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Published in *Nature* **430** (August 12, 2004), pp. 778-781; doi:10.1038/nature02723
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Submitted April 7, 2004; accepted June 3, 2004.

The authors thank N. Howe and E. A. Simpson for assistance in data collection and B. Luke Stafford for help in designing Figure 1.
This research was supported by University of Nebraska Research Enhancement Funds and an NSF grant to Northern Arizona University.

Pinyon jays use transitive inference to predict social dominance

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Abstract

Living in large, stable social groups is often considered to favor the evolution of enhanced cognitive abilities, such as recognizing group members, tracking their social status and inferring relationships among them.[1–4] An individual's place in the social order can be learned through direct interactions with others, but conflicts can be time-consuming and even injurious. Because the number of possible pairwise interactions increases rapidly with group size, members of large social groups will benefit if they can make judgments about relationships on the basis of indirect evidence.[5] Transitive reasoning should therefore be particularly important for social individuals, allowing assessment of relationships from observations of interactions among others. Although a variety of studies have suggested that transitive inference may be used in social settings,[6–10] the phenomenon has not been demonstrated under controlled conditions in animals. Here we show that highly social pinyon jays (*Gymnorhinus cyanocephalus*) draw sophisticated inferences about their own dominance status relative to that of strangers that they have observed interacting with known individuals. These results directly demonstrate that animals use transitive inference in social settings and imply that such cognitive capabilities are widespread among social species.

Pinyon jays are among the most social of North American corvids. They live in large permanent flocks of up to 500 individuals, breed colonially and establish long-term multigenerational relationships with linear dominance hierarchies.[11, 12] In operant experiments using colored stimuli, pinyon jays track implicitly ordered dyadic relationships more accurately and display more robust transitive inferences than western scrub jays (*Aphelocoma californica*), a closely related, less social species.[13] This suggests that the differing demands of the social systems in the two species may have selected for differential cognitive abilities,[14] but there has been no direct evidence that pinyon jays or any other non-human species use transitive inference to make social judgments.

Sixteen adult male pinyon jays, sexed by DNA analysis, were captured in northern Arizona, housed individually and kept mildly hungry (at 90% of their free-feeding weight) by controlled daily feedings. They were divided into three groups such that, although some birds may have known each other from the wild, no birds from separate groups had been in direct contact for at least five years (see Methods). Within the three groups dominance relationships were established in a series of six 5-minute staged encounters between each of the 36 possible pairs of individuals (Figure 1a). All sessions were recorded on digital videotape and the frequencies of five behavioral events—one dominant display (stare at) and four submissive ones (look away, crouch, chin-up and beg)—were determined for each bird.[11, 12]

From each encounter session, we extracted two weighted indices for each bird (one of dominant and one of subordinate behaviors) on the basis of the event frequencies. Weights were obtained by canonical discriminant analysis on a subset of dyads in which the relationships were clear and unequivocal (see Methods). The difference between dominant and subordinate behaviors for a given individual provided a direct measure of the strength of its relative social status (see Methods). Using the average differences in relative social status between individuals in all 36 dyads over the last three encounters, we constructed inferred within-group dominance hierarchies and coded the bird designations accordingly. In all three groups the hierarchies were linear and fully transitive (group 1, A > B > C > D > E > F; group 2, 1 > 2 > 3 > 4 > 5 > 6; and group 3, P > Q > R > S). For 62% of the dyads, relative social status was consistent from the first or second encounter. In those dyads in which both birds were low-ranking, however, the process often took much longer: over 25% of the dyads showed transient status reversals as late as the fourth or fifth encounter.

Once within-group dominance relationships had been established, we conducted a limited set of cross-group dominance encounters between similarly ranked individuals to establish a basis for predicting the relationships between other, untested cross-group dyads. During the cross-group encounters we avoided using birds at the top or bottom of their group hierarchies, because the next stage of the experiment ("exhibition" encounters, below) required birds that could both win and lose encounters with members of their group. There were 32 possible cross-group dominance relationships, of which we determined eight (see Methods). The information from these cross-group pairings plus the knowledge of each within-group hierarchy made it possible to establish our experimental and control conditions in the next stage of the experiment.

We designed a set of 12 instances that tested the ability of pinyon jays to draw social inferences. In each instance, an observer bird watched a series of "exhibition" encounters between another bird (the "demonstrator") and two different opponents (Figure 1b, c). Although the observer had never previously interacted with the demonstrator, the results of the cross-group dominance tests predicted that the demonstrator should dominate the observer. On each of three consecutive days, the observer watched

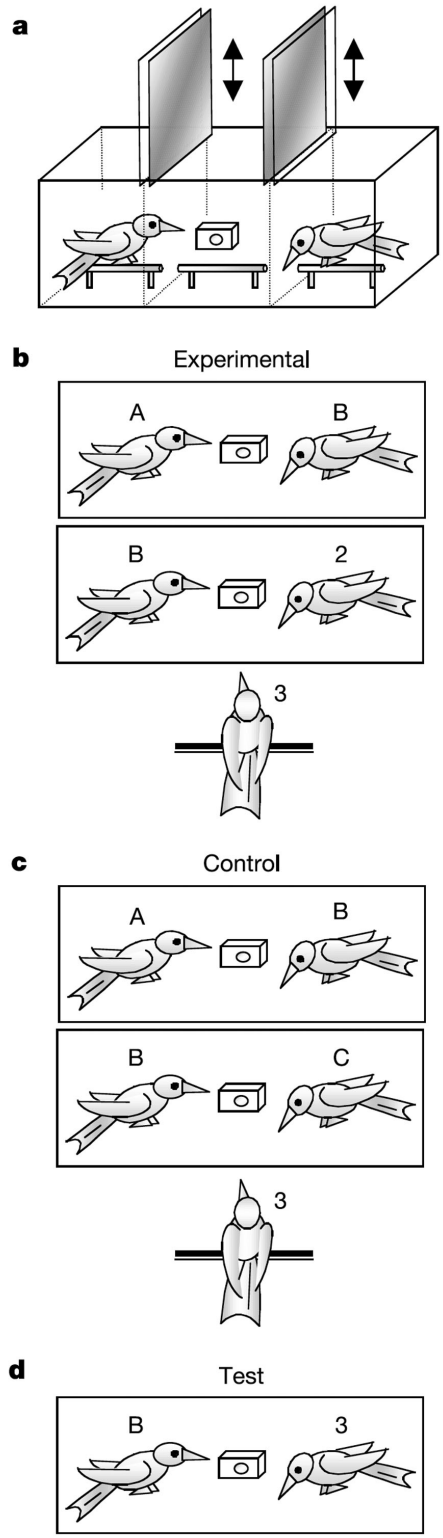

Figure 1. Dominance encounters were conducted in a transparent acrylic chamber (100 × 40 × 40 cm) separated into three compartments by sliding opaque and transparent dividers. On each trial, a feeder box in the central compartment was baited with a single unshelled peanut. **a**, To establish relative dominance, all dyads within each of the social groups were tested. Birds were placed in each of the two end chambers and were released simultaneously to compete over access to the peanut. **b**, **c**, Next, exhibition encounters were observed by a third bird whose prior knowledge of contestants was systematically controlled. If bird 3 was in the experimental condition, for example, he watched A > B, B > 2 (only 2 known to 3). If bird 3 was in the control condition, he watched A > B, B > C (all strangers to 3). **d**, In either case, following these exhibition encounters 3 was tested with B.

his demonstrator lose encounters with one opponent and win encounters with another, giving a total of six exhibition encounters per observer/demonstrator dyad. In all cases, the outcomes of the exhibition encounters coincided with our predictions. This sequentially balanced design was employed to ensure the use of transitive inference on the basis of observations of encounters between specific individuals, rather than simply the general effects of having seen another animal win or lose.[15, 16, 17]

In the exhibition encounters, the observer's prior knowledge about one of the demonstrator's opponents was varied systematically. In experimental instances the demonstrator and one opponent were strangers, but the opponent that repeatedly lost to the demonstrator was familiar to the observer, because that opponent had dominated the observer in earlier staged encounters. For example, suppose that cross-group testing had established that B was dominant to 2. We could then use 3 in an experimental treatment by allowing him to observe that A > B and B > 2 (Figure 1b). In this case, A and B would be strangers to 3, but the relationship 2 > 3 would have been established in earlier within-group interactions. Using transitive reasoning, 3 should expect to be subordinate to B. In contrast, in control instances the demonstrator and both of his opponents were all strangers to the observer. If 3 were assigned to the control condition, he would watch A > B and B > C, all unknown to 3 (Figure 1c). Therefore, 3 could not subsequently use transitive reasoning to predict his status relative to B.

Following the exhibition encounters, each observer was given six 5-minute staged encounters with his demonstrator (testing, in our example, B versus 3; Figure 1d), and the behavior of both participants in these test trials was evaluated for evidence of transitive social inference. We conducted six sets of experimental and six sets of control exhibition and test encounters, each using different observer/demonstrator dyads (see Methods). Because the data violated assumptions of parametric analysis, differences between groups were analyzed using Wilcoxon two-sample exact probability tests.[18] Dyads were assigned to treatments in a balanced fashion, such that experimental and control dyads had statistically indistinguishable differences in relative social status scores ($W^+ = 44$, $P = 0.48$).

If experimental observers use transitive social inference to predict their relationship to the demonstrator, they should exhibit higher initial levels of submissive behavior than control observers. This proved to be the case. During the first minute of the first encounter experimental observers displayed subordinance levels that were nearly four times as high as those of controls (Figure 2a). The effect faded rapidly, however, and there were no significant treatment differences in subordinance between observers in subsequent intervals or in later encounters. Experimental observers also displayed lower initial levels of dominant behaviors than controls, though the effect was only statistically significant in the second minute of the first encounter (Figure 2c). There were no significant differences in subordinance between demonstrators paired with experimental or control observers (Figure 2b), but experimental demonstrators showed higher levels of dominance than controls (Figure 2d) during the second and third minutes of the first encounter, apparently in response to the initially higher level of subordinance displayed by experimental observers. As with the observer's behavior, the effect on the demonstrator's dominance was transient and no significant differences were apparent in later encounters.

In addition to win or lose information, exhibition encounters also provided information about the relative disparity between a demonstrator and his opponents. Observers could, therefore, have made more subtle, graded assessments of their relative status, inferring the probable degree of difference in dominance between themselves and the demonstrator. To determine whether observers made use of this information, we calculated the difference in relative dominance for each demonstrator between the exhibition encounters he won and those he lost. We tested this measure as a predictor of observer subordinance during the first test encounter. Whereas there was a strong positive relationship for experimental observers, there was no such relationship for control birds (Figure 3). These findings suggest that observers estimated the actual disparity in their dominance status relative to the demonstrator, but only when they knew the losing opponent.

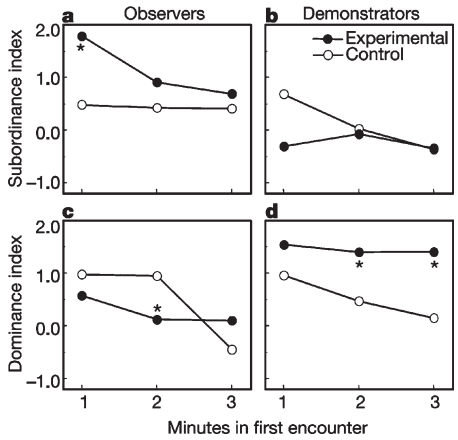

Figure 2: Mean dominance and subordinance indices for each of the first 3 min of the first test session. **a**–**d**, Behavior of the observers (**a**, **c**) and the corresponding demonstrators (**b**, **d**); filled circles correspond to experimental birds, open circles to control birds. **a**, Experimental observers were significantly more subordinate during the first minute than control observers ($W^+ = 53$, $P = 0.026$), but this effect disappeared after the first minute ($W^+ = 41$, $P = 0.41$). **b**, There were no significant differences in subordinate behavior between demonstrators paired with experimental or control observers ($W^+ \leq 47$, $P \geq 0.12$). **c**, Experimental observers displayed lower levels of dominant behaviors than controls, though the difference was only significant during the second minute of the first encounter (second: $W^+ = 53$, $P = 0.022$; first and third: $W^+ \leq 47$, $P \geq 0.12$). Because of their higher level of subordinate behavior in the first minute (**a**), relative social status (= dominance – subordinance) was markedly lower for experimental observers during the first minute of the first encounter ($W^+ = 54$, $P = 0.015$). **d**, Demonstrators showed higher levels of dominance than controls, but the effect was significant only in the second and third minutes of the first encounter (first: $W^+ = 42$, $P = 0.34$; second and third: $W^+ \geq 52$, $P \leq 0.039$).

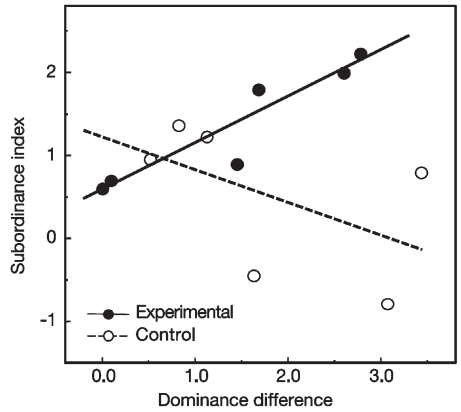

Figure 3: Subordinance index for observers during the first 5-min test encounter with the demonstrator. The subordinance index is a function of the mean difference in dominance between demonstrators and opponents during the exhibition encounters. Experimental dyads are shown as filled circles with a continuous regression line; control dyads as open circles with a dashed regression line. There was a strong positive relationship ($F_{1,5} = 26.64$, $P = 0.007$, $r^2 = 0.87$) for experimental birds, but none for control birds ($F_{1,5} = 1.55$, $P > 0.25$, $r^2 = 0.28$), and analysis of covariance (ANCOVA) indicated that the regression slopes for the two treatments were significantly different ($F_{1,2} = 8.01$, $P = 0.022$).

The results are fully in accord with the hypothesis that pinyon jays use transitive reasoning to make inferences of relative dominance. Jays that had previously interacted with one of the birds they observed drew inferences about their rank relative to the demonstrator, and showed a graded, quantitative response based on their observations. Jays that observed very similar interactions, but had never interacted directly with any of the birds they observed, failed to show either effect. This pattern rules out alternative general explanations, such as badges of status [19] or dispositional responses to seeing another bird win or lose.[15, 16, 17] This work constitutes a direct demonstration of transitive inference in social settings, and supports the hypothesis that social complexity provided a crucial context for the evolution of cognitive abilities.

Methods

Test procedures

To familiarize the birds with the apparatus, each jay was placed alone in one of the end compartments of the encounter chamber. After 30 seconds the dividers were raised and the bird was allowed to explore the apparatus until it discovered and consumed a peanut. Each bird received six such familiarization trials before beginning staged encounters. During staged encounters (Figure 1a), each member of a dyad was initially placed in one of the end chambers (randomly selected). After 10 seconds the opaque divider was lifted, providing visual contact between dyad members through the second, transparent divider. After an additional 10 seconds the transparent divider was lifted, giving the birds simultaneous access to the central contest area. To facilitate recognition of individuals for video scoring, one of the dyad members in each encounter was marked on the wing primaries with water-soluble white paint. After the encounter the paint was removed.

Group formation and selection of pairs for testing

Our experimental design required sets of birds of relatively similar rank who were unknown to each other, but whose relative dominance could be predicted accurately. We first divided the birds into three groups; two groups of six birds and one group of four. The small size of the groups minimized the possibility of nonlinear relationships. Once the within-group hierarchies were established, we then determined eight of the 32 possible cross-group dominance relationships by pairing the second-, third- and fourth-ranked birds in group 1 with those of the same rank in group 2, and the second- and third-ranked birds in group 3 with the second- and third-ranked birds in both groups 1 and 2. The outcomes of these within- and cross-groups dominance encounters were subsequently used to select sets of observers and demonstrators.

During exhibition sessions the demonstrator was paired with two other birds, one dominant and one subordinate to the demonstrator. In experimental conditions one of these other birds had to be a stranger to the observer and the other a known dominant. In control conditions both birds had to be strangers to the observer. In addition, because the experimental design required birds that could both win and lose encounters with members of their group, birds at the top or bottom of their group hierarchies were not used as observers. These constraints limited the number of possible pairings that could be generated, with the result that some individuals were used in more than one trial. Nine observers and six demonstrators participated in the six experimental and six control pairings.

To control for prior experience in winning and losing, we arranged daily maintenance encounters between each of the demonstrators and observers and members of their own groups. During the three weeks before testing, each observer had an average of 15 encounters with five other birds, of which he won 47%; for the four observers that were tested more than once, at least two months passed between successive trials. In the same time period, each demonstrator had an average of 16 prior encounters with four other birds, of which he won 56%; for the three demonstrators tested more than once, at least 10 days passed between successive trials.

Behavioral indices

Because display behavior is often a more reliable indicator of dominance than gaining access to food,[20] we used relative frequencies of behavioral acts to assess dominance. To obtain an empirically valid index of relative dominance in which the contributions of the different behavioral events were appropriately weighted, we first calculated (for each individual in each encounter) the difference between the raw counts of dominant and subordinate actions divided by their sum. Differences between dyad members in the value of this ratio, which weighted all action patterns equally, provided an initial approximate measure of relative dominance. From the 36 within-group dyads in the study, we extracted a set of 15 exemplars, dyads in which the mean of this ratio (averaged over all six encounters) was larger than 0.5 and in which one of the dyad members consistently dominated in all six encounters. Because some behaviors are better indicators of social status than others, however, a simple sum of event frequencies is often misleading as an indicator of relative dominance. To obtain a more sensitive measure, we subjected the raw counts from the last three encounters from each exemplar to canonical discriminant analysis,[18] which produces the weighted linear combination of standardized variables that best distinguishes between data classes. In the final configuration, three variables—the frequencies of stare at and look away, and the sum of the frequencies of the three other submissive displays—were log-transformed, standardized and combined into two weighted discriminant functions that constituted dominance and subordinance indices. The difference between dominance and subordinance provided a direct measure of each individual's relative social status (relative social status = dominance - subordinance), and in this combination the discriminant functions correctly categorized 93% of the encounters in the exemplar data set.

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