## Research Article #3—Transitive Learning Research Requirement Psychology 350

This is one of the articles you may read and report about for your research component. Critiquing this article is **worth 3 research credits**. Each report will be graded on a pass/fail basis. To get a passing grade, it must be clear that you read the article and have a basic understanding of it. Only passing grades count towards the research component. **Remember you must pass the research requirement to receive a grade for this class.** 

## Instructions

- 1. Read the vocabulary words and background information.
- 2. Read the questions you will be asked to answer about the article.
- 3. Read the article, making notes on the answers to the questions as you find them.
- 4. Type up your responses to the questions on separate paper.
- 5. Keep a copy of your paper (if I can't find it, you have to produce a copy for me or lose the points)
- 6. Put the complete answers in my mailbox in room 237 Burnett Hall or email it to cgarbin@unl.edu

On the top of the page put **your name, section number, and student ID number**. Please number each question, type out the complete question and then type your answer. Single or double spacing is fine. Make sure your responses use complete sentences.

## Vocabulary

These are the key scientific terms that you may not know. There may be other vocabulary with which you are not familiar. Check a dictionary.

*Transitive inference/Transitive reasoning*-Logical reasoning that takes the form if A>B and B>C, therefore A>C.

*Linear dominance hierarchy*-Dominance within the flock follows the pattern of transitive reasoning (if Bird A dominates Bird B and Bird B dominates Bird C, Bird A will also dominate Bird C).

Staged encounter-The bird was placed inside the cage with another bird and was able to interact.

Exhibition encounter-The bird was able to watch two other birds interact from a separate cage.

## Background Information

The third author on this article is Prof. Al Kamil, a faculty member at UNL with a joint appointment in both the Psychology and Biology departments. His current research is focusing on social cognition, transitive inference, and episodic memory in birds. If you find this article interesting and would like to continue learning more, you could take a class from Prof. Kamil or speak with him about helping with his research for course credit. His office is in Manter Hall.

### Questions for the Report

- 1. What is the title of this article?
- 2. What is this article about, and why does it say it is important for psychologists to study this topic? Use your own words.
- 3. The independent variable is what the researcher manipulates. How many independent variables and what were they?
- 4. The dependant variable(s) is what the researcher measures to see what happens with the independent variable. How many dependent variables were there and what were they?
- 5. Who were the participants in this experiment?
- 6. If you had been in this experiment, what would you have seen/heard/done? In other words, generally describe what the researcher asked the participants to do. Not all participants did exactly the same thing so be sure to indicate those differences. Use your own words.
- 7. What was done to control confounds in this study? What confounds were controlled and what do you think were uncontrolled be explicit!
- 8. In your own words, describe the primary conclusions from this research.
- 9. How might the findings in this study be applied (say something that the author(s) didn't!!).

# letters to nature

intermediates. The organ of balance attained its modern proportions quickly and seemingly without transitional forms<sup>27</sup>, and the locomotor system underwent a protracted and complex sequence of changes, representing a variety of functional patterns<sup>3,28</sup>. The changes of the ear were complex because the physical properties of sound in air are very different from those in water. As a result, cetaceans totally reorganized sound transmission through the outer and middle ear (Fig. 4), while keeping the cochlea in the inner ear relatively unchanged.

This macroevolutionary change in the ear of cetaceans was nearly completed in four to seven million years. The functional end members of this evolutionary sequence-generalized mammalian hearing and modern whale hearing<sup>12</sup>-are widely distributed in modern forms; they can be seen as evolutionarily stable configurations<sup>29</sup>. We propose that in these evolutionary end members all parts of the ear are optimized for collaboration with each other and are kept stable by internal selection<sup>29</sup>. As the ancestors of cetaceans took to the water, the environmental tolerances of this system were exceeded and natural selection for the transmission of waterborne sound played its part. In pakicetids this resulted in a functional trade-off for the existing transmission mechanism, in which anatomical elements used for generalized sound transmission are now also important in bone-conducted hearing. The result is a sound transmission mechanism that works in air and in water, but performs poorly in both when compared with either land mammals or modern whales. A new evolutionarily stable configuration was not reached until new anatomical elements assumed a function in hearing in remingtonocetids and protocetids, and some old elements were eliminated as sound transmitters. The mandible is one of the most important elements added to the cetacean hearing mechanism and could be considered a keystone character<sup>29</sup> that catalysed the major transformation of the cetacean ear. 

### Methods

In Fig. 3, sound input areas are those parts of the middle ear that are the sound receiver. For modern land mammals and phocid seals the sound input area is the tympanic membrane area, whereas for modern cetaceans it is the tympanic plate area. The tympanic membrane and tympanic plate are functionally analogous, but they are not evolutionarily homologous. For *Pakicetus* (H-GSP 91035), the tympanic membrane is the sound receiver; its area was plotted on the *x* axis. *Remingtoncetus* (RUSB 2914) used the tympanic membrane for receiving airborne sound, but the tympanic plate for receiving waterborne sound; hence, it was plotted twice in this figure. *Indocetus* is not shown because no incus is known for this taxon. The point for *Zygorhiza* was made on the basis of LSUMG V160A. The areas of the tympanic membrane and tympanic plate were determined using a method described elsewhere<sup>16,30</sup>. Fossil taxa are plotted as ranges on the *y* axis because their density can only be estimated. The lower and upper range for the ossicular mass presented were calculated by multiplying the measured volumes by the minimum and maximum ossicular densities; that is, those for land mammals (2.0 g cm<sup>-3</sup>) and modern cetaceans (2.7 g cm<sup>-3</sup>), respectively<sup>30</sup>. For data sources see Supplementary Information.

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# Pinyon jays use transitive inference to predict social dominance

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Living in large, stable social groups is often considered to favour the evolution of enhanced cognitive abilities, such as recognizing group members, tracking their social status and inferring relationships among them<sup>1-4</sup>. 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<sup>5</sup>. 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<sup>6–10</sup>, 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<sup>11,12</sup>. In operant experiments using coloured 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<sup>13</sup>. This suggests that the differing demands of the social systems in the two species may have selected for differential cognitive abilities<sup>14</sup>, 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-min staged encounters between each of the 36 possible pairs of individuals (Fig. 1a). All sessions were recorded on digital videotape and the frequencies of five behavioural events—one dominant display (stare at) and four submissive ones (look away, crouch, chin-up and beg)<sup>11,12</sup>—were determined for each bird.

From each encounter session, we extracted two weighted indices for each bird (one of dominant and one of subordinate behaviours) 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 behaviours 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 crossgroup 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 (Fig. 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 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





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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<sup>15–17</sup>.

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(Fig. 1b). In this case, A and B would be strangers to 3, but the relationship 2 > 3 would have been established in earlier withingroup 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 (Fig. 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-min staged encounters with his demonstrator (testing, in our example, B versus 3; Fig. 1d), and the behaviour 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 analysed using Wilcoxon two-sample exact probability tests<sup>18</sup>. Dyads were assigned to treatments in a balanced fashion,



Figure 2 Mean dominance and subordinance indices for each of the first 3 min of the first test session. **a-d**, Behaviour 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 behaviour between demonstrators paired with experimental or control observers  $(W^+ \le 47, P \ge 0.12)$ . **c**, Experimental observers displayed lower levels of dominant behaviours 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:  $W^+ \le 47$ ,  $P \ge 0.12$ ). Because of their higher level of subordinate behaviour 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:  $W^+ \ge 52, P \le 0.039$ ).

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 behaviour 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 (Fig. 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 behaviours than controls, though the effect was only statistically significant in the second minute of the first encounter (Fig. 2c). There were no significant differences in subordinance between demonstrators paired with experimental or control observers (Fig. 2b), but experimental demonstrators showed higher levels of dominance than controls (Fig. 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 behaviour, 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 (Fig. 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.

The results are fully in accord with the hypothesis that pinyon jays use transitive reasoning to make inferences of relative dominance.



**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 ( $F_{1,2} = 8.01, P = 0.022$ ).

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<sup>19</sup> or dispositional responses to seeing another bird win or lose<sup>15–17</sup>. 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.  $\Box$ 

### 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 s the dividers were raised and the bird was allowed to explore the apparatus until it discovered and consumed a peanut. Each bird encounters (Fig. 1a), each member of a dyad was initially placed in one of the end chambers (randomly selected). After 10 s the opaque divider was lifted, providing visual contact between dyad members through the second, transparent divider. After an additional 10 s 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 watersoluble 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.

### **Behavioural indices**

Because display behaviour is often a more reliable indicator of dominance than gaining access to food<sup>20</sup>, we used relative frequencies of behavioural acts to assess dominance. To obtain an empirically valid index of relative dominance in which the contributions of the different behavioural 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 behaviours 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<sup>18</sup>, 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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# **Complex auditory behaviour emerges from simple reactive steering**

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The recognition and localization of sound signals is fundamental to acoustic communication<sup>1,2</sup>. Complex neural mechanisms are thought to underlie the processing of species-specific sound patterns even in animals with simple auditory pathways<sup>3,4</sup>. In female crickets, which orient towards the male's calling song, current models propose pattern recognition mechanisms based on the temporal structure of the song<sup>5–7</sup>. Furthermore, it is thought that localization is achieved by comparing the output of the left and right recognition networks, which then directs the female to the pattern that most closely resembles the speciesspecific song<sup>8–10</sup>. Here we show, using a highly sensitive method for measuring the movements of female crickets, that when walking and flying each sound pulse of the communication signal releases a rapid steering response. Thus auditory orientation emerges from reactive motor responses to individual sound Copyright of Nature is the property of Nature Publishing Group and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.