



Coordination of Chimpanzees (*Pan troglodytes*) in a Stag Hunt Game

Anke F. Bullinger · Emily Wyman · Alicia P. Melis ·
Michael Tomasello

Received: 17 January 2011 / Accepted: 5 July 2011
© Springer Science+Business Media, LLC 2011

Abstract Group-living animals frequently face situations in which they must coordinate individual and sometimes conflicting goals. We assessed chimpanzees' ability to coordinate in a Stag Hunt game. Dyads were confronted with a situation in which each individual was already foraging on a low-value food (hare) when a high-value food (stag) appeared that required collaboration for retrieval, with a solo attempt to get the stag resulting in a loss of both options. In one condition visibility between partners was open whereas in the other it was blocked by a barrier. Regardless of condition, dyads almost always (91%) coordinated to choose the higher valued collaborative option. Intentional communication or monitoring of the partner's behavior before decision making—characteristic of much human coordination—were limited. Instead, all dyads adopted a leader–follower strategy in which one partner took the risk of going first, presumably predicting that this would induce the other to join in (sometimes communicating if she was slow to do so). These results show that humans' closest primate relatives do not use complex communication to coordinate but most often use a less cognitively complex strategy that achieves the same end.

Keywords Chimpanzees · Collaboration · Communication · Coordination · Stag hunt

Introduction

Group-living animals must constantly make group decisions. Most prominently, they must decide on group travel direction (Conradt and Roper 2005; Petit and Bon 2010; Pillot and Deneubourg 2010). Given that no individual wants to travel alone, each

Electronic supplementary material The online version of this article (doi:10.1007/s10764-011-9546-3) contains supplementary material, which is available to authorized users.

A. F. Bullinger (✉) · E. Wyman · A. P. Melis · M. Tomasello
Department of Developmental and Comparative Psychology,
Max Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany
e-mail: bullinge@eva.mpg.de

must take into account the others' behavior to travel together. However, if different individuals prefer different travel directions, a coordination problem can arise (Kummer 1968; Nunn and Lewis 2001): individuals are reciprocally dependent on one another's decisions, and so their goals and intentions need to be coordinated to benefit from the advantages of group living. One way in which chimpanzees (*Pan troglodytes*) have resolved this kind of challenge can be seen in the case of their crossing dangerous roads. In such situations, dominant adult males often take the riskier front and rear positions (Hockings *et al.* 2006), in a sense guiding the rest of the group.

Another context in which coordination becomes a major issue is during chimpanzees' group hunting (Watts and Mitani 2002), which poses special challenges. A moving prey puts hunters under externally imposed time pressure, and mistakes may be irreparable, leading to complete failure of the hunt and wasted energy (Gilby and Wrangham 2007). When a party of male chimpanzees spies a vulnerable monkey (a food of very high value), they are typically on their way to feed on some kind of lower-value vegetation (Mitani and Watts 1999). Each individual knows that he cannot capture the monkey alone, and so he wants to pursue it only if others do also (see Mitani and Watts (1999) for observational evidence on the influence of party size on hunting bouts and Hirata and Fuwa (2007) and Melis *et al.* (2006a) for experimental evidence that chimpanzees understand when they do and do not need partners in collaboration problems). Each chimpanzee must therefore decide whether to take the risk of forgoing the vegetation to pursue the more rewarding, but also riskier, monkey, which each will do only if he predicts that the others will also. The contingencies in this situation are most naturally modeled in game theoretic terms as a Stag Hunt problem: all individuals benefit by going for the stag so long as all decide to do it (Skyrms 2004).¹ Because all individuals would prefer the stag, the players' personal interests do not conflict with those of others and hence they are all better off cooperating so that defection or deception are not major issues (Alvard and Nolin 2002).

At the point of decision making, there are 2 main classes of solution to this problem: collective decision making and individual decision making. The first solution is that individuals make a group decision, wherein group members try to estimate each other's goals and intentions *before* decision making (Tomasello and Carpenter 2007). This can be achieved, e.g., by mutual eye contact or on a more advanced level by intentional communication, wherein individuals explicitly inform one another of what they are going to do (Brinck and Gärdenfors 2003; King *et al.* 2009; Tomasello 1995; Fischer and Zinner 2011). Intentional communication is here defined as motor acts, e.g., attention getters, gestures, that are directed to a recipient via body orientation or eye gaze with the sender expecting a response as evidenced by looking to the recipient, waiting for a response, or persisting in the communicative interaction (Liebal *et al.* 2004).

¹ The precise reward structure is not our main concern here. But in chimpanzee group hunting each individual knows that he has a chance of capturing the monkey himself, in which case he will get a very high reward. He also knows that if someone else captures the monkey he will still get some meat by begging and harassing the captor afterwards. Moreover, even a scrap of meat is worth considerable effort as it supplies many micronutrients not available in vegetation (Tennie *et al.* 2009).

The second solution requires individuals that impulsively decide in favor of their own selfish interests and hence become passive leaders, i.e., by taking the lead they unintentionally prompt others to join in (King *et al.* 2009; Van Vugt 2006). This strategy can be realized without a detailed knowledge of the goals and intentions of other individuals, but simply relies on the individual's ability to observe and react to a change in the partner's behavior (Rands *et al.* 2003). So *after* one individual has made her decision, coordination can be achieved via 3 ways (Conradt and Roper 2005): 1) followers monitor the behavior of their group members and use social cues that are unintentionally spread, e.g., vocalization, to adjust their behavior accordingly; 2) followers use nonsocial cues, i.e., external outstanding cues, e.g., the rustling noise of the prey, to infer the partners behavior and adjust their actions accordingly; or 3) leaders use intentional communication to influence the followers' decision.

One way in which individual decision making could lead to a group hunt is the following: If there is a chimpanzee—perhaps a juvenile—that believes that he can capture the monkey alone, he may start chasing it, taking the leader position without considering the consequences for the group. The others now see ≥ 1 other individual already committed to the chase, and because 2 is quite often enough for success, they are taking very little risk in joining in now. Alternatively, an individual may know from past experience (Fang *et al.* 2002) that if he starts things going others will soon join in (because their joining in immediately creates sufficient manpower). That is to say, by beginning the chase this individual knows that he is changing the situation for the others such that it is now in their interest to follow in to the chase, which is not implausible given that chimpanzees understand things about how the behavior of others is driven by their goals and perceptions (Hare *et al.* 2000, 2001). Either way, 1 individual becomes the stimulator for the group: an outcome that is not the result of a group decision, but emerges from the interaction between dictating individuals and followers. Recently there has been much discussion about the important role of such risky leadership decisions in coordinating the social behavior of a number of animal species (King *et al.* 2009; Sueur and Deneubourg 2011).

Previous research suggests that chimpanzees are more likely to adopt the leader–follower strategy than the group decision strategy in attempting to solve the coordination problem presented by Stag Hunt type situations. In terms of communication, there are no reliable reports of chimpanzees intentionally communicating to initiate a group hunt. Mitani and Watts (1999) reported very cautiously that male chimpanzees in their study group sometimes vocalized before mobilizing with others to go off in search of monkeys (though it is not a unique vocalization), but there is no such report for the moment of decision when the monkey is spied. Experimental studies of collaborative problem solving mostly find no communication among chimpanzees to initiate the collaboration (Hirata and Fuwa 2007; Povinelli and O'Neill 2000; *cf.* Crawford 1937 for juvenile chimpanzees pulling at their recalcitrant companions). Even when a pair of chimpanzees with conflicting preferences must coordinate and agree on 1 out of 2 possible collaborative tasks, they mainly solve this problem without intentional communication (Melis *et al.* 2009).

In terms of a potential leader–follower strategy, 2 observations are relevant. First, in many group hunts in the wild, the initiator is a juvenile chimpanzee (Boesch and Boesch-Achermann 2000). It may thus be that such a young individual has not yet

learned that he cannot catch the monkey alone. Second, in an analysis of many group hunts over many years in several different groups, Gilby *et al.* (2008) reported the critical role of what they call impact hunters, which initiate many group hunts. These individuals may be ones who have figured out that if they initiate things, others will likely follow (because their following will immediately constitute a group hunt with sufficient hunters), and thus reducing the risk associated with a leadership role.

In the current study, we investigated chimpanzees' coordination experimentally in a Stag Hunt type situation (Skyrms 2004). Pairs of chimpanzees were confronted with a situation in which each had to choose within a certain time interval to either continue foraging a low-value food individually (hare) or to forsake the hare and go for a high-value food collaboratively (stag). Throughout testing both individuals continuously demonstrated an understanding that leaving the hare meant forsaking it for good, and that obtaining the stag required that the partner go for it also, so that both would need to collaborate. Subjects thus clearly understood that a solo attempt to get the stag would lead to the loss of everything.

Of major interest were the cues that individuals might use in making a decision to go for the stag, including most prominently seeing or hearing the other go first (or possibly just hearing or seeing the stag appear) and any acts of intentional communication toward the partner (Crawford 1998; Skyrms 2002). To try to influence these cues experimentally, we ran 1 condition in which the partners had full visual access to each other and another condition in which a barrier impeded visual access to the partner at the critical moment in which they had to make the decision. We also looked at the timing of situations to assess the likelihood of a leader–follower strategy.

Our prediction based on past research was that chimpanzees would not rely heavily on intentional communication to coordinate a decision to go for the stag. Instead, we predicted, at least in some pairs, a leader–follower strategy. The barrier manipulation had the potential to force individuals to modify their strategy no matter which of these options they were pursuing. The barrier made both overt communication with the partner and visual monitoring of the partner extremely difficult in the time interval before ≥ 1 of the partners reached the stag (at which point visual access was possible if limited).

Methods

Participants

Eight chimpanzees (*Pan troglodytes*; 1 male, 5 females, and 2 juveniles) ranging from 5 to 33 yr of age participated in the study (Table I). An additional 7 chimpanzees (2 males, 5 females) took part in the study but were excluded from further testing because they failed in the training or pretest. All individuals were housed at the Wolfgang-Köhler-Primate-Research-Center (WKPRC) in Leipzig, Germany. They were paired into dyads ($N=12$). Some individuals had previously participated in collaborative problem-solving studies (Greenberg *et al.* 2010; Melis *et al.* 2006a). Subjects could choose to stop participating at any time. They were never food deprived and water was available *ad libitum*. Animal husbandry and

Table 1 Sex, age, rank, and grouping for each subject tested as well as individual results

Group	Subject	Sex	Age	Rank	Role	Leader's behaviour at Stag		Comments
						Monitoring	Intentional Communication	
1	Fraukje	Female	33	1	Leader	18.6%	18.6%	Mother of Pia
1	Lobo	Male	5	3	Leader	20.8%	6.3%	
1	Natascha	Female	29	1	mixed	17.2%	3.4%	
1	Pia	Female	10	2	Follower	23.5%	0.0%	
2	Lome	Male	8	4	Mixed	52.6%	13.2%	
2	Robert	Male	33	1	Follower	0.0%	27.8%	Father of Lome and Sandra
2	Sandra	Female	16	3	Leader	21.1%	52.1%	
2	Ulla	Female	32	2	Follower	23.5%	0.0%	

1= no-barrier followed by barrier condition; 2= barrier followed by no-barrier condition.

research comply with the EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria and the WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquarium.

Materials and Design

Subjects sat in adjacent rooms (47 m²) on either side of a booth and were separated at all times from the experimenter (E) by caging (Fig. 1).

Hare In each testing room a box hung at the mesh-wall farthest away from the partner's testing room, so that when individuals fed on it they had their backs oriented toward the partner. Each box contained 60 holes stuffed with raisins and was closed with a sliding door. The ape could get access to the raisins by sliding the

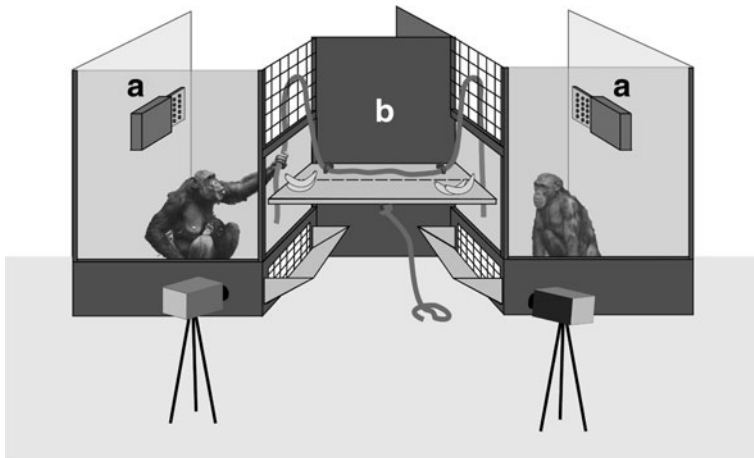


Fig. 1 Experimental setup (barrier condition). (a) Hare. (b) Stag. Distances are minimized for purposes of this illustration.

door to one side and then picking them out of the holes. However, as soon as the ape let go of the door, it shut irreversibly so no more raisins could be obtained.

Stag A platform lay inside the booth between the 2 testing rooms but out of the subjects' reach. Two metal loops were attached to the platform, and a rope lay threaded through these loops, with 1 of the 2 rope ends extending 1.3 m into each of the subject's testing rooms. Equal amounts of food (6-cm-long pieces of banana) were placed on either side of the platform. If subjects pulled both ends of the rope simultaneously, they raised the platform and the food fell down into 2 collecting trays below, from which each ape could retrieve its reward. However, if only 1 end of the rope was pulled, the rope became unthreaded so the food could not be retrieved by either individual. Critically, food on the stag was available for only a limited time period: once food was placed on the platform, E began to pull a chain for 20 s that made a loud audible noise during the second half of the interval, signaling to the apes that they had only a further 10 s in which to secure the food. At the end of this interval, the food platform was pulled sharply, causing the food to fall away so it was lost to the apes altogether.

We tested 2 groups of 4 individuals in all possible dyads (6 in each group). Dyads participated in 2 types of test conditions. In the *barrier condition*, the dyad partners could not see each other while feeding on the hare and thus had no visual information about their partner's decision. In the *no-barrier condition*, the dyad partners could see each other and potentially communicate their decisions before leaving the hare. One group started with the barrier condition and the other with the no-barrier condition, in an intrasubjects design (Table 1). We randomly assigned subjects to the groups and the order of partners.

Procedure

Training and Pretests Before entering the test phase, subjects received a series of training phases and pretests to ensure that they understood the different apparatuses and the basic principles of the game. If subjects failed to complete all training phases successfully, or failed any of the pretests, we excluded them from further testing.

Stag Training Subjects learned over 5 training phases how to retrieve food from the stag platform, and that the stag could be retrieved only together with a partner (see the Electronic Supplementary Material [ESM] for details of the different training phases and results). The partner was either the experimenter or a conspecific, acting as a stooge, so that no subject had prior experience with a later test partner.

Hare Training Subjects learned over 3 training phases how to retrieve food from the hare box and that food could no longer be retrieved from the hare once the door had closed (see ESM for details of the different training phases and results). In addition, subjects were exposed to a partner who was occupied feeding on the hare and not from the first waiting at the stag to collaborate (see ESM for details). Thus, subjects learned to pay attention to the partner's behavior.

Nonsocial Pretest This pretest ensured subjects' knowledge that the stag could be obtained only with a partner (see [ESM](#) for details of the results). Subjects received 5 trials in which they alone entered their testing room, i.e., no stooge present. As soon as the subject started feeding on the hare, the stag platform was baited. Subjects had to refrain from pulling the rope on 4 out of 5 trials to continue with the next pretest.

Stooge Pretest This pretest ensured subjects' knowledge that the stag was available for only a 20-s time interval (see [ESM](#) for details of the results). Subjects received 5 trials in which both the subject and the stooge entered their respective testing rooms, though the hare was set up only in the subject's room. As soon as the subject started feeding on the hare, the stag platform was baited. Subjects had to pull the rope within the given time interval on 4 out of 5 trials to continue with the next pretest. In addition, this pretest served as preference test to ensure that the stag food was higher in value than the hare food.

Experimental Sessions Refresher pretest. To continually ensure that subjects were sensitive to the contingencies of the game, both subjects of a dyad received up to 3 blocks of 1 nonsocial pretest trial and 1 stooge pretest trial. Subjects had to pass both of these trials consecutively to continue with the test on the same day. Subjects not passing after the second block were not allowed to enter the test session and received a third block as training (see [ESM](#) for details of the results).

Test. Subjects were now paired in dyads and entered their respective testing rooms. As soon as both started feeding on the hare, the stag platform was baited. Now subjects faced a decision: either continue to feed on the hare, or attempt to retrieve the stag collaboratively together with their partners. Each dyad participated in 12 trials per condition administered in 3–6 sessions of 2–4 trials each. The time interval between 2 consecutive trials was ≥ 3 min.

Scoring and Analysis The central questions of interest were 1) the conditions under which dyads would give up their hares to coordinate in retrieving the stag; 2) whether they might adopt leader-follower roles; and 3) whether coordination would be achieved primarily through the monitoring of each other's behavior or by intentional communication. A trial started when the first subject opened its hare and finished when the stag was lifted by the dyad or removed by E. We videotaped all sessions, and coded the following variables from live coding and from tapes:

- 1) Choice to either stay on the hare or go for the stag. Whenever the subject's hand left the hare and it moved toward the stag, it was coded as "going for stag." (To control for subjects' understanding of making an either-or-decision we further coded whether subjects returned and tried to reopen the hare. In addition, we checked whether raisins were left in the hare after each trial to make sure subjects really gave up one option for the other.)
- 2) Coordination at the stag. This was coded as successful if both subjects pulled the rope simultaneously within the time interval and obtained their food.
- 3) Role taking. A subject was coded as *leader* if its hand left the hare before its partner's and as *follower* if its hand left the hare after its partner's.

- 4) Communication. Communication was differentiated temporally as that occurring a) still at the hare or b) at the stag. We also differentiated between i) visual monitoring of the partner, i.e., 1 individual observes the behavior of the partner without actively trying to get the partner's attention and ii) intentional communication, wherein attention getters, such as hand-clapping, grid-banging, and stomping as well as signs of impatience, such as running along barrier and rocking toward the direction of the partner, were coded.
- 5) Follower's reason to leave the hare. This was divided into 5 categories: a) social auditory cues, i.e., auditory cues spread unintentionally by the leader, e.g., hear the hare of leader close; b) nonsocial auditory cues, i.e., auditory cues spread in the course of the procedure, e.g., hear stag placement, hear start of chain rattling; c) visual monitoring of the leader (see 4); d) intentional communication (see 4); and e) not discernible. Whenever the follower left the hare ≤ 2 s after one of the categories applied, we assigned it to the respective category a–d. In cases of not attributable or ambiguous reasons, e.g., unable to distinguish between 2 reasons, we coded it conservatively, assigning it to category e.
- 6) Temporal relationship between communication and participant actions. Once the leader had left the hare it was coded whether or not the leader communicated to the follower relative to its waiting time.

To assess interobserver reliability, a second coder, unaware of the hypotheses of the study, coded 25% of the trials. Agreement on subjects switching to the stag, coordinating at the stag, taking roles, and returning and trying to reopen the hare was excellent at 100.0% (Cohen's $K=1.00$). Further reliability estimates were determined for followers' reason to leave the hare (Cohen's $K=0.922$), the monitoring behavior (Cohen's $K=0.809$), and intentional communication (Cohen's $K=0.758$). Agreement on whether or not the leader communicated relative to its waiting time was high (Spearman's $\rho=0.999$, $p<0.001$, $n=69$).

Statistics To check for an order effect of condition, we used a repeated measures ANOVA with 1 intersubject factor (group) and 1 intrasubject factor (condition) because the same subjects received all conditions in repeated test trials. Both factors had 2 levels: group consisted of group 1 that started with 12 trials without the barrier and group 2 that started with 12 trials with the barrier. The factor condition had the levels without barrier and with barrier. To check for role taking we used the χ^2 test to determine whether the observed frequencies (counts) of taking the lead markedly differed from the frequencies that we would expect by chance. Using a paired-samples t -test (2-tailed) we compared the number of trials on which communication occurred or did not occur at the different times of the leader waiting at the stag.

Results

Overall, dyads understood the game extremely well: Based on their training performance and the pretests before each test session, subjects in the study clearly understood that 1) collaboration was needed to obtain the stag and 2) leaving the hare meant forsaking it for good. In addition, once an individual had left the hare to

go for the stag, it almost never returned (only 3% of the time), and when it did it never tried to open the door forcefully, even though there were still raisins in the hare on 99% of these trials. Once both partners had arrived at the stag, they pulled successfully together on 94.7% of the trials; the failures were due to bad coordination (0.3%), late arrival on the stag of 1 individual (1.9%), or pulling the rope too early (3.1%).

Of main interest was what subjects would choose. Dyads were highly successful in coordinating to their mutually preferred option. Subjects chose the stag option in 91% of the trials (95% in the barrier and 87% in the no-barrier condition). In 7% of the trials only 1 individual went for the stag, and in 2% both individuals stayed on the hare. There was no main effect of condition (ANOVA: $F_{1,10}=2.255, p=0.164, \eta^2=0.184$), no main effect of order of conditions (ANOVA: $F_{1,10}=4.746, p=0.054, \eta^2=0.322$), and no interaction between condition and order (ANOVA: $F_{1,10}=3.01, p=0.113, \eta^2=0.231$) on choosing the stag. So, regardless of whether chimpanzees could see the other or not, both partners overwhelmingly chose the collaborative stag option. There was also no effect of condition on latency to go to the stag (t -test: $t(7)=1.159, p=0.284$).

Examining the timing of participation, in most instances we found a clear leader-follower strategy. For the most part, individuals adopted specific roles across trials (Fig. 2), with very little role switching. Three individuals consistently took the role of the leader (Lobo: $\chi^2=21.795, p<0.001$; Fraukje: $\chi^2=8.042, p=0.005$; Sandra: $\chi^2=136.111, p<0.001$), whereas 3 individuals consistently took the role of the follower (Pia: $\chi^2=34.087, p<0.001$; Ulla: $\chi^2=40.111, p<0.001$; Robert: $\chi^2=36.000, p<0.001$). Both of these groups comprise a mixture of males and females, older and younger individuals, and more and less dominant individuals (Table I). Two individuals took different roles depending on the specific pairing (1 of which was consistent across trials with a specific partner).

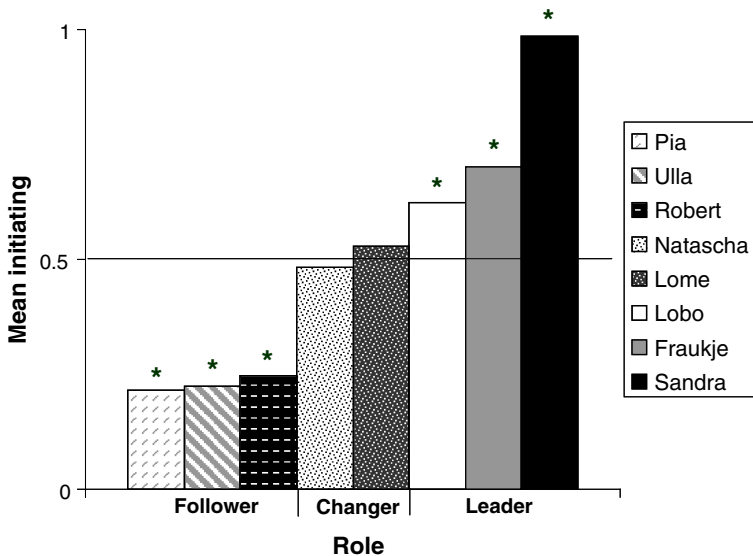


Fig. 2 Individual role taking. The stars over the bars indicate significant differences from chance rate of 50% (on the basis that within any dyad, each individual had a 50% chance of taking leader vs. follower role).

Because coordination was so prevalent, the next question was what cues subjects used to make their decision. By definition, leaders left their hare first and could communicate their decision to their partners either before leaving the hare or after arriving at the stag. Before leaving the hare, they never intentionally communicated to the partner, and they visually monitored the partner's behavior on only 6.0% of the trials. Leaders more often left the hare quickly for the stag, and then after having made this decision just waited at the stag, or intentionally communicate from the stag if the follower was slow to follow. Leaders intentionally communicated from the stag in 15.2% (range 0–52.1%) of the trials, and they visually monitored the potential follower in an additional 22.2% (range 0–52.6%) of the trials (for individual differences see Table 1).

For 66.8% of the trials, we could determine what prompted the followers to leave the hare based on the timing of the response (Fig. 3). Followers mainly left the hare in response to auditory cues, 26.3% of which were social auditory cues, i.e., the sound of the leader's hare closing, and 27.1% of which were nonsocial auditory cues, i.e., the sound of the stag placement and the sound of the chain indicating the stag leaving. Monitoring the leader led to followers departing from the hare in only 1.2%. This small amount can be explained by the inefficiency of this behavior because visual monitoring requires stopping eating on the hare, turning around, checking for the leader's location, and then deciding whether or not to leave. Followers were prompted to leave for the stag by the intentional communication of the leader in 12.2% of the trials.

This small amount of communication was due at least in part to the fact that followers tended to leave immediately after the leader. Figure 4 shows that no intentional communication took place when leaders waited only a short time for their partners to join them at the stag (mean=4.73 s \pm SE 0.31 s). However, significantly more intentional communication occurred when leaders had to wait a relatively long time for their partner to join them at the stag (mean=11.05 s \pm SE 0.44 s); *t*-test: *t*(20)=

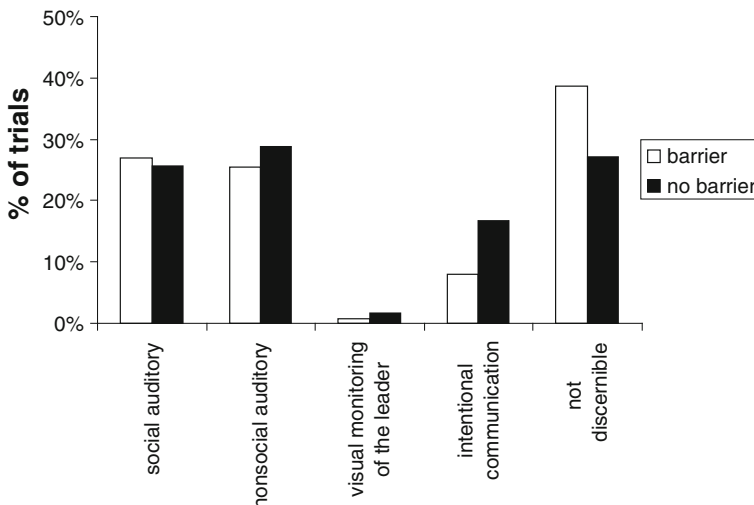


Fig. 3 Percentage of trials in which the follower switched to stag for the different cues used.

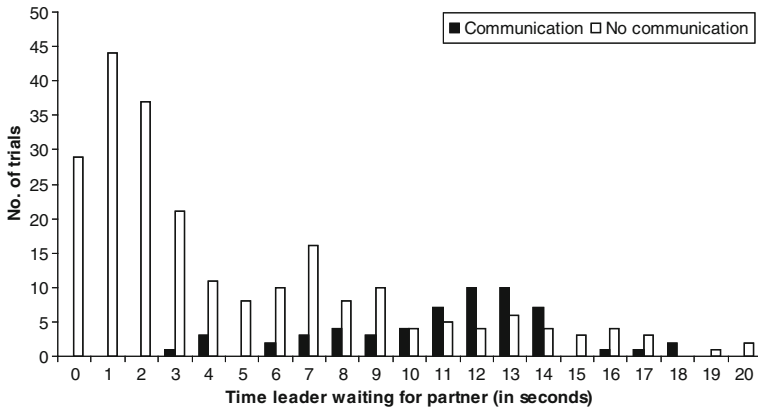


Fig. 4 Number of trials the leader communicated or did not communicate in relation to time leader waited for the partner.

2.775, $p=0.012$. This indicates that only if the follower did not join the leader on the stag immediately did the leader communicate intentionally.

To maximize rewards, there might have been pressure over time for a mutual strategy in which both individuals stayed with the hare for as long as possible, and then simultaneously went for the stag at the end of the time interval. Thus, the 2 partners should have waited until the last moment before going together to get the stag. However, we did not observe the development of any such strategies over the course of trials for any pairs of individuals in the current study.

Discussion

In discussions of humans in Stag Hunt situations, the emphasis is typically on the need for some kind of mutual knowledge, as often brought about by communication, in coordinating on a maximally beneficial solution for all (Cooper *et al.* 1994). Human children most often go for the stag if they see that the partner not only has seen the stag, but also—through mutual eye contact—has seen them seeing the stag as well. The current study shows that humans' closest primate relatives most often use another, less cognitively complex strategy that quite often achieves the same end. This is in line with simulation models showing that very simple individual rules of thumb can be sufficient to generate seemingly complex patterns of social behavior (Conradt and Roper 2009; Rands *et al.* 2003).

Chimpanzees in the current study overwhelmingly chose the collaborative stag option, and they did so regardless of whether they had visual access to their partners at the moment of decision. However, they were not just going for the stag out of excitement or failure to inhibit because in the nonsocial pretests they refrained from going for the stag if there was no partner present. Nor were they solving the coordination problem by communication because there was no intentional communication at the initial point of decision making, and even very little visual monitoring of the partner before decision making. One could argue that subjects had learned throughout the pretraining that partners were always willing to collaborate to

retrieve the stag and were thus primed to always go for the stag option. We cannot completely rule out that this was the case. However, subjects also had prior experience with a stooge that was occupied feeding on the hare while the subject waited at the stag.

Instead, the chimpanzees in the current study seemed to be using a leader–follower strategy. For the follower, things were fairly simple. There were a few visual and a number of auditory cues that followers used to determine that their partners had already made her decision to go for the stag, e.g., the visual sighting of the leader at the stag, the sound of the leader’s hare closing, or some intentional communication, all of which were possible in both the barrier and no-barrier condition. In such cases, going for the stag presented very little risk (see Conradt and Roper 2005 and Rands *et al.* 2003 on factors limiting risk in foraging and traveling behavior). However, there were also indications that followers might have been making guesses about their partners’ likely behavior (rather than just hearing them leave or responding to their presence at the stag). Quite frequently they abandoned their hare in response to nonsocial auditory cues (mainly the sound of the stag), suggesting potential inferences to the effect that the partner must have heard the cue also and so would likely go for the stag. This is consistent with the fact that chimpanzees understand what others see and hear, and that this affects their ensuing behavior (Hare *et al.* 2000; 2001; Melis *et al.* 2006c).

The leader, by contrast, had to take some risk (see Gilby and Wrangham 2007; Heilbronner *et al.* 2008 for risk proneness of chimpanzees). Given their demonstrated knowledge that they needed a partner, they had to have been making guesses about what their partner would do. In the no-barrier condition, they could reason that as soon as the partner saw them going for the stag, it would follow (see Meunier *et al.* 2008 and Sueur and Petit 2009 on monitoring behavior in monkeys). However, in the barrier condition, they had to reason that the partner would come to the stag only upon hearing them going there, e.g., their hare closing or other sounds, or else when the partner spied them actually at the stag waiting. Indeed, if the partner did not come early in the process, leaders sometimes intentionally communicated via some kind of attention getters to induce the partner to come. The fact that leaders tended to communicate only after some time with a recalcitrant partner suggests that they assumed it would come to the stag immediately after the leader, and so communicated only as time was running out. Overall, if leaders were confident that followers would indeed join them at the stag if they saw them there—and if not they would communicate—then leaders would seem to have found an effective strategy that was also not particularly risky.

King *et al.* (2009) and Pyritz *et al.* (2011) note that leadership roles are often adopted by individuals that receive the most benefit from a collaboration, e.g., dominants who can monopolize the food at the end. Our sample size was too small to analyze effects of dominance, sex, or age, but from the raw data there was no hint that any of these factors consistently characterized leaders vs. followers (Table 1). However, this could be the case because individuals received the equally divided food in separate rooms, thus removing the dominant’s chance to assert its position. In line with this, Melis *et al.* (2006b) showed that dominance constrains chimpanzees’ ability to solve a cooperative problem if sharing of food is involved. It would be interesting to know if the removal of the partition or presence of clumped food would lead to consistent leader role taking of dominants.

We did not observe any major changes in strategy over trials: neither leaders nor followers appeared to maximize their outcome (neither learned to deplete the hare maximally and wait until the last moment before leaving for the stag). In contrast to other experimental studies (Jensen *et al.* 2007), we did not observe such maximization strategies of coordination over repeated trials in our Stag Hunt task.

Some commentators on human evolution have singled out for special attention the way that humans can so readily solve coordination problems with use of various kinds of mutual knowledge and communication (Alvard *in press*; Tomasello 2009). The current research demonstrates that there are simpler ways to solve coordination problems that are available to—and actually used by—humans' closest great ape relatives (Melis *et al.* 2009). However, it is possible that there are particular kinds of Stag Hunt and other coordination problems for which chimpanzees' leader–follower strategy would work less well, e.g., if leaving the hare was more costly for the leader (requiring more assurance of the partner's behavior before risking loss of the hare), or if visual and auditory cues were not present, or were unreliable for the follower. These are questions for future research for investigators interested in how specific incentive structures and specific amounts and kinds of information (Bearden 2001; Crawford 1998) affect joint decision making in different species.

Acknowledgments We thank Dr. Joanna Setchell and the *International Journal of Primatology* (IJP) for the generous fund from Springer–IJP that made this special issue possible. We thank Josefine Kalbitz and Hanna Petschauer from the Max Planck Institute for Evolutionary Anthropology for assistance in study preparation and Raik Pieszek for technical support, as well as Roger Mundry for statistical advice. In particular, we appreciate the hard work of the Wolfgang-Köhler-Primate-Research-Center animal caretakers, mainly Daniel Geissler and Stefan Leideritz. We also thank Lisa Klepfer, Katja Karg, Franziska Schleger, Nadja Miosga, Maria Baumeister, Nele Zickert, Carolin Kade, Mandy Rogalla, Christian Nawroth, Sina Mackay, Caroline Mayer, Christina Meier, Franka Köpp and Julia Löpelt for help with our tests, along with Claudia Menzel for the reliability coding. We thank Julia Greenberg, Anna-Claire Schneider, and Katharina Hamann for fruitful discussions throughout the study and the reviewers and editors for the very helpful comments on the manuscript. The research of A. F. Bullinger is supported by a grant from the German National Academic Foundation.

References

- Alvard, M. (in press). Human social ecology. In J. Mitani (Ed.), *The evolution of primate societies*. Chicago: University of Chicago Press.
- Alvard, M., & Nolin, D. (2002). Rousseau's whale hunt? Coordination among big game hunters. *Current Anthropology*, 43(4), 533–559.
- Bearden, J. (2001). The evolution of inefficiency in a simulated stag hunt. *Behavior Research Methods, Instruments, & Computers*, 33(2), 124–129.
- Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Tai Forest: Behavioural ecology and evolution*. Oxford: Oxford University Press.
- Brinck, I., & Gärdenfors, P. (2003). Co-operation and communication in apes and humans. *Mind & Language*, 18(5), 484–501.
- Conradt, L., & Roper, T. J. (2005). Consensus decision making in animals. *Trends in Ecology & Evolution*, 20(8), 449–456.
- Conradt, L., & Roper, T. J. (2009). Conflicts of interest and the evolution of decision sharing. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364, 807–819.
- Cooper, R., DeJong, D., Forsythe, R., & Ross, T. (1994). Alternative institutions for resolving coordination problems: Experimental evidence on forward induction and preplay communication. In J. Friedman (Ed.), *Problems of coordination in economic activity*. Dordrecht: Kluwer Academic.

- Crawford, M. P. (1937). The cooperative solving of problems by young chimpanzees. *Comparative Psychology Monographs*, *14*, 1–88.
- Crawford, V. (1998). A survey of experiments on communication via cheap talk. *Journal of Economic Theory*, *78*, 286–298.
- Fang, C., Kimbrough, S. O., Valluri, A., Zheng, Z., & Pace, S. (2002). On adaptive emergence of trust behavior in the game of stag hunt. *Group Decision and Negotiation*, *11*(6), 449–467.
- Fischer, J., & Zinner, D. (2011). Communication and cognition in primate group movement. *International Journal of Primatology*. doi:10.1007/s10764-011-9542-7.
- Gilby, I. C., & Wrangham, R. W. (2007). Risk-prone hunting by chimpanzees (*Pan troglodytes schweinfurthii*) increases during periods of high diet quality. *Behavioral Ecology and Sociobiology*, *61*, 1771–1779.
- Gilby, I. C., Eberly, L. E., & Wrangham, R. W. (2008). Economic profitability of social predation among wild chimpanzees: Individual variation promotes cooperation. *Animal Behaviour*, *75*(2), 351–360.
- Greenberg, J. R., Hamann, K., Warneken, F., & Tomasello, M. (2010). Chimpanzee helping in collaborative and non-collaborative contexts. *Animal Behaviour*, *80*, 873–880.
- Hare, B., Call, J., Agnetta, B., & Tomasello, M. (2000). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, *59*(4), 771–785.
- Hare, B., Call, J., & Tomasello, M. (2001). Do chimpanzees know what conspecifics know? *Animal Behaviour*, *61*(1), 139–151.
- Heilbrunner, S. R., Rosati, A. G., Stevens, J. R., Hare, B., & Hauser, M. D. (2008). A fruit in the hand or two in the bush? Divergent risk preferences in chimpanzees and bonobos. *Biology Letters*, *4*, 246–249.
- Hirata, S., & Fuwa, K. (2007). Chimpanzees (*Pan troglodytes*) learn to act with other individuals in a cooperative task. *Primates*, *48*(1), 13–21.
- Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2006). Road crossing in chimpanzees: A risky business. *Current Biology*, *16*(17), R668–R670.
- Jensen, K., Call, J., & Tomasello, M. (2007). Chimpanzees are rational maximizers in an ultimatum game. *Science*, *318*, 107–109.
- King, A. J., Johnson, D. D. P., & van Vugt, M. (2009). The origins and evolution of leadership. *Current Biology*, *19*, R911–R916.
- Kummer, H. (1968). *Social organization of hamadryas baboons: A field study*. Basel: Karger.
- Liebal, K., Pika, S., & Tomasello, M. (2004). Social communication in siamangs (*Symphalangus syndactylus*): Use of gestures and facial expressions. *Primates*, *45*(1), 41–57.
- Melis, A. P., Hare, B., & Tomasello, M. (2006a). Chimpanzees recruit the best collaborators. *Science*, *311* (5765), 1297–1300.
- Melis, A. P., Hare, B., & Tomasello, M. (2006b). Engineering cooperation in chimpanzees: Tolerance constraints on cooperation. *Animal Behaviour*, *72*(2), 275–286.
- Melis, A. P., Call, J., & Tomasello, M. (2006c). Chimpanzees (*Pan troglodytes*) conceal visual and auditory information from others. *Journal of Comparative Psychology*, *120*, 154–162.
- Melis, A. P., Hare, B., & Tomasello, M. (2009). Chimpanzees coordinate in a negotiation game. *Evolution and Human Behavior*, *30*, 381–392.
- Meunier, H., Deneubourg, J. L., & Petit, O. (2008). How many for dinner? Recruitment and monitoring by glances in capuchins. *Primates*, *49*, 26–31.
- Mitani, J. C., & Watts, D. P. (1999). Demographic influences on the hunting behavior of chimpanzees. *American Journal of Physical Anthropology*, *109*(4), 439–454.
- Nunn, C. L., & Lewis, R. J. (2001). Cooperation and collective action in animal behavior. In R. Noë, J. A. R. A. M. van Hooff, & P. Hammerstein (Eds.), *Economics in nature*. Cambridge: Cambridge University Press.
- Petit, O., & Bon, R. (2010). Decision-making processes: The case of collective movements. *Behavioural Processes*, *84*, 635–647.
- Pillot, M.-H., & Deneubourg, J.-L. (2010). Collective movements, initiation and stops: Diversity of situations and law of parsimony. *Behavioural Processes*, *84*, 657–661.
- Povinelli, D. J., & O'Neill, D. K. (2000). Do chimpanzees use their gestures to instruct each other? In S. Baron-Cohen, H. Tager-Flusberg, & D. J. Cohen (Eds.), *Understanding other minds: Perspectives from autism*. New York: Oxford University Press.
- Pyritz, L., Kappeler, P. M., & Fichtel, C. (2011). Coordination of group movements in wild red-fronted lemurs (*Eulemur rufifrons*): Processes and influence of ecological and reproductive seasonality. *International Journal of Primatology*. doi:10.1007/s10764-011-9549-0.

- Rands, S. A., Cowlshaw, G., Pettifor, R. A., Rowcliffe, J. M., & Johnstone, R. A. (2003). Spontaneous emergence of leaders and followers in foraging pairs. *Nature*, *423*, 432–434.
- Skyrms, B. (2002). Signals, evolution and the explanatory power of transient information. *Philosophy of Science*, *69*(3), 407–428.
- Skyrms, B. (2004). *The stag hunt and the evolution of social structure*. New York: Cambridge University Press.
- Sueur, C., & Petit, O. (2009). Signals use by leaders in *Macaca tonkeana* and *Macaca mulatta*: Group-mate recruitment and behaviour monitoring. *Animal Cognition*, *13*(2), 239–248.
- Sueur, C., & Deneubourg, J. L. (2011). Self-organization in Primates: Understanding the rules underlying collective movements. *International Journal of Primatology*. doi:10.1007/s10764-011-9520-0.
- Tennie, C., Gilby, I. C., & Mundry, R. (2009). The meat-scrap hypothesis: Small quantities of meat may promote cooperative hunting in wild chimpanzees (*Pan troglodytes*). *Behavioral Ecology and Sociobiology*, *63*(3), 421–431.
- Tomasello, M. (1995). Joint attention as social cognition. In C. Moore & P. J. Dunham (Eds.), *Joint attention: Its origins and role in development*. Hillsdale: Lawrence Erlbaum Associates.
- Tomasello, M. (2009). *Why we cooperate*. Cambridge: MIT Press.
- Tomasello, M., & Carpenter, M. (2007). Shared intentionality. *Developmental Science*, *10*(1), 121–125.
- Van Vugt, M. (2006). Evolutionary origins of leadership and followership. *Personality and Social Psychology Review*, *10*(4), 354–371.
- Watts, D. P., & Mitani, J. C. (2002). Hunting behavior of chimpanzees at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, *23*(1), 1–28.