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Social complexity predicts transitive reasoning in prosimian primates

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Transitive inference is a form of deductive reasoning that has been suggested as one cognitive mechanism by which animals could learn the many relationships within their group's dominance hierarchy. This process thus bears relevance to the social intelligence hypothesis, which posits evolutionary links between various forms of social and nonsocial cognition. Recent evidence corroborates the link between social complexity and transitive inference and indicates that highly social animals may show superior transitive reasoning even in nonsocial contexts. We examined the relationship between social complexity and transitive inference in two species of prosimians, a group of primates that diverged from the common ancestor of monkeys, apes and humans over 50 million years ago. In experiment 1, highly social ringtailed lemurs, *Lemur catta*, outperformed the less social mongoose lemurs, *Eulemur mongoz*, in tests of transitive inference and showed more robust representations of the underlying ordinal relationships between the stimuli. In experiment 2, after training under a correction procedure that emphasized the underlying linear dimension of the series, both species showed similar transitive inference. This finding suggests that the two lemur species differ not in their fundamental ability to make transitive inferences, but rather in their predisposition to mentally organize information along a common underlying dimension. Together, these results support the hypothesis that social complexity is an important selective pressure for the evolution of cognitive abilities relevant to transitive reasoning.

Explaining the emergence of generalized forms of intelligence is among the greatest challenges in evolutionary psychology and biological anthropology. In the primate literature, considerable attention has been given to the social intelligence hypothesis, which suggests that life in complex social environments was the primary selective pressure for primate cognitive evolution (Jolly 1966b; Humphrey 1976; Byrne & Whiten 1988; Kummer et al. 1997). Although the social intelligence hypothesis was

developed specifically to explain the evolution of primate intelligence, its predictions apply across taxa. Therefore, one experimental approach for testing the social intelligence hypothesis is to examine whether species with complex social environments show unusual intelligence in nonsocial domains compared to closely related, less social species (Bond et al. 2003). If social complexity promotes selection for generalized forms of intelligence, convergent evolution predicts that species facing similar social demands should show similar cognitive adaptations (Shettleworth 1998; Hare et al. 2002; Hare et al. 2005; Byrne & Bates 2007).

One form of reasoning that has proved useful in testing this hypothesis is transitive inference (if A > B and B > C, then A > C). Although transitive inference is useful in many domains, it has been suggested that this ability may be particularly important for animals living in large

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social groups with linear dominance hierarchies (Cheney & Seyfarth 1990; Hogue et al. 1996). For example, it is unlikely that an animal living in such a group could determine the overall dominance hierarchy by observing all possible dyadic interactions among group members. Rather, animals would benefit by observing a subset of dominance interactions and inferring the remaining rank relationships through transitive inference (e.g. if A dominates B and B dominates C, then A dominates C). Indeed, recent studies have shown that several species correctly infer dominance relationships between unknown conspecifics after observing a subset of relevant dominance interactions (Paz-y-Miño et al. 2004; Grosenick et al. 2007).

Thus a critical question arises: do animals living in large hierarchical social groups show enhanced transitive reasoning in nonsocial domains? To test this hypothesis Bond et al. (2003) compared the performance of two closely related corvid species in a nonsocial transitive inference task. Consistent with the social intelligence hypothesis, highly social pinyon jays, *Gymnorhinus cyanocephalus*, performed significantly better than less social western scrub-jays, *Aphelocoma californica*, in a task that required the birds to learn multiple dyadic relationships between arbitrary visual stimuli. Furthermore, in tests of transitive inference, pinyon jays had a response profile consistent with cognitive accounts of transitive inference, which invoke complex mental representations of the underlying order, whereas scrub-jays showed hallmarks of an associative representation driven by simple conditioning processes.

While these results support the hypothesis that social complexity is an important selective pressure for the evolution of transitive reasoning, additional comparative studies with other strategically chosen species are required to rule out alternative hypotheses and corroborate the trends observed in corvids. Although pinyon jays and scrub-jays differ in their social organization, the two species also differ greatly in their feeding ecology, a behaviour with strong ties to spatial cognition (Krebs et al. 1989; Shettleworth 1990). Indeed, pinyon jays also outperform scrub-jays on open-room tests of spatial cognition (Balda & Kamil 1989; Kamil et al. 1994). If transitive inference is supported by underlying spatial representations, as several theorists contend (Davis 1992; Roberts & Phelps 1994; Terrace & Mcgonigle 1994; Lazareva et al. 2000), then the observed cognitive differences may have evolved in response to selection pressures that relate to feeding ecology rather than social organization. Secondly, prior to transitive tests, pinyon jays reached an accuracy level with the training pairs that far exceeded that of scrub-jays even after scrub-jays were given considerable remedial training. It is therefore possible that the differences observed during transitive tests also reflected differences in the two species proficiency with the training pairs.

As noted by Bond et al. (2003), additional comparative studies using similarly designed tasks with other carefully chosen species are important next steps in testing the hypothesis that social complexity selected for transitive reasoning. In the current experiments we examined the relationship between social complexity and transitive inference in two species of prosimian primates that were closely matched in their feeding ecology. Prosimian primates diverged from the common ancestor of monkeys, apes and humans approximately 63 million years ago (Yoder et al. 1996) and are thus our best living model of the ancestral primate mind. We compared the performance of highly social ringtailed lemurs, *Lemur catta*, to that of less social mongoose lemurs, *Eulemur mongoz*. Ringtailed lemurs live in larger social groups than any other lemur species (10–20 animals per group) and their groups are organized around probabilistically linear dominance hierarchies (Jolly 1966a, b; Sauther et al. 1999). In contrast, mongoose lemurs live in small family units with a typical group consisting of a mating pair and their offspring (Curtis & Zaramody 1999). Both species subsist on a highly variable diet consisting of fruits, leaves, flowers and insects (Sauther et al. 1999; Curtis 2004). Because these species have similar feeding ecology, yet differ greatly in their social organization, they can provide critical data regarding the relationship between social complexity and transitive reasoning.

GENERAL METHODS

Subjects and Housing

We tested three adult male mongoose lemurs (12–15 years old, $\overline{X} = 14$ years), and three adult male ringtailed lemurs (12–14 years old, $\overline{X} = 13$ years). Subjects were housed in indoor enclosures at the Duke University Lemur Center. Animals were singly housed with the exception of one mongoose lemur, which was pair-housed and easily separated during testing. (Housing decisions are made by the Duke Lemur Center staff and unrelated to the experiment.) Two mongoose lemurs and one ringtailed lemur had approximately 2 months prior experience in unrelated operant tasks and all other animals were experimentally naïve. All animals had unlimited access to water and received fresh fruit and Purina monkey chow daily.

Apparatus

We tested all lemurs in their home enclosures. Equipment for stimulus presentation, data acquisition and reward delivery was housed in a custom-built, stainless steel, portable testing station (86 × 43 × 35 cm) and brought into the enclosure for the duration of each session. Stimuli were displayed on a 15-inch touch-sensitive computer monitor and a custom-built REALbasic (REAL Software, Austin, TX, U.S.A.) program presented the stimuli and recorded responses. Choice stimuli were presented in two central screen locations and the left–right location of the correct stimulus was determined randomly (see Supplementary Material).

Lemurs were required to press a rectangular start-stimulus located at the bottom centre of the screen in order to initiate a trial. A clear Plexiglas panel with circular openings (diameter = 5 cm) centred on each stimulus location was mounted in front of the screen to prevent lemurs from making unnecessary contact with areas of the