RESEARCH ARTICLE

Sex Ratio Affects Sex-Specific Innovation and Learning in Captive Ruffed Lemurs (*Varecia variegata* and *Varecia rubra*)

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Recent years have witnessed extensive research into problem solving and innovation in primates, yet lemurs have not been subjected to the same level of attention as apes and monkeys, and the social context in which novel behavior appears has rarely been considered. We gave novel foraging puzzlebox devices to seven groups of ruffed lemurs (*Varecia variegata* and *Varecia rubra*) to examine the factors affecting rates of innovation and social learning. We found, across a range of group sex ratios, that animals of the less-represented sex were more likely to contact and solve the puzzlebox sooner than those of the more-represented sex. We established that while some individuals were able to solve the puzzleboxes there was no evidence of social learning. Our findings are consistent with previously reported male deference as a sexual strategy, but we conclude that the need for male deference diminishes when, within a group, males are rare. Am. J. Primatol. 73:1–12, 2011. © 2011 Wiley-Liss, Inc.

Key words: innovation; problem solving; social learning; sex ratio; lemur

INTRODUCTION

Although the social environment is widely thought to have had an impact upon the evolution of intelligence and behavioral plasticity [Byrne & Whiten, 1997; Humphrey, 1976; Jolly, 1966; MacLean et al., 2008], the relationship between social complexity and learning has been subjected to comparatively little empirical attention. Theoretical work implies that variable, changing, and challenging environmental conditions promote reliance upon individual problem solving and the devising of new solutions, henceforth "innovation" [Boyd & Richerson, 1985; Reader & Laland, 2003]. However, this "variability" is generally interpreted with respect to the physical or ecological environment. For instance, Day et al. [2003] found evidence supporting the "extractive foraging hypothesis" [Parker & Gibson, 1977], which proposes that those species that employ complex manipulations to forage for their food and extract it from the substrate are likely to be more intelligent than those species that do not. However, various life history traits, such as sex, age, and social status, have been found to impact upon the likelihood of the spread of acquired information [Reader & Laland, 2001]. For instance, Nicol and Pope [1999] found that domestic hens tended to copy high-ranking female demonstrators more than either males or low-ranking females. Similarly, capuchin monkeys have been reported to follow the method of the dominant male to open a puzzlebox even when they have found an alternative solution [Dindo et al., 2009]. Reader and Laland

[2001] found, in a meta analysis, that, when sex-ratio was controlled for, male primates had a higher propensity to innovate than females. They speculated that this may be due to lower risk aversion in males driven by greater intensity of sexual selection. Behavioral characteristics, such as neophobia, perception, and cognitive differences, may also covary to some degree with social status, and may in turn affect innovation and social learning propensities [Lefebvre, 2000; Lewis, 2002, Reader et al., 2011].

There has been little consideration of the effect of factors such as group size and sex ratio on problem solving, innovation, and social learning. Plausibly, as group size increases, time spent on antipredator behavior typically decreases, creating more opportunities for exploration and innovation [Dukas and Kamil, 2000]. "Social facilitation" and "local enhancement" may act to promote greater rates of innovation and social learning in larger compared with smaller groups [Day et al., 2001; see Hoppitt

and Laland, 2008 for definitions]. Moreover, to the extent that the aforementioned sex difference in rates of primate innovation is the product of sexual selection, we might expect innovation rates to be sensitive to the sex ratio, since this would shape the degree of competition between individuals of the same sex. In addition, the sex ratio might plausibly affect access to desired resources such as foods, and hence problem-solving in foraging tasks, if being in the minority sex inadvertently enhances dominance relations relative to individuals in the majority sex, or affects the extent to which the members of each sex are observed, or have others in close proximity.

We investigated these factors in captive groups of ruffed lemurs (Varecia variegatassp.). Lemurs were chosen for two reasons. First, multiple groups are accessible to observation in zoos where they are housed in a range of group sizes and sex ratios. Second, there are reports of both female aggression toward males, and male deference to females, during foraging [Overdorff et al., 2005; White et al., 2007]. These effects are potentially sensitive to the sex ratio within the group, and might be expected to affect sex differences in the rate of problem solving, particularly the solving of foraging tasks. Although now regarded as two species, until recently ruffed lemurs were classified as two subspecies, partly due to the similarities in their ecology, social structure, and diet [Vasey & Tattersall, 2002]. The social structure of ruffed lemurs was once thought to be small family troops [Klopfer & Boskoff, 1979] although current thinking suggests that they live in a fission–fusion society with small foraging groups [Morland, 1991; Vasey, 2005]. Although some other lemur species (e.g. Lemur catta) have been found to have strong female dominance, there is a less conclusive pattern among ruffed lemur groups. Studies from both captivity and the wild have, however, reported female led aggression and feeding priority [Kaufman, 1991; Morland, 1991; Raps & White, 1995; Vasey, 2006]. Accordingly, there are reasons to anticipate natural variation in, and sensitivity to, group size and sex ratio in these primates.

There are conflicting findings concerning the problem-solving abilities of strepsirhines (of which lemurs are a member). Strepsirhines usually do not perform as well as other primate species in cognitive tasks, performing a smaller range of manipulations of puzzles, particularly with respect to unbaited manipulandi [Jolly, 1964a,b; Parker, 1974; Torigoe, 1985]. In experiments in which subjects have been presented with puzzleboxes, where they are required to slide open a horizontal door to access food, lemurs are reported to have shown little comprehension of the task, where even after solving, no marked refinement in method was observed [Anderson et al., 1992; Fornasieri et al., 1990]. However, scrounging opportunities with this task provided a little incentive for naïve individuals to learn the method.

In contrast, in two recent studies social learning has been reported in lemur species. Using a two-action task, Kendal et al. [2010] found evidence consistent with social learning in wild ring-tail lemurs (Lemur catta). While subjects did not tend to use the same access point that they had seen used over an alternative, nonetheless the technique used to open one of the access points appeared to be socially transmitted. When Stoinski et al. [2011] presented captive black-and-white lemurs with a two-action puzzlebox, they found significant differences between the actions performed by individuals depending upon the action they had seen demonstrated, although one action was more faithfully replicated than the other.

Similarly, some recent studies have also suggested that lemurs are capable of solving tasks requiring cognitive abilities not previously associated with them. For instance, Santos et al. [2005] found that both ring-tailed and brown lemurs were able to choose the correctly shaped one of two manipulandi to pull a reward toward them. Similarly, Ruiz et al. [2008] suggested that a group of lemurs, viewing a picture of a conspecific, were able to follow the depicted head orientation in order to access a box containing a reward. This suggests that lemurs may possess a rudimentary capacity for gaze following. Work by Genty et al. [2004, 2010] has also tested whether brown and black lemurs (Eulemur fulvus and Eulemur macaco) could learn a reverse-reward contingency task. Through repeated iterations and training, in common with some monkey species, some individuals learned to pick the smaller of two rewards, which resulted in them being given the larger reward [Genty et al., 2004, 2010].

In sum, while the studies detailed above have investigated problem solving, innovation, social learning, and a variety of other cognitive capabilities in lemurs, the social context in which these abilities are deployed has not been greatly examined. Here we explore the extent to which group size and sex ratio impact upon innovation and social learning in captive ruffed lemur groups. Seven zoo groups of Ruffed lemurs were presented with novel foraging puzzleboxes to investigate the extent to which the latency with which individuals approached and solved the puzzlebox was predicted by the size and sex ratio of the group. A second objective was to determine whether the lemurs in the groups were learning to use the puzzleboxes by social or asocial means.

METHODS

Subjects

In total, we studied 43 individuals, including one recently born-dependent infant whose sex was undetermined, in seven groups at four zoos, between May and August 2007 (Table I). Groups were housed in a variety of enclosure types, with differing group

TABLE I. The Primate Groups Used in This Studying Showing Composition of the Groups

Group	Zoo	Species	Group size	Males	Females	Proportion of males in group	Adults	Juveniles	Enclosure type
1	Woburn Safari Park	Black and white	9	9	0	1	9	0	Large walk-through
2	Twycross Zoo	Black and white	7	6	1	0.86	7	0	Indoor and outdoor areas of similar size
3	Fife wildlife park	Black and white	7	6	1	0.86	7	0	Large outdoor run with small indoor area
4	Twycross Zoo	Red	4	1	3	0.25	3	1[a]	Indoor and outdoor enclosures of similar size
5	Fife Wildlife Park	Red	4	1	3	0.25	4	0	Large outdoor run with small indoor area
6	Trotters World of Animals	Red	3	0	3	0	3	0	Large outdoor run with small indoor area
7	Trotters World of Animals	Black and white	9	6	3	0.66	8	1	Large outdoor run with small indoor area

[a]Still traveling on mother.

sizes and compositions and various husbandry regimes. Within these groups, which ranged from all male to all female, there were 29 males and 14 females. Sex ratios within each species (male:female) were: *V. rubra* 2:9, *V. variegata* 27:5. Although efforts were made to study groups with a range of group sizes and sex ratios, this was limited by the groups available at zoos within the United Kingdom. The precise age of individuals was not always known and for this reason individuals were allocated to age categories. These categories are based upon information from individual keepers and follow the classification of Rowe [1996]. Individuals in six groups were identified by their markings, however, to aid identification, individuals in the seventh group were marked with colored paints (Ritchey Super Sprayline). This method caused no distress and the markings were ignored after a few minutes by the subjects. Henceforth, groups with more males than females will be described as "male-biased" and groups with more females than males will be described as "female-biased."

Apparatus

Each group was presented with three puzzle-boxes (Fig. 1A–C), made of opaque white acrylic, each for one 30-min trial. The puzzleboxes followed the design of those used by Day et al. [2003] and Kendal et al. [2005] and required manipulation to gain access to sultanas, a highly desirable food to the lemurs.

The puzzleboxes were all designed to provide two, spatially separate and color differentiated, means of access to the food, each of which required the same type of manipulation. A mechanism inside each box prevented the two points of access from being used simultaneously. Ruffed lemur vision can be both di- and tri-chromatic so colors distinguishable for both di- and tri-chromatic individuals were used [Surridge et al., 2003]. The puzzleboxes were designed to be solved with ecologically valid extractive foraging actions, such as turning over leaf litter and exploring crevices. Puzzlebox 1 (the "fliptop" puzzlebox—Fig. 1A) was 170 mm long, 150 mm wide and 115 mm high; the doors had to be lifted to retrieve sultanas contained below. Puzzlebox 2 (the "round-top" puzzlebox- Fig. 1B) was a cylinder 152 mm in diameter and 117 mm tall. The top had two access points through which individuals reached and pushed aside a pendulum door to obtain sultanas. Puzzlebox 3 (the "cylinder" puzzlebox—Fig. 1C) was a cylinder 152 mm in diameter and 237 mm tall. At a height of 152 mm, there were two access points opposite one another, one bordered in red, one bordered in blue, individuals could reach into these access points and push a pendulum aside to obtain sultanas. The puzzleboxes were bolted to a piece of clear polycarbonate 500 mm by 300 mm. For each trial, two handfuls of sultanas as measured by LGD were placed in the puzzlebox (approximately 150 g).
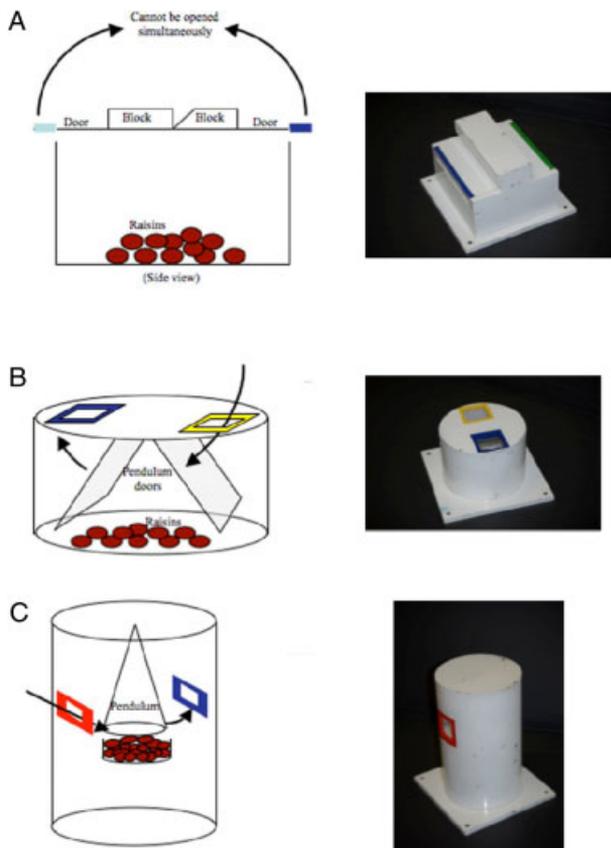
Fig. 1. Diagrams and photographs of the puzzleboxes used in the experiments. **A** is the fliptop puzzlebox, **B** is the round-top puzzlebox, and **C** is the cylinder puzzlebox. Arrows indicate the movement of the devices that prevent simultaneous manipulation of both options.

The puzzleboxes were located on the ground within the enclosures in the position that the animals were usually fed or the area which, according to the zoo-keeping staff, was most favored by the animals when they fed. If this area was not visible to the experimenters, the puzzlebox was placed in the closest suitable location. Before the start of the experiment, an area of 1 m around the puzzlebox was categorized as "in proximity," when in this area subjects were assumed likely to observe the individual manipulating the puzzlebox. When outside of the area individuals were categorized as "outside proximity" and it was assumed that they were unlikely to observe the exact movements of individuals manipulating the puzzlebox. Therefore, we used being "in proximity" during a conspecific's manipulation as a proxy for observation of that manipulation.

Procedure

Baseline data

As a baseline we gathered feeding data, on days both before and after the presentation of the puzzleboxes, forming two 30-min sessions per group.

These baseline trials were randomly distributed throughout the day, although none were carried out within the hour following a regular feed. Food used in regular feeds was placed on the ground in the same area used for puzzlebox presentation and spread over an area of less than $1 m^2$ (exact dimensions depending on the policy of the zoo).

All occurrences sampling was used to collect data on the latency to first feed of each individual, the number of feeding bouts (defined as the number of times an individual picked up a new piece of food having finished that which it was previously eating) for each individual, and the identity of conspecifics within 1 m proximity to an individual when it was feeding at the feeding site. These data were collected by LGD. In addition, the identity of individuals in proximity to the feeding site at 10-sec intervals was recorded using instantaneous sampling techniques [Martin & Bateson, 1993].

Puzzlebox data

Each group was presented with all of the three puzzleboxes, one at a time, in separate trials. The puzzleboxes were presented on consecutive days, with the order in which they were presented randomized. No more than one box was presented each day. Timing of the puzzlebox presentation was randomly distributed throughout the day, although puzzleboxes were not presented within the hour following a regular feed.

The puzzleboxes were introduced by an experimenter or by an experimenter and a zoo-keeper, depending upon the zoo. Observations started immediately after the puzzlebox was set down and continued for 30 min or until all sultanas were consumed.

Data were collected on the latency of each individual to first contact the box and for each unsuccessful and successful manipulation of the box. Box manipulations were defined as those that involved the use of front limbs or snout, focused on the food access points (the doors or pendulums behind which food was contained). Unsuccessful and successful manipulations were categorized as those manipulations of the puzzlebox when a subject did not and did gain food, respectively. For each unsuccessful or successful manipulation of the box, the color of the access point was recorded. For each contact and manipulation, whether unsuccessful or successful, the identity of conspecifics who were within 1 m proximity was recorded. If the first contact an animal had with the puzzlebox was a manipulation, this was recorded as both the first contact and the appropriate manipulation (either successful or not).

Analyses

The statistics program *R* was used for all data analyses [R-Development-Core-Team, 2006].

Predicting contact, manipulation, and successful solution of the puzzleboxes

We fitted Cox Models in the ''survival'' package [Therneau, 2010; Therneau & Grambsch, 2000] to determine whether the sex and age of an individual and the size and sex ratio of the group was correlated with the latency to contact the puzzle-box, latency to first manipulate one of the access points (whether successful or unsuccessful), and latency to first successfully manipulate the box. Survival analysis models, such as Cox Models, while initially designed for survival data, can be used for any time-to-event data. Here the event of interest is not death, but the contact, manipulation or solution of the puzzle-box. The Cox model allows us to estimate the effect that each independent variable has on the ''hazard rate'' for each of these events: the instantaneous rate at which the event of interest occurs. Fitting Cox Models allows a ceiling value to be applied, allowing those animals that did not manipulate or solve a particular puzzlebox to be included in the analyses as ''censored'' data points, without distorting the results, as would occur if ceiling values were included in a standard regression analysis. The Cox Model has the additional advantage that it does not make any assumptions about the underlying distribution of latencies [Therneau & Grambsch, 2000]. We refined the models, allowing first-order interactions, using the stepAIC function of the MASS package [Venables & Ripley, 2002]. All Cox Models were assessed to ensure that they obeyed the assumption that hazards were proportional across the 21 trials (that is, the presentation of the three puzzleboxes to each of the seven groups) [Therneau & Grambsch, 2000]. When constructing the models we were able to fit a frailty (random) effect allowing for within-individual correlation in latency, thus allowing the modeling of multiple events per subject without pseudo-replication. We examined the dfbeta residuals [Therneau & Gramsbsch, 2000] to assess the influence of each observation on the fitted model, finding that there were no extreme cases. As zoos had different management regimes, which were similar to all groups within a zoo, we examined zoo as a variable to account for these management differences. In all cases, we report the minimum adequate model, as judged by the Akaike information criterion (AIC), with the significance of the remaining terms judged by Wald tests.

Social learning

To examine whether animals were using social learning or asocial learning to successfully manipulate the puzzlebox, we used data on the color of the access point manipulated. This was then analyzed using Kendal et al.'s [2009] Option Bias method. This method assumes that when social learning is taking place individuals are more likely to choose the same option as others in the group (e.g. access point in the puzzleboxes in Fig. 1) than would be expected by chance; that is, social learning promotes within-group homogeneity in behavior. The method uses randomization of the data at the level of individuals to make an estimate of the likelihood that asocial learning could generate the observed level of homogeneity in the option choices exhibited in the study groups, and infers social learning if this probability is small (i.e. $P < 0.05$). The analysis was performed on all groups in which more than two individuals successfully manipulated the puzzlebox. Analyses were performed separately for each puzzlebox.

We also analyzed the data for social learning using model-fitting methods developed by Kendal et al. [2007]. Under these methods, data from the instantaneous ''proximity'' sampling, which was taken every 10 sec, were used to estimate values for four parameters:

(i) Intrinsic (asocial) movement (Mn) is defined as the proportion of naïve individuals (individuals who have not successfully manipulated the puzzlebox) outside the 1-m proximity area in the 10-sec timestep t, that move into proximity of the puzzlebox in the timestep $t+1$, when there have been no successful manipulations of the puzzlebox in timestep t. This was calculated only for time steps when the number of naïve individuals at distance from the puzzlebox was > 0.
(ii) Movement due to stimulus enhancement (s) is calculated from the proportion of naïve individuals who move into proximity at timestep $t+1$, when there was at least one successful manipulation of the puzzlebox at timestep t. The mean intrinsic (asocial) movement rate across the trial is subtracted in order to account for the rate at which individuals may approach the box without being attracted by a demonstration. It is scaled for the number of successful manipulations in timestep t in order to calculate the stimulus enhancement effect per successful manipulation.
(iii) Asocial learning (a) is defined as the proportion of naïve individuals in proximity to the puzzlebox at timestep t that successfully manipulate the puzzlebox at timestep $t+1$ when there has been no successful manipulation of the puzzlebox at timestep t.
(iv) Observational learning (b) is calculated from the proportion of naïve individuals at the puzzlebox at timestep t who observe an individual successfully manipulating the puzzlebox who subsequently go on to successfully manipulate the puzzlebox at timestep $t+1$. The mean asocial learning rate across the trial is subtracted in order to account for the rate at which individuals may solve the puzzlebox without using observational learning. It is scaled for the

number of successful manipulations in timestep t in order to calculate the observational learning effect per successful manipulation.

We calculated the mean rates of these parameters calculated across all timesteps for all individuals in the populations to estimate the effect of social and asocial learning and movement on the individuals in the group for each trial. The stimulus enhancement (ii) and observational learning (iv) parameters respectively quantify the difference in movement to the puzzle box, and solving the puzzlebox under social conditions from asocial conditions, for each time step. Therefore, we used a Wilcoxon signed ranks test to test whether these measures were significantly elevated under social conditions.

All research complied with the ethics requirements of the zoos and with UK legislation and with the American Society of Primatologists' Principles for the Ethical Treatment of Primates.

RESULTS

Baseline Data

In the baseline data, there were no significant effects of sex, age, sex ratio, group size, zoo or species on each individual's latency to first consumption of food.

Species Differences

There was no significant difference between the two species in latency to contact the puzzlebox (Black and white ruffed: median = 589, IQ range = 1,744.5, $n = 96$; Red ruffed: median = 780, IQ range = 1,747, $n = 33$; Mann–Whitney test: $W = 1,578.5$, $P = 0.978$). Similarly, there was no significant difference between the two species in latency to first manipulation (Black and white ruffed: median = 1,800, IQ range = 1,616.75, $n = 96$; Red ruffed: median = 1,800, IQ range 1,562, $n = 33$; Mann-Whitney test: $W = 1,603.5$, $P = 0.911$). Nor was there a significant difference between species of latency to first successful manipulation (Black and white ruffed: median = 1,800, IQ range = 905.75, $n = 96$; Red ruffed: median = 1,800, IQ range = 0, $n = 33$; $W = 1,519.5$, $P = 0.662$). As there were no significant differences between the two species, data were collapsed across species for all further analyses.

There were not enough degrees of freedom to include zoo and species in the survival analysis models. Therefore, as an additional test of species differences, models were constructed with species as a factor, without zoo as a factor. In these models, there was no significant effect of species, supporting our decision to collapse species for all further analyses. Henceforth, all analyses reported contain zoo as a factor, but not species.

Latency to First Contact

Thirty-eight of the 43 individuals contacted at least one of the puzzleboxes (Table III). When modeling the latency to first contact the puzzlebox, there were significant effects of *sex, sex ratio, group size, zoo*, and a *sex by sex ratio* interaction. There was a significant negative effect of group size (Wald test: $\chi^2 = 6.63$, df = 1.00, $P = 0.01$, Table IIa), with individuals in the larger groups tending to contact the puzzlebox later than those in the smaller groups.

Overall, there was a tendency for males to contact the puzzleboxes faster than females and for individuals in male-biased groups to contact the puzzlebox sooner than those in female-biased groups. These effects were overwhelmed by a significant interaction between sex and sex ratio (Wald test: $\chi^2 = 7.89$, df = 1, $P = 0.005$), meaning that the relative rate of first contact of males and females depended on sex ratio (95% confidence interval (CI) for slope, on the scale of the linear predictor: males: -0.52 to 6.57; females $2.18–12.24$). In female-biased groups, males tended to contact the puzzlebox sooner than females, whereas in male-biased groups, females tended to contact the puzzlebox sooner than males (see Fig. 2A for estimated effect sizes).

Individuals at Twycross Zoo showed a small but significant increase in latency to first contact the puzzleboxes relative to other groups in contacting the puzzlebox (Wald test: $\chi^2 = 9.89$, df = 1.00, $P = 0.0017$).

Latency to First Manipulation

Thirty-three individuals manipulated at least one of the puzzleboxes. The latency to first manipulation showed a significant effect of *zoo* and a significant interaction of *sex by group size*. Males were slower to manipulate the box than females when in larger groups, but females were slower to manipulate the box than males when in smaller groups (Wald test: $\chi^2 = 4.28$, df = 1.00, $P = 0.038$, Table IIb).

Groups at Twycross zoo, all other factors being equal, were more than three times slower to first manipulate the puzzlebox than those at Fife Wildlife Park (Wald test: $\chi^2 = 5.26$, df = 1.00, $P = 0.022$; 95% CI: 0.70–6.70).

Latency to Solve the Puzzlebox

All groups solved at least one of the puzzleboxes, with four of the seven groups solving all the puzzleboxes during the trials. Across all the groups, the mean number of puzzleboxes solved was 2.43. Of the 43 individuals, 23 solved at least one of the puzzleboxes (13 individuals solved one puzzlebox, 8 solved two, and 3 solved all three puzzleboxes).

The latency to solve the puzzlebox showed a significant effect of *zoo, sex, sex ratio, group size*, and

sex by sex ratio interaction (Table IIc). There was a negative effect of group size on hazard rate, suggesting that as group size increases individuals within the group were slower to solve the puzzlebox (Wald test: $\chi^2 = 7.79$, df = 1.00, $P = 0.00530$). The estimated effect size translates to a 15-fold increase (95% CI: 3.56–49.87) in the rate of solving as group size decreased across the range of group sizes observed (smallest group: $n = 3$, largest group: $n = 9$).

Although males solved the task faster than females, and although individuals in male-biased groups solved the tasks faster than individuals in female-biased groups, on average, there was once again a significant interaction between sex and sex ratio (Wald test: $\chi^2 = 11.85$, d.f. = 1.00, $P = 0.00058$; see Fig. 2C and D), meaning the relative rate of first successful manipulation of the puzzlebox by males and females depended on sex ratio (95% CI for slope: Males: −0.96, 9.62; Females: 4.86, 20.81). In female-biased groups, males tended to solve the puzzlebox sooner than females, whereas in male-biased groups, females tended to solve the puzzlebox sooner than males.

Individuals at Fife Wildlife Park were significantly faster to solve the puzzlebox than individuals at Twycross zoo, all other things being equal, with a rate of solving 10 times faster (Wald test: $\chi^2 = 8.28$, df = 1.00, $P = 0.004$, 95% CI: 0.39–37.29). Individuals at Trotters World of Animals were an estimated 32.6 times faster at solving the puzzlebox than individuals at Fife Wildlife Park (Wald test: $\chi^2 = 5.28$, df = 1.00, $P = 0.02200$, 95% CI: 2.33–457.2).

Social Learning

We found no evidence that social learning was taking place for any of the puzzleboxes. Using the Option Bias method [Kendal et al., 2009], we found with all three puzzleboxes that the bias for the use of one colored option over the other was not sufficiently extreme to reject the null hypothesis of asocial learning (fliptop puzzlebox: OB $\chi^2 = 38.6$, $P = 0.16$, $N = 15$ individuals; round-top puzzlebox: OB $\chi^2 = 6.51$, $P = 0.69$, $N = 8$ individuals; cylinder puzzlebox: OB $\chi^2 = 27.15$, $P = 0.42$, $N = 8$ individuals). Therefore, the data are consistent with the hypothesis that individuals chose options

TABLE II. The Output From the Cox Model Analyses of Factors Affecting the Latency of Lemurs to (a) Contact the Puzzlebox, (b) Unsuccessfully Manipulate the Puzzlebox, and (c) Successfully Manipulate the Puzzlebox

	Coefficient	Standard error of coefficient	Chi-squared	Degrees of freedom	*P*-value
(a)[a]					
Zoo (Trotters)	1.667	0.929	3.22	1.0	0.0730
Zoo (Twycross)	−1.359	0.432	9.89	1.0	0.0017***
Zoo (Woburn)	0.577	0.641	0.81	1.0	0.3700
Sex (Male)	2.237	1.065	4.41	1.0	0.0360***
Sex Ratio (M/F)	7.209	2.567	7.89	1.0	0.0050***
Group size	−0.815	0.317	6.63	1.0	0.0100***
Age (Juvenile)	0.745	0.659	1.28	1.0	0.2600
Sex (Male)*Sex Ratio	−4.185	1.663	6.34	1.0	0.0120***
Frailty (Individual)			18.29	11.4	0.0880
(b)[b]					
Zoo (Trotters)	0.915	0.967	0.90	1.0	0.3400
Zoo (Twycross)	−1.126	0.491	5.26	1.0	0.0220***
Zoo (Woburn)	1.110	0.686	2.62	1.0	0.1100
Sex (Male)	2.917	1.626	3.22	1.0	0.0730
Sex Ratio (M/F)	2.472	2.051	1.45	1.0	0.2300
Group Size	−0.234	0.291	0.64	1.0	0.4200
Sex (Male)*Group Size	−0.483	0.233	4.28	1.0	0.0380***
Frailty (Individual)			21.26	13.6	0.0830
(c)[c]					
Zoo (Trotters)	3.48	1.516	5.28	1.0	0.0220***
Zoo (Twycross)	−2.28	0.793	8.28	1.0	0.0040***
Zoo (Woburn)	1.87	0.927	4.05	1.0	0.0440***
Sex (Male)	4.54	1.654	7.54	1.0	0.0060***
Sex Ratio (M/F)	12.84	4.070	9.95	1.0	0.0016***
Group size	−1.32	0.473	7.79	1.0	0.0053***
Sex (Male)*Sex Ratio	−8.52	2.475	11.85	1.0	0.0006***
Frailty (Individual)			12.11	7.68	0.1300

[a]Variance of random effect = 0.276, *I*-likelihood = −337.2, Likelihood ratio test = 55.8 on 17.2 df, $P = 5.76 \times 10^{-06}$, $n = 129$.
[b]Variance of random effect = 0.439, *I*-likelihood = −265.8, Likelihood ratio test = 54 on 17.8 df, $P = 1.63 \times 10^{-05}$, $n = 129$.
[c]Variance of random effect = 0.276, *I*-likelihood = −337.2, Likelihood ratio test = 55.8 on 17.2 df, $P = 5.76 \times 10^{-06}$, $n = 129$.
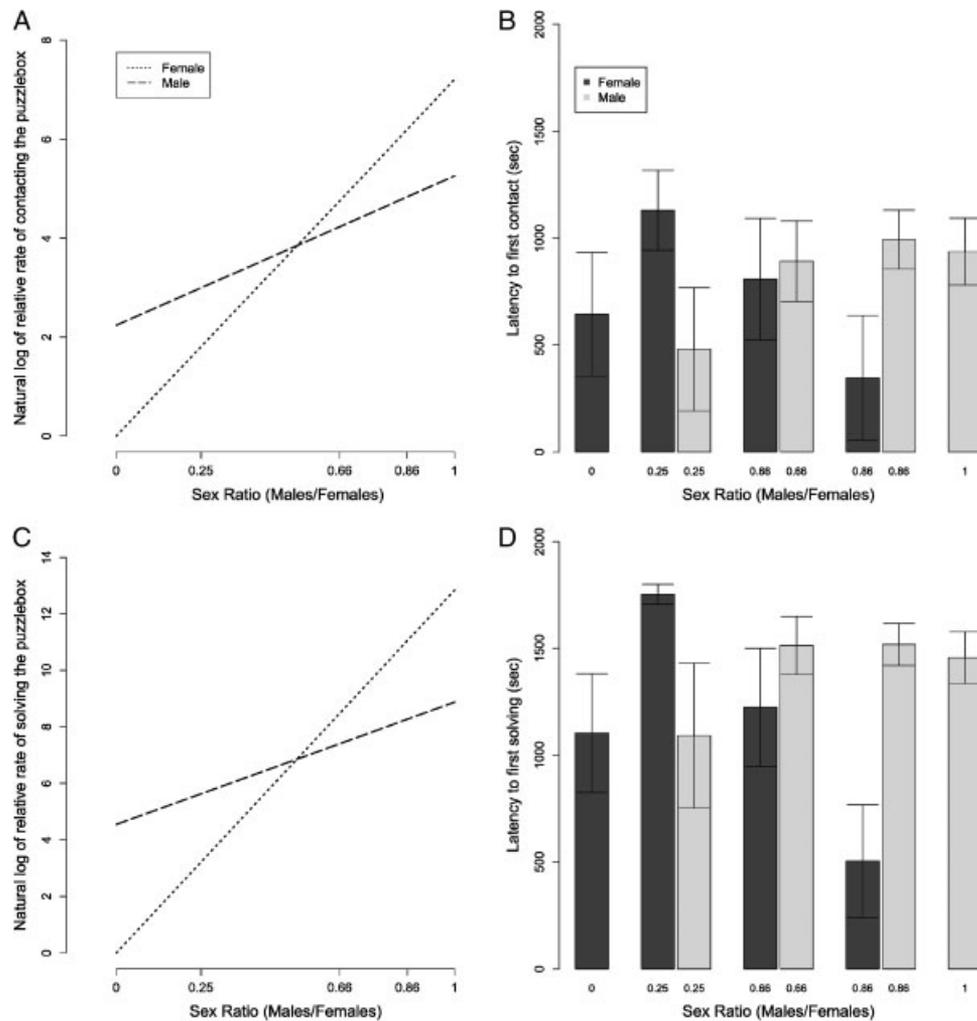
Fig. 2. (**A**) Interaction plot showing the natural logarithm of the relative rate of first contact of the puzzlebox plotted for males and females across the sex ratios present in the experiment relative to females in an all-female group. Rates are calculated using hazard rate from the Cox Model in Table IIa. (**B**) The mean latency ($\pm$standard error) to first contact of the puzzlebox for females (dark gray) and males (light gray) across the sex ratios present in the experiment. (**C**) Interaction plot showing the fitted model (Table IIc) for the relative rate of solving the puzzlebox for males and females across the sex ratios present in the experiment. Effects are plotted on the scale of the linear predictor used in a Cox model. The plot therefore shows the natural logarithm of the ratio with the rate with that of the baseline, in this case, females in all-female groups. (**D**) The mean latency ($\pm$standard error) to first solve the puzzlebox for females (dark gray) and males (light gray) across the sex ratios present in the experiment. All latencies are in seconds.

independently of the other members of their group in all three tasks.

Using the modeling methods developed by Kendal et al. [2007], Figure 3 shows that the mean values for both of the social parameters were significantly different from zero (Wilcoxon test: Stimulus enhancement (s): $V = 0$, $P = 0.0225$; Observational learning (b): $V = 0$, $P = 0.0360$). However, the mean rates of the social parameters (stimulus enhancement and observational learning) were negative, indicating that individuals were less likely to approach and use the box, respectively, if others in the group had been using the puzzlebox in the previous time step, suggesting that the puzzlebox solution was not socially transmitted, but rather

inhibited by other individuals learning to solve the puzzlebox.

Rates of intrinsic movement, that is the movement individuals make without any social influence (mean = 0.0196), were significantly higher than movement toward the puzzlebox induced by the presence of another individual interacting with it (mean = -0.0133) (Paired Wilcoxon: $V = 78$, $P = 0.00253$). The same occurred with the learning parameters, with asocial learning rates (mean = 0.0136) significantly higher than rates of observational learning, that is the rate of transition from naïve to informed after being in the 1-m proximity zone during a conspecific's puzzlebox solution (mean = -0.0118; Paired Wilcoxon: $V = 28$, $P = 0.0225$).

TABLE III. The Number of Individuals Contacting and Solving Each Puzzlebox by Group, Including the Latency of the First Individual to Contact and Solve Each Puzzlebox, in Seconds

Group	Puzzlebox	Number contacting puzzlebox	Latency to first contact (sec)	Number solving puzzlebox	Latency to first solving (sec)
1	Circular	3	50	1	145
	Cylinder	6	17	2	163
	Fliptop	7	6	5	40
2	Circular	3	6	1	261
	Cylinder	4	46	1	267
	Fliptop	1	341	0	NA
3	Circular	7	1	3	185
	Cylinder	5	1	2	76
	Fliptop	5	57	5	104
4	Circular	2	780	0	NA
	Cylinder	2	46	0	NA
	Fliptop	2	47	1	909
5	Circular	3	13	1	72
	Cylinder	2	53	0	NA
	Fliptop	3	26	2	160
6	Circular	2	10	1	24
	Cylinder	2	16	2	16
	Fliptop	2	42	1	371
7	Circular	7	6	3	79
	Cylinder	5	9	2	220
	Fliptop	5	12	3	32
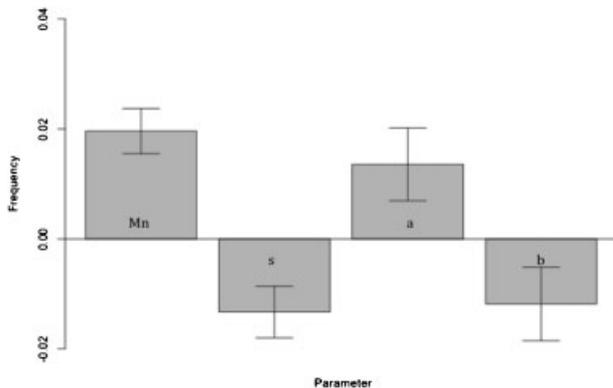
Fig. 3. Mean for the parameters in social learning modeling ($\pm$SE). Mn is intrinsic (asocial) movement, s is stimulus enhancement, a is asocial learning, and b is observational learning.

There were no significant correlations between any of the four fitted parameters.

Kendal et al. [2007] suggested that latency to solve a task should be negatively correlated with parameters critical for the solving of the task, as if the parameter was critical, in those populations in which it was more prevalent, individuals would learn to solve the puzzlebox sooner. Neither of the movement parameters, nor observational learning, was correlated with the latency to solve the puzzlebox (Intrinsic Movement: Spearman's correlation: -0.310, df $= 11$, $P = 0.303$; stimulus enhancement: Spearman's correlation: 0.461, df $= 11$, $P = 0.113$; observational learning: 0.538, df $= 11$, $P = 0.581$).

However, asocial learning (that is, transition from naïve to informed without observation of a conspecific's task solution) was found to be negatively correlated with latency to solve the puzzlebox (Spearman's correlation: -0.804, df $= 11$, $P \leq 0.001$) implying that individuals learned asocially how to solve the puzzlebox to retrieve the reward.

DISCUSSION

We carried out an experimental study to investigate the effects of group size and sex ratio on latency to contact, manipulate, and solve novel foraging puzzleboxes in zoo groups of ruffed lemurs. We found that latency to contact and to solve the puzzleboxes was significantly affected by the size of the groups. On average, the larger the group the slower individuals were to contact and solve the puzzlebox. This result contrasts with other work which suggests that larger groups of fish and birds are less neophobic than smaller groups and are more able to discover novel objects as there are simply more pairs of eyes to observe the environment [Day et al., 2001; Greenberg, 2003]. However, in the case of our lemurs there may be group dynamics in which differences between ranks in dominance hierarchies are wider in larger groups. This would ensure that some individuals, in larger groups, are more able to dominate the puzzlebox than individuals in smaller groups, meaning that subordinate individuals are unable to gain access to the puzzlebox until later in

the trial [Coussi-Korbel & Fragaszy, 1995; Fragaszy & Visalberghi, 2004].

With respect to both the latency to solve the puzzlebox and the latency to contact the puzzlebox, there was a significant interaction effect of sex and sex ratio. Both males and females in male-biased groups contacted and solved the puzzlebox sooner than males and females, respectively, in female-biased groups. However, females were faster than males to contact and solve the puzzlebox in male-biased groups but not female-biased groups. The ability of females to gain faster access to the puzzlebox, and to solve it sooner, than males in male-biased groups may relate to the reported female dominance in these species [Overdorff, et al., 2005]. It has been argued that the apparent female dominance observed in lemur species could have evolved in two ways, either due to female agonistic superiority or due to male deference [Kappeler, 1990; Pereira et al., 1990; White et al., 2007]. It is possible that the female dominance effect is only a feeding priority and does not extend to other domains. Alternatively, male deference may represent a reproductive strategy in which males defer to females when feeding to seek mating priority with them, thus females gain leverage over males [Kappeler, 1990; Lewis, 2002].

Our data suggest that male rates of contact with the puzzlebox and solving the puzzlebox increase as the groups become more male-biased. However, the female rate of contact and solving increases even more rapidly as the group becomes more male-biased, thus females outstrip males at contacting and successfully manipulating in male-biased groups. Our findings suggest that females, over a period of time, may be able to increase their status in the groups as they become rarer. In female-biased groups, it is likely that dominance hierarchies among the females resulted in some females being much less likely to contact or solve the puzzlebox than others. However when in a group with a higher proportion of males, females were more likely to be able use the puzzlebox sooner than in female-dominated groups, since there are fewer other females that might be dominant over them.

Data from the baseline trials do not suggest female dominance, as females were not significantly quicker to eat than males, regardless of group sex-ratios, and juveniles were not significantly slower than adults. However, as food in baseline trials was dispersed over a larger area than in the puzzleboxes any effect of male deference or female feeding priority was likely reduced as females could not monopolize the dispersed food as effectively [White et al., 2007]. Novel food resources, particularly those that contain highly desirable food, such as in our puzzlebox, may also provide a prized resource and are therefore more likely to be monopolized.

Our study has shown that lemurs can learn novel cognitive tasks. However, species-specific dominance relationships probably influence how individuals interact with objects and innovate [Coussi-Korbel & Fragaszy, 1995; Fragaszy & Visalberghi, 2004]. Our data are also consistent with other studies that have failed to find social learning in lemur species [Anderson et al., 1992; Fornasieri et al., 1990; but c.f. Kendal et al., 2010; Stoinski et al., 2011]. The Option Bias method found no evidence for social learning in any puzzlebox.

This conclusion of a lack of social learning in the lemur groups is supported by our modeling of learning processes where we found that only the asocial learning parameter was significantly negatively correlated with the latency of the group to solve the puzzlebox. This suggests that asocial learning was critical to the solving of the puzzleboxes, providing further evidence that the lemurs did not engage in social learning in this context, but rather learned through trial-and-error. Indeed when modeling the data we found a negative effect of the two social learning parameters, which is consistent with Anderson et al. [1992] who found that there was a socially mediated inhibition of performance in some groups when presented with novel feeding puzzleboxes. Thus, we do not conclude that lemurs are unable to learn socially and indeed in circumstances where social inhibition is weakened there is reason to expect social learning [Kendal et al., 2010]. Although the occurrence of aggression was generally low during the trials in this experiment, dominance-related effects cannot be ruled out. The presence of high-ranking individuals may inhibit low-ranking individuals from approaching the puzzlebox, in order to avoid aggression [Custance, pers comm., Fragaszy & Visalberghi, 2004]. Social hierarchy may have a significant impact upon the ability of individuals in a group to learn socially, either by subordinates playing dumb [Drea & Wallen, 1999] or by restricting the spread of information due to the tolerance of individuals to one another [Coussi-Korbel & Fragaszy, 1995].

Theory suggests that individuals may be more likely to copy difficult or costly tasks than simple ones [Boyd & Richerson, 1985]. It is possible that the puzzleboxes were not of sufficient difficulty for the lemurs to require social learning in order to solve them. However, this explanation for the lack of social learning seems unlikely, compared with the role of social hierarchy, as social learning was evidenced for at least one of these three puzzleboxes in callitrichid monkeys [Kendal et al., 2009].

In summary, our data demonstrate that group size and sex ratio can mediate the propagation and spread of innovations within groups of lemurs. This effect may be due to restricted individual access to a resource, here mediated by inhibition of proximity or deference to another, or the amount of attention that an individual can devote to a resource (being little when a subordinate individual) when in proximity to it.

ACKNOWLEDGMENTS

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