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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.

Keywords: cognition; cognitive evolution; *Eulemur mongoz*; *Lemur catta*; mongoose lemur; primate; prosimian; ringtailed lemur; social intelligence; transitive inference

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 underyling 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 touchscreen that did not contain stimuli. We trained lemurs to sit on a small plastic crate in front of the cart (33 × 43 × 35 cm) to facilitate contact with the touchscreen. We rewarded correct responses with positive visual and auditory feedback and a 190 mg fruit punch-flavoured TestDiet pellet (Division of Land O'Lakes Purina Feed, LLC, Richmond, IN, U.S.A.). Incorrect responses yielded a warning tone and a black screen for 2–3 s. We terminated each session once the subject scored 30 correct responses because of dietary management issues.

Design and Procedure

We used seven black and white pictures throughout the experiment and used three arbitrary orderings of these pictures to control for salience of individual photos. One mongoose and one ringtailed lemur was assigned to each of the three orders. We trained the lemurs with an incremental procedure across three distinct phases but the basic trial structure remained the same throughout the experiment. Two images from the ordinal sequence were simultaneously presented in a side-by-side configuration on each trial. We rewarded subjects for pressing the higher-ranking stimulus (Fig. 1).

EXPERIMENT 1

Methods

Training

In the initial phase of training, each session consisted of a single pair of adjacently ranked stimuli. Lemurs were required to press the higher ranked of these two stimuli for reward. Lemurs were advanced to the next stimulus pairing in the ordinal sequence after performing at or above 80% correct for two consecutive days on a given pair. For instance, criterial performance choosing stimulus A in the AB pairing was followed by training requiring a response to stimulus B in the BC pairing. Lemurs began this phase of training with the AB pairing and progressed through to the final FG pair. In the second phase of training, two adjacent stimulus pairs were presented in each session (e.g. AB, BC). The order of pair presentations within each session was random with the restriction that each pair was presented three times per six trials. Again, we rewarded lemurs for choosing the higher-ranked stimulus in each paired presentation. Lemurs were advanced to the next grouping of adjacent pairs in the ordinal sequence after completing at least 80% of trials correctly on two consecutive days with the current pairs. For example, criterial performance choosing stimulus A in the AB pairing and stimulus B in the BC pairing was followed by training with the BC and CD pairs. We concluded the second phase of training once a lemur met criterion on the EF and FG pairings.

In the final phase of training, lemurs were required to order all six adjacent pairs of stimuli in every session. The six pairs were presented in random order with the restriction that each pair was shown once every six trials and all pairs were shown with equal frequency in each session. Again, lemurs were rewarded for selecting the higher ranked of the two stimuli presented on each trial. As in previous training phases, we terminated sessions after 30 correct responses with the exception that sessions continued until all six pairs occurred with equal frequency. Lemurs received 65 sessions of six pair training before advancing to transitive test sessions.

Testing

Test sessions consisted of 30 trials of familiar adjacent pairs (five trials per pair) and six probe trials of novel nonadjacent stimulus pairs (one trial per pair). Every test session began with at least six familiar trials. A probe trial was presented once per five trials for the remaining trials in each session. In addition, at least two familiar trials occurred between probe trials. Probe pairs were presented

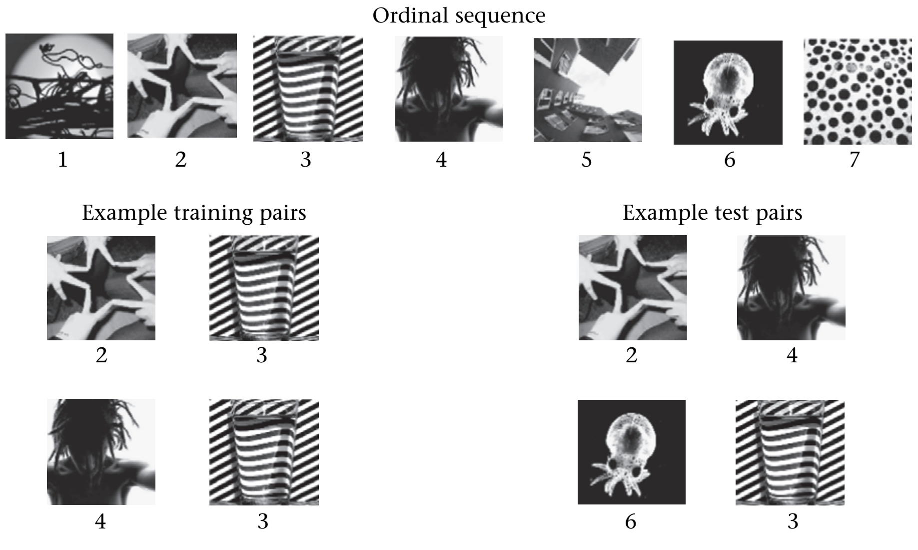

Figure 1. Stimuli and example training and test pairs. In training, subjects were rewarded to for selecting the higher-ranked image in a pair. All test trials were reinforced regardless of the subject's choice.

in a random order with the restriction that all pairs were presented once per session. All possible probe pairs were tested (combinations with at least one intervening stimulus) with the exception of pairs involving the highest- or lowest-ranked stimuli (A and G), which resulted in six different probe pairs (BD, BE, BF, CE, CF, DF). We reinforced all trials with probe pairs regardless of the animal's choice; however, we differentially reinforced responses to adjacent pairs as in training. We conducted 10 test sessions.

Results

Training

Both species learned to discriminate pairs of adjacently ranked stimuli during the initial phase of training (Fig. 2a). We conducted a multiple regression with predictors of species, pair and individual on the number of trials to criterion for each adjacent pair to assess learning rates across successive discriminations. Because the AB pair did not require the partial reversal inherent to subsequent adjacent pair discriminations, this pair was excluded from the analysis. On average, both species required fewer trials for each successive discrimination (linear regression: $t_{26} = -2.67$, $P < 0.05$) and no differences were detected between species (linear regression: $t_{26} = 1.95$, $P = 0.06$; partial eta$^2 = 0.39$, power $= 0.15$). A similar pattern was observed for the second phase of training for which two pairs were presented in each session (Fig. 2b). A multiple regression with the predictors of species, individual and pair combination yielded no effect of species (linear regression: $t_{26} = 0.49$, $P = 0.63$, partial eta$^2 = 0.09$, power $= 0.08$) but again showed an effect of pair combination (linear regression: $t_{26} = -3.957$, $P < 0.05$), reflecting faster learning with each successive discrimination.

In the final phase of training, when all six pairs occurred in random order, both species performed at a high level of accuracy even during the first session, as revealed by a one-sample *t* test comparing accuracy to that expected by chance (one-sample *t* test: $t_5 = 4.30$, $P < 0.05$). Both species maintained this level of performance but showed no further learning across the final 65 training sessions (linear regression: ringtailed: $t_{63} = 0.47$, $P = 0.64$; mongoose: $t_{63} = 0.1$, $P = 0.92$).

Testing

Both species showed evidence of transitive inference. However, there were important differences between the two species. Accuracy on adjacent pair combinations during test sessions was similar for the two species (Fig. 3). A repeated measures two-way ANOVA with the factors of species (ringtailed, mongoose) and pair (AB, BC, CD, DE, EF, FG) on accuracy for familiar adjacent pairs revealed a main effect of pair (ANOVA: $F_{5,10} = 11.80$, $P < 0.05$) but no effect of species (ANOVA: $F_{1,2} = 0.04$, $P = 0.86$, partial eta$^2 = 0.02$, power $= 0.05$) and no interaction between pair and species (ANOVA: $F_{5,10} = 0.25$, $P = 0.93$, partial eta$^2 = 0.11$, power $= 0.09$).

In contrast, ringtailed lemurs had markedly better performance than mongoose lemurs on the nonadjacent pairs that required transitive inference (Fig. 4). A repeated measures two-way ANOVA with the factors of species (ringtailed, mongoose) and pair (AB, BC, CD, DE, EF, FG) on accuracy for nonadjacent probe pairs revealed a main effect of species (ANOVA: $F_{1,2} = 23.76$, $P = 0.04$) but no effect of pair (ANOVA: $F_{5,10} = 0.73$, $P = 0.62$) and no interaction between pair and species (ANOVA: $F_{5,10} = 2.65$, $P = 0.09$). Ringtailed lemurs responded above chance to five of the six adjacent pairs, whereas mongoose lemurs responded above chance to only three of the adjacent pairs (binomial tests: $P < 0.05$). In addition to overall differences in transitive performance, ringtailed and mongoose lemurs showed striking differences in accuracy as a function of the symbolic difference separating stimuli in a test pair (Fig. 5). Specifically, ringtailed lemurs showed greater accuracy as the number of intervening elements increased (linear regression: $t_2 = 7.10$, $P < 0.05$), whereas mongoose lemurs showed no difference in accuracy as a function of symbolic distance (linear regression: $t_2 = -1.52$, $P = 0.27$, partial eta$^2 = 0.54$, power $= 0.12$).

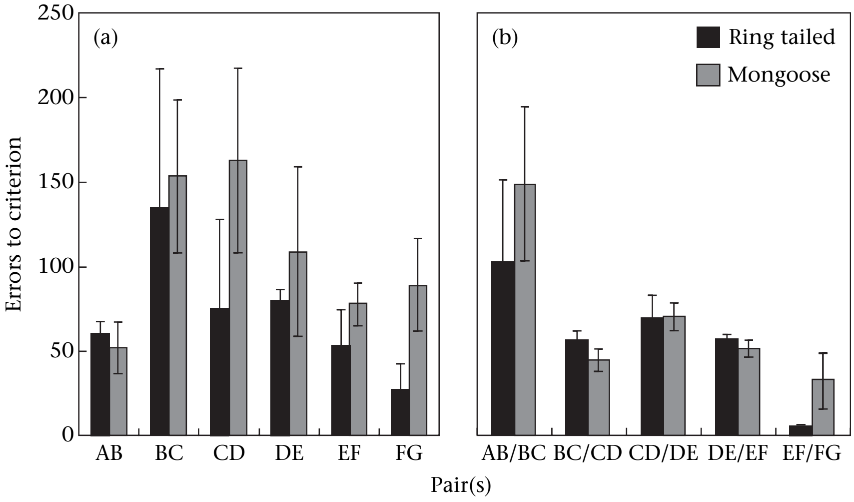

Figure 2. Mean ± SE number of errors before meeting the accuracy criterion in training sessions with (a) one or (b) two adjacent pairs.

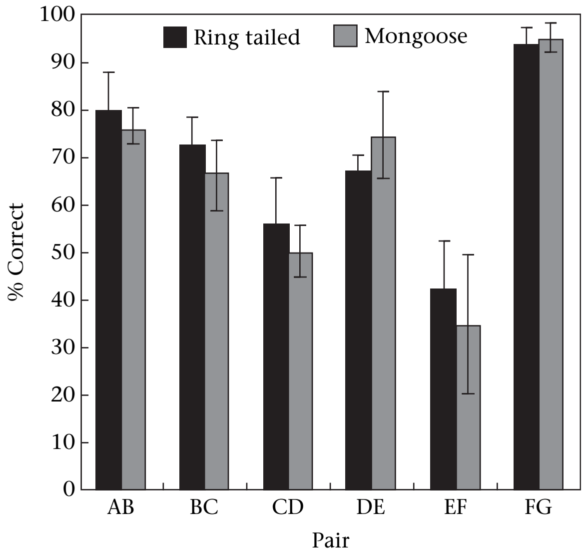

Figure 3. Mean ± SE accuracy on adjacent pairs for experiment 1 test sessions.

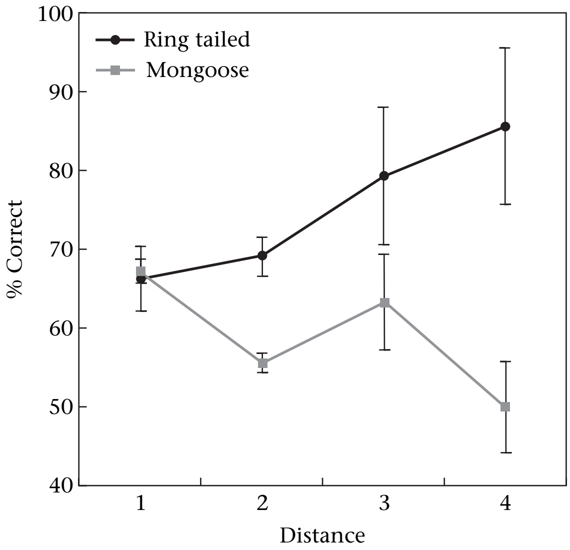

Figure 5. Mean ± SE accuracy as a function of symbolic distance for experiment 1 test sessions.

Lastly, ringtailed and mongoose lemurs showed different patterns of response time to adjacent pairs as a function of the pair's position in the ordinal sequence. Only ringtailed lemurs showed response times to adjacent pairs that increased monotonically with the pair's position in the ordinal sequence (linear regression: ringtailed: $t_4 = 3.07$, $P < 0.05$; mongoose: $t_4 = 1.06$, $P = 0.35$, partial eta$^2 = 0.22$, power $= 0.08$).

Discussion

These species differences are consistent with the predictions of the social intelligence hypothesis. Ringtailed lemurs, which live in large social groups oriented around dominance hierarchies, showed robust representations of transitive relationships compared to less socially oriented mongoose lemurs. This result is evidenced in both overall accuracy and in the strikingly different patterns of accuracy and response time as a function of symbolic distance and position in the series. The symbolic distance effect (Moyer & Landauer 1967) refers to the phenomenon that the speed and accuracy with which two stimuli are compared varies inversely with the distance between the stimuli on the compared dimension. The presence of a symbolic distance effect in the current task can be interpreted as evidence that an animal represented and compared stimuli along a common underlying dimension. Interestingly, only ringtailed lemurs showed increased accuracy at greater symbolic distances. Ringtailed lemurs also showed response times to adjacent pairs that increased monotonically with a pair's position in the ordinal sequence. Such position effects are predicted by models in which ordinal stimuli are represented along a linear psychological continuum and evaluated in memory according to their distance from fixed reference points (Banks 1977; Polich & Potts 1977; Holyoak & Patterson 1981). If the highest-ranked item in the series (A) is the reference point to which other values are compared, one would expect response times to adjacent pairs to increase with a pair's distance from this marker (Terrace et al. 2003). Only ringtailed lemurs had response times that reflected such an underlying representation.

Importantly, the species difference cannot be attributed to differences in proficiency with the training pairs. Ringtailed and mongoose lemurs learned to discriminate the adjacent pairs at comparable rates and performed equally well with the training pairs during test sessions. Given their closely matched accuracies on the adjacent pairs (ringtailed: 67%, mongoose: 66%), one would expect similar levels of transitive inference if the two species represented the ordinal series in similar ways.

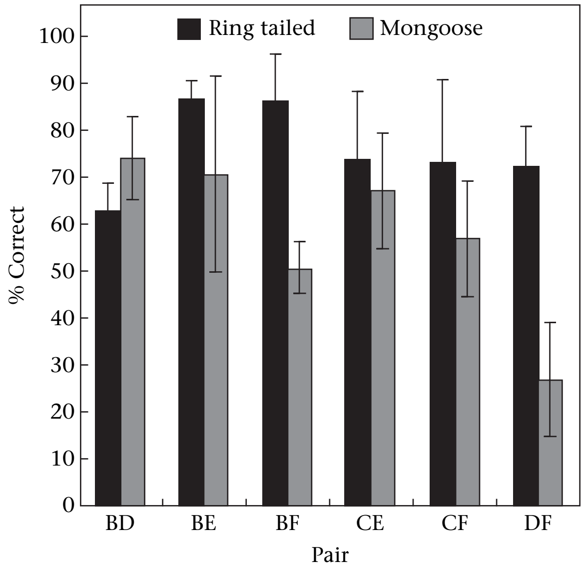

Figure 4. Mean ± SE accuracy on nonadjacent pairs for experiment 1 test sessions.

EXPERIMENT 2

Experiment 1 showed that two species of prosimian primates are capable of transitive inference. Both species were able to order pairs of nonadjacent items after training with the adjacent pairs. However, important species differences emerged. Although accuracy for the two species was equivalent for adjacent pairs, ringtailed lemurs showed superior performance on pairs requiring transitive inference. In addition, only ringtailed lemurs' accuracy was modulated by the symbolic distance between the stimuli in a pair. The goal of experiment 2 was to further probe the transitive inference abilities of the two species and to ask whether emphasizing the linear nature of the underlying series would assist mongoose lemurs in constructing a mental representation of the series more similar to that of ringtailed lemurs. To do this, we used a correction procedure in experiment 2 that re-trained all adjacent pairs in an order consistent with their ordinal ranks (e.g. AB followed by BC, etc.).

Methods

Training

We began correction sessions with the presentation of the AB pair and we required subjects to respond correctly to this pair (i.e. select stimulus A) for five trials before they could advance to the BC pair. Each successive pair required five correct responses to the higher-ranked stimulus in the pair before a subject advanced to the next pair in the ordinal sequence. We terminated sessions upon criterial performance with the final pair in the series (FG). Thus, all adjacent pairs were trained each day in an order consistent with their ordinal ranks (AB, BC, CD, DE, EF, FG). All subjects received correction sessions until they performed above 70% with each pair in the series for two consecutive sessions. Lemurs then received two additional training sessions with a random mixture of all adjacent pairs before advancing to transitive test sessions.

Testing

Each subject participated in 20 test sessions identical to those in experiment 1.

Results

On average, ringtailed and mongoose lemurs required an equivalent number of sessions to reach the 70% accuracy criterion for the correction procedure (t test: $t_4 = -1.45$, $P = 0.22$). Again, both species responded with equal accuracy to the adjacent pairs during test sessions. A repeated measures two-way ANOVA with the factors of species (ringtailed, mongoose) and pair (AB, BC, CD, DE, EF, FG) on accuracy revealed a main effect of pair (ANOVA: $F_{5,10} = 6.93$, $P < 0.05$) but no effect of species (ANOVA: $F_{1,2} = 0.04$, $P = 0.86$, partial eta$^2 = 0.02$, power $= 0.05$) and no interaction between pair and species (ANOVA: $F_{5,10} = 0.89$, $P = 0.52$, partial eta$^2 = 0.30$, power $= 0.20$). In contrast to experiment 1, ringtailed and mongoose lemurs showed no difference in overall accuracy on nonadjacent test pairs (ANOVA: $F_{1,2} = 0.07$, $P = 0.82$, partial eta$^2 = 0.03$, power $= 0.05$). Both species responded above chance expectation on all six nonadjacent pairs, showing robust transitive inference (binomial tests: $P < 0.05$). Both ringtailed and mongoose lemurs showed greater accuracy for test pairs with greater symbolic distances (linear regression: ringtailed: $t_2 = 9.40$, $P < 0.05$; mongoose: $t_2 = 11.6$, $P < 0.05$; Fig. 6). Similarly, both species showed shorter response latencies at greater symbolic distances, although this difference in response latency was not significant in mongoose lemurs (linear regression: ringtailed: $t_2 = -22.19$, $P < 0.05$; mongoose: $t_2 = -3.28$, $P = 0.08$). Lastly, both species showed a position effect whereby response times to adjacent pairs increased monotonically with a pairs' distance from the highest-ranked item (A) in the sequence (linear regression: ringtailed: $t_4 = 3.58$, $P < 0.05$; mongoose: $t_4 = 4.84$, $P < 0.05$; Fig. 7).

Discussion

The species difference observed in experiment 1 was eliminated when the adjacent pairs were re-trained in an order consistent with their ordinal ranks. Both ringtailed and mongoose lemurs responded above chance to all six pairs requiring transitive inference and both species showed symbolic distance effects in response time and accuracy. The finding that mongoose lemurs performed as well as ringtailed lemurs after the correction procedure suggests that the species difference in experiment 1 did not reflect absolute limits in the species' abilities to make transitive inferences. Rather, it appears that ringtailed lemurs were simply better able to detect the linear nature of the series when the stimuli were presented in a pseudorandom order.

GENERAL DISCUSSION

The results of the current experiments provide strong support for the social intelligence hypothesis.

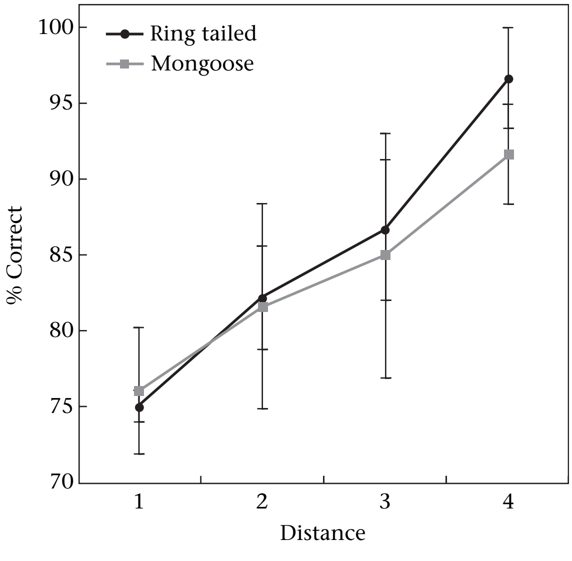

Figure 6. Mean ± SE accuracy as a function of symbolic distance for experiment 2 test sessions.

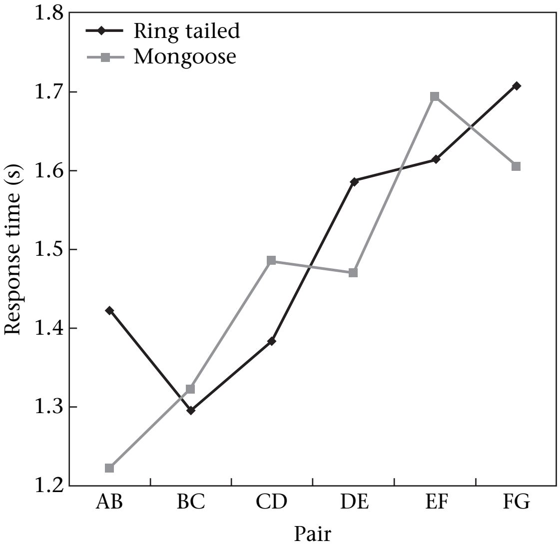

Figure 7. Mean response time to adjacent pairs for experiment 2 test sessions. The higher-ranked stimulus in each adjacent pair decreases from left to right along the *X* axis.

In experiment 1, both species learned to discriminate adjacent pairs at comparable rates and with similar accuracy. However, in tests of transitive inference, ringtailed lemurs outperformed mongoose lemurs and showed richer representations of the underlying linear order of the test series. In experiment 2, lemurs were given a correction procedure that emphasized the linear nature of the test series and both species performed equally well during transitive tests. This finding suggests that the two species are not fundamentally different in their ability to make transitive inferences, but rather, differ in their proclivity to detect the underlying linear order of an ordinal series.

Given that ringtailed lemurs live in large social groups with roughly linear dominance hierarchies, the ability to detect and reason about the rank order of conspecifics is probably an essential cognitive ability for survival. However, it seems likely that even if transitive reasoning evolved for a specific social context, it was subsequently exploited for use in more generalized realms, since ringtailed lemurs excel at reasoning about rank relationships in nonsocial contexts (as evidenced by the current experiments). Indeed, it is this very notion of co-opting traits that were originally selected for social purposes upon which the social intelligence hypothesis attempts to explain the multifarious intelligence of primates (Byrne & Bates 2007). Although mongoose lemurs showed some evidence of transitive inference in experiment 1, their performance was markedly poorer than that of ringtailed lemurs. Mongoose lemurs responded above chance to only half of the test pairs requiring transitive inference and, unlike ringtailed lemurs, did not show a symbolic distance effect. Because mongoose lemurs live in small family groups oriented around a single breeding pair and their offspring, it is unlikely that they face substantial cognitive demands relevant to tracking dominance relationships. Accordingly, mongoose lemurs may have been less likely to spontaneously detect the underlying linear dimension of the test series.

In contrast, there were no differences between the two species in transitive reasoning performance after both species underwent an extensive correction procedure that emphasized the linear ordering of the pairs. However, it is noteworthy that animals in the wild are unlikely to experience anything like the ordered presentations used in experiment 2. Instead, the final phase of training in experiment 1, during which the six adjacent pairs were presented in random order, resembles the manner in which animals are likely to witness dyadic social interactions in their natural environment. Given this scenario, animals living in large social groups with linear dominance hierarchies would face a premium not only on representing the overall order of the dominance hierarchy, but also on being able to mentally construct this order when the relevant information is acquired in a piecemeal fashion. The results of the current experiments suggest that it is this tendency to spontaneously organize an interconnected series of items along a continuous dimension that marks the greatest difference between ringtailed and mongoose lemurs. Even when the training pairs were presented in an order inconsistent with their ordinal ranks, ringtailed lemurs showed a natural tendency to organize this information along a continuous underlying dimension. In contrast, mongoose lemurs required training that emphasized the underlying linear dimension before they showed robust transitive inference.

Although species comparisons have great utility for testing hypotheses about the selective pressures in cognitive evolution, the results of such experiments must be interpreted cautiously (Bitterman 1975). It is always possible that differences between species reflect the influence of extraneous variables unrelated to the hypothesis at hand. At present we know very little about cognition in prosimians and it is possible that ringtailed and mongoose lemurs differ cognitively in other regards relevant to the current experiments. However, as noted by Bond et al. (2003), species comparisons are most effective when applied iteratively across carefully chosen sets of species. These data supplement the results previously obtained with corvids in several important ways. First, both lemur species were closely matched in accuracy on the training pairs at the time of transitive tests. Therefore, it is unlikely that the species difference in transitive inference can be attributed to differences in proficiency with the training pairs or general differences in memory capacity. It is also unlikely that the species difference was the result of differences in spatial cognition as ringtailed and mongoose lemurs do not differ radically in their home range use or feeding ecology. Taken together, the trends observed in corvids and prosimians suggest that there has been convergent evolution on the cognitive abilities relevant to the representation of order, and that social complexity was probably a selective pressure in this process.

When Alison Jolly first hypothesized that complex social environments provided the evolutionary context in which primate intelligence evolved, she did so on the basis of the differences that she observed between prosimian and anthropoid primates (Jolly 1966b). Although some lemur species formed social structures similar to those observed in Old World monkeys, lemurs appeared to lack the intelligence that characterized the anthropoid primates. Thus, it appeared that monkey-like societies preceded monkey-like intelligence in the course of primate evolution. While prosimians and anthropoids undoubtedly differ in many important ways, there is also great social and cognitive variation within each of these primate lineages. A critical examination of the relationships between socioecology and cognition across the primate order will be paramount in our quest to understand the evolution of primate intelligence.

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Supplementary Material

Supplementary material for this article may be found, in the online version, at doi:10.1016/j.anbehav.2008.01.025.

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