

Bonobos (*Pan paniscus*) Perform Branch Drag Displays before Long-Distance Travel



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Abstract Many primates use objects in courtship and dominance displays, but little is known about such displays in other contexts. Bonobos (*Pan paniscus*) frequently perform “branch drag” displays in which an individual runs along the ground while holding a branch in one hand. We aim to understand how bonobos use branch drags in the context of group travel. Using observational data collected from a community of free-ranging bonobos at the Lui Kotale field site in the Democratic Republic of Congo we compare group travel that occurs after branch drags to travel in the absence of branch drags. We found that bonobos are much more likely to perform branch drags before travel to a distant feeding tree than before shorter bouts of travel. At some locations, bonobos also perform branch drags before a change in travel direction. Our results suggest that in specific contexts branch drags may provide information about upcoming group travel, and likely function to coordinate group movement.

Keywords Bonobo · Communicative display · Object use · Travel coordination

Introduction

Many primates use objects in communicative displays (Beck 1980). Most of these displays involve individuals throwing rocks or causing branches or other debris to fall

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from trees. The use of objects appears to attract attention, amplify a display, and may intimidate group mates or deter predators (Leca *et al.* 2008; van Schaik *et al.* 1999; Boninski *et al.* 2000). For example, Japanese macaques (*Macaca fuscata*), capuchins (*Cebus apella*), chimpanzees (*Pan troglodytes*), and gorillas (*Gorilla gorilla*) all use sticks, stones, or other objects in agonistic displays (Leca *et al.* 2008; Moura 2007; Nishida *et al.* 1999; Wittiger and Sunderland-Groves 2007).

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 (Liebal *et al.* 2013; Zuberbühler 2012). 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 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).

The bonobo (*Pan paniscus*) “branch drag” display—in which an individual breaks a small tree (1–2 m), then runs or walks along the ground while holding the tree in one hand—presents researchers with an opportunity to increase understanding of the ways in which primate use objects to communicate. Previous studies have described branch drags but no systematic research has been carried out on their usage (Hohmann and Fruth 2003a; Ingmanson 1996; Kanō 1992).

Broadly, bonobos seem to use branch drags in two contexts: agonistic interactions and travel bouts (Kanō 1992). We here examine branch drags in the context of group travel, focusing on three related questions. First, do branch drags precede travel to a distant location? Second, do they precede a change in travel direction? Third, do they predict the subsequent direction of travel? A reliable association between branch drags and specific aspects of travel could potentially provide receivers with information about the likelihood, distance, and direction of travel, thereby reducing the costs of travel coordination.

To address these questions, we investigate branch drags performed at locations where bonobos likely make decisions about group movement: nest sites, feeding trees, and “wait-and-see events” (defined later). Our decision to focus on these three locations derives both from previous empirical work and our understanding of bonobo travel-related behaviors. Sleeping sites and feeding trees appear to be locations at which many primate species make key foraging decisions [baboons (*Papio ursinus*): Noser and Byrne 2007; capuchins: Janson 2007; chimpanzees: Janmaat *et al.* 2014], and observers identified wait-and-see events as potentially pivotal locations for group travel. Thus, 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. If bonobos use branch drags to signal their motivation to travel or change the direction of travel, we predict that movement that occurs after a branch drag will differ from movement that occurs in the absence of a branch drag. Specifically, we predict that 1) bonobos travel farther after a branch drag than in the absence of a branch drag, 2) branch drags predict a party’s subsequent travel direction, and 3) parties change travel direction after a branch drag, regardless of the direction in which the branch drag was performed.

Methods

Bonobos form long-term, stable communities in which all members share a home range and regularly associate with each other (Kanō 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 and composition. We defined a party as all individuals visible to observers or known to be within 50 m based on observations in the previous 15 min (Lehmann and Boesch 2004).

For 13 mo, 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 2003b). In addition to the data collection protocol for branch drags (detailed later), observers also conducted focal animal observations and ad libitum sampling on social and vocal behavior (Altmann 1974).

Branch drags were highly conspicuous events, so observers were able to collect data on all branch drags that occurred while following the subjects. Whenever an individual performed a branch drag, observers noted the identity of the actor and the identities of all individuals within a 10-m radius.

Whenever possible, 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 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.

We considered a branch drag to have occurred in the context of travel if at least one individual performed at least one branch drag at a location of interest (defined later) either before the group began traveling but had already descended to the ground, or within the first 5 min of traveling. We included branch drags performed within the first 5 min 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 >5 min after the initiation of travel, we excluded the travel from our analysis; i.e., when an individual performed a branch drag en route to another feeding tree, we could not consider the travel to have occurred after a branch drag, but nor could we consider it to have occurred in the absence of a branch drag). Thus, we categorized each location of interest as 1) a location where a branch drag occurred; 2) a location where a branch drag did not occur; or 3) a location that we excluded from our analyses because a branch drag occurred, but took place ≥ 5 min after the initiation of travel. For our analyses on subsequent distance traveled and change in travel direction, each location of interest was the relevant data point, not individual branch drag displays. For this reason, our sample sizes are much smaller than the number of individual branch drag displays that we observed; i.e., we recorded 321 individual branch drags, but our analyses were conducted on only 61 locations of interest where a branch drag occurred.

Locations of Interest

We identified three locations of interest as the location of the initial movement from the nest site; the initial movement from one feeding tree to another; and the initial movement after a pause in travel at wait-and-see locations:

Nest Sites

Bonobos make sleeping nests in trees. These nests are very rarely made in feeding trees, so most mornings bonobos descend from their nest site and travel to a feeding tree (Fruth and Hohmann 1993). Sometimes, however, bonobos travel arboreally from nest sites to nearby feeding trees. In these cases, the travel from nest site to feeding tree was not included in our analyses; and the terrestrial travel after the first feeding tree was considered to be part of the feeding tree context (see later).

Feeding Trees

Bonobos often travel directly between feeding trees in what appears to be a goal-oriented manner (Schamberg *pers. obs.*). We examined the role of branch drags during travel between feeding trees. For a feeding tree to be considered in our analysis, bonobos had to feed in the tree for a minimum of 10 min (mean \pm SD time spent in feeding trees was 49 ± 53 min).

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. In these contexts, 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.

In our analyses, we combined data from the nest sites and feeding trees because of their similarity: in both contexts, bonobos descended to travel the ground after a period of time in trees. In contrast, we analyzed wait-and-see events separately because 1) they did not involve bonobos descending to the ground and 2) their designation as a location of interest involved more observer judgment than nest sites or feeding trees, which were very clearly salient locations for bonobos.

Measurements and Statistical Analyses

Rate of Branch Drags Performance and Associations with Party Size

We report several descriptive statistics as background on branch drags. We tabulated the rate at which each male performed branch drags by dividing the number of branch drags observed during focal animal sampling by the number of observation hours. The overall rate of branch dragging that we report is the mean of each individual's rate.

We also examined the association between party size and the likelihood of a branch drag by performing a generalized linear model (glm function lmerTest package in R version 3.1.2) with party size at each location of interest as the independent variable and occurrence of a branch drag (yes/no) as the dependent variable.

Distance Traveled after Locations of Interest

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 Garmin Basecamp to calculate the distance (in meters) between two points. To test the association between branch drags and subsequent distance traveled we created two linear models (using the lm function in R version 3.1.2): one using data from nest sites and feeding trees, and the other using data from wait-and-see events. In the nest site/feeding tree model, presence of branch drag (yes/no), context (nest site/feeding tree), and an interaction term (context \times branch drag) were independent variables, and meters traveled to next feeding tree was the dependent variable. In the wait-and-see model, presence of branch drag (yes/no) was the independent variable, and meters traveled to the next feeding tree was the dependent variable.

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 in Garmin Basecamp to calculate the bearing from the location of the branch drag to the location of the party 10 min after the onset of travel. We used a 10-min window because we felt that a shorter duration might not measure a party's true travel direction, but would instead reflect the direction of the sometimes desultory initiation of travel. We compared this bearing to the bearing of the final branch drag given at the location of interest. At each location of interest, a variable number of individuals performed a variable number of branch drags. We included only the final branch drag of each of these bouts in our analysis. Using only first branch drag or the penultimate branch drag, instead of the final branch drag, did not change the pattern of our results (Electronic Supplementary Material [ESM] Table SI). If the difference between these two bearings was $<30^\circ$, we considered the branch drag 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 the receiver. Our pattern of results remained consistent if we increased or decreased the criterion by 10° .

To assess whether a branch drag predicted subsequent travel direction we used a chi-squared test to compare the number of branch drags that were consistent with subsequent travel direction to the number of branch drags that would have been expected to do so by chance. We conducted two chi-squared tests: one with data from nest sites and feeding trees, another with data from wait-and-see events.

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 chance. 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.

We chose not to use circular statistical tests because our data violate two assumptions of such tests. First, we have no evidence that small directional differences are meaningful to bonobos; e.g., a bonobo may not easily distinguish between a branch drag performed at 300° and another performed at 320°. As a result, our data are not really suitable for correlational statistical analysis, which assumes interval measures and tests for a consistent relation throughout a numerical range. Second, a correlational analysis would also assume that bonobos could perform a branch drag in any direction (360°), but this assumption is also violated by our data, as explained earlier. We, therefore, used the more conservative statistical analysis that takes account of the nature of our data.

To investigate whether the branch drags of dominant individuals were more likely to predict the party's subsequent travel direction, we compared the branch drags performed by the alpha male to those compared by all other males by conducting a Fischer's exact test.

We determined male dominance rank by using the outcomes of dyadic agonistic interactions (unpublished data). We used "fleeing upon aggression" as a signal of subordination, following previous work showing this to be a reliable measure of dominance rank in bonobos (Stevens *et al.* 2005, 2006).

Change in Travel Direction

We also tested whether parties changed travel direction after branch drags, regardless of the direction in which the branch drag was performed. We calculated the change in direction by subtracting the bearing from the previous feeding tree to the location of interest from the bearing from the location of interest to the party's location 10 min after the initiation of travel. To test the association between branch drags and the magnitude of a party's change of direction we created two linear models (using the *lm* function in R version 3.1.2): one using data from feeding trees, and the other using data from wait-and-see events. In both models, the presence of branch drag (yes/no) was the independent variable, and direction change in navigational degrees was the dependent variable.

We also conducted a generalized linear model (*glm* function *lmerTest* package in R 3.1.2) with the data from wait-and-see-events. Occurrence of a branch drag (yes/no) was the independent variable and change in party direction (above/below median change) was the outcome variable. This binomial outcome model was our original analysis of the data. We later ran the linear model in order to test the data using continuous variables, as we do in all other analyses.

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 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

Branch Drags

Male bonobos performed branch drags at a mean rate of $1.08 \pm \text{SD } 0.76$ branch drags per hour per individual. Only one female was observed to perform a branch drag during 117 h of focal animal sampling. There was 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 libitum data). The remaining five males performed 32% (103/321) of all branch drags (see ESM Table SI for complete list of all branch drags and associated data). Branch drags were also more likely to be performed in larger, than smaller, parties (GLM: party size: $\beta = 0.31$, $\text{SE} = 0.15$, $Z = 2.01$, $P = 0.044$).

Branch Drags at Nest Sites and Feeding Trees

Distance Traveled to Next Feeding Tree

Our analysis included 23 instances of travel between nest sites and feeding trees (mean distance traveled: $438 \pm \text{SD } 450$ m) and 133 instances of travel between feeding trees ($447 \pm \text{SD } 492$ m). Bonobos performed branch drags at 12 of the nest sites and 31 of the feeding trees (Fig. 1).

A linear model that included branch drag, context, and an interaction term between the two as predictor variables fit the data significantly better than a null model ($F = 12.7$, $\text{df} = 3$, $P < 0.001$). The results of the full model indicate that parties traveled significantly farther after a branch drag than in the absence of a branch drag, regardless of whether the branch drag was performed at a nest site or a feeding tree (Table 1). Plotting the data shows that this relationship holds until the distance to the next feeding tree was 600 m, at which point the likelihood of a branch drag plateaued for feeding trees, and dropped for nest sites (Fig. 2).

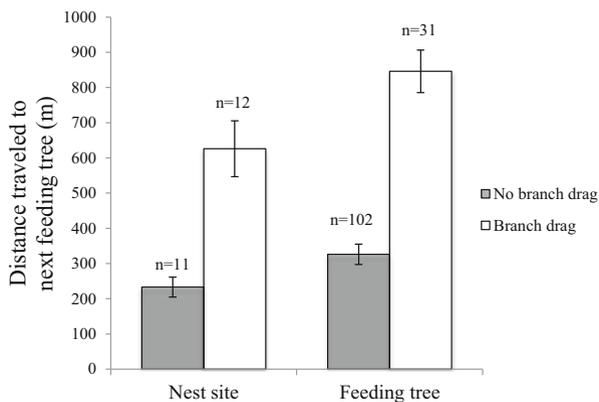


Fig. 1 Mean \pm SE distance bonobos (*Pan paniscus*) at Lui Kotale, Democratic Republic of Congo, traveled from a nest site or feeding tree to the next feeding tree, split by the occurrence or absence of a branch drag. Data are from July 2011 to March 2014.

Table 1 Results of a linear model testing the influence of whether a branch drag occurred, the context, and the interaction between the two on the distance bonobos (*Pan paniscus*) at Lui Kotale, Democratic Republic of Congo, traveled to the next feeding tree

Predictor variables	Estimate	SE	T value	P value
Intercept	326.0	43	7.5	<0.001
Branch drag	519.8	90	5.8	<0.001
Context (nest site)	-92.2	139	-0.7	0.508
Branch drag × nest site	-127.7	204	-0.6	0.531

Data are from July 2011 to March 2014

Association between Direction of Branch Drags and Direction of Subsequent Travel

The direction in which a branch drag was performed predicted subsequent travel direction in 45% (5/11) of instances at nest sites and 24% (5/21) of instances at feeding. Overall the direction of the branch drag correctly signaled a party's subsequent travel direction in 32% (10/32) of cases, significantly more than would be expected by chance (16.67%) ($\chi^2 = 7.22$, $df = 1$, $P = 0.007$).

Branch drags performed by the first-ranking male were no more likely to predict subsequent travel direction than branch drags performed by other individuals ($P = 0.659$, Fischer's exact test).

Change in Travel Direction

We obtained accurate information on the party's travel bearing before and after 80 feeding trees ($66^\circ \pm SD 47^\circ$). The mean change in travel direction before and after feeding in a tree did was $68^\circ \pm SD 47^\circ$ in the absence of a branch drag and $56^\circ \pm SD 45^\circ$ when a branch drag did occur, but occurrence of a branch drag was not significantly associated with the magnitude of directional change (LM: $\beta = 12.19$, $SE = 13.05$, $Z = -0.9$, $P = 0.353$).

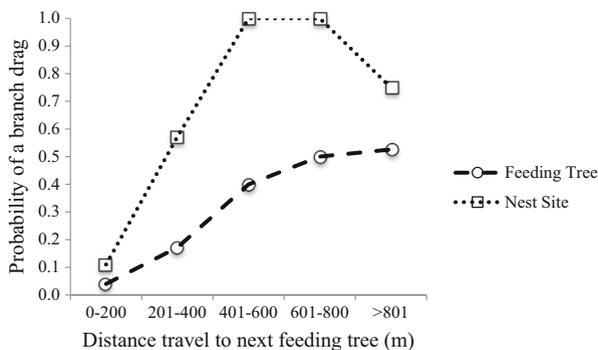


Fig. 2 Relationship between the occurrence of a branch drag and subsequent distance traveled by bonobos (*Pan paniscus*) at Lui Kotale, Democratic Republic of Congo at nest sites and feeding trees. Data are from July 2011 to March 2014.

Wait-and-See Events

Distance Traveled to Next Feeding Tree

Our analysis included 41 instances of travel between wait-and-see events and feeding trees ($466 \pm \text{SD } 386$ m). The occurrence of a branch drag at a wait-and-see event was not significantly associated with distance traveled to the next feeding tree (LM: $\beta = 73.81$, $\text{SE} = 122.06$, $Z = 0.6$, $P = 0.551$).

Association between Direction of Branch Drags and Direction of Subsequent Travel

We collected data on the direction of the final branch drag at 14 wait-and-see events. The direction in which a branch drag was performed predicted subsequent travel direction in 36% (5/14) of instances, which is not significantly different from chance ($\chi^2 = 3.66$, $\text{df} = 1$, $P = 0.056$).

We knew the identity of the final branch dragger at wait-and-see events in 13 instances. Branch drags performed by the first-ranking male predicted subsequent travel direction in 100% (4/4) of instance and were significantly more likely to predict travel direction than branch drags performed by all other individuals (11% (1/9) of instances; $P = 0.007$, Fischer's exact test).

Change in Travel Direction

The mean change in travel direction before and after wait-and-see events was $35^\circ \pm \text{SD } 33^\circ$ in the absence of a branch drag and $54^\circ \pm \text{SD } 42^\circ$ when a branch drag occurred (Fig. 3). This difference was not significant (LM: $\beta = 19.23$, $\text{SE} = 11.34$, $Z = 1.7$, $P = 0.097$).

When a branch drag occurred, parties changed their direction by more than 35° in 72% (13/18) of instances, compared to 36% (9/25) of instances in the absence of a branch drag. 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 $<35^\circ$ (GLM: $\beta = 1.5$, $\text{SE} = 0.7$, $Z = 2.3$, $P = 0.023$). Plotting the data suggests that branch drags were more likely to be performed before larger directional changes (Fig. 4).

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. Additionally, as the probability of a branch drag increased, the distance subsequently traveled increased. At wait-and-see events, by contrast, performance of branch drags was unrelated to subsequent travel distance.

There was some indication that branch drags also functioned to signal the direction of subsequent travel. Across all contexts, the orientation of branch drag predicted the

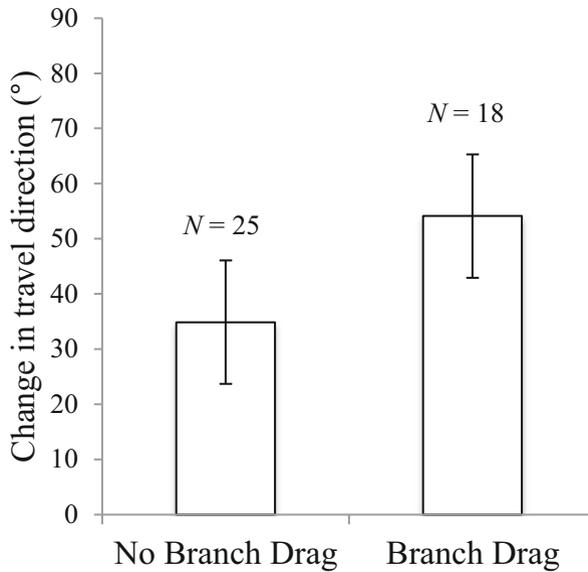


Fig. 3 Mean \pm SE change in travel direction of bonobos (*Pan paniscus*) at Lui Kotale, Democratic Republic of Congo at wait-and-see events, split by the occurrence or absence of a branch drag. Data are from July to March 2014.

orientation of subsequent travel more than would have been predicted by chance, though this agreement occurred in only 32% of all cases. Additional research and larger sample sizes are needed to further understand the relationship between branch drags and travel direction.

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

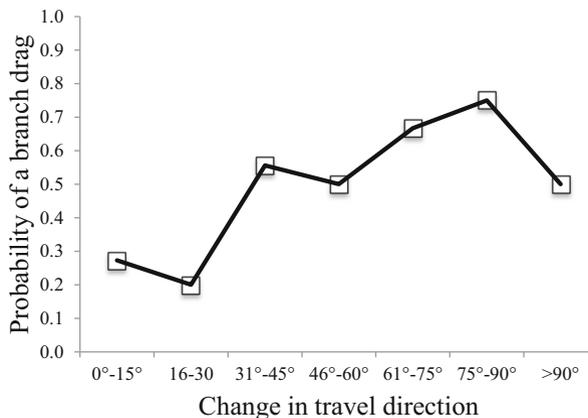


Fig. 4 Relationship between occurrence of a branch drag and the magnitude of directional change at wait-and-see events in free-ranging bonobos (*Pan paniscus*) at the Lui Kotale field site. Data are from July 2011 to March 2014.

individual's motivation to do so determines the function of any particular display. A similar explanation has been proposed for the interpretation of chimpanzee travel "hoos" (Gruber and Zuberbühler 2013), and may also be applicable to observations of buttress drumming (Boesch 1991).

At nest sites and feeding trees, individuals may have produced 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 846 m, 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 326 m, a distance over which bonobos can easily communicate (Hohmann and Fruth 1994; White *et al.* 2015).

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 site (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. For example, individuals may have performed branch drags because they were motivated to leave a particular area of the forest, rather than because they knew their eventual destination.

If branch drags were used as travel signals, it is puzzling that males performed the overwhelming majority of these displays. 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). One explanation for why females did not perform a larger proportion of branch drags is that branch drags, like most primate displays, may have evolved as a signal of male dominance, and only later were co-opted for use in the travel context. Another, mutually compatible hypothesis, is that, because of 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 of group coordination such as soft calls or individual movement (Meunier *et al.* 2006) might reveal female influence more effectively than our focus on branch drags. Additionally, our results are largely based on data from only a few individuals, so should be interpreted cautiously.

Conclusion

Bonobos use branch drag displays in the context of group travel. 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 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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Compliance with Ethical Standards

Conflicts of Interest We have no conflicts of interest to declare.

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