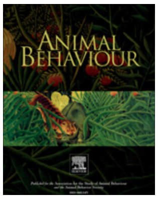
Animal Behaviour 79 (2010) 1277–1283

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Transitive inference in free-living greylag geese, *Anser anser*

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ARTICLE INFO

Article history:
Received 25 October 2009
Initial acceptance 14 December 2009
Final acceptance 24 February 2010
Available online 8 April 2010
MS. number: 09-00702

Keywords:
Anser anser
cognition
greylag goose
social complexity
transitive inference

Living in large, stable groups is often considered to favour the evolution of cognitive abilities related to social living, such as the ability to track relationships among group members and to make transitive inferences about relationships based on indirect evidence. Greylag geese are relatively small brained, but live in complex societies with social support and clan structures. They form dominance hierarchies in which families dominate pairs and unpaired individuals. However, competition is costly and the ability to transitively infer relationships among flock members may be highly advantageous. We tested five free-living, juvenile greylag geese embedded in a flock of 150 birds for their ability to track multiple dyadic relationships and their transitive inference competence. Individuals were trained on discriminations between successive pairs of five implicitly ordered colours (A–E). All individuals learned to track four dyadic relationships simultaneously and showed transitive inference when presented with nonadjacent colours. Remarkably, the amount of training required was related to the individual's early social environment. Our study is one of the first to show transitive inference in a precocial bird and suggests an influence of early social experience on sociocognitive abilities. Furthermore, it improves our understanding of social complexity as an important selection pressure for the evolution of cognition.

Living in large, stable social groups is often considered to favour the evolution of cognitive abilities related to social living (e.g. Jolly 1966; Byrne & Whiten 1988; Balda et al. 1996). For instance, knowledge about relationships among group members may substantially reduce the number of unprofitable encounters, which can be time consuming, energetically demanding or even injurious. However, the number of possible pairwise interactions increases rapidly with group size, and it is unlikely that an individual in a large social group can observe all possible pairs of group members together. Members of such groups may thus benefit if they can make judgements about relationships on the basis of indirect evidence. Basing relationship judgements on transitive inference enables individuals to conclude that if A is dominant to B and B is dominant to C, then A is probably also dominant to C, even if A and C have never been seen together.

Transitive inference has long been considered a hallmark of humans but has also been shown in several nonhuman animals (e.g. Gillan 1981; von Fersen et al. 1991; Davis 1992; Treichler & van Tilburg 1996; Lazareva et al. 2004). It is usually tested in operant two-choice tasks based on colour or symbol discrimination, and field observations indicate that primates may also use transitive information when they enter a new society (Altmann 1962; Kummer 1982). Paz-y-Mino et al. (2004) and Grosenick et al. (2007) demonstrated in controlled laboratory experiments that pinyon jays, *Gymnorhinus cyanocephalus*, and African cichlids, *Astatotilapia burtoni*, indeed use transitive inference to assess dominance rank based on observed social interactions. A comparative study in jays furthermore showed that the ability to track and transitively infer dyadic relationships relates to social complexity (Bond et al. 2003), suggesting that transitive inference may indeed be an adaptation to living in complex social environments and as such may be widespread among social vertebrates. As sociality is common in vertebrates, we also might expect transitive inference to be widespread, yet the taxonomic survey of such cognitive skills is currently limited. We sought to fill this gap by extending studies of transitive inference to a precocial avian species tested under seminatural conditions.

Greylag geese are precocial birds and as such relatively small brained (Iwaniuk & Nelson 2003), but they live in complex societies that are in many aspects comparable to those of primates or corvids (Scheiber et al. 2008). They are long-term monogamous, biparental

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doi:10.1016/j.anbehav.2010.02.029

birds which form large flocks for most of the year. Parents and offspring maintain extended associations well beyond fledging that typically last for a year or longer (Weiß et al. 2008; Scheiber et al. 2009a) and females form loose clans with other female relatives as adults (Frigerio et al. 2001; Weiß et al. 2008). Social allies provide active and passive social support (Frigerio et al. 2003; Weiß & Kotrschal 2004; Scheiber et al. 2005, 2009a, b), and increased aggression against individuals that were recently involved in conflicts with the aggressor's social allies suggests that greylag geese may even understand third-party relationships (Weiß et al. 2008). Furthermore, greylag geese develop dominance hierarchies in which families typically dominate pairs and pairs tend to win against singletons. Hence, individual geese may benefit if they can track and transitively infer relationships among flock members and thus avoid costly interactions.

For these reasons, we tested transitive inference in greylag geese by using well-established procedures in which the ordering of arbitrary stimuli can be inferred from a series of dyadic comparisons (e.g. Gillan 1981; von Fersen et al. 1991; Bond et al. 2003). Importantly, we did so in a field setting with individuals embedded in the social web of a free-living flock of about 150 greylag geese, whose individual life histories and social backgrounds have been monitored continuously since hatching. Only a few studies so far have tested cognitive abilites of noncaptive, experimentally naïve animals (e.g. Sovrano et al. 2002; Chiandetti & Vallortigara 2008; Rugani et al. 2009). Hauser et al. (2000) showed that untrained, semifree-ranging rhesus monkeys, *Macaca mulatta*, were able to represent numbers spontaneously. However, they failed at values greater than three, which is in striking contrast to laboratory results, where rhesus monkeys showed preferences for nine versus eight items after some training on smaller quantities (Washburn & Rumbaugh 1991). While these ambiguities may have resulted from methodological differences between the studies, it has to be considered that performance in cognitive tasks may vary between free-living and laboratory-housed animals owing to variation in ecology, social or experimental experience (see Boesch 2008 and Tomasello & Call 2008 for a recent debate on this issue). Furthermore, cognitive studies on birds have focused mainly on altricial birds and, to our knowledge, transitive inference in precocial birds has only been shown once in laboratory-reared chickens, *Gallus gallus domesticus* (Daisley et al. 2009, in press).

The aim of our approach was thus four-fold: we wanted to determine whether free-living, experimentally naive geese (1) can be tested with standard procedure operant tasks in their natural (social) environment, (2) are capable of tracking dyadic relationships in a series of five coloured stimuli and (3) show transitive inference when confronted with novel stimulus pairs; (4) we also investigated whether individual performances relate to the complexity of their early social environment (i.e. group size).

METHODS

Animals

A free-flying, nonmigratory flock of greylag geese was introduced into the valley of the river Alm, Austria, by Konrad Lorenz and coworkers in 1973 (Lorenz 1988). The flock is unrestrained but habituated to the presence of humans and is provisioned with pellets and grain twice daily. At the time of this study, the flock consisted of 150 birds individually marked with coloured leg bands, whose life histories have been monitored continuously. About 25% of the individuals were hand-raised by human foster parents. Hand-raised goslings are in contact with the flock from the time they hatch and after fledging integrate fully into the flock. They establish pair bonds and raise offspring indistinguishable from the goose-raised geese, but maintain a life-long confidence towards familiar humans.

We experimentally tested five hand-raised greylag geese. As time investment in training each individual was large (see below) our sample size was small but within the range of comparable studies. Three juvenile females and one male were 4 months old and one subadult female 1 year and 4 months old at the start of the experiments. All individuals had fledged and were well integrated into the flock but still spent ample time around familiar humans. The subadult female was loosely paired to a young male. The three juvenile females had participated in a gaze-following study in their first 6 weeks of life (S. Kehmeier, I. B. R. Scheiber, C. Schloegl & B. M. Weiß, unpublished data), but all birds were naïve to operant testing. The five subjects were unrelated and had been hand-raised in sibling groups of four to seven birds; however, at the start of the experiments only the juvenile male still had two siblings in the flock, while the other birds' siblings had all died or dispersed after fledging. Hence, life history parameters were the same in most of the birds except for a variation in early sibling group size.

Training Procedures

Experiments were conducted in a small outdoor arena (1.5 × 1.4 m) that allowed testing without interference from other geese and did not allow the other geese participating in the experiments to watch the trials. The focal geese were well familiarized with the experimenters and thus readily followed them to the arena and, when offered a piece of bread, into it. In the few instances when a goose wanted to leave the arena it was allowed to do so and the experiment was finished outside. During weather conditions with much snow or continuous temperatures well below 0 °C the geese did not venture far from the nearby river and experiments were therefore run along a calm stretch of the river bank, where no other geese were close by and could disturb the experiment. Experiments were conducted daily between August 2008 and January 2009, with typically a 1-day break per week. During the entire time, experiments were never interrupted for more than 3 consecutive days. Experiments were conducted by B.M.W. and, during training steps 5, 6 and 7 (see below) by B.M.W. and S.K.

Preliminary Training

Subjects were trained to retrieve a favoured food item, that is, a small piece of bread, from a grey cup (height 8.5 cm, diameter 7.5 cm) by pushing or pulling off a square grey lid (10 × 10 cm). After this, they were offered two cups with grey lids. They were allowed to open both, but only one cup was baited. When birds reliably opened both cups, the formal training started.

Training on Dyadic Relationships

Each bird was trained on a series of discriminations between successive pairs of a five-colour series defining an implicit hierarchy: A > B > C > D > E. Colours in the series were yellow, blue, green, red and black, chosen to be maximally discriminable to the human eye. Colours were assigned a unique ordering for each bird, ensuring that the relative discriminabilities of the stimulus pairs could not confound the main effects of stimulus order. Birds received daily sessions of 16 trials, in which the two cups were covered with differently coloured lids, representing adjacent colours in the hierarchical series. Both cups were shown to the goose for 1 s and were then placed in front of the goose about 40 cm apart. The subject was allowed to choose only one of the cups and only the higher ranking colour was rewarded. Thus, if colours B and

C were presented together, B was rewarded, while C was rewarded when presented together with D. The position (left or right) of the correct stimulus was randomized, under the restriction that the same position did not occur on more than three successive trials.

Birds were trained on the hierarchical colour series in seven steps (Fig. 1) similar to the training procedures used by Gillan (1981), Lazareva et al. (2004) and Lazareva & Wasserman (2006). We first trained birds on colour pair AB by presenting AB in all trials in a session. Thereupon, birds were trained on colour pair BC. Once birds had learned the first two colour pairs, these pairs were intermixed within sessions, that is, they were presented in equal numbers and randomized order within sessions. In the same fashion, birds continued to learn the next colour pair in the series, followed by all learned colour pairs intermixed within sessions, until in step 7 all four colour pairs were fully intermixed within sessions. Birds were advanced from one training step to the next, when they performed above chance, that is, reached a criterion of 13 or more correct responses, in each of two consecutive sessions as well as in the 16 consecutive trials of each colour pair.

Correction Training

If a bird developed a side bias, that is, chose the same position 13 or more times in a session, the following session was started with the correct stimulus presented repeatedly on the opposite side. Once the bird chose correctly three times in a row, the position of the correct stimulus was randomized again. If a bird did not reach this criterion within two sessions, it was allowed to open both cups in the next session. After this, side bias correction training continued as described above. Similarly, if a bird chose one colour pair incorrectly in 75% or more of the trials that colour pair was presented in 75% of the trials in the next session, with the other colour pair(s) equally split on the remaining 25% of trials. This colour correction training was continued until the bird chose 75% or more trials of that colour pair correctly. Sessions with either type of correction training were not considered for determining the criteria to move on to the next training step.

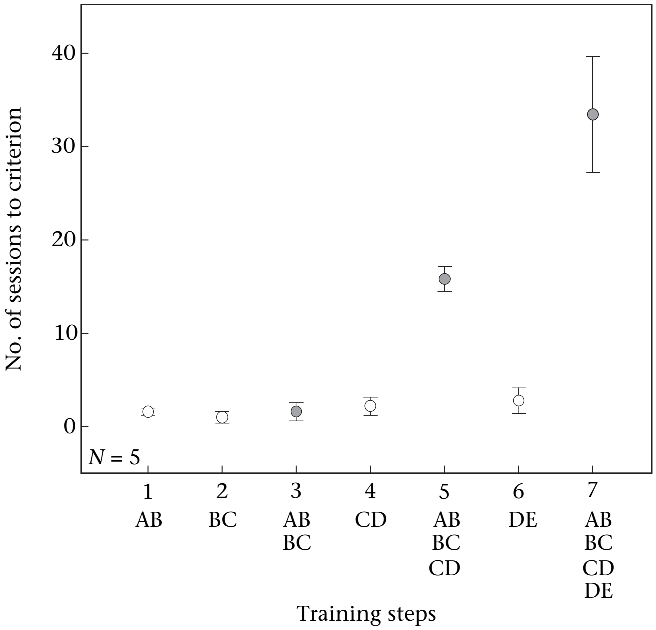

Figure 1. Number of sessions required to perform above chance level for training steps 1–7. Plots show mean ± SE. White circles indicate training steps with one colour pair presented, grey circles training steps with multiple colour pairs intermixed within sessions.

Overtraining

Once birds had reached the criterion in step 7, training was continued for an additional eight sessions. If performance remained above chance over all eight sessions as well as in each colour pair, birds were advanced to testing. If performance dropped below chance level during overtraining, the bird was returned to step 7.

Transitive Inference Tests

We presented each bird with eight daily test sessions. In each session, birds received 14 familiar adjacent colour pairs and two probe trials consisting of the novel, nonadjacent colour pair BD, whereby a consistent choice of B in this novel pairing would indicate a transitive inference from the implicit ordinal sequence. In this first test phase we did not test nonadjacent pairs including A or E, because responses to A had always been rewarded and those to E never rewarded during training (‘end-anchor effect’, Bryant & Trabasso 1971). To avoid biasing choice on subsequent presentations, choices during probe trials were not rewarded. To emphasize the otherwise unchanged reinforcement, the first and last three trials of a session as well as three trials in between the probe trials were always familiar colour pairs. If a side or colour bias emerged during testing, no correction sessions were conducted.

After the first eight test sessions were completed, each bird received another eight sessions of overtraining. This was followed by a second test series of 24 sessions, in which also nonadjacent, transitive pairs including the end-anchors A and E were presented as probe trials. To keep symbolic distance, that is, the distance between items along the implicit sequence (Moyer & Bayer 1976) the same as in BD, we paired both A and E with colour C. Tests were conducted as above, with BD, AC and CE intermixed 16 times each across the 24 sessions. Because of the long training duration for one of the birds and subsequent seasonal constraints the second test series could only be conducted with four of the five birds.

Control Sessions

After the transitive inference test series, birds received five final sessions, in which each adjacent, familiar colour pair as well as a control pair, consisting of two equally coloured grey lids, were presented 16 times each and in randomized order within sessions. The control pair thus did not provide a colour cue about the reward location. As in trials with familiar pairs one of the cups was baited in control trials to control for visual, aural or olfactory cues about the correct choice.

Statistical Analyses

We tested individual results using binomial tests. Mean performances did not deviate from a normal distribution (Shapiro–Wilk: all $P > 0.05$) and were analysed using paired t tests and repeated measures ANOVA with Holm–Sidak post hoc comparisons. Correlations of sibling group size with training duration and test performance were calculated using Pearson correlation coefficients. Data were analysed using SPSS 11.5 (SPSS Inc, Chicago, IL, U.S.A.) and Sigma Stat 3.5 (Systat Software, San Jose, CA, U.S.A.). Results of all tests are two tailed with α set to 0.05. Means are given ±SD.

RESULTS

All five birds successfully learned to track four dyadic relationships simultaneously. The number of sessions needed to complete the training phase (steps 1–7 and overtraining) ranged from 67 to

110 (83.4 ± 17.1 sessions). Throughout this time, birds developed a side bias 5.4 ± 2.8 times and a colour bias 8.2 ± 2.8 times. Birds needed an average of 1.3 ± 0.5 correction sessions to overcome a side bias and 2.1 ± 0.7 correction sessions to overcome a colour bias. Performance remained stable during overtraining in four of the birds, while individual W dropped below chance level and had to repeat step 7 and overtraining.

The number of sessions birds required to reach a significant level of performance in single colour pairs was low and did not differ between the colour pairs (repeated measures ANOVA: $F_{4,29} = 0.699$, $P = 0.57$; Fig. 1). However, performance differed significantly depending on the numbers of colour pairs intermixed within sessions (repeated measures ANOVA: $F_{4,29} = 38.857$, $P < 0.001$; Fig. 1). While the number of sessions required to track two colour pairs simultaneously did not differ from the mean number of sessions required for single colour pairs, birds needed significantly more training sessions to successfully track three or four colour pairs simultaneously than in the other conditions (Table 1).

Throughout the test phase (from the first test series to the control sessions) choice accuracy in the familiar colour pairs was well above chance (binomial tests: all $P < 0.05$), with performance in the end-anchor pairs (AB/DE) significantly better than in the middle pairs (paired t test: $t_4 = 3.999$, $P = 0.016$; Fig. 2). Only individual P showed a colour bias in two sessions of the first test series. In the first test series, birds showed a significantly higher accuracy in nonadjacent transitive inference probe trials than expected by chance (paired t test: $t_4 = 8.485$, $P = 0.001$; Fig. 2). Birds chose B over D in 87.5% of the trials; individual performance was above chance in four of the individuals and showed a trend in the fifth (Table 2). In the second test series, each of the four tested birds performed above chance in all three nonadjacent colour pairs (Table 2). Choice accuracy was particularly high in probe trials containing end-anchors (AC: 96.8%; CE: 98.4%), while it was again 87.5% in BD probe trials, but because of the lower number of individuals a statistical comparison with the first test series was not feasible.

Choice accuracy did not deviate from chance in the control trials (51.3%; paired t test: $t_4 = 0.535$, $P = 0.621$), indicating that birds could not pick the correct cup based on visual, aural or olfactory cues. Furthermore, birds performed significantly worse in the first trial of a new condition than in the last trial of the previous condition (two-way repeated measures ANOVA: $F_{1,119} = 10.602$, $P = 0.01$; Fig. 3). This difference was significantly larger towards the end of the training (two-way repeated measures ANOVA: condition*difference interaction: $F_{5,119} = 5.586$, $P < 0.001$; Fig. 3), indicating that the birds had increasing difficulties with solving the task as the number of colours and simultaneously presented pairs increased.

Finally, our focal subjects showed little or no variation in most life history aspects, but differed in one aspect of their early social environment, namely sibling group size before fledging. An analysis of individual performance in the experiments in relation to sibling group size showed that individuals raised in larger groups required significantly more sessions to complete the training phase than those raised in smaller sibling groups ($r_3 = 0.936$, $P = 0.019$; Fig. 4). Individuals raised in larger groups also tended to have more correct choices in the transitive colour pair ($r_3 = 0.832$, $P = 0.081$); however, these individuals had also received more training and owing to our small sample size it was not feasible to control for training duration statistically. It thus remains unclear whether performance in the transitive colour pair was directly influenced by sibling group size or via effects on training duration.

Table 1
Statistical results of Holm–Sidak post hoc tests comparing training steps with one, two, three or four colour pairs intermixed within sessions

No. of colour pairs	t	P	Adjusted alpha
One versus two	0.067	0.947	0.05
One versus three	3.343	0.006	0.025
One versus four	9.312	<0.001	0.01
Two versus three	3.411	0.005	0.017
Two versus four	9.38	<0.001	0.009
Three versus four	5.969	<0.001	0.013

DISCUSSION

Our results are clear-cut: greylag geese are capable of simultaneously tracking multiple dyadic relationships; and they can transitively infer relationships among novel pairs of stimuli. Furthermore, we demonstrated that operant discrimination procedures are a suitable tool for cognitive tests with free-ranging geese and that individual performance in cognitive tasks may be influenced by the social environment. Hence, this study not only provides an experimental approach for testing cognitive skills in free-living birds, but also supports recent ideas that transitive inference may be a widespread skill among social vertebrates and that social complexity provided a significant context for the evolution of cognitive abilities not just in primates, but in all highly social animals.

Our results lie well within the range of performance observed in other social animals: choice accuracies in greylag geese appeared to be similar to those of squirrel monkeys (*Saimiri* sp.: McGonigle & Chalmers 1977), pigeons, *Columba livia* (Lazareva & Wasserman 2006) and the highly social pinyon jays, and better than those of the less social scrub jays, *Aphelocoma californica* (Bond et al. 2003). In comparison to studies using similar training sequences to ours, greylag geese acquired the five-colour sequence only marginally slower than chimpanzees, *Pan troglodytes* (Gillan 1981), rhesus macaques (Treichler & van Tilburg 1996) and hooded crows, *Corvus cornix* (Lazareva et al. 2004), but they were considerably faster than pigeons (Lazareva & Wasserman 2006). Hence, accuracy and speed of performance in our free-living geese compared well to results obtained from other social animals in the laboratory. As this study was not designed to study mechanisms of transitive inference, it remains unknown whether geese use simple mechanisms such as reward ratios or cognitively more advanced mechanisms (see e.g. Lazareva & Wasserman 2006) to solve the task. However, our results provide a sound basis for future studies investigating the underlying cognitive mechanisms.

The first two colour pairs were learned at similar speed even though the second pair involved partial reversal learning, that is, the previously unrewarded stimulus was now rewarded. This may indicate that geese tend to avoid a novel stimulus and that they naturally choose a familiar stimulus over a novel one, similar to what has been described for pigeons (Clement & Zentall 2003). However, as the task became more complex, the birds needed more sessions to complete a training step, and choice accuracy dropped significantly from the last session of one condition to the first session of the next condition. While this was to be expected upon the introduction of a new colour, performance also dropped significantly when previously learned colour pairs were mixed and no new colour was introduced. Furthermore, the drop in performance became more pronounced the longer the training continued (see Fig. 3). This suggests that involuntary cues by the experimenter ('Clever Hans effect') did not play a role, although our field method was based on direct interactions with the experimenters. Had the birds learned to respond to experimenter cues, they should have shown no pronounced drop in performance, and any drop should

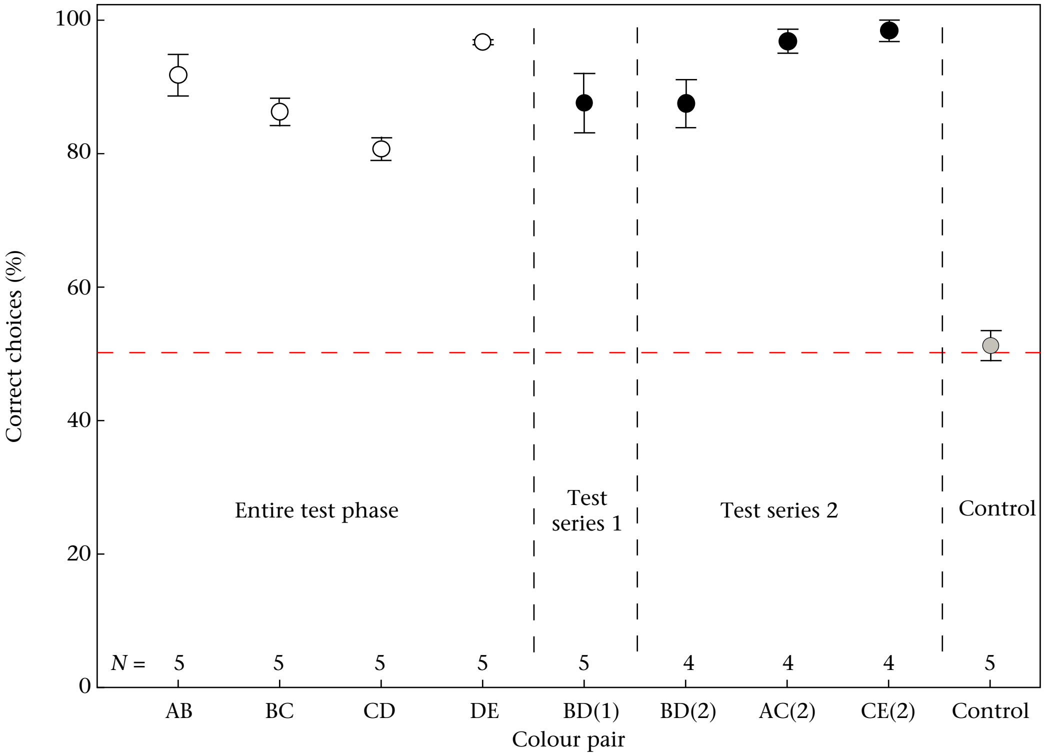

Figure 2. Choice accuracy during transitive inference testing for familiar (white circle), transitive (black circle) and control (grey circle) pairs. Accuracies are calculated for the indicated test phases, which are separated by vertical dashed lines. Numbers in parentheses indicate first or second test series; horizontal dashed line indicates chance level. Plots show mean ± SE.

have become smaller over time as birds became more familiar with the experimenter and procedure. However, as the exact opposite was the case, the ‘Clever Hans’ effect is an implausible explanation for the results of our study.

Transitive inference in nonhuman animals has mostly been studied in adults and little is known about the development of this cognitive skill in animals (Gillan 1981; Lazareva et al. 2004). In domestic chicks, the ability seems to develop before fledging (Daisley et al., in press). Also in our geese, transitive inference developed well before adulthood as even juveniles chose transitively, thus providing evidence that transitive inference may emerge early in life. The early existence of the birds’ skills corresponds with critical life stages in greylag geese. At the start of testing in autumn, tracking relationships among flock members becomes increasingly relevant when breeders and nonbreeders reaggregate after moult and young geese will be confronted with an increased level of agonistic interactions. During this time, however, juveniles still form tight family units with their parents and siblings. These tight units may allow juveniles to learn about the social relationships in the flock when mistakes are not yet very costly because family members provide active and passive social support (Weiß & Kotrschal 2004; Scheiber et al. 2005, 2009a, b). At the end of the winter, when our birds demonstrated transitive inference, family units typically break up and juveniles will increasingly have to manage their social interactions in the flock without support from their family.

In our experimental paradigm geese demonstrated the use of transitive inference in a foraging context; however, there is increasing evidence that animals indeed use transitive inference in social settings (Paz-y-Mino et al. 2004; Grosenick et al. 2007). In pinyon jays transitive inference skills were demonstrated both in an operant foraging task and in the context of social dominance (Bond et al. 2003; Paz-y-Mino et al. 2004). Furthermore, jays’ and lemurs’ performance in operant transitive inference tasks were related to the complexity of the social system (Bond et al. 2003; MacLean et al. 2008), suggesting that the concept of transitive inference may be applied flexibly across contexts. Also, domestic chickens showed observational learning of dominance relationships (Hogue et al. 1996) as well as transitive inference abilities in a food-related task (Daisley et al., in press). In geese, ample

Table 2
Individual performances and binomial test statistics for nonadjacent probe trials

Individual	First test		Second test					
	BD		BD		AC		CE	
	% Correct	*P*	% Correct	*P*	% Correct	*P*	% Correct	*P*
O	87.5	0.004	93.8	0.001	93.8	0.001	100	<0.001
P	75	0.077	93.8	0.001	100	<0.001	100	<0.001
S	81.3	0.021	81.3	0.021	93.8	0.001	100	<0.001
T	100	<0.001	81.3	0.021	100	<0.001	93.8	0.001
W	93.8	0.001						

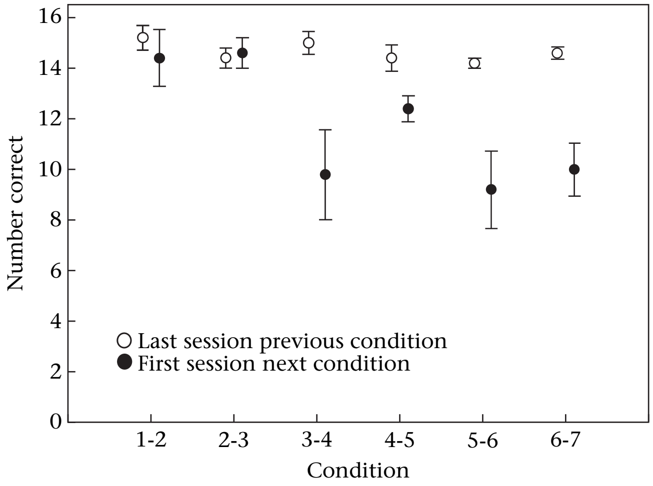

Figure 3. Choice accuracy during first (black circle) and last (white circle) sessions of a condition. Conditions 2, 4 and 6 introduced new colour pairs; conditions 3, 5 and 7 mixed previously learned colour pairs. Plots show mean ± SE.

evidence exists for learning of social information (i.e. individual recognition: Weiß & Kotrschal 2004; Black et al. 2007; I. B. R. Scheiber, A. Hohnstein & B. M. Weiß, unpublished observations). Still, it took our focal birds 2–4 months to learn about four dyadic relationships, while social dominance hierarchies require a much larger number of relationships to be learned and rapidly relearned whenever changes occur. However, unlike dominance hierarchies, the experimenter-imposed ordering on the stimuli used has neither an intrinsic biological relevance to the animals nor any connection to any naturally transitive relationship (Allen 2006). Indeed, animals tested with a dominance-related paradigm learned about dyadic relationships between conspecifics from considerably fewer and even just single observations (Hogue et al. 1996; Paz-y-Mino et al. 2004; Grosenick et al. 2007), suggesting that rapid learning of dyadic relationships may be conditional upon biologically meaningful stimuli.

The studies demonstrating a relationship between the performance in operant transitive inference tasks and the complexity of the social system (Bond et al. 2003; MacLean et al. 2008) further suggest that relatively nonsocial species may require more extensive training in such tasks than their more social relatives. Comparative data from closely related species are not yet available for greylag geese, but transitive inference performance in geese compared well to that in pinyon jays, which have similar flock sizes and stability as our flock of geese (Marzluff & Balda 1992). Furthermore, our results also indicate that individual differences in training performance may relate to the complexity of the social environment. The tested individuals grew up in sibling groups of four to seven birds, but most of these had dispersed or died by the time training started so that four of the five tested birds had no siblings left in the flock during training and testing. The amount of training required to successfully track four colour pairs simultaneously correlated significantly with the sibling group size birds were raised in and thus with their early rather than their current social environment. However, we found that birds from smaller and presumably less complex sibling groups performed better during training. This may seem intuitively surprising, but families with fewer offspring are typically involved in more agonistic interactions with other flock members than families with more offspring (Scheiber et al. 2005). Scheiber et al. (2005) attributed this to smaller families being attacked more often than large ones and other flock members avoiding interactions with large families. Hence, goslings from smaller families may have had more experience and/or opportunities to learn about dyadic relationships in the flock. Alternatively, learning to track dyadic relationships may be facilitated in smaller groups with fewer dyads. Our small sample size does not yet allow substantiated conclusions on this promising topic and more research will be needed to understand the relationships between the early social environment and cognitive abilities in later life.

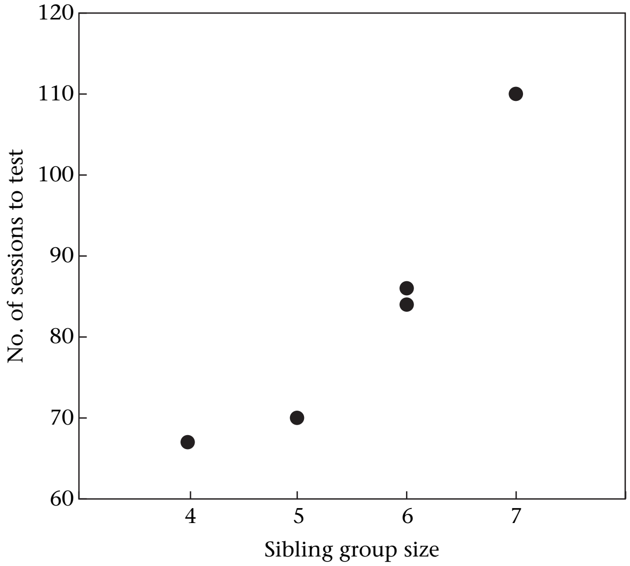

Figure 4. Relationship between sibling group size during rearing and number of sessions required to complete the training phase.

In conclusion, this study demonstrated that free-living greylag geese tracked and transitively inferred relationships similar to other highly social and cognitively advanced vertebrates. Furthermore, our results provide evidence that the complexity of the early social environment may contribute not only to species differences in cognitive skills but also to individual differences within a species, and thereby add to the understanding of cognitive processes in a comparative perspective.

Acknowledgments

We are grateful to I.B.R. Scheiber and F. Schweiger for help with data collection and T. Bugnyar, K. Kotrschal and S. Mikolasch for fruitful discussions on the topic. Funding was provided by the FWF (Projekt P20538-B17), by the 'Verein der Förderer', and the 'Herzog von Cumberland Stiftung'.

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