Goats' behaviour in a competitive food paradigm: Evidence for perspective taking?

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Summary

Many mammalian species are highly social, creating intra-group competition for such things as food and mates. Recent research with nonhuman primates indicates that in competitive situations individuals know what other individuals can and cannot see, and they use this knowledge to their advantage in various ways. In the current study, we extended these findings to a non-primate species, the domestic goat, using the conspecific competition paradigm developed by Hare et al. (2000). Like chimpanzees and some other nonhuman primates, goats live in fission-fusion societies, form coalitions and alliances, and are known to reconcile after fights. In the current study, a dominant and a subordinate individual competed for food, but in some cases the subordinate could see things that the dominant could not. In the condition where dominants could only see one piece of food but subordinates could see both, subordinates' preferences depended on whether they received aggression from the dominant animal during the experiment. Subjects who received aggression preferred the hidden over the visible piece of food, whereas subjects who never received aggression significantly preferred the visible piece. By using this strategy, goats who had not received aggression got significantly more food than the other goats. Such complex social interactions may be supported by cognitive mechanisms similar to those of chimpanzees. We discuss these results in the context of current issues in mammalian cognition and socio-ecology.

Keywords: social cognition, goats, visual perspective taking, comparative cognition.

Introduction

Mammalian species tend to be highly social. Although this sociality can confer many benefits, it also precipitates competition among individuals for

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valuable commodities such as food and mates. Consequently, competition is a pervasive and influential aspect of many animals' lives. Indeed, recent research suggests that some species may demonstrate complex cognitive abilities in competitive situations that they do not display elsewhere. Specifically, some nonhuman primates know what competitors can and cannot see, and they use this knowledge to their advantage in various ways. However, such cognitive skills may not be confined to primates – other mammalian species also possess complex social structures in which competition is an important part of everyday interactions. Here we examine whether one such species, the domestic goat, can take the visual perspective of others.

Past research has shown that chimpanzees can take the visual perspective of others when competing with a conspecific for food. Hare et al. (2000; see also Bräuer et al., in press) placed a subordinate and a dominant chimpanzee into two separate rooms with a third room in between. Each chimpanzee's room contained a guillotine door leading into the third room; when these doors were opened slightly, the chimpanzees could see food that had been placed in the room, as well as the other individual looking under her door. In the test, two pieces of food were placed at various locations within the room. Then the doors for both individuals were opened, allowing them to enter the third room. In this situation, the subordinate faces a problem: the dominant individual will take all of the food that it can see. Indeed, in all the conditions in which dominants had good visual and physical access to the two pieces of food, they took them both on most occasions. However, in some conditions the subordinate could see a piece of food that the dominant could not see. For example, the food might be placed on the subordinate's side of a small barrier. If subordinates knew that the dominant could not see that piece of food, making it safe for them to take, they should prefer it over the visible piece. Results indicated that, indeed, subordinates took the food that only they could see much more often than the food that both they and the dominant could see. Moreover, subordinates' preferences were not simple reactions to the behaviour of the dominant competitor: in conditions where the subordinate was given a small head start, forcing them to make their choice before the dominant was released into the area, they still preferred the hidden piece. Hare et al. (2003) used this same basic experimental paradigm with capuchin monkeys and found that, unlike chimpanzees, subordinate monkeys used the behaviour of the dominant animal to determine where to go.

Recently, Karin-D'Arcy & Povinelli (2002) failed to replicate the results of Hare et al. (2000) with a new group of chimpanzees. However, Bräuer et al. (in press) did replicate the original results, and suggested that the earlier failure occurred because of alterations to the physical dimensions of the testing setup. In particular, Karin-D'Arcy & Povinelli (2002) used a substantially smaller arena then Hare et al. (2000), and reduced the distance between pieces from 2 meters (as in the Hare et al. (2000) study) to 1.25 meters. Bräuer et al. (in press) showed that varying the distance between food pieces and the competitors directly effects subordinate behaviour, and thus determines whether the original finding is replicated. Moreover, recent experiments have demonstrated visual perspective-taking in chimpanzees using a novel paradigm. Hare et al. (in press) had chimpanzees compete for food with a human competitor. Pieces of food were placed on two separate trays on either side of a booth; if the human saw the chimpanzee approaching either tray, he retracted it and thus prevented the subject from retrieving the food. In the first experiment, the human looked at one piece of food and had his back to the other. In a second experiment, one piece of food was placed behind a clear barrier, and the other behind an opaque barrier. In both studies, chimpanzees preferentially went for the piece of food the human did not have visual access to. Flombaum & Santos (2005) used a similar paradigm and demonstrated that rhesus macaques are also sensitive to human visual perspective in a competitive context.

Together, these findings suggest that some nonhuman primates know what conspecifics (or humans) can and cannot see. Furthermore, they use this knowledge to maximize their food intake in competitive situations. These cognitive skills, however, may not be confined to primates. Indeed, in recent research has demonstrated that a number of non-primate species possess related cognitive skills, such as sensitivity to gaze direction or attentional state in others. Such species include domestic dogs (Call et al., 2003), corvids (Bugnyar et al., 2004; Emery & Clayton, 2004), dolphins (Xitco et al., 2004), and the domestic goat (Kaminski et al., 2005). These findings raise the possibility that some non-primate species may understand something about what others can and cannot see. Here we specifically examine whether goats (*Capra hircus*) can take the visual perspective of conspecifics.

Many characteristics of domestic goats suggest that they may possess this sort of sophisticated cognitive ability. As previously mentioned, they are sensitive to the gaze direction of other individuals, following the gaze of conspecifics to outside objects above and behind them and even using some human gestures (like, e.g., pointing) to locate hidden food in an object choice paradigm (Kaminski et al., 2005). Moreover, in the wild, goats live in relatively complex social groups that share some characteristics with those of non-human primates. Their groups contain a strong hierarchy featuring contest competition (Barroso et al., 2000), and their groups have a fission-fusion structure (Shi et al., 2005) similar to that of chimpanzees. That is, they encounter other individuals from their group irregularly across the day. Such a fission-fusion structure is thought to add another layer of complexity to the group, as party composition can frequently shift (Barrett et al., 2002). Goats also form coalitions and alliances, and engage in reconciliation after fights (Schino, 1998), as many primates do.

The nature of goat social groups, therefore, suggests that goats may possess cognitive skills allowing them to effectively navigate their complex, competitive social landscape. Specifically, they may also be able to determine what others can and cannot see. In the current study, we tested domestic goats in a conspecific competition paradigm analogous to the one previously used with chimpanzees (Hare et al., 2000). A dominant and a subordinate individual competed over food across situations in which different kinds of barriers were present. In some of these situations, the subordinate could see things that the dominant could not. However, we modified the original paradigm of Hare et al. (2000) to control for two additional factors. First, we attempted to account for the relationship between the specific individuals, which can play an important role in determining the nature of dyadic interactions. For example, tolerant chimpanzee pairs are more likely to cooperate and solve a novel problem than intolerant pairs (Melis et al., in press). As such, we measured the social tolerance of the goat pairs during experimental trials, assessing the degree to which aggressive encounters influenced the subjects' decisions. Secondly, we controlled for an issue originally raised by Karin-D'Arcy & Povinelli (2002). Those authors suggested that a predisposition to feed in the vicinity of barriers (the peripheral feeding hypothesis), independent of whether others can or cannot see such activities, could explain a preference for selecting the hidden food option. They tested this hypothesis with chimpanzees, placing an opaque barrier to the side of the food such that both subjects could see the food, but the food was still near a barrier. Although this hypothesis did not account for the behaviour of chimpanzees (e.g., Hare et al., 2001), it is conceivable that other species may show such a predisposition. Therefore, following Karin-D'Arcy & Povinelli (2002), we included a control condition in which the barrier was placed next to the food.

Methods

Subjects and housing

Twenty female domestic goats (*Capra hircus*) housed in social groups in three different zoos in Germany participated in this study. They were tested with the permission of the Zoo's veterinarians and caretakers. We tested eight subjects from group 1 (Leipzig), four subjects from group 2 (Hirschfeld) and five subjects from group 3 (Weissenfels). Three individuals, one from each group, only participated as competing dominants as they were the highest ranking females of the group.

For all animals, water was available ad libitum, and subjects were not food deprived at any time. All groups were fed two times per day throughout the study. Food consisted of vegetables, fruits, pellets and hay. Additionally, animals in group 3 (Weissenfels) received grass depending on the season. The zoo visitors were allowed to feed all animals except those in group 1 (Leipzig).

Group 1 (Leipzig)

This group consisted of 13 adults (one male and 12 females) and a varying number of juveniles. All animals were raised by their mothers except Knickohr, who was raised by humans. The group had access to an outdoor (130 m^2) and an indoor enclosure (13 m^2). Therefore animals had an overall available space of approximately 11 m^2 per animal.

Group 2 (Hirschfeld)

This group consisted of 12 adults (one male and 11 females) and a varying number of juveniles. All animals were raised by their mothers. The group had access to an outdoor (256 m^2) and an indoor enclosure (11.5 m^2). Therefore animals had an overall available space of approximately 22.3 m^2 per animal.

Group 3 (Weissenfels)

This group consisted of 8 adults (one male and 7 females) and a varying number of juveniles. All animals were raised by their mothers. The group had access to an outdoor (182 m^2) and an indoor enclosure (6.4 m^2). Therefore animals had an overall available space of approximately 23.6 m^2 per animal.

Procedure

The study was conducted from March 2001 to June 2003. Testing took place in the mornings before the first feeding time to ensure that the animals were highly food motivated. Subjects were tested in pairs consisting of a dominant and a subordinate animal. Before the actual test began, we conducted a preliminary test of dominance using a food competition test. We introduced a single pair of animals into the same cage and placed a piece of apple inside the cage approximately equidistant between them. Subjects who never obtained the food in the presence of another individual were considered subordinate to this individual. In accordance with previous findings (Barroso et al., 2000), all three groups had linear hierarchies and dominance relations could clearly be determined.

In the actual test, pairs of a dominant and a subordinate animal, as identified with the dominance pretest, were tested in three adjacent cages. These cages differed in size for the three groups because housing conditions varied at the different zoos. One or two wooden barriers (35 × 60 cm) were used to hide food from the dominant subjects depending on the condition. These occluders were placed at the extreme sides of the cages, equidistant from the two competitors; although the distances between the food pieces varied at each zoo, the distance from each participant to the food pieces was a constant 1.4 m for all three groups. At the beginning of each trial, the subjects were confined separately in the two extreme cages while E1 placed two pieces of apple in the middle cage. Both subjects' doors were completely closed, ensuring that neither subject could observe the hiding process. Food pieces were placed on the floor in one of two predetermined places.

In each condition, subordinate animals could see both pieces of food, whereas the dominants' visual access to the food varied depending on the condition. There were three experimental conditions (following Hare et al., 2000, Experiment 3):

Visible–Visible:
No occluders were present, and both individuals could see both pieces of food.

Hidden–Visible:
One occluder was present, preventing the dominant animal (but not the subordinate) from seeing one of the pieces of food.

Hidden–Hidden:
Two occluders were present, such that only the subordinate animal could see both pieces of food.

Each subject was grouped with every possible dominant individual. Altogether 46 dyads were tested and for each possible dyad, subjects completed 4 trials in the Visible-Hidden condition and 2 trials in each of the other conditions. Because of the linearity of the dominance hierarchy in all groups, some subjects received fewer trials than others (e.g., the individuals which were second in rank could only be grouped with the alpha females, while the lowest in rank could be grouped with several individuals). We therefore calculated the mean for each subject across dyads.

Each pair of subjects was run in the three conditions one after the other, typically with one session per day and no more than a few days between sessions. Across subjects, order of conditions and food location was counterbalanced and randomized with the stipulation that condition and food location was not the same in more than two consecutive trials. To control for preference for the barrier, each individual also completed 8 trials of a non-social control condition. In this control, one occluder was present, but the subordinate individual was alone in the cage (that is, she did not compete with a dominant over the food). Food location was counterbalanced and randomized across subjects, with the stipulation that it was not the same in more than two consecutive trials. Individuals from two groups (Leipzig + Weissenfels) also completed 8 trials in two additional social controls (described below), where they had to compete with a dominant animal.

Side barrier:
One occluder was present but placed next to the food, such that both individuals could see both pieces of food.

Transparent barrier:
One transparent occluder (35 × 60 cm) was present, such that both individuals could see both pieces of food but one piece of food was physically blocked from the dominant individual. To make it easier for the subjects to perceive the transparent barrier as an object, this barrier had a black frame.

Each pair of subjects was run in each of the two conditions one after the other, typically with one session per day and no more than a few days between sessions. Across subjects, order of conditions and food location was counterbalanced and randomized with the stipulation that condition and food location was not the same in more than two consecutive trials.

To control for order effects, the order in which the different conditions were given varied in all three groups.

Leipzig: Experimental/Non-social control/Side and transparent control
Hirschfeld: Non-social Control/Experimental
Weissenfels: Side and transparent control/Non-social Control/Experimental

After the baiting and the placement of the barriers were completed, E1 left the cage and together with E2 raised both subjects' doors simultaneously, which allowed both individuals to see the physical arrangement of the occluders, the food, and the other participant looking under its door. Once both subjects had looked through their respective doors, the subordinate subject was released first giving it a clear head start while the dominant subject, whose door remained slightly open, was delayed until the subordinate clearly approached one of the two food locations, at which point the dominant was released as well.

To see whether the size of the room had an influence on the aggressive behaviour of the animals in the experimental setup, we conducted additional experimental trials in the Leipzig zoo using the same room measurements as in the Weissenfels zoo. To do that we artificially shrank the room by placing wooden walls inside it in a way that the floor space was the same as in Weissenfels. As the smaller room did not seem to influence the behaviour of the Leipzig goats, all trials were collapsed for further analysis.

Scoring and data analyses

All trials were videotaped and scored from the videotapes. We took several measurements. We scored how many food pieces the subject managed to eat and whether or not the subordinate ever received aggressive hits from a dominant during the experiment. An aggressive hit was coded if the dominant individual physically hit the subordinate individual with its horns at any body part. All aggressive encounters during experimental trials occurred exclusively in group 1 (Leipzig). At no point did aggressive encounters lead to injuries nor was there any sign of severe distress. This was confirmed by the fact that subordinate individuals would keep on moving towards the food and also eat the food in many of the trials in which they actually received aggression. If aggression occurred subordinate subjects usually received no more than one hit per trial with an overall aggressionrate of: $X \pm \mathrm{SD} = 0.322 \pm 0.263$, $N = 8$. The subordinate animals received aggression mainly (except in two cases) *after* they had eaten the first piece of food.

We also scored which food piece the subject approached; when the animal's body was clearly directed towards one piece of food, this was designated as an approach. A second coder who was unaware of the experimental condition coded 20% of the material for reliability. Interobserver reliability for approach behaviour was good: Cohen's kappa $= 0.82$, $N = 104$.

Results

First, we tested whether subjects retrieved different amounts of food in the various conditions. An ANOVA on the percent of food obtained, with condition as within-subject factor and aggression as between-subject factor, indicated that subjects got comparable amounts of food in all three conditions ($F_{2,30} = 1.86$, $p = 0.173$). This result was independent from whether subjects received aggression during the experiment ($F_{2,30} = 0.09$, $p = 0.916$). However, subjects who received aggression obtained significantly less food than those who received no aggression ($F_{1,15} = 8.15$, $p = 0.012$).

Focusing on the visible-hidden condition, we investigated whether subjects approached the hidden over the visible piece of food in a competitive situation, as well as whether aggressiveness had an influence on this behaviour (see Figure 1). A visual inspection of plots of residuals versus predicted values did not show any hints for violations of the assumptions of normatlity and homogeneity of error variances. Although subjects did not show an overall preference for the hidden piece ($F_{1,15} = 0.69$, $p = 0.42$), there was

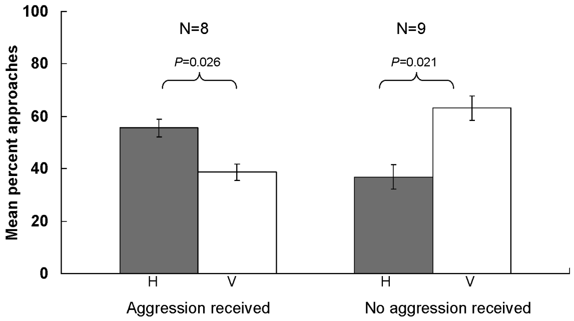

Figure 1. Mean percentage of approaches to the visible piece of food as a function of aggressive encounters received.

an interaction between preference for the hidden food and received aggression ($F_{1,15} = 14.58$, $p = 0.002$). Posthoc tests indicated that subjects who received aggression approached the Hidden piece significantly more often than the Visible piece ($t_7 = 2.81$, $p = 0.026$) whereas subjects who received no aggression during the experiment showed the opposite pattern – they approached the Visible piece significantly more often than the Hidden piece ($t_8 = 2.86$, $p = 0.021$).

If we concentrated the analysis on the mean percent of approaches in trials in which the subjects received aggression then it turns out that there is no significant difference between approaches to visible and approaches to the hidden piece of food ($t = 0.607$, df $= 7$, $p = 0.563$). This indicates that aggression is not more or less probably depending on the behavior of the subject but rather reflects the general aggression level within the group.

An ANOVA on the non-social control showed that subjects did not prefer the hidden or visible piece of food if they were in a non-social situation. This result was independent from whether they received aggression during the experiment ($F_{1,13} = 0.24$, $p = 0.631$). The same was true for the 'side'-control condition: subjects did not prefer the piece of food with the barrier over the other piece ($F_{1,7} = 0.72$, $p = 0.425$), and there was no interaction between preference and aggression ($F_{1,7} = 0.27$, $p = 0.142$). Similarly, in the 'transparent' control subjects also choose randomly between the piece of food behind the clear barrier and the other piece of food ($F_{1,7} = 0.25$, $p = 0.63$), and there was no interaction with aggression ($F_{1,7} = 0.05$, $p = 0.831$).

In a further analysis we investigated whether there were any learning effects in the visible-hidden condition, comparing each subjects' first half of trials with their second half of trials. An ANOVA with the variable 'choice' (visible vs hidden), 'half' (first half vs second half) and 'aggression received' revealed an interaction of all three factors ($F_{1,15} = 23.39$, $p < 0.0001$). We therefore conducted two additional ANOVAs. First we looked at the group of goats which received aggression, conducting the same analysis again. There was a significant effect of choice ($F_{1,6} = 6.4$, $p = 0.045$) but no interaction with 'half': the goats that received aggression during the trial significantly choose one food place over the other but do not learn to do so over time. We then examined the goats that did not received aggression. This analysis showed that these goats also significantly chose one food piece over the other (Choice: $F_{1,9} = 6.057$, $p = 0.036$) but that this behaviour changed over time ($F_{1,9} = 25.5$, $p = 0.001$). A posthoc analysis showed that the goats that did not receive aggression during the experiment significantly preferred the visible over the hidden piece in the first half of the trials ($t_9 = 3.974$, $p = 0.005$) but not in the second half of the trials ($t_9 = 0.429$, $p = 0.678$), suggesting that this preference was not learned, but in fact vanished over time.

However, an analysis of the mean amount of food eaten in the first half of trials compared to the second half of trials showed that this did not affect subjects success rate ($t_8 = 0.274$, $p = 0.791$). This suggests that, as inter-individual competition was relaxed, subjects did not have to maintain their initial strategy entirely to be successful.

Discussion

The results of this experiment indicated that in a competitive situation, subordinate goats' preferences depended on whether or not they received aggression from the dominant animal during the experiment. The subjects who received aggression preferred the hidden piece of food, whereas the goats who never received aggression significantly preferred the visible piece. By using this strategy, the latter group of goats got significantly more food than the former group. That is, these goats first acquired the visible piece of food and then the hidden piece. The other goats, in contrast, retrieved only the hidden piece, as the competitor ate the visible piece once they were released into the room. These findings have both socio-ecological and cognitive implications.

To begin with, the difference in behaviour between the goats that received aggression and those that did not is paralleled by differences in these groups' socio-ecology. Specifically, the individuals who received aggression were all from the Leipzig group, whereas the goats from the other zoos showed no aggressive behaviours in the test. As previously mentioned, goats are a species with a strong, linear dominance hierarchy (Barroso et al., 2000), and the pretest established that the groups in this study were indeed organized along these lines. Moreover, this form of dominance hierarchy suggests that the predominant type of competition for goats is within-group content (WGC) competition (van Schaik, 1989). Despite these similarities in hierarchy for subjects from the different zoos, there are obvious differences in the housing conditions of the three groups. The Leipzig group had more individuals, and each individual has about half as much overall space than individuals in the other two groups. In addition, visitors at the Leipzig zoo are not allowed to feed the animals, whereas visitors are allowed to feed the animals at the other two zoos. These differences both in feeding and overall space suggest that while food sources may be relatively clumped at the Leipzig Zoo, food is more spatially dispersed at the other two zoos. The food in the Leipzig group, therefore, is probably easier for dominant individuals to monopolize compared to the other groups. These conditions may lead to a stronger hierarchy as well as more aggression between individuals (van Schaik, 1989; Pruetz & Isbell, 2000). Indeed, primate species appear to develop a stronger linear hierarchy under clumped-food conditions compared to dispersed food conditions (Pruetz & Isbell, 2000). As such, the different behaviours of the goats may stem from the way their local feeding ecologies have altered their social relationships. This implies that a current model accounting for differences in primate socio-ecology may also be valid for some non-primate species

The current findings also have cognitive implications, specifically with respect to the behaviour of subordinate goats that received no aggression during the experiment. These goats significantly preferred the visible over the hidden piece of food, and by using this strategy they obtained significantly more food than the goats from the other group. The behaviour of these goats is therefore comparable to the behaviour of dominant chimpanzees confronted with a situation in which they have to compete with a subordinate individual and both pieces of food are now on the dominant's side ('the dominant test' Hare et al., 2000).

One hypothesis which explains these findings is that the goats are sensitive to the dominant individual's visual access—because the visible piece of food is at risk relative to the hidden piece, subordinate individuals approach that piece first. Other explanations that do not involve visual perspective-taking provide weak accounts of the goats' behaviour. For example, it is unlikely that these goats' preferences arose because they read the behaviour of their competitor. All that subordinates could see was the dominant's feet in the center of the door, which was raised 15 cm from the ground. In addition, the dominant individual was not released until the subordinate made her choice. Therefore, it is very unlikely that the subordinate's choice was based on reading the dominant's behaviour. It is also unlikely that the goats' preference arose because they sought physical protection from the dominant, as there was nothing to protect them on the side of the visible piece of food. Moreover, since these goats could expect to receive no aggression, seeking protection behind the barrier was not necessary. As such, if the goats were not sensitive to what their competitor could and could not see, they should choose randomly between the two pieces. Conversely, these results can not be explained by avoidance of the barrier in general, since goats in the non-social control condition did not prefer to take either piece of food first. Finally, the goats do not appear to have a preference for social feeding, as they attempt to retrieve both the visible piece and the piece hidden behind a barrier.

In contrast to those goats living in groups with relaxed competition, the subordinate goats from the Leipzig group with more intense competition significantly preferred the hidden piece of food. This strategy is similar to that of subordinate chimpanzees in competitive contexts (Hare et al., 2000). However, unlike chimpanzees in previous research, the goats studied here may have sought protection behind the barrier. Chimpanzees were tested with very small barriers (20 cm in height) that offered no protection and were not big enough for subjects to hide behind. The barriers used in the current study, however, were larger and did afford some protection. Therefore, we cannot rule out that the goats which received aggression probably preferred the hidden over the visible piece of food because they wanted to be protected by the barrier. The transparent barrier was introduced to rule out that goats simply sought physical protection by the barrier as in this condition the barrier would allow physical protection but not visual obstruction. The behaviour of the goats in this condition indicated that as soon as visual obstruction was not assured even though physical protection would be goats did not prefer approaching the food behind the barrier. However, observational evidence suggests that, in the transparent barrier control condition, the goats did not understand that the transparent barrier was a physical object. Rather, they appeared to try to reach the food through the barrier. Consequently, we cannot rule out that these goats probably exhibited a preference for the hidden food simply because the barrier protected them from the dominant.

The different strategies of the two groups indicates that socio-ecological factors, such as the level of inter-individual aggression, may effect the expression of certain cognitive abilities Since there is generally less competition in the groups from Hirschfeld and Weissenfels, subordinate goats from these groups could utilize a strategy in which they attempted to monopolize all the food. Taken together with the results of other studies stressing the importance of contextual factors such as space availability (Bräuer et al., in press), these findings emphasize that observable behaviour is determined through a complex interplay of contextual, social, and cognitive factors.

From an evolutionary perspective, the goats' sensitivity to others' visual perspective suggests that Level 1 visual perspective taking, that is the understanding if another individual can or cannot see an object based on whether the visual access to the object is or is not obstructed (Flavell et al., 1978) may be widespread in the animal kingdom. There is now evidence that a variety of mammalian species have an understanding of the visual perspective of others. These species include chimpanzees (Hare et al., 2000), orangutans (*Pongo pygmeus*) (Shillito et al., 2005), rhesus monkeys (*Macaca mulatta*) (Flombaum & Santos, 2005), and dogs (*Canis familiaris*) (Call et al., 2003; Bräuer et al., 2004; Kaminski et al., subm.). There is also growing evidence that multiple corvid species understand something about other's visual perception (Emery & Clayton, 2001; Bugnyar et al., 2004; Dally et al., 2004; Dally et al., 2005). Yet despite the growing evidence that some type of visual perspective taking is present across diverse taxa, chimpanzees may have more complex visual perspective skills than other species tested so far. For example, chimpanzees not only understand which piece of food another individual can see in the present, but also which piece of food another individual had seen in the recent past (Hare et al., 2001). Such an ability may require more sophisticated representational skills then those necessary to make judgements about ongoing competitive situations (such as in the current study): since subjects have to remember what other individuals have seen or have not seen, their decision must be based on memory and not on currently present stimuli. When tested with a paradigm comparable to that used with chimpanzees, dogs did not show the kind of sophisticated understanding that chimpanzees did (Kaminski et al., subm.). However, in a very different context, scrub jays (*Aphelocoma coerulescens*) appear to be sensitive to the knowledge of others over a longer temporal span. That is, they re-cache food significantly more often when another individual had witnessed the initial caching compared to when there was no observer during the caching (Emery & Clayton, 2001). These results are suggestive of chimpanzee-like visual-perspective taking; however, this specific result may be explained based purely on the presence or absence of an observer at the time of initial caching, rather than memory of others' past visual perspective. Therefore, this study is not directly comparable to those with chimpanzees (but see Dally et al., 2004). Future studies are needed to investigate whether other species also display this sophisticated level of perspective taking.

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