led primarily to approaches that involved the movement of the caller to another party (Schamberg et al. submitted).

Two observations support the view that callers who gave LHs+HHs were motivated to facilitate a recruitment. First, callers who gave LHs+HHs were more likely than others to be on the periphery of their own party, possibly to direct calls towards separated parties. Second, when LHs+HHs did not result in recruitment, callers often continued to call. In contrast, when LHs+HHs were followed by recruitment, callers were unlikely to produce additional calls.

The use of LH+HH combinations in the context of inter-party travel recruitment may have evolved in response to the demands a low-visibility fission-fusion social structure. While bonobos frequently divide into small parties, they also seem to be highly motivated to reunite with individuals from other parties, perhaps in order to maintain social relationships or gain access to mates (Suer et al. 2011). As a result, natural selection may have favored the use of LH+HH combinations because they allow callers to efficiently recruit out-of-sight individuals to their own party, and thereby reduce the costs of separation from group mates.

The use of vocalizations to facilitate travel coordination and behavioral synchronization is not unique to fission-fusion societies. In species with more cohesive
social structures, however, single call types not tightly linked to travel behavior may suffice to synchronize group movement because additional visual cues allow listeners to correctly interpret such underspecified calls (see Kondo and Watanabe 2009 for a review of contact calls and their use in group movement and group cohesion). Species that communicate over long distances, however, may require signals that convey more specific information in order to coordinate group movement. For example, the loud ‘whoops’ produced by spotted hyenas (Crocuta crocuta) during conflicts with lions differ acoustically from those given as contact calls. These differences may have evolved because of the need to recruit distant individuals in the joint defense of a carcass against lions, allowing callers and listeners to coordinate their movements for mutual benefit (Gersick et al. 2015).

For bonobos, HHs alone undoubtedly play an important role in interparty communication and travel coordination (Hohmann and Fruth 1994). However, they likely provide listeners with ambiguous information about a caller’s motivation and subsequent behavior because they are produced in a variety of contexts. By combining HHs with LHs, bonobos may overcome some of the constraints imposed by long-distance vocal communication and provide listeners with more precise, potentially useful information about group travel.

Our results here complement previous findings on bonobos’ combination of HHs with another call type, the ‘whistle’ (Schamberg et al. submitted). The previous analysis indicated that individuals who produced ‘whistle-high hoot’ (W+HH) combinations were likely to approach and join another party. While LHs+HHs also appear to signal caller motivation to reunite with separated parties, three differences between LHs+HHs and
W+HHs underscore their distinct, complementary roles in the bonobo communicative repertoire (see Table 2).

First, the two call combinations appeared to be associated with different motivations regarding interparty movement. W+HHs seemed to signal the caller’s motivation to move to another party, whereas LHs+HHs appeared to reflect the caller’s motivation to recruit others to join its own party. In the unpredictable context of fission-fusion movements—will A move to B or vice versa?—individuals may benefit from providing signals related to the relative direction of movement between parties.

The second important distinction is that LHs+HHs were more strongly associated with group travel than W+HHs. While W+HHs appeared to signal a caller’s motivation to approach another party, once the caller had joined its new party the group was unlikely to travel (Schamberg et al. submitted). In contrast, the recruitments associated with LHs+HHs commonly occurred while both parties were traveling, and the newly formed party often continued to travel after the reunion of the parties.

Finally, patterns of call production suggest that individuals produced both LHs+HHs and W+HHs persistently—that is, individuals continued to call until their putative goal had been achieved. This goal, however, appeared to vary according to the type of call combination. Callers producing LHs+HHs ceased calling once other individuals joined their own party, whereas callers producing W+HHs ceased calling once they had received a vocal response from another party. Such call patterns support the hypothesis that the two call combinations served complementary functions. W+HHs appeared to be produced in order to facilitate the caller’s own movement; vocal exchanges may have aided callers to locate the other party or to reassure them that they would not receive aggression if they approached the other party. LHs+HHs, on the other
hand, seemed to be produced in order to recruit extra-party individuals to the caller’s party. Under these circumstances, vocal exchanges may not have aided callers in achieving their goal. Such an interpretation is also supported by the observation that occurrence of a vocal exchange was related to post-call approaches for W+HHs, but did not predict recruitments following LHs+HHs.

**Conclusion**

Bonobos use call combinations and persistent call production in order to recruit extra-party individuals for bouts of group travel. The use of call combinations in this context may have been favored by natural selection because of limitations of long-distance communication. In most species, vocalizations that facilitate group travel are produced in a context in which listeners can use visual information to correctly interpret that the vocalizations signal imminent travel. The absence of visual cues during long-distance communication may have placed additional pressures on callers to provide more informative vocalizations by producing call combinations.

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Republic of the Congo. Research was approved by the Animal Care and Use Committee of the University of Pennsylvania (Protocol no. 804117).

References


CHAPTER 3: Bonobos perform branch drag displays before long-distance travel

Abstract

Many primates use objects in courtship and dominance displays, but very little is known about such displays in other contexts. Bonobos (Pan paniscus) frequently performed ‘branch drag’ displays in which an individual runs along the ground while holding a branch in one hand. We show that these displays were used in the context of group travel. In particular, individuals were much more likely to perform branch drags before travel to a distant feeding tree than prior to shorter bouts of travel. Additionally, at certain locations, individuals performed branch drags prior to a change in travel direction. Previous research had suggested that the direction in a branch drag itself was performed ‘predicted’ subsequent travel direction, but we found mixed evidence for this claim. Our results demonstrate that in specific contexts branch drags can potentially provide individuals information about upcoming group travel.
Introduction

Many primates use objects in communicative displays (reviewed in Beck 1980). Most of these displays involve individuals throwing rocks or causing branches or other debris to fall from trees. The use of objects appears to attract attention, amplify a display, and may intimidate group mates or deter predators (van Schaik et al. 1999; Leca et al. 2008). For example, Japanese macaques (*Macaca fuscata*), capuchin monkeys (*Cebus apella*), chimpanzees (*Pan troglodytes*), and gorillas (*Gorilla gorilla*) have all been observed to use sticks, stones, or other objects in agonistic displays (Nishida et al. 1999; Moura 2007; Leca et al. 2008; Wittiger and Sunderland-Groves 2007).

Displays incorporating objects appear to be most common during aggression, though animals also use objects in courtship displays. For example, chimpanzees perform leaf-clipping displays, in which individuals tear or bite a leaf, apparently in order to make a distinctive sound. The display is given in several contexts, but often functions as a copulation solicitation (Nishida 1980). Similarly, female capuchins throw rocks at males as a courtship display (Falótico and Ottoni 2013).

Compared to research on vocal and gestural communication, investigations into the use of objects during displays are relatively rare, and our understanding of the phenomenon is limited. Here we investigate bonobos’ use of the ‘branch drag’ display, in which an individual breaks a small tree (1-2 meters), then runs or walks along the ground while holding the tree in one hand. Previous studies have described this behavior, but no systematic research has been carried out on its usage (Kano 1992; Ingmanson 1996; Hohmann and Fruth 2003). Broadly, branch drags seem to be performed in two contexts: during agonistic interactions and prior to and during travel.
In this paper, we focus on branch drags performed in the context of group travel. We examine if branch drags, 1) precede travel to a distant location; 2) precede a change in travel direction; and 3) ‘predict’ subsequent direction of travel (i.e., if the branch drag is performed in the same direction as the subsequent travel). In order to test these hypotheses, we analyze branch drags performed at locations where bonobos likely make decisions about group movement: nest sites, feeding trees, and ‘wait-and-see events’ (defined below). In each of these contexts, we compare travel after the occurrence of a branch drag(s) with travel in the absence of a branch drag. We find evidence that branch drags precede travel to a distant location and also precede change in travel direction. We find mixed evidence that branch drags ‘predict’ the direction of subsequent travel.

Methods

Bonobos form long-term, stable communities in which all members share a home range and regularly associate with each other (Kano 1992). Within a community, individuals form temporary subgroups, or ‘parties,’ that travel and forage separately from other parties. Parties are unpredictable in size (ranging from one individual to the entire community), duration (lasting from several minutes to several days), and composition.

For 13 months, between July 2011 and March 2014, we sampled behavior and recorded vocalizations from 18 free-ranging adults (7 males and 11 females) at the LuiKotale field site in the Mai-Ndombe province of the Democratic Republic of Congo (Hohmann and Fruth 2003). In addition to the data collection protocol for branch drags (detailed below), observers also conducted focal animal observations, ad lib sampling, and scan sampling (Altman 1974) for related research into bonobo communication.
We observed 61 branch drag events that occurred before travel. In 47 of these events, only one individual performed one or more branch drags. In all other events, one or more individuals were observed to branch-drag within the same five-minute period. Branch drags were highly conspicuous events, so observers were able to collect data on all branch drags (n=321) that occurred while following the animals.

Whenever an individual performed a branch drag, observers noted the identity of the actor, the identities of all individuals within a 10-meter radius, and whether the branch drag was targeted at any individual. A branch drag was considered ‘targeted’ if it was aimed at, and terminated within one meter of, another individual, or if the branch drag appeared to be aimed at another individual, but the targeted individual fled before the branch drag terminated. All branch drags that did not meet one of these criteria were considered ‘untargeted.’

We did not distinguish between targeted and untargeted branch drags in our analysis for two reasons. First, out of the 61 branch drag events we examined, only 7% (4/61) consisted solely of targeted branch drags. All other events consisted of either only untargeted branch drags (35/61) or a combination of both targeted and untargeted branch drags (22/61), making exclusively targeted branch drag events a relatively small portion of our dataset. Second, while targeted branch drags may constitute a form of aggression, they may also serve as a type of herding behavior and might, therefore, be relevant to group travel.

Observers also recorded the bearing (in degrees) of the branch drag—i.e., the navigational direction in which the signaler was moving while performing the display. To do so, observers oriented themselves in the same direction as the branch drag and recorded the bearing from a compass. Finally, observers recorded the location of each
branch drag and recorded the daily travel route and feeding trees of the bonobos on a GPS device (Garmin Map62SC). The travel route consisted of a series of GPS locations recorded every minute.

A branch drag was considered to have occurred in the context of travel if at least one individual performed at least one branch drag either before the group began traveling or within the first five minutes of traveling. We included branch drags performed within the first five minutes of travel because the onset of travel was often desultory and uncohesive, making it difficult to determine when a party’s movement had actually begun. If a branch drag did not occur at a location of interest, but did occur more than five minutes after the initiation of travel, we excluded the travel from our analysis.

**Travel contexts**

Our analysis included three contexts of travel: the initial movement from the nestsite; between feeding trees; and after wait-and-see locations.

*a. Nestsites*

Bonobos make sleeping nests in trees. These nests are very rarely made in feeding trees, so each morning bonobos descend from their nest site and travel to a feeding tree (Fruth and Hohmann 1993). In baboons (*Papio ursinus*) and chimpanzees, investigations of this ‘first travel’ event have shown that groups make key foraging decisions when departing from sleeping sites (Noser and Byrne 2007; Janmaat et al. 2014). For this reason, we compared travel from nest sites after a branch drags occurred with travel in the absence of a branch drag.

*b. Feeding trees*
Bonobos are primarily frugivorous but eat a wide range of other foods as well (Hohmann et al. 2010). Non-fruit food items such as terrestrial herbaceous vegetation and small mammals are exploited opportunistically throughout the year. In contrast, fruiting trees are highly seasonal and patchily distributed. Bonobos often travel directly between feeding trees in what appears to be a goal-oriented manner. For these reasons, we examined the role of branch drags during travel between feeding trees, but not other feeding sites. For a feeding tree to be considered in our analysis, bonobos had to feed in the tree for a minimum of 10 minutes (mean ± SD time spent in feeding trees was 49 ± 53 minutes).

c. Wait-and-see events

Bonobos spend most of their time traveling, feeding, searching for food, grooming or sleeping. There were periods of time, however, when they were not engaged in any of these activities, but instead seemed to be waiting for some event that would precipitate travel. Individuals were often vigilant, looking at other members of their party or oriented toward distant, out-of-sight parties. We termed these periods ‘wait-and-see’ events and recorded their location because they seemed to be potentially pivotal points in group travel.

Measurements

To measure the distance between the location of interest (nest site, feeding tree, or wait-and-see event) and the next feeding tree we used the Measure tool in the Garmin Basecamp software to calculate the distance (in meters) and bearing (in navigational degrees) between two points. We also used the Measure tool to determine whether parties changed their travel direction at wait-and-see events and feeding trees.
To calculate the direction of travel, we measured the party’s bearing from the previous feeding tree to next feeding tree or wait-and-see location. To calculate the direction of travel after the branch drag, we measured the bearing from the location of interest to the party’s location 10 minutes after the initiation of travel.

Association between direction of branch drag and subsequent travel direction

To determine whether a branch drag ‘predicted’ a party’s subsequent travel direction, we used the Measure tool to calculate the bearing from the location of the branch drag to the location of the party 10 minutes after the onset of travel. We then compared this bearing to the bearing of the branch drag itself. If the difference between these two bearings was less than 30°, the branch drag was considered to ‘predict’ subsequent travel direction. We used bearings accurate to 30° or less as our criterion because such angles were small enough to potentially provide receivers with useful information about subsequent travel direction, but large enough to account for the fact that very small directional differences may not have been meaningful to individuals. Our pattern of results remained consistent if the criterion was increased or decreased by 10°.

At each location of interest, the number of individuals that performed a branch drag and the number of branch drags that each individual performed varied. We used only the final branch drag at each location in our analysis. To assess whether a branch drag ‘predicted’ subsequent travel direction we used a chi-squared test to compare the number of branch drags ‘predicted’ subsequent travel direction to the number of branch drags we would expect to ‘predict’ subsequent travel direction by chance. One method of calculating an expected value would be to assume that bonobos could perform a branch drag in any direction (360°), which would result in 12 separate 30° windows. In this case, we would expect 1/12 of all branch drags to ‘predict’ subsequent travel direction by
This assumption, however, may not be conservative enough because individuals may have been more likely to perform a branch drag in the direction they were facing, which may also have been the direction in which the party was about to travel. This potential confound biases the possible bearing of each branch drag. Therefore, we assumed that bonobos were only likely to perform branch drags in the approximate direction they were facing, resulting in an expectation that 1/6 of all branch drags would 'predict' subsequent travel direction by chance.

Statistical analysis

To examine whether the parties’ travel differed more after a branch drag than in the absence of a branch drag we used Linear Models (‘lm’ function in R version 3.1.2 GUI 1.65 Snow Leopard build (6833) with continuous outcome measures and Generalized Linear Models (‘glm’ function ‘lmerTest’ package in R) for binomial outcome measures.

Results

Branch drags

Male bonobos performed branch drags at a mean ± SD rate of 1.08 ± 0.76 branch drags per hour per individual. Only one female was observed to perform branch drags during 117 hours of focal animal sampling. There was also a strong effect of dominance rank on performance of branch drags, with the two highest-ranking males accounting for 64% (204/321) of all branch drags (combining focal and ad lib data). The remaining five males performed 32% (103/321) of all branch drags.
Branch drags and subsequent travel distance

Our analysis included 43 instances of travel between nest sites and feeding trees (mean ± SD distance traveled: 270m ± 386m), 133 instances of travel between feeding trees (447m ± 492m), and 41 instances of travel between wait-and-see events and feeding trees (466m ± 386m). In each context, the distance traveled to the next feeding tree was greater after a branch drag than when no branch drag occurred (Fig. 1).

![Travel to feeding trees in 3 contexts](image)

**Figure 1.** The mean ± SE distance traveled from the location of interest (nest site, feeding tree, or wait-and-see event) to the next feeding tree, based on the occurrence or absence of a branch drag.

To test the association between branch drags and travel distance in each of the three contexts, we performed a linear model in which distance to the next feeding tree was the outcome measure and occurrence of a branch drag (yes or no), context (nest...
site, feeding tree, wait-and-see event), and the interaction between context and branch
drag were predictor variables (Table 1).

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>Estimate</th>
<th>SE</th>
<th>t value</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>326.0</td>
<td>41</td>
<td>8.0</td>
<td>0.000</td>
</tr>
<tr>
<td>Branch drag</td>
<td>519.8</td>
<td>84</td>
<td>6.2</td>
<td>0.000</td>
</tr>
<tr>
<td>Context (nest site)</td>
<td>-203.2</td>
<td>86</td>
<td>-2.3</td>
<td>0.020</td>
</tr>
<tr>
<td>Context (wait-and-see)</td>
<td>107.9</td>
<td>95</td>
<td>1.1</td>
<td>0.256</td>
</tr>
<tr>
<td>Branch drag x Nest site</td>
<td>-16.7</td>
<td>164</td>
<td>-0.1</td>
<td>0.919</td>
</tr>
<tr>
<td>Branch drag x Wait-and-see</td>
<td>-446.0</td>
<td>154</td>
<td>-2.9</td>
<td>0.004</td>
</tr>
</tbody>
</table>

**Table 1.** Results of a linear model in which distance traveled to the next feeding tree was the dependent measure.

Overall, results indicate that parties traveled significantly farther after a branch
drag than in the absence of a branch drag. This main effect, however, varied across
contexts because the effect of a branch drag was significantly attenuated in wait-and-
see contexts. Finally, as already noted, parties at nest sites tended to travel shorter
distances to their first feeding tree of the day (mean: 270m) than parties in other
contexts (means: 447m and 446m), so context by itself was a significant predictor of
distance traveled. Nonetheless, parties leaving nest sites traveled longer distances after
a branch drag than in the absence of a branch drag.
Figure 2. The relationship between the occurrence of a branch drag and subsequent travel distance across three contexts (nest site, feeding tree, and wait-and-see event), based on meters traveled to the next feeding tree.

Figure 2 presents more detailed data on the distance traveled after the occurrence or absence of a branch in the three contexts. In the nest site and feeding tree contexts, the likelihood of a branch drag occurring increased as the distance to the next feeding tree also increased. This relationship held until the distance to the next feeding tree was 600m at which point the likelihood of a branch drag plateaued. At wait-and-see events, there was an inconsistent relationship between branch drags and subsequent distance traveled.

**Branch drags and change in travel direction**

We obtained accurate information on the party’s travel bearing before and after 43 wait-and-see events (mean ± SD change of travel direction: 43° ± 37°) and 80 feeding trees (66° ± 47°). At wait-and-see events, the magnitude of a party’s directional change was larger after a branch drag than in the absence of a branch drag. For feeding
trees the pattern was reversed: the magnitude of a party’s directional change was smaller after a branch drag than in the absence of a branch drag (Fig. 3). Statistical analysis (Table 3) revealed no significant effect of a branch drag, but a significant effect of context on the magnitude of directional change.

![Change in travel direction](image)

**Fig 3.** The mean ± SE change in travel direction (in degrees) in two contexts, in the presence or absence of a branch drag.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Estimate</th>
<th>SE</th>
<th>t value</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Branch drag</td>
<td>-0.9</td>
<td>0.14</td>
<td>-0.7</td>
<td>0.494</td>
</tr>
<tr>
<td>Context</td>
<td>-0.4</td>
<td>0.12</td>
<td>-3.1</td>
<td>0.003</td>
</tr>
<tr>
<td>Branch drag x context</td>
<td>0.3</td>
<td>-0.2</td>
<td>1.5</td>
<td>0.146</td>
</tr>
</tbody>
</table>

**Table 3.** Results of a linear model in which context and occurrence of a branch drag were predictors and a party’s directional change before and after a given location (feeding tree or wait-and-see event) was the dependent measure.

Focusing exclusively on wait-and-see events, where the occurrence of a branch drag did appear to influence directional change, we found some evidence for a relationship between the probability of a branch drag and the magnitude of directional change.
change. Using a somewhat weaker statistical measure, we tested whether branch drags were more likely to occur when the change in direction was greater than the median change of direction (35°) for all wait-and-see events. When a branch drag occurred, parties changed their direction by more than 35° in 72% (13/18) of instances, compared to 40% (10/25) of instances in the absence of a branch drag. A Generalized Linear Model with performance of a branch drag (yes or no) as the predictor variable and change of direction (above or below the median) as the outcome measure revealed that branch drags were significantly more likely to occur when the party changed its travel direction by more than 35° than when the party changed its direction less than 35° (β=1.15, SE=0.7, z=2.3, p=0.022). There was also a general trend that branch drags were more likely to be performed before larger directional changes (Fig. 4).

**Fig 4.** The relationship between occurrence of a branch drag and the magnitude of directional change at the wait-and-see events.

*Association between direction of branch drags and direction of subsequent travel*
The direction in which a branch drag was performed ‘predicted’ subsequent travel direction (i.e., differed less than 30° from the party’s subsequent travel direction) in 50% (6/12) of instances at nest sites, 43% (10/23) of instances at feeding trees, and 38% (6/16) of instances at wait-and-see events. Overall the direction of the branch drag correctly signaled a party’s subsequent travel direction in 43% (22/51) of cases, significantly more than would be expected by chance (16.67%) ($X^2=25.719$, df=1, p<0.0001).

*Branch drags and party size*

Branch drags were more likely to be performed in larger, than smaller, parties than (GLM: party size: $\beta=0.31$, SE=0.15, z=2.01, p=0.044). However, in a model that included both party size and occurrence of a branch drag, only occurrence of a branch drag was related to distance to the next feeding tree (party size: $\beta=-3.9$, SE=6.4, z=-0.6, p=0.541; branch drag: $\beta=404.6$, SE=75.0, z=5.4, p=0.000).

*Discussion*

In contexts where bonobos likely make decisions about group movement, branch drags were associated with certain features of a party’s subsequent travel. Specifically, at nest sites and feeding trees, branch drags were significantly associated with travel to a distant, as opposed to a nearby, feeding tree. As the probability of a branch drag increased, there was a concomitant increase in the distance subsequently traveled. At wait-and-see events, by contrast, performance of branch drags was less strongly associated with subsequent travel distance.
Branch drags also showed some association with a change in travel direction, but here again context was important. When bonobos were at a feeding tree, we found no association between the occurrence of a branch drag and a change in travel direction. By contrast, at wait-and-see events branch drags were associated with a larger change in travel direction, and as the probability of a branch drag increase so did the magnitude of the change of direction. Finally, across all contexts the orientation of branch drag ‘predicted’ the orientation of subsequent travel more than would have been predicted by chance, though this agreement occurred in only 43% of all cases. Results thus provide only limited support for the hypothesis that branch drags function to signal the direction of subsequent travel.

Our results suggest that bonobos used branch drags to facilitate group movement, but this does not rule out possibility that branch drags also function as dominance displays. One possible explanation for use of branch drags in multiple contexts is that all branch drags serve to draw attention to the individual performing the display, but the individual’s motivation to do so determines the function of any particular display.

At nest sites and feeding trees, individuals may have been motivated to produce branch drags to facilitate travel initiation and party cohesion when the next feeding tree was far away because maintaining contact with separated individuals is more difficult over longer distances. Indeed, the mean distance to the next feeding tree after a branch drag was 846m, a distance approaching the limit at which bonobos’ long-distance calls are audible (personal observation). In contrast, the mean distance to the next feeding tree in the absence of a branch drag was 326m, a distance over which bonobos can
easily communicate (Hohmann and Fruth 1994; White et al. 2015; Schamberg et al. submitted).

One potential implication of our results is that bonobos plan their travel routes. Selective performance of branch drags when the next feeding tree was distant may indicate that individuals knew the location of their next feeding (for evidence that bonobos remember distant food sources see Menzel et al. 2002; cf. Rosati and Hare 2012). However, our data cannot distinguish between this possibility and other hypotheses that do not rely on bonobos having a mental map of their home range.

If branch drags were used as travel signals, it is puzzling that males performed the overwhelming majority of these displays. Indeed, one limitation of our results derives from the fact that they are largely based on data from only a few male individuals. The paucity of branch drags by females is somewhat surprising because female bonobos are often dominant to males (Surbeck and Hohmann 2013) and likely play an important role in determining group movements (Furuichi 2011). Why, then, did females not perform a larger proportion of branch drags? One explanation is that branch drags, like most primate displays, may have evolved as a signal of male dominance, and were only later co-opted for use in the travel context. Another, mutually compatible hypothesis, is that, due to their high status, females do not need to perform such conspicuous—and potentially energetically costly—displays in order to influence group movement. Attention to other mechanisms group coordination like soft calls or individual movement (e.g., Meunier et al. 2006) might more effectively reveal female influence than our focus on branch drags.

Conclusion
Bonobos use branch drag displays in the context of group travel to alter their party’s movement. During departures from nest sites and feeding trees branch drags occur before bout of long travel. At so-called wait-and-see events, branch drags occur when a party changes its direction. Individuals likely perform branch drags to draw attention to themselves and their own travel behavior in order to influence others’ travel behavior. The use of branch drags in facilitating group movement represents one of the first examples of animals using an object during a display outside the context of aggression or courtship.

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References


