Articles

Evidence from four lemur species that ringtailed lemur social cognition converges with that of haplorhine primates

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ARTICLE INFO

Many haplorhine primates flexibly exploit social cues when competing for food. Whether strepsirrhine primates possess similar abilities is unknown. To explore the phylogenetic origins of such skills among primates, we tested ringtailed lemurs, *Lemur catta*, for their ability to exploit social cues while competing for food. We found that in two contexts ringtailed lemurs spontaneously approached food out of their competitor's view. To assess whether these skills are related to the relatively complex social structure seen in ringtailed lemurs or shared more broadly across a range of strepsirrhines, we then compared ringtailed lemurs to three lemur species with less complex societies in the same food competition task ($N = 50$ lemurs). Although all species skilfully avoided food proximate to a competitor in a pretest, only ringtailed lemurs performed above chance in the food competition task that required subjects to avoid food that an experimenter was facing in favour of one that he was not facing. We also compared all four species in a noncompetitive gaze-following task. Ringtailed lemurs were again the only species that looked up more frequently when an experimenter gazed into space than when an experimenter gazed forward (although at relatively low frequencies). These results are consistent with the hypothesis that ringtailed lemurs have undergone convergent social-cognitive evolution with haplorhines, possibly as an adaptation for living in the largest and most complex social groups among strepsirrhines. Results are discussed in terms of lemur cognitive evolution as well as the social intelligence hypothesis.
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Competition for resources within and between social groups has been suggested as one of the key selective pressures driving the evolution of complex cognitive skills in animals. The social intelligence hypothesis predicts that the evolution of social-cognitive skills is favoured in species living in large, complex social groups because social skills allowing individuals to outcompete conspecifics for access to resources and mates will confer significant fitness advantages (Jolly 1966; Humphrey 1976; Byrne & Whiten 1988; Dunbar 2003; Seyfarth et al. 2005; Byrne & Bates 2007).

The initial stage of testing this hypothesis has involved documenting the presence or absence of social-cognitive skills in a range of species. A variety of tasks have now been developed that allow for the assessment of social skills in a range of species in tasks of differing complexity. The simplest tasks examine a species' ability to locate food or make social decisions using basic positional cues such as the head or body orientation of others (Marino 2002; Call et al. 2003; Virányi et al. 2004; Hare et al. 2006; Schwab & Huber 2006; von Bayern & Emery 2009; Ruiz et al. 2009). Other

tasks have measured subjects' ability to make inferences about what others can and cannot perceive in the context of social competition. Most notably, there is now growing evidence that some primates and corvid species are sensitive to the perceptual states of others (reviewed in: Emery & Clayton 2004; Call & Tomasello 2008; Rosati & Hare 2009). For example, rhesus macaques, *Macaca mulatta*, spontaneously avoid approaching food near a person whose eyes and face are visible over a person whose has his face averted or his eyes closed (Flombaum & Santos 2005). Experiments also suggest that chimpanzees know what another individual can or cannot see and whether they themselves can be seen or heard, and can even reason about the precise target of another individual's attention (Hare et al. 2000, 2001, 2006; Melis et al. 2006; Brauer et al. 2007; Kaminski et al. 2008; E.L.M. & B.H., unpublished data).

Strepsirrhines (lemurs, lorises and galagos) represent an important group of primates to consider when reconstructing the evolution of any primate trait(s) as they are believed to be the most evolutionarily conserved primates. Strepsirrhines last share a common ancestor with haplorhines (monkeys and apes) about 75 million years ago (Horvath et al. 2008), and based on anatomical comparisons to extinct basal primates, they are thought to be both morphologically and behaviourally similar to the last common

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ancestor of all primates (Tattersall 1982). This means that if the majority of strepsirrhine and haplorhine species possess a social-cognitive skill, it is likely that this trait was present early in primate evolution and has been inherited in extant species through common descent. Alternatively, if a trait that is common among haplorhines is not present in strepsirrhines, this suggests that the trait evolved in haplorhines after the initial strepsirrhine–haplorhine split. To explore whether any strepsirrhines posses social-cognitive abilities that have been documented in haplorhines, we tested ringtailed lemurs, *Lemur catta*, in two tasks similar to those that have been used with monkeys and apes (Flombaum & Santos 2005; Hare et al. 2006).

GENERAL METHODS

Lemurs were housed in pairs or in groups in indoor enclosures and in outdoor semi-free-ranging enclosures at the Duke Lemur Center, Durham, NC, U.S.A. Subjects were tested in their home enclosures and separated from all other group members for the duration of the session. Food was temporarily removed during the experimental session, but water was available ad libitum.

Experiments 1–3 each consisted of three phases: (1) an introductory trial, (2) a competitive pretest and (3) a test. In the introductory trial, the experimenter(s) placed two food trays on either side of a table. The experimenter(s) then immediately stood up and faced away from the subject until the lemur had eaten the food at both locations. This trial served both to habituate the lemur to the trays and to assure that the subject understood that there could be food positioned on both trays. In the competitive pretest, the experimenter placed two food trays on either side of the table (~1 m apart) and knelt behind one, facing the lemur. The subject was allowed to eat the food to the side of the experimenter (uncontested food), but if the subject approached the food in front of the experimenter (contested food), the experimenter removed the tray immediately, and placed it under the table out of the subject's view. In all experiments a subject was scored as having approached a food tray if its head or hand came within 5 cm of the food tray.

EXPERIMENT 1

In experiment 1, we tested whether ringtailed lemurs preferentially target food that is proximate to a human competitor who is facing away from the subject (and the food) compared to food that is proximate to a competitor who is facing the subject and the food.

To do so, we modified the methods of Flombaum & Santos (2005), who used an analogous paradigm with rhesus monkeys, *M. mulatta*.

Methods

Ten ringtailed lemurs participated (Table 1), all of which had some experience in pilot experiments. Pilot experiments consisted of sessions similar to the present experiments, but were conducted on the floor of the lemur's enclosure, with the experimenter kneeling on the ground and his head well above the subjects' eye level.

Subjects did not discriminate between forward- and backward-facing experimenters during these pilot sessions. Consequently, we conducted the current experiments on an elevated table so that the experimenter's head was at the lemur's eye level and was thus more salient at the time of choice. Data were collected between February and March 2010. After the introductory trial, subjects first participated in a pretest that served to establish a competitive relationship between the subject and the human experimenter. Two food trays were placed 1 m apart on a table (73 cm height, 61 cm width, 123 cm length) and the experimenter knelt directly behind one of these trays with his face level with the tray. If a subject approached the food in front of the experimenter, the experimenter quickly removed this tray (taking it off the table and out of the subject's view) and the subject was allowed 1 min to feed from the uncontested food tray. If the subject approached the uncontested food tray she was allowed to feed freely and was given 1 min to approach the contested food tray. If the subject approached the contested food tray during this period, the experimenter quickly removed the tray. Experimenters 1 and 2 rotated every other trial, with each experimenter completing four trials. Experimenter 1 always began the first trial, followed by experimenter 2 on the same side as experimenter 1. The side (left or right) experimenter 1 knelt behind in the first trial was counterbalanced between subjects.

In the test, food was again positioned on two trays at each side of the table, but one experimenter was present behind each tray. One experimenter knelt at the left side of the table and the other knelt at the right and each experimenter remained on the same side of the table throughout the session. In each trial the subject was first attracted to a food reward at a central location 1 m away from the experimenters and equidistant from both food trays. The experimenter who baited this location was alternated on every trial.

Both experimenters then placed a tray with a piece of grape on the table, and one experimenter faced forward so that he could see the food and the lemur, while the other experimenter faced backwards so that the food tray was positioned behind his head and he

Table 1
Subject information and the percentage of trials that each subject approached the uncontested food in the pretest and the test for experiments 1–2

Subject	Experiment 1		Experiment 2	
	Pretest (% of 8 trials)	Test (% of 12 trials)	Pretest (% of 6 trials)	Test (% of 12 trials)
Average	**95***	**78***	**95***	**69***
Aracus (M, 18.4 years)	—	—	50	50
Dory (F, 16.7 years)	100*	75	—	—
Sosiphanes (F, 8.6 years)	100*	58	100*	92*
Aristides (M, 16.6 years)	—	—	100*	75
Cleis (F, 20.6 years)	100*	75	100*	58
Ivy (M, 1.5 years)	75	50	100*	75
Cap N' Lee (M, 5.6 years)	100*	100*	100*	83*
Fern (F, 2.6 years)	100*	100*	100*	83*
Persephone (F, 0.7 years)	100*	100*	100*	75
Alena (F, 4.7 years)	—	—	100*	42
Berisades (M, 1.7 years)	100*	75	100*	58
Licinius (M, 16.9 years)	88*	75	—	—

* Binomial probability (or one-sample *t* test for groups): $P < 0.05$.

could not see the lemur or the food tray. Subjects were then allowed 2 min to approach one of the food trays. If the subject first approached the tray in front of the experimenter facing backward, the subject was allowed to feed, and the forward-facing experimenter removed the tray in front of him and placed it out of sight beneath the table. If the subject first approached the tray in front of the experimenter facing forward, the experimenter quickly removed the tray and positioned it out of sight, and on half the trials, the subject was then allowed to approach the other food tray. This was done to encourage participation. We conducted a total 12 trials, and the experimenter facing forward (left or right) was counterbalanced within sessions for each subject. The side facing forward (left or right) on the first trial was counterbalanced between subjects.

Results and Discussion

During the pretest, ringtailed lemurs showed a strong preference to approach the uncontested food tray (mean ± SE approach to uncontested food: $95 \pm 2.8\%$; two-tailed one-sample t test: $t_9 = 16.3$, $P < 0.001$). During the test, subjects approached the food proximate to the backward-facing experimenter at levels exceeding that expected by chance (mean ± SE approach to backward-facing experimenter: $75.8 \pm 6.1\%$ one-sample t test: $t_9 = 4.2$, $P = 0.002$, two-tailed; Fig. 1). There was no difference in approaches to the uncontested food between the first half and second half of the session (mean ± SE approach to uncontested food, first half versus second half of session: $75 \pm 6.2\%$ versus $76.6 \pm 6.7\%$; paired-sample t test: $t_9 = -0.43$, $P = 0.678$, two-tailed). At an individual level, 3 of 10 lemurs approached the food proximate to the backward-facing experimenter more frequently than expected by chance (Table 1). These results suggest that ringtailed lemurs are sensitive to basic social cues such as the head orientation of potential competitors, and use this information to guide foraging decisions.

EXPERIMENT 2

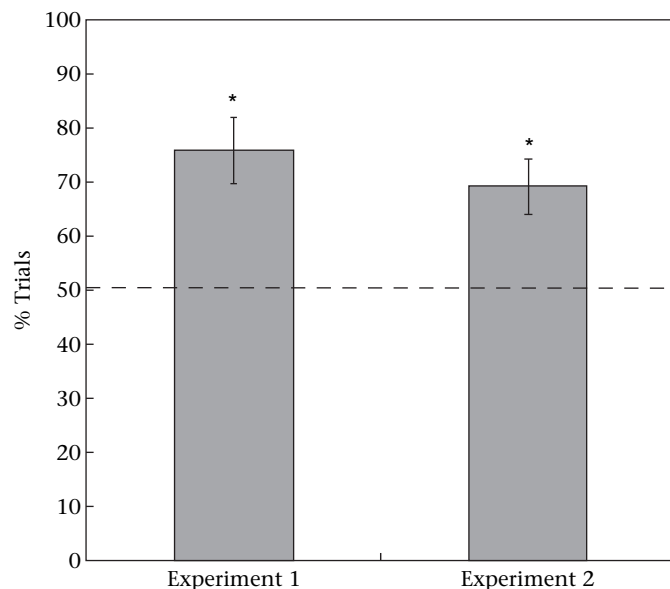In experiment 2, we tested ringtailed lemurs in a modified version of the food competition task that required the subjects to reason about a single competitor's visual orientation towards two food trays. This paradigm differed from experiment 1 in that subjects could not use a simple heuristic regarding the proximity of a visible face to the contested food items. Rather, subjects were required to exploit information about the orientation of the competitor's head towards two potential food items. The design of this experiment was modelled after that of Hare et al. (2006), who tested chimpanzees, *Pan troglodytes*, in a similar task.

Methods

Ten ringtailed lemurs participated, seven of which participated in experiment 1 (Table 1). The experiment took place on a table (73 cm height, 122 cm width, 122 cm length). Again, subjects first participated in an introductory trial and then a pretest (identical to experiment 1) to establish a competitive relationship with the experimenter (Supplementary Material, Movie S1). During the test, a single experimenter knelt equidistantly between the two food trays placed at the sides of the table, but was oriented in profile so that one of the food trays was in front of his face while the other was behind his head (Fig. 2). If the subject first approached the tray behind the experimenter, the lemur was allowed to feed from this tray, the tray in front of the experimenter was removed, and the next trial was conducted. If the subject first approached the tray in front of the experimenter, the experimenter quickly removed the tray (Supplementary Material, Movie S1). As in experiment 1, on half of trials the subject was then allowed to approach the other food item.

Results and Discussion

As in experiment 1, subjects showed a strong preference to approach the uncontested food during the pretest (mean ± SE

Figure 1. Mean ± SE percentage of trials that subjects approached the uncontested food in experiments 1 and 2. *$P < 0.05$.
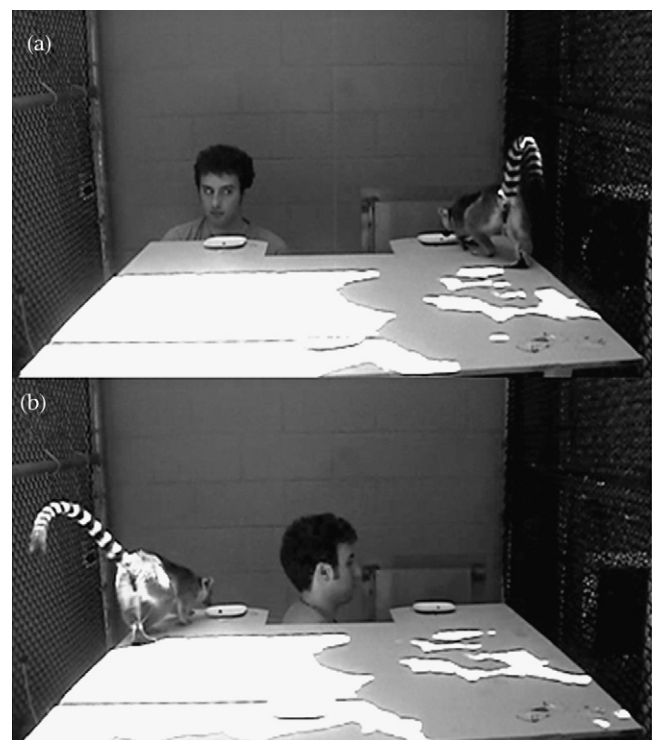

Figure 2. Procedure for the (a) pretest and (b) test in experiments 2 and 3. In the pretest, an experimenter knelt behind one of two food trays and subjects were allowed to feed from the tray to the side, but not in front of the experimenter. In the test, the experimenter knelt equidistantly between the two trays, oriented in profile, so that one tray was in front of him and the other was behind him.

approach to uncontested food: $95 \pm 5\%$; one-sample t test: $t_9 = 9$, $P < 0.001$, two-tailed). In the test, ringtailed lemurs approached the food located behind the experimenter's head more frequently than expected by chance (mean $\pm$ SE approach to uncontested food: $69.2 \pm 5.1\%$, one-sample t test: $t_9 = 3.7$, $P = 0.005$, two-tailed; Fig. 1). There was no difference in the amount of approaches to the uncontested food between the first half and second half of the session (mean $\pm$ SE approach to uncontested food, first half versus second half of session: $71.7 \pm 4.3\%$ versus $66.7 \pm 9.3\%$; paired-sample t test: $t_9 = 0.487$, $P = 0.638$, two-tailed). At an individual level, 3 of 10 lemurs approached the food proximate to the backward-facing experimenter more frequently than expected by chance (Table 1). There was no correlation in performance for subjects that completed experiment 1 and experiment 2 (Pearson correlation: $r_5 = 0.07$, $P = 0.88$).

This preference to approach food behind a human experimenter is consistent with the results of experiment 1 and suggests that ringtailed lemurs' responses were not driven by simple preferences to avoid food near a competitor whose face and eyes were visible. Together, the results of experiments 1 and 2 indicate that ringtailed lemurs share social-cognitive skills with monkeys and apes, and suggest that these skills may have been present in an ancestral primate before the divergence of the two primate suborders 75 million years ago. However, it is also possible that ringtailed lemurs, which live in larger, more complex social groups than any other lemur species (Jolly 1966; Sauther et al. 1999), evolved these abilities in parallel with monkeys and apes. This possibility is supported by the fact that ringtailed lemurs are convergent with Old World monkeys in many aspects of their social behaviour (Sauther et al. 1999) and have outperformed other lemur species in other cognitive tasks linked to social complexity (MacLean et al. 2008). These cases of independent evolution are critical for identifying the selective pressures that have favoured the evolution of the trait in question (Felsenstein 1985; Harvey & Purvis 1991; Nunn & Barton 2001). Therefore, in experiment 3, we collected data from three additional lemur species to determine whether the skills detected in experiments 1 and 2 are general to lemurs, or uniquely derived in ringtailed lemurs and convergent with haplorhine primates.

EXPERIMENT 3

In the case of social cognition, strepsirrhines provide a strong comparative test of the social intelligence hypothesis because they are characterized by a diverse range of social systems (Mittermeier et al. 2008). If sophisticated social-cognitive abilities coevolve with complex social systems, we should expect to see corresponding variance in lemur social cognition. To test whether the skills shown by ringtailed lemurs in experiments 1 and 2 are unique to this species and associated with social complexity, or are shared more broadly across lemurs, we collected data from three other lemur species (mongoose lemurs, *Eulemur mongoz*, $N = 10$; black lemurs, *Eulemur macaco*, $N = 10$; ruffed lemurs, *Varecia variegata rubra*, $N = 10$) and an experimentally naïve group of 10 ringtailed lemurs in the food competition task from experiment 2. We chose to test 10 experimentally naïve ringtailed lemurs so that any potential species differences would not be confounded with the experience that ringtailed lemurs had accrued in experiments 1 and 2 or during pilot sessions. Although closely related to ringtailed lemurs (Horvath et al. 2008), the additional species we tested all live in smaller and less hierarchically arranged social groups, and do not show social convergences with Old World monkeys similarly to ringtailed lemurs (Curtis & Zaramody 1999; Bayart & Simmen 2005; Vasey 2007). If the ability to exploit social cues is shared across all primates, we predicted that other strepsirrhine species would show similar abilities to ringtailed lemurs. Alternatively, if the ability to

exploit social cues in ringtailed lemurs is convergent with that of monkeys and apes, we predicted that ringtailed lemurs would outperform other, less socially complex, strepsirrhine species.

Methods

The procedure for experiment 3 was identical to that of experiment 2 with the exception that we instituted a criterion that subjects must choose the uncontested food on six consecutive trials or seven of eight consecutive trials during the pretest before advancing to the test. We implemented this criterion to assure that all subjects perceived the experimenter as a food competitor before beginning the test. Test trials were identical to those in experiment 2.

Results and Discussion

Importantly, in the pretest, all species showed a strong preference for the uncontested food item (mean $\pm$ SE approach to uncontested food, one-tailed one-sample t tests: *L. catta*: $97 \pm 3\%$, $t_9 = 15.7$, $P < 0.001$; *E. mongoz*: $85.2 \pm 3.9\%$, $t_9 = 9.0$, $P < 0.001$; *E. macaco*: $88.0 \pm 3.7\%$, $t_9 = 10.3$, $P < 0.001$; *V. variegata*: $86.6 \pm 3.6\%$, $t_9 = 10.1$, $P < 0.001$) and there were no differences between species (one-way ANOVA: $F_{3,36} = 2.2$, $P = 0.10$). Thus, all species proved competent in the choice component of the task, and avoided food positioned near the competitor. In the test condition, however, only ringtailed lemurs preferentially approached the food item out of the competitor's view (mean $\pm$ SE approach to food behind the experimenter, one-tailed one-sample t tests: *L. catta*: 63.3 ± 5, $t_9 = 2.7$, $P = 0.013$; *E. mongoz*: $35 \pm 5.2\%$, $t_9 = -2.9$, $P = 0.991$; *E. macaco*: $47.5 \pm 5.6\%$, $t_9 = -0.45$, $P = 0.668$; *V. variegata*: $45 \pm 4.0\%$, $t_9 = -1.3$, $P = 0.881$; Fig. 3). To assess species differences and learning effects, we conducted a mixed model ANOVA with the between-subjects factor of species and the within-subjects factor of session half. This analysis revealed a significant effect of species ($F_{3,36} = 5.6$, $P = 0.003$) but no effect of session half ($F_{1,36} = 1.50$, $P = 0.23$) and no species $\times$ session half interaction ($F_{3,36} = 0.08$, $P = 0.97$). Tukey HSD post hoc tests indicated that ringtailed lemurs performed significantly better than mongoose lemurs ($P = 0.002$), and tended to outperform ruffed lemurs ($P = 0.06$), but no other pairs of species differed. To test directly for
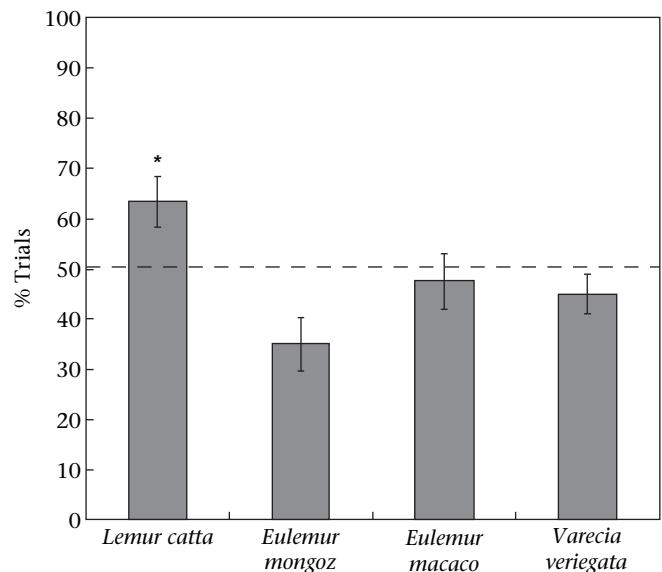

Figure 3. Mean $\pm$ SE percentage of trials that each species approached food behind the experimenter in experiment 3. *$P < 0.05$.

learning in ringtailed lemurs, we compared these subjects' performance in the first and second half of the test session using a paired-samples t test. Ringtailed lemurs' performance did not differ between the first and second halves of the test session ($t_9 = -0.67$, $P = 0.52$), suggesting that subjects' performance was not dependent on learning within the test session. At an individual level across all species, the only subject to approach the food behind the experimenter more frequently than expected by chance was a ringtailed lemur (Table 2).

The results of experiment 3 are consistent with the social intelligence hypothesis and suggest that the ability to exploit social cues indicative of others' attention may be tightly coupled with social complexity in strepsirrhine primates. These results mirror those reported for comparisons of ringtailed lemurs and mongoose lemurs in tests of transitive reasoning (MacLean et al. 2008), an ability thought to be important for learning social dominance hierarchies (Cheney & Seyfarth 1990; Bond et al. 2003; Paz-y-Miño et al. 2004; Grosenick et al. 2007), and raise the possibility that ringtailed lemurs may possess a suite of social-cognitive abilities unlike those of other closely related, but less socially complex, lemur species. To test this possibility further, we compared the same four species in a second social-cognitive task in experiment 4.

EXPERIMENT 4

In experiment 4, we tested 17 ringtailed lemurs, 14 ruffed lemurs, 8 black lemurs and 10 mongoose lemurs in a gaze-following task. Although initial studies of gaze following produced negative results in black lemurs (Anderson & Mitchell 1999), the results of experiment 3 suggest that there may be considerable social-cognitive variation between lemur species. Furthermore, several recent studies using innovative methods have produced evidence that some lemur species may be attuned to the gaze of conspecifics (Shepherd & Platt 2008; Ruiz et al. 2009).

Methods

We compared lemurs' tendency to look upward in a control condition where an experimenter looked directly at the subject, and an experimental condition in which the experimenter repeatedly looked upward in view of the subject. In both conditions the experimenter first attracted the subject to the centre of the table approximately 1 m in front of him with a food reward. In the 'gaze' condition the experimenter fixated on the lemur and then looked directly up (moving his entire head), repeating this motion for 10 s. In the 'control' condition, the experimenter looked directly at the subject for 10 s. In both conditions, the experimenter held a small piece of grape below his chin and made clicking noises throughout the trial to ensure that subjects were looking in the right direction and capable of viewing the social cue (similar to Herrmann et al. 2007).

Subjects received eight trials total (4 gaze, 4 control), and all trials were videotaped with two digital video cameras, one facing the subject on the table in front of the experimenter, and one behind and to the side of the table with both the experimenter and the subject visible. Behaviours were scored from video. On each trial we coded whether subjects looked upward, operationally defined as any movement of the subject's head in an upward direction while oriented towards the experimenter. A second observer coded 20% of trials and inter-rater reliability was good (Cohen's $\kappa = 0.74$). Most subjects received one block of four trials (ABBA or BAAB) before and after the session in experiment 3, but seven subjects who were initially apprehensive to approach received all eight trials consecutively after the test session. The condition of the first trial was counterbalanced within species.

Results and Discussion

A mixed model ANOVA with the within-subjects factor of condition (gaze, control) and the between-subjects factor of species revealed no main effects of condition ($F_{1,45} = 2.39$, $P = 0.13$) or species ($F_{3,45} = 0.18$, $P = 0.91$) and no condition by species interaction ($F_{3,45} = 1.43$, $P = 0.25$), indicating that, as a group, lemurs did not follow the experimenter's gaze. However, separate analysis of each species revealed that ringtailed lemurs, but no other species, looked up more frequently in the gaze condition than in the control condition (mean $\pm$ SD number of trials subjects looked up in gaze versus control condition, out of four total trials, one-tailed paired-sample t test: L. catta: 0.35 ± 0.61 versus 0.12 ± 0.33: $t_{16} = 2.22$, $P = 0.021$; E. mongoz: 0.50 ± 0.85 versus 0.20 ± 0.42: $t_9 = 1.12$, $P = 0.14$; E. macaco: 0.13 ± 0.35 versus 0.38 ± 0.74: $t_7 = -1.0$, $P = 0.82$; Varecia: 0.50 ± 0.76 versus 0.14 ± 0.36: $t_{13} = 1.59$, $P = 0.07$; Fig. 4).

Table 2
Subject information and the percentage of trials that each subject approached the uncontested food in the pretest and the test in experiment 3

Subject (species average)	Pretest (% of (N) trials)	Test (% of 12 trials)
Lemur catta	**97**[*]	**63**[*]
Cebes (M, 4.0 years)	100* (6)	75
Herodotus (M, 4.1 years)	100* (6)	92*
Dorieus (F, 10.1 years)	100* (6)	67
Sophia (F, 4.9 years)	100* (6)	58
Chandler (M, 10.7 years)	100* (6)	75
Alexander (M, 5.2 years)	100* (6)	42
Justine (F, 5.2 years)	70 (10)	67
Fanta (F, 3.2 years)	100* (6)	67
Randy (M, 4.2 years)	100* (6)	42
Shasta (F, 2.1 years)	100* (6)	50
Eulemur mongoz	**85.2**[*]	**35**
Guadalupe (F, 14.9 years)	70 (10)	25
Maddie (F, 4.0 years)	75 (8)	58.3
Pedro (M, 19.8 years)	87.5* (8)	50
Flor (F, 23.8 years)	87.5* (8)	8.3
Sancho (F, 27.4 years)	66.7 (12)	33.3
Felipe (M, 14.0 years)	100* (6)	25
Julio (M, 20.0 years)	85.7* (14)	41.7
Paco (M, 12.9 years)	100* (6)	25
Fabio (M, 21.9 years)	80 (10)	25
Moheli (F, 22.9 years)	100* (6)	58.3
Eulemur macaco	**88**[*]	**47.5**
Foster (F, 14.1 years)	100* (6)	83.3
Olivier (M, 19.0 years)	72.7 (11)	33.3
Belushi (M, 1.2 years)	100* (6)	41.7
Hopkins (M, 14.1 years)	100* (6)	66.7
Tarantino (M, 11.0 years)	90* (10)	33.3
Redford (M, 18.0 years)	75 (12)	41.7
Akroyd (M, 1.3 years)	80 (10)	41.7
Lamour (F, 21.0 years)	87.5* (8)	50
Deucalion (M, 21.0 years)	75 (12)	25
Teucer (M, 21.0 years)	100* (6)	58.3
Varecia variegata	**86.6**[*]	**45**
Esther (F, 1.1 years)	87.5* (8)	41.7
Phoebe (F, 1.1 years)	66.7 (12)	50
Aries (M, 2.9 years)	90.9* (11)	58.3
Hunter (M, 13.9 years)	100* (6)	50
Borealis (M, 21.9 years)	80 (10)	41.7
Antlia (F, 20.9 years)	85.7 (7)	58.3
Minias (F, 16.0 years)	100* (6)	50
Hydra (F, 2.1 years)	75 (12)	33.3
Alphard (M, 20.9 years)	100* (6)	16.7
Avior (M, 2.1 years)	80 (10)	50

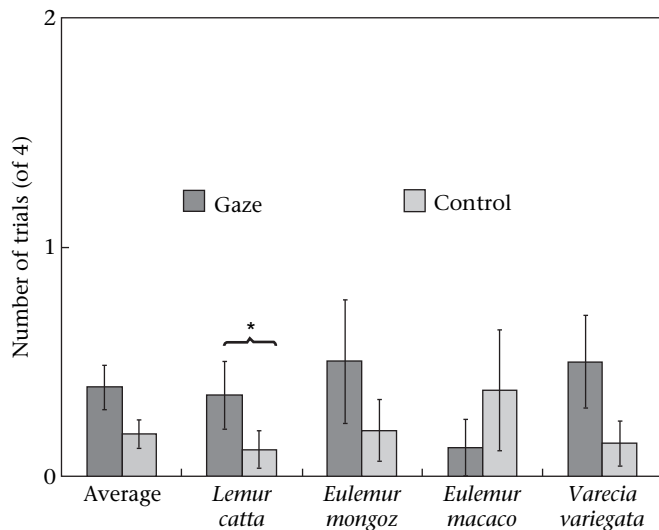[*] Binomial probability (or one-sample t test for groups): $P < 0.05$.

Figure 4. Mean ± SE number of trials that subjects looked upward in the 'gaze' and the 'control' conditions for experiment 4. *$P < 0.05$.

GENERAL DISCUSSION

Together, the results of these experiments suggest that the ability to exploit social cues such as a competitor's visual orientation is not shared among all extant primates and was probably not present in the last common ancestor of strepsirrhines and haplorhines. The only strepsirrhine species in these experiments that demonstrated spontaneous social skills analogous to those reported in monkeys and apes is a species known for having social complexity that has often been compared to that of Old World monkeys (Jolly 1966; Sauther et al. 1999). Our results suggest that convergences between ringtailed lemurs and monkeys extend to the cognitive domain, and may reflect similar cognitive adaptations for living in complex social groups.

In one of the initial formulations of the social intelligence hypothesis, Jolly (1966, page 504) noted that '[ringtailed] lemurs seem to have 'monkey-type' societies without having evolved monkey-level intelligence' and concluded that complex cognition evolved after increased sociality, rather than the other way around. While ringtailed lemurs surely differ from monkey species in important and interesting ways, our results suggest that the cognitive similarities between these taxa may be equally striking. Additional comparative studies between these groups will be important for uncovering the extent, and mechanisms of these convergences. Whether these similarities are specific to social cognition or are domain general remains an important question. One interesting prediction of the social intelligence hypothesis is that cognitive skills that initially evolved for social functions are frequently exapted for use in more generalized contexts (Cheney & Seyfarth 1990; Byrne & Bates 2007). Thus, socially and nonsocially derived intelligence may be difficult to tease apart experimentally (Herrmann et al. 2010).

Although ringtailed lemurs showed social skills resembling those reported in monkeys and apes, the present experiments cannot determine whether the cognitive mechanisms underlying these abilities are the same across these taxa. For example, in the food competition task, ringtailed lemurs may have preferentially targeted food behind the experimenter after having simply learnt to avoid food in front of social competitors over a lifetime of experience dealing with other lemurs and humans. Alternatively, it could be that lemurs solved these problems using a more sophisticated understanding of others' visual perception. To distinguish

between different mechanistic hypotheses, future research will need to replicate and extend work designed to assess similar cognitive skills in haplorhines (Hare et al. 2000, 2003; Flombaum & Santos 2005; Burkart & Heschl 2007). Importantly, however, this mechanistic question is orthogonal to that of establishing convergence between lemurs and haplorhine primates, as different proximate mechanisms frequently underlie analogous functional adaptations. It is also important to note that although ringtailed lemurs performed above chance in the food competition experiments, the percentage of approaches to the uncontested side were relatively low compared to monkeys and apes tested in similar tasks (Flombaum & Santos 2005; Hare et al. 2006). Although this quantitative difference may be due to a number of factors (e.g. differences in food motivation, visual acuity, temperament, etc.), it may be that ringtailed lemurs are simply less sensitive to this set of social cues than are haplorhine primates. Nevertheless, the fact that ringtailed lemurs performed above chance indicates some sensitivity to basic social cues that are indicative of another's attentional state.

In the gaze-following task, differences between lemurs and monkeys and apes are more readily apparent. The overall rate of gaze following for all lemur species was remarkably low ($\sim 10\%$ of trials) compared to that reported for monkeys and apes (30–85% of trials) (Tomasello et al. 1998, 2001) and the tendency for ringtailed lemurs to look upward in the 'gaze' condition can be explained by a number of mechanisms, including increased vigilance in response to the experimenter's head movements. Nevertheless, other studies suggest that some lemur species may co-orient with others (Shepherd & Platt 2008; Ruiz et al. 2009), raising the possibility that gaze following in lemurs is more common between conspecifics. For example, Ruiz et al. (2009) presented brown lemurs, *Eulemur fulvus*, and black lemurs, *E. macaco*, with a photograph of a lemur with its head and eyes oriented towards the left or right. In that study, subjects first oriented in the same direction as the photographic model of a conspecific.

Our findings emphasize the importance of adopting a phylogenetic approach to the study of cognition and demonstrate the necessity of testing multiple species, without assuming that data from any single taxon are representative of larger taxonomic groups (i.e. the model species approach). Lemurs provide an ideal group for comparative methods given their phylogenetic affinity but social and ecological diversity. However, tests of other strategically targeted species will prove important for assessing the breadth of the social intelligence hypothesis (Beach 1950; Shettleworth 1993; Arnold & Nunn 2010). For example, whether the social-cognitive skills observed in various species of corvids, canids and cetaceans are uniquely derived in these species or are shared across larger taxonomic groups remain open empirical questions. The results of these tests will be critical in our understanding of both the phylogeny and function of social cognition.

Supplementary Material

Supplementary material for this article is available, in the online version, at doi:10.1016/j.anbehav.2011.01.020.

References

Anderson, J. R. & Mitchell, R. W. 1999. Macaques but not lemurs co-orient visually with humans. *Folia Primatologica*, **70**, 17–22.

Arnold, C. & Nunn, C. L. 2010. Phylogenetic Targeting of research effort in evolutionary biology. *American Naturalist*, **176**, 601–612.

Bayart, F. & Simmen, B. 2005. Demography, range use, and behavior in black lemurs (*Eulemur macaco macaco*) at Ampasikely, northwest Madagascar. *American Journal of Primatology*, **67**, 299–312.

von Bayern, A. M. P. & Emery, N. J. 2009. Jackdaws respond to human attentional states and communicative cues in different contexts. *Current Biology*, **19**, 602–606.

Beach, F. A. 1950. The snark was a boojum. *American Psychologist*, **5**, 115–124.

Bond, A. B., Kamil, A. C. & Balda, R. P. 2003. Social complexity and transitive inference in corvids. *Animal Behaviour*, **65**, 479–487.

Brauer, J., Call, J. & Tomasello, M. 2007. Chimpanzees really know what others can see in a competitive situation. *Animal Cognition*, **10**, 439–448.

Burkart, J. M. & Heschl, A. 2007. Understanding visual access in common marmosets, *Callithrix jacchus*: perspective taking or behaviour reading? *Animal Behaviour*, **73**, 457–469.

Byrne, R. W. & Bates, L. A. 2007. Sociality, evolution and cognition. *Current Biology*, **17**, R714–723.

Byrne, R. W. & Whiten, A. W. 1988. *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans*. Oxford: Clarendon Press.

Call, J. & Tomasello, M. 2008. Does the chimpanzee have a theory of mind? 30 years later. *Trends in Cognitive Sciences*, **12**, 187–192.

Call, J., Brauer, J., Kaminski, J. & Tomasello, M. 2003. Domestic dogs (*Canis familiaris*) are sensitive to the attentional state of humans. *Journal of Comparative Psychology*, **117**, 257–263.

Cheney, D. L. & Seyfarth, R. M. 1990. *How Monkeys See the World: Inside the Mind of Another Species*. Chicago: University of Chicago Press.

Curtis, D. J. & Zaramody, A. 1999. Social structure and seasonal variation in the behaviour of *Eulemur mongoz*. *Folia Primatologica*, **70**, 79–96.

Dunbar, R. I. M. 2003. The social brain: mind, language, and society in evolutionary perspective. *Annual Review of Anthropology*, **32**, 163–181.

Emery, N. J. & Clayton, N. S. 2004. The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science*, **306**, 1903–1907.

Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist*, **125**, 1–15.

Flombaum, J. I. & Santos, L. R. 2005. Rhesus monkeys attribute perceptions to others. *Current Biology*, **15**, 447–452.

Grosenick, L., Clement, T. S. & Fernald, R. D. 2007. Fish can infer social rank by observation alone. *Nature*, **445**, 429–432.

Hare, B., Call, J., Agnetta, B. & Tomasello, M. 2000. Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, **59**, 771–785.

Hare, B., Call, J. & Tomasello, M. 2001. Do chimpanzees know what conspecifics know? *Animal Behaviour*, **61**, 139–151.

Hare, B., Addessi, E., Call, J., Tomasello, M. & Visalberghi, E. 2003. Do capuchin monkeys, *Cebus apella*, know what conspecifics do and do not see? *Animal Behaviour*, **65**, 131–142.

Hare, B., Call, J. & Tomasello, M. 2006. Chimpanzees deceive a human competitor by hiding. *Cognition*, **101**, 495–514.

Harvey, P. H. & Purvis, A. 1991. Comparative methods for explaining adaptations. *Nature*, **351**, 619–624.

Herrmann, E., Call, J., Hernandez-Lloreda, M. V., Hare, B. & Tomasello, M. 2007. Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. *Science*, **317**, 1360–1366.

Herrmann, E., Hernandez-Lloreda, M. V., Call, J., Hare, B. & Tomasello, M. 2010. The structure of individual differences in the cognitive abilities of children and chimpanzees. *Psychological Science*, **21**, 102–110.

Horvath, J., Weisrock, D., Embry, S. L., Fiorentino, I., Balhoff, J. P.,I., Kappeler, P., Wray, G. A., Willard, H. & Yoder, A. D. 2008. The development and application of a phylogenomic toolkit: resolving the evolutionary history of Madagascar's lemurs. *Genome Research*, **18**, 489–499.

Humphrey, N. K. 1976. The social function of intellect. In: *Growing Points in Ethology* (Ed. by P. P. G. Bateson & R. A. Hinde), pp. 303–317. Cambridge: Cambridge University Press.

Jolly, A. 1966. Lemur social behavior and primate intelligence. *Science*, **153**, 501–506.

Kaminski, J., Call, J. & Tomasello, M. 2008. Chimpanzees know what others know, but not what they believe. *Cognition*, **109**, 224–234.

MacLean, E. L., Merritt, D. J. & Brannon, E. M. 2008. Social organization predicts transitive reasoning in prosimian primates. *Animal Behaviour*, **76**, 479–486.

Marino, L. 2002. Convergence of complex cognitive abilities in cetaceans and primates. *Brain Behavior and Evolution*, **59**, 21–32.

Melis, A. P., Call, J. & Tomasello, M. 2006. Chimpanzees (*Pan troglodytes*) conceal visual and auditory information from others. *Journal of Comparative Psychology*, **120**, 154–162.

Mittermeier, R., Ganzhorn, J., Konstant, W., Glander, K., Tattersall, I., Groves, C., Rylands, A., Hapke, A., Ratsimbazafy, J. & Mayor, M., et al. 2008. Lemur diversity in Madagascar. *International Journal of Primatology*, **29**, 1607–1656.

Nunn, C. L. & Barton, R. A. 2001. Comparative methods for studying primate adaptation and allometry. *Evolutionary Anthropology*, **10**, 81–98.

Paz-y-Miño, C. G., Bond, A. B., Kamil, A. C. & Balda, R. P. 2004. Pinyon jays use transitive inference to predict social dominance. *Nature*, **430**, 778–781.

Rosati, A. G. & Hare, B. 2009. Looking past the model species: diversity in gaze-following skills across primates. *Current Opinion in Neurobiology*, **19**, 45–51.

Ruiz, A., Gomez, J. C., Roeder, J. J. & Byrne, R. W. 2009. Gaze following and gaze priming in lemurs. *Animal Cognition*, **12**, 427–434.

Sauther, M. L., Sussman, R. W. & Gould, L. 1999. The socioecology of the ringtailed lemur: thirty-five years of research. *Evolutionary Anthropology*, **8**, 120–132.

Schwab, C. & Huber, L. 2006. Obey or not obey? Dogs (*Canis familiaris*) behave differently in response to attentional states of their owners. *Journal of Comparative Psychology*, **120**, 169–175.

Seyfarth, R. M., Cheney, D. L. & Bergman, T. J. 2005. Primate social cognition and the origins of language. *Trends in Cognitive Sciences*, **9**, 264–266.

Shepherd, S. V. & Platt, M. L. 2008. Spontaneous social orienting and gaze following in ringtailed lemurs (*Lemur catta*). *Animal Cognition*, **11**, 13–20.

Shettleworth, S. J. 1993. Where is the comparison in comparative cognition? Alternative research programs. *Psychological Science*, **4**, 179–184.

Tattersall, I. 1982. *The Primates of Madagascar*. New York: Columbia University Press.

Tomasello, M., Call, J. & Hare, B. 1998. Five primate species follow the visual gaze of conspecifics. *Animal Behaviour*, **55**, 1063–1069.

Tomasello, M., Hare, B. & Fogleman, T. 2001. The ontogeny of gaze following in chimpanzees, *Pan troglodytes*, and rhesus macaques, *Macaca mulatta*. *Animal Behaviour*, **61**, 335–343.

Vasey, N. 2007. The breeding system of wild red ruffed lemurs (*Varecia rubra*): a preliminary report. *Primates*, **48**, 41–54.

Virányi, Z., Topál, J., Gácsi, M., Miklósi, Á & Csányi, V. 2004. Dogs respond appropriately to cues of humans' attentional focus. *Behavioural Processes*, **66**, 161–172.