EVIDENCE FOR SOCIAL LEARNING IN WILD LEMURS (*LEMUR CATTA*).

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ABSTRACT

Interest in social learning has been fuelled by claims of 'culture' in wild animals. These remain controversial because alternative explanations to social learning, such as asocial learning or ecological differences, remain difficult to refute. Compared to in the laboratory, the study of social learning in natural contexts is in its infancy. Here, we apply two new statistical methods (Option Bias Analysis and Network Based Diffusion Analysis) for the first time to data from the wild, complemented by standard inferential statistics. Contrary to common thought regarding the cognitive abilities of prosimian primates, we find evidence consistent with social learning, within sub-groups, in the Ring-tailed lemur (*Lemur catta*), supporting the theory of directed social learning (Coussi-Korbel & Fragaszy, 1995). We also caution that, as the tool-box for capturing social learning in natural contexts grows, care is required in ensuring the methods employed are appropriate, in particular regarding social dynamics of study subjects.

Running Head: social learning in wild lemurs

Key words: social learning, lemur, rank, directed social learning, option-bias analysis, network based diffusion analysis.

INTRODUCTION

Social learning, or learning from others, is of widespread current interest because it potentially provides a means by which animals can acquire adaptive information about their environment rapidly and efficiently. Social learning is thought to underlie the rapid diffusion of novel behavioral variants, inter-population variation in behavior, and cultural traditions, in animals from fishes to apes (Lefebvre & Palameta, 1988; Rendell & Whitehead 2001; Warner, 1988; Whiten, 1999). Interest in animal social learning has also been fuelled by reports of intra- and inter-population variation in the behavioral repertoires of animal populations, spawning claims of 'culture' in apes (McGrew 1998; van Schaik et al., 2003; Whiten et al., 1999) cetaceans (Krützen et al., 2005; Rendell & Whitehead 2001), and monkeys (Leca, Gunst, & Huffman, 2007; Perry et al., 2003). However, claims that these data demonstrate animal cultures remain controversial because alternative explanations to social learning, such as genetic proclivities or ecological differences, remain difficult to refute (see Laland et al., 2009) despite innovative work in captivity (eg. Whiten, Spiteri, Horner, Bonnie et al. 2007). Moreover, as learning is frequently functional, adaptive, based on genetic proclivities, and responsive to ecological resources, the current 'ethnographic' method, which proclaims culture where the alternatives can be dismissed, is vulnerable to excluding genuine cases of social learning. Thus, compared to the controlled laboratory study of social learning, and despite pioneering work with apes and cetaceans (see Whiten et al., 1999; Sargeant & Mann 2009; Whitehead, 2009), we are lacking in tools for unequivocally capturing social learning in natural contexts, whether in the wild or captivity.

Recently, however, several statistical methods have been created to aid in the task of identifying social learning in naturalistic contexts (eg. Boogert, Reader, Hoppitt, & Laland, 2008; Kendal, Kendal, & Laland, 2007; Kendal, Kendal, Hoppitt, & Laland, 2009a; Franz & Nunn, 2009; Matthews, 2009). We presented a solution to the problem, in the form of a method known as *option-bias analysis* (Kendal et al., 2009a). The method is based on the well-established premise of social learning research, that –when ecological and genetic differences are accounted for - social learning can generate greater homogeneity in behavior between animals than expected in its absence (but see Thornton & Malapert 2009). For example, when probing for termites in their mound, chimpanzees are reported to use either a short- or long-twig method (Whiten et al., 1999) and when manufacturing 'wide' *Pandanus* leaf tools New Caledonian Crows, *Corvus moneduloides*, have three variants available to them (Holzhaider, Hunt & Gray, this issue). If this behavior is learned socially then a given population may disproportionately use one method, whereas if it is learned asocially one might expect use of both methods in proportion to their opportunity and profitability. Thus, provided alternative forms of bias can be ruled out (e.g. genetic or ecological), the level of homogeneity of behavior within a population potentially provides a metric that can be used probabilistically to detect a social influence on learning. In order to test for social learning in the observed data, however, the probability that option biases of the magnitude observed in the actual data could be the result of chance or asocial learning alone must be computed.

The option-bias method compares the observed level of homogeneity to a sampling distribution generated utilizing randomization and other procedures, allowing claims of social learning to be evaluated according to consensual standards. The approach circumvents the inherent problems arising from the lack of a controlled ‘demonstrator-observer’ scenario, tasks that afford few alternatives for solution, incomplete data, small group sizes and low statistical power. Thus it was hoped that the method would prove useful to other researchers attempting to distinguish social and asocial learning in social contexts and provide a new and potentially valuable tool for the identification of cultural traditions. Accordingly, the R code is freely available[1] for others to apply this method, which can be deployed within controlled experimental and captive animal settings and to natural datasets too. Crucially, the method does not require the researcher to record the inception and initial spread of the trait which further enhances its utility in natural populations. The method was illustrated through application to data from groups of Callitrichid monkeys provided with novel two option extractive foraging tasks, providing evidence that social learning could be distinguished from unlearned processes and asocial learning, and revealing that the monkeys only employed social learning for the more difficult tasks (Kendal et al., 2009a). The method was further validated against published datasets, showing social learning using standard statistics, and through simulation, and exhibited higher statistical power than conventional inferential statistics (ibid).

An alternative technique, recently developed by Franz and Nunn (2009; this issue) and extended upon by Hoppitt and colleagues (Hoppitt, Boogert & Laland, 2010; Hoppitt, Kandler, Kendal & Laland, this issue) is Network Based Diffusion Analysis (NBDA). Here, rather than focusing on homogeneity of behavior, the social network of a group is utilized to

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[1] Much of the freeware for these methods can be found at http://lalandlab.st-andrews.ac.uk/freeware.html

identify social learning. The method is based on the intuitive yet understudied and unsupported (see Boogert et al., 2008) theory of directed social learning (Coussi-Korbel & Fragaszy 1995) that information is transmitted or directed through sub-sections of non-human primate populations at different rates according to age, sex, status or association patterns. Accordingly in NBDA social learning opportunities are assumed to be constrained by a social network such that the probability of learning from skilled individuals is dictated by the strength of connection to them. The approach requires as inputs (i) a social network which may be asymmetrical, for example grooming, or symmetrical, for example proximity and (ii) diffusion data represented as either the order of acquisition - (OADA, Hoppitt et al. 2010) or timing of acquisition - (TADA, Franz & Nunn, this issue) of a novel behavior pattern. In the extended NBDA/TADA method, agent based models of social and asocial learning (relating to the social network) and pure asocial learning (regardless of the network) are fit to the observed diffusion data using maximum likelihood estimation. The model with the best fit to the data is then identified using the Akaike information criterion. The authors designed the method as a more reliable alternative to the use of diffusion curve analysis (Reader, 2004) in assessing evidence for social learning in free-living animals and as such made the R code freely available alongside their paper (Franz & Nunn 2009) and assess its utility in the field (this issue). Although the method requires more substantial data than the option-bias method it has the potential to be used to asses the evidence for social learning strategies (Laland, 2004), especially regarding from whom individuals learn. Development of the embryonic empirical investigation of social learning strategies (Kendal, Coolen, van Bergen & Laland, 2005; Kendal, Coolen & Laland, 2009b) in the wild can contribute extensively to our understanding of the evolution of human cultural capacities by facilitating comparative analysis.

These alternative simulation and modeling methods will be most powerful when used alongside more conventional inferential statistics such as those used by other researchers of free-living groups. For example, Perry (2009) in analysis of an extensive long-term data set used generalized linear models to investigate the assumption that the proportion of learned behavioral variants observed by an individual predicts the proportion of learned behavioral variants performed. Specifically, such regression analyses revealed that the technique most frequently observed for accessing seeds from *Luehea candida* fruits, during development, significantly predicted the technique adopted by female, and to a lesser extent, male white faced capuchins (*Cebus capucinus*) in the wild. An alternative measure of the influence of observational opportunities on subsequent learning is an investigation of the relationship between the ‘learning time’ (latency between first contact and first success) and the latency of first contact (Day, 2003; Boogert et al., 2008). Here, a negative relationship is assumed to indicate social learning as those who contacted the task later are thought to have had increased observational opportunities and would thus have a reduced ‘learning time’. Finally, we may profit, if only opportunistically where groups are not exposed to demonstrations of a novel behavioral variant by the experimenter, from techniques developed by researchers using the ‘two group with control’ method in captivity (e.g. Hopper et al., 2007; Whiten, Horner, & de Waal, 2005). Consistent with the option-bias assumptions, traditions are identified by determining whether there is a statistical difference between groups, seeded with demonstrators trained in alternate techniques to gain a resource, in the proportion of one (of the two) alternative techniques used.

Our aim is to use a variety of methods in combination to test for social learning in foraging data collected from wild ring tailed lemurs (*Lemur catta*), and to reflect on any constraints upon their use and other methodological considerations. As the observation of a novel behavior (or innovation) in the wild is opportunistic, we adopt the strategy of a field experiment (see Reader & Biro, this issue). Here we introduce artificial extractive foraging tasks and monitor the spread of the novel behavior pattern. This has the advantage that we may observe the inception of the novel trait and test for social learning to solve the task and also the preference for extraction variants afforded by the task’s design. Also as transmission of information may only occur when the task is in place, we may be sure that we do not miss any transmission events – a common worry with more opportunistic data collection regarding naturally occurring ‘tasks’(eg. termite fishing) in the field (see Franz & Nunn, this issue).

Lemur catta live in multimale-multifemale groups of 5 to 27 individuals with a 1:1 sex ratio, female philopatry and male dispersal (Gould 1997; Nakamichi, Rakototiana & Koyama, 1997). They exhibit top-down ‘despotic hierarchies’ (Sapolsky, 2005) and adult females are dominant over males (Jolly 1996) and although rank order in both sexes is usually linear, it can occasionally be triangular (Koyama, Ichino, Nakamichi & Takahata, 2005). Unlike Cercopithecine monkeys, adult daughters are not always ranked below their mothers (Koyama *et al*., 2005). Mothers, daughters and sisters often form affiliated pairs or triads, while barely tolerating more distantly related relatives (such as cousins or granddaughters) (Jolly & Pride, 1999). There are conflicting reports regarding the cognitive abilities of lemurs with some reporting minimal comprehension when presented with novel foraging tasks (Fornasieri, Anderson, & Roeder, 1990; Anderson, Fornasieri, Ludes, & Roeder, 1992) or objects (Jolly, 1966), and others suggesting that lemurs learn to use tools as quickly as haplorhine species and, in some cases, more flexibly (Santos, Mahajan & Barnes, 2005). Lemur species are, however, understudied in the field of social learning. An early open diffusion study of a single captive group of *Lemur catta* faced with a novel foraging task (Kappeler, 1987), whilst describing possible patterns of innovation and social transmission, did not attempt to assess the learning mechanisms (social or asocial) involved. Likewise, a study of the naturally occurring phenomenon of 'drinking from tails' in captive *Lemur catta* although suggestive of social learning offered no information regarding the transmission of the novel behavior pattern as it was already well established in the group (Hosey, Jacques & Pitts, 1997). Several studies of the introduction of novel foraging tasks in lemurs have, however, reported a strong influence of social rank upon access to novel tasks and consequent expression of the novel trait in individuals, whether through social or asocial learning (Kappeler, 1987; Anderson et al., 1992; Fornasieri et al., 1990).

In this paper we aim to apply the Option Bias and NBDA methods for the first time to data from the wild, complemented by standard inferential statistical techniques. In doing so, we examine the use of the methods in a species with strong social hierarchies and in particular extend the option bias method for use with tasks of more than two options and with underlying biases in their use.

METHODS

II Data Collection

Study Site and Participants

Two medium-sized groups of ring-tailed lemurs (*Lemur catta*) from Berenty Reserve, Southern Madagascar, were selected for the purposes of this study. Berenty Reserve consists of a 200 ha area of natural gallery forest, transitional scrub and spiny desert (Budnitz & Dainis, 1975). The home ranges of the selected lemur troops overlapped with tourist accommodation so they were very well habituated to humans. In addition, the demographic histories of most troop members were known since they have been studied on a regular basis since the 1990s (Nakamichi, Rakototiana & Koyama 1997).

The two study troops were given the letter and number codes YF and T1B by Koyama and his colleagues, henceforth labeled group 1 and group 2, respectively. Group 1 comprised 13 lemurs: six adult females (three years or older), two unweaned infants, one juvenile female (1-2 years old) and four adult males. Group 2 consisted of 15 lemurs: six adult females, three unweaned infants, one juvenile female and five adult males. The ages, dominance ranks (as indicated by Nakamichi) and kin relationships are illustrated in figure 1.

[Figure 1 – group diagram]

Materials

The lemurs were presented with a two-action puzzle feeder (Figure 2). The feeder was comprised of an 8cm long by 8cm wide transparent Perspex or plexiglass tube that was enclosed at each end by 1cm thick pieces of wood. A 4cm diameter hole was cut halfway down the length of the tube into which was inserted a plastic food cup. A hinged aluminum metal flap (6cm wide by 7cm high) was attached to the tube. The flap was curved so that it fitted snugly against the tube. A 2cm high by 1cm wide aluminum rod was fixed just above the flap's hinge. The rod ensured the flap fell back into place over the food cup unless it was continually held up. The flap had a 4cm diameter hole cut into it, which was aligned with the food cup. A 0.5cm thick aluminum disc of 5cm diameter was fixed to the flap just above the hole using a metal pin. A lug-nut was fitted to the top right of the disc so that it would only swivel to the left. A combination of banana pellets, mashed banana, papaya and custard apple was loaded into the food cup as reinforcement. Thus, the lemurs could access the food reward by either *swivelling* the disc to the left or lifting/*flipping* the flap (Figure 2a&b).

To prevent monopolization of a single task by dominant individuals, four to six tubes were presented simultaneously during each day of testing. The tubes were positioned approximately 30cm from the ground and were wedged between forks in the branches of trees or between the trunks of close growing saplings. Pilot studies using small open wooden boxes indicated that if test apparatus were placed too close together, one or two high ranking lemurs would monopolize access. Thus the tubes were presented at two sites 10 to 15 meters apart. At each site, the tubes were placed three to four meters apart from one another (Figure 2c). The lemurs' behavior was recorded using two Sony camcorders fixed to tripods.

[Figure 2 – task apparatus here]

Procedure

Group 1 was tested first (between 4th to the 14th of October 2006). Testing commenced at 07:00 on each of ten consecutive days. Each testing session was 30 minutes long. There were two experimenters each of whom stood by one of the two camcorders and called out the names of each lemur that approached the tubes. The tubes were removed, refilled with food and replaced after 15 minutes of testing.

Following completion of testing with group 1, testing commenced with Group 2 (between 21st October to 7th November 2006). Since group 1 showed a preponderance of flipping over swivelling, group 2 was seeded with swivelling demonstrators to ascertain whether they would learn a relatively non-preferred method. Two tubes, that could only be swivelled as the flaps were screwed shut, were placed into position. The two highest ranking females (TP and PE) monopolized these tubes during the demonstration phase and quickly learned to swivel. The tubes were presented in this manner, for 15 minutes, on each of eight consecutive days. During that time, only one other female (HC: the three year old daughter of PE) managed to gain access on one occasion and swivelled the disc twice. Thus, she was counted as a demonstrator thereafter. Throughout the demonstration phase only HC, PE and TP approached the tubes. Most of the other lemurs sat between 5 and 10 meters away; if they approached any closer they were chased away by TP or PE, thus we are confident that non-demonstrators only observed task manipulations, rather than interacted with the task, during this phase.

After the demonstration phase, tubes that could be opened by either swivelling or flipping were placed in the same configuration as for group 1 for 30 minutes on each of 10 consecutive days (Figure 2). The same procedure was followed as when testing group 1 except for one day. On day 6, a subgroup of three males was located approximately 30 meters away from the usual testing area. Since males were habitually chased away by females whenever they approached a tube, we took this opportunity to give them access to the apparatus. Thus, we placed the tubes in trees adjacent to the peripheral subgroup of males rather than in the usual testing area.

Once testing was complete, two independent observers analyzed the digital video film of the testing sessions. The latency since session start, the subject’s letter code, their action upon the tube (Table 1), the tube part manipulated (disc, right side of flap, left side of flap or bottom of flap), the body part used (nose, left hand or right hand), whether the subject was successful or unsuccessful in obtaining a food reward, who was in proximity and at what distance from the tube (within zones of approximately 0-1m and >1m to 3m) and whether they were observing (the face being orientated towards the task) during a conspecific's task manipulation were noted. There was 'very good' (Altman 1991) inter-observer reliability according to Cohen Kappa scores for two sessions from one site (5% of total testing with 273 separate task manipulations) for the action (0.85) and body part used (0.94), as well as for proximity (<1m and >1-3m) of conspecifics to the task (0.92) and whether they were 'observing' during manipulations (0.83).

Baseline data were collected in the mornings and afternoons after testing to determine social dynamics outside of testing sessions. Proximity data were collected using focal subject sampling. Each focal session was 3 minutes long with data taken as point samples each minute. The identification of each lemur that was within one metre proximity of the focal subject was noted. Sixty such focals were collected per lemur between 30th September to the 23rd of November 2006. The subjects were sampled in a randomized order.

[Table 1 – definitions]

Asocial Learning Controls

Control subjects were four adult male ring tailed lemurs (ages 6-7 years) living in a social group at Zoo Atlanta. Each lemur was tested individually and out of visual range of the other group members. For each subject a device similar to that described above, was loaded with 5 grapes and hung from the cage mesh with both defenses (flip and swivel) enabled before the start of the session. Sessions began when a single subject was shifted into the cage with the device and ended after 10 minutes (for 4 of 6 sessions) or after 10 minutes of no interaction with the device (2 of 6 sessions). Two subjects that interacted with the device immediately received one session; one subject refused to interact with the device on his first session but did successfully interact on a second session. The final subject refused to interact with the device on two sessions; given his fear response to the device, no additional sessions were attempted. A video camera set up in an adjacent cage at a 45 degree angle was used to record all interactions with the device, and data on 1) latency of and method used (swivel or flip), 2) body part used (nose or L or R hand) and 3) success/no success in obtaining a food reward were extracted from the video recording.

II Statistical Methods

Assessing Social Dynamics

During testing of each group DC made qualitative estimates of any apparent sub-groupings. Sociograms, a systematic method for representing subjects as points or nodes, with the relationships between them illustrated using lines (Moreno 1960), were constructed using the baseline proximity data collected outside of testing sessions. Finally, to test whether our assignment of individuals to subgroups was reasonable, we carried out permutation (randomization) tests on a measure of modularity (Newman and Girvan 2004, see Kasper & Voelkl 2009) in a directed social network within each group, where the strength of the connection (edge weighting) between any two individuals was measured by the number of times two individuals were within 1m proximity of each other during the baseline data collection sessions (using the modularity function in the R (2.10.1) package 'igraph' (v0.5.3), written by Gabor Csardi). Individuals that were members of a group but not assigned to a subgroup were assigned membership to their own unique singleton 'subgroups'. The null distribution of modularity scores was derived by randomly assigning individuals to subgroups, repeated over 10,000 iterations (keeping subgroup sizes constant).

Standard Inferential Statistics

In all analyses the behavior of the trained demonstrators (found only in group 2) is excluded, with the exception of task manipulations produced by the demonstrators that are observed by conspecifics, which are incorporated into analyses of the predictive power of observational opportunities on behavior. Non-parametric tests were used when parametric assumptions were not met. Where multiple tests were conducted, the family-wise error rate was controlled for by modifying the significance level of alpha, designated in the text as α^*. For each family of tests $\alpha^* = \alpha/c$, where α=0.05 and c denotes the number of tests.

To examine 'learning time' in the despotic *Lemur catta* we adapted the method of using success latency minus contact latency (Day, 2003), developed with the more egalitarian Callitrichid species. Thus, we calculated a 'total time at the task prior to success' [success latency - (contact latency + time not present at task)] to account for the skewed pattern of access to resources within groups (Sapolsky, 2005). In addition, we did not assess the relationship between learning time and task contact latency as an indicator of social learning, as this assumes that later contactors have observed more task manipulations than earlier contactors (Day, 2003; Boogert et al., 2008). Instead, we investigated the relationship between 'learning time' and the number of successful manipulations observed prior to success, as the latter provides a direct measure of observational opportunities.

Option-Bias Analysis

As emphasized by Kendal et al. (2009a) the underlying assumption of the method – social learning leads to homogeneity of behavior – calls for researchers to assess whether homogeneity is expected in their context, to account for other factors (eg. genetics, ecology) responsible for homogeneity, and to use a level of population analysis appropriate to the given context. It was also emphasized that the method may be used where there are more than two options for solution. The presentation of novel tasks to wild ring tailed lemurs allowed us to apply the method where these factors come into play.

Group structure or modes of transmission may cause heterogeneity of behavior between cliques within groups. As there were distinct sub-groups, only within which the close proximity of members was tolerated, the option bias analyses were conducted at the level of group and sub-group. The options used were categorized, and analyses conducted accordingly, into 2 broad options (flip/swivel); 3 options related to the subjects' approach to flip (forward flip (ff)/over the top flip (ottf)/ up and under flip (uuf); see Table 1); and 6 body-part options (flip vs. swivel by body part used – left or right hand and nose). Swivel was not broken down into further options as the disc's left-turn only movement, restricted variability in methods used.

The option-bias method calculates a chi-square value as a metric of within-group homogeneity of behavior. In contrast to the callitrichid data previously analyzed using the method (Kendal, et al., 2009a), there appeared to be prior biases for use of the different options. Thus, we altered the original method by deriving *expected* values for the chi-square metric probabilistically to assume independence across the cells of an option-by-group contingency table, rather than assuming an equal probability of each option for the expected value, as used in Kendal et al (2009a) (see supplementary material for the new function code).

The method explicitly allows for the inputting of any underlying biases in option use when conducting power analyses or gaining estimates of Type I error. For the broad option bias analyses we calculated the underlying bias in use of flip vs. swivel using the asocial learning controls (from Zoo Atlanta) and overall option use in the two open diffusions (note that the latter measure gives us a conservative assessment of social learning on within-group homogeneity over and above the influence of genetic/ecological biases and is used on the basis that any overall bias need not necessarily reflect within group homogeneity that results from social learning). Of the four asocial learning control individuals, one did not interact with the task and 3 did. Of these, one showed no clear preference (f:s=3:4) and two showed some preference for flip (f:s=10:3, 5:2) giving an average of flip being 2.9 times more likely than swivel. Excluding demonstrators, the overall option use in the two open diffusion groups (flip=3237, swivel=437) indicated that flip was 7.4 times more likely than swivel. The average of these preference values (for the controls and open diffusions) gives an underlying ratio for each option of 5 to 1 (f:s) which may be input as an underlying bias in option use. We also conduct a more accurate measure of the power to detect social learning by including, in the model, an estimate of the probability of asocial learning causing repeated use of one option over the other. This is as opposed to the initial option-bias calculation which sets alpha at 0.5. Here, we used the three asocial learning controls and the innovator from the unseeded open diffusion. All four individuals used the same option in their first and second manipulation, giving a strength of association (α) causing return to the same option of one (4/4 (using same) - 0/4 (using different, equivalent to chance probability of using same) = 4/4). Finally, in analyses of option bias in the three flip options, we were limited in parametization of both the underlying bias and uncertainty in alpha as the asocial learning controls did not provide useful data: due to task placement, they were unable to conduct manipulations requiring them to approach the task from behind and over the top (ottf) or behind and underneath (uuf), but were restricted to approaching the tube from the front and forward flipping (ff). However, excluding demonstrators, the overall flip option use in the two open diffusion groups gave an estimated underlying bias for ff:ottf:uuf of 94:4:1.

All simulations were repeated 10,000 times.

Network Based Diffusion Analysis

The NBDA analysis does not assess social learning of particular task options but of the task in general. In applying the method we used diffusions based on the time of acquisition (first successful task manipulation), coded using 20 second time intervals, for each for each individual. Two social networks were used in this analysis: (1) As we were interested in the role of rank-related directed social learning, the social network used in the analysis was a matrix of absolute rank differences among individuals (rank being indicated by Nakamichi). We used two symmetrical matrices, one in which high values indicated a large difference in rank and one in which they indicated a small difference in rank. Thus any significant finding of social learning would indicate that individuals are more likely to learn from (and follow in the diffusion) individuals that have a large rank difference to themselves or a very similar rank, respectively. (2) As within group structuring is strong in *Lemur catta* we also ran the analysis using proximity matrices for each group. Here the symmetrical matrices represented the number of point samples in which individuals were within 1m of each other during baseline data collection. As all matrices had a high average connection strength, analyses began with the parameter *tau* (which determines the probability of social learning at each time step given the connection strengths between naïve and experienced individuals) bounded between 0 and 1 and the asocial learning parameter set at 0.5.

RESULTS

Following assessment of the groups' social dynamics, the results section is divided into a series of standard inferential statistics and a series of modeling/simulation based methods for assessing the evidence for social learning in the data.

Social Dynamics

The qualitative sub-groupings apparent to DC during testing (1: TA-TI-AL, CA-CU-RA, remainder singletons; 2: HE-SE-WM, WH-RE, TP-PE-HC (demonstrators), remainder singletons) were reflected to an extent in the sociograms constructed from the baseline data (figure 3). The permutation tests (Newman & Girvan 2004), using this baseline proximity data, indicated that in both groups the observed modularity was very low (Group 1: 0.033; Group 2: 0.186), possibly due to a lack of data. However, the observed sub-group structures gave modularity scores that lay at the 100th and 99.98th percentile of the simulated distribution, based on the baseline data, for group 1 and 2 respectively. Thus our assignment of individuals to sub-groups gives a significantly higher modularity than expected by chance.

As the proximities of individuals outside of testing sessions corresponds to the sub-groupings observed during task presentations, we may be reasonably confident in our assignment of individuals to sub-groups.

[Figure 3 - sociograms]

Standard Inferential Social Learning Statistics

Group Comparisons of Option Use

The possible existence of traditions in each of the open diffusion groups was assessed by comparing their relative frequencies of task option use and assessing the level of asocial bias for one option over the other using the asocial learning control individuals. As can be seen in table 2, the control individuals did not exhibit a strong bias for use of either flip or swivel in their first successful manipulation. Task positioning negated the use of over the top flip (ottf) or up and under flip (uuf) as subjects could not approach the task from behind but only from the front, resulting in forward flips (ff) only.

[Table 2 about here]

There was no significant difference between the two open diffusion groups in the percentage of swivel manipulations ([number of swivels/(number of swivels + flips)] x 100) produced (median: group 1 =10.2%, group 2=9.4%; two-tailed Mann-Whitney U test: U=27, N1=8, N2=7, p=0.9) despite the fact that group 2 was seeded with swivel-trained demonstrators. When the category 'flip' was broken down into over the top-flip (ottf), up and under-flip (uuf) and forward-flip (ff) (with swivel) a Kruskall Wallis analysis indicated a significant difference between the groups in the use of the uu-flip option only (χ_1^2=5.65, p=0.017) with group 2 (median=0.42) producing more than group 1 (0) (see figure 4), however the result should not be treated as valid as it treats multiple manipulations from the same individuals as independent data points. As can be seen in figure 4, group 2 produce more ott-flips (median =4.35%; 5/7 individuals exhibiting them) than group 1 (0.311%; 3/8 individuals). This is despite the fact that, ecologically, ottf manipulations are at least two times more likely in group 1 than group 2 (there were 4 trees at which ottf was possible for group 1 and only 1-2 trees for group 2). There was no significant difference between the two groups in option use at the level of flip or swivel using left or right hand or nose.

[Figure 4 about here]

Influence of Observation Opportunities upon Behavior

The proportion of each type of successful manipulation used was assessed as a function of the proportion of the successful manipulation types observed. We also investigated, across successful and unsuccessful manipulations, the number of different options used as a function of the number of different options an individual had observed others to use. Full details may be seen in the supplementary material, but in summary, there was no indication that observation opportunities, either of actual manipulation type (eg. flip vs. swivel / ff vs. ottf vs. uuf / flip vs. swivel by body part) or of manipulation variety (number of options), had any influence on the type or variety of manipulations an individual produced.

If social learning reduced the time taken to learn the task ('learning time') we would expect a negative relationship between learning time and the frequency of successful manipulations observed (from a zone of within 3m around the task) prior to success. There was, however, a significant *positive* effect of 'learning time' (latency between first contact and first success accounting for time away from the task) as a function of the number of successful manipulations observed prior to first successful manipulation (Linear mixed model (LMM), with group as a random variable: $t_{1,12}$=6.36, $p<0.0001$). Thus, the more successful manipulations individuals observed prior to success, the greater the total time at the task prior to first success. Similarly, we found a significant positive correlation of absolute latency to first success and the number of successful manipulations observed prior to this success (Spearman's rho_{13}= 264.66, $p=0.043$, data pooled across groups). It is possible that our 'learning time' measure was a poor indicator of learning. If it were representative of learning we would expect a higher proportion of successful to unsuccessful task manipulations in individuals that were at the task for only a short, rather than extended, period prior to their first success. Across individuals there was, however, no relationship between the proportion of successful manipulations produced (successful/ (successful+unsuccessful)) and the learning time. These results may indicate that time at the task is more representative of task monopolization than learning and those monopolizing the task, are tolerated in proximity to conspecifics at the task and thus observe more task manipulations than less dominant individuals.

Investigating the Role of Rank

Linear mixed models, with group as a random variable, failed to find relationships fitting success order to either rank or the total time at the task prior to success. When non-solvers are included in the analysis by giving them a ceiling success order value, there is however, a positive relationship between success order and rank (LMM with group as a random variable: $t_{1,18}$= 2.74, p =0.01) suggesting that subordinate individuals are prevented from solving the task by dominant individuals (see figure 5). Of those individuals that did solve the task, there was a significant negative effect of rank on the total time to solve the task (LMM: $t_{1,12}$= -2.16, p=0.05). In other words, subordinate individuals that gained sufficient access to solve the task learned the solution more quickly than dominant individuals (see figure 5). There was, however, no significant correlation between the proportion of successful manipulations (successful / (successful+unsuccessful)) produced by individuals and their rank. There is thus no hint that more dominant individuals have an extended trial and error period (represented by a greater proportion of unsuccessful to successful manipulations) compared to subordinate individuals, during their greater total time at the task prior to success. Total time at the task prior to success, may thus have more to do with monopolization than learning.

[figure 5 about here]

Due to the apparent role of rank in individuals' interactions with the task we conducted an analysis of 'learning time' as a function of the opportunities to observe successful manipulations prior to first success, including rank as an explanatory variable. As reported above, there was a significant main effect of observation of successful manipulations (LMM excluding non-solvers: $t_{1,10}$=4.3976, df=10, p=0.0013), but no main effect of rank yet a significant interaction of successful manipulations observed and rank ($t_{1,10}$=-2.4612, df=10, p=0.0336). Thus, as can be seen in figure 6, more dominant individuals tend to observe many successful manipulations and have a relatively long total latency to task solution, whilst more subordinate individuals tend to observe little and have short latencies to task solution. However, extreme caution is required in interpretation of all rank related results as it is only in group 1 that the top ranking individuals feature in the data, as ranks 1,2 and 5 in group 2 were 'trained demonstrators' and thus excluded.

[figure 6 about here]

Option Bias Analysis

The option bias analysis was conducted at the level of flip vs. swivel and also, as flip could be broken down into 3 options, at the level of over the top-flip (ottf), vs. up under-flip (uuf) vs. forward-flip (ff). Likewise, one can consider body part used for each manipulation, giving 6 options (left or right hand or nose for flip or swivel). All details can be found in the supplementary material, but in summary, the majority of option bias analyses (across the 2 groups or 4 sub-groups, for all manipulations or successful manipulations only) yielded non-significant results, despite high power.

There was however, one significant option bias analysis when conducted on all manipulations of ff vs. ottf vs. uuf, across the 4 sub-groups (option bias: χ^2=591.278, p=0.0001; LLM=292.6169, p=0.0001; see figure 7a). The Type I error rates at *p*=0.0001, (where social learning (*s*) is set to zero and the asocial learning rate (α) to 0.5) with an underlying bias of 94 (ff) to 4 (ottf) to 1 (uuf), were <0.0001 for both methods. The family wise error rate does not need to be taken into account here as the option-bias method itself is highly conservative in this respect. In addition, the *p* value is so small that it would remain significant after a reduction in α. We therefore have evidence consistent with social learning of different flip-specific methods for extracting food from the tasks. As previously mentioned, such an analysis as regards swivel was not conducted as the subjects appeared largely restricted to approaching the task from the front when swivelling. As can be seen in figure 6b it is largely the proportion of option use in sub-group 4 that results in the significant difference between the observed and simulated null distribution, although sub-groups 1-3 also deviate from the global proportions. As highlighted above, the bias for ottf and uuf in sub-group 4 (of group 2) cannot be accounted for by ecological differences as there were actually more tasks available at which these options were possible for group 1 than group 2. It should also be noted that sub-groups were not restricted to the use of particular tasks (of the 4-6 simultaneously presented) and thus differing possibilities of flip options afforded by each tasks position cannot account for the significant option-bias result.

[Figure 7 about here]

Network Based Diffusion Analysis

When conducting extended NBDA (or TADA as re-classified by Franz & Nunn, this issue) analyses, using difference in rank between individuals as indicative of the social network, there is no evidence for social learning. For both groups, regardless of whether social network matrices allow similarity or dissimilarity in rank to indicate high connection strengths between individuals, the purely asocial learning model is always better supported than the model including both social and asocial learning (Akaike probabilities around 0.73%; see supplementary information). Thus, the difference in rank between individual A and B does not give any indication as to the likelihood that B will produce a successful manipulation given that A has already done so. When using inter-individual proximity levels (outside of testing sessions) as an indicator of the social network, for both groups, neither the social and asocial learning model nor the pure asocial learning model is favoured over the other (see supplementary information).

DISCUSSION

We have applied the option-bias method and NBDA method to data from wild animals for the first time, as well as compared their outcomes with those of standard inferential statistical tests. To our knowledge, we present the first evidence consistent with social learning in prosimian primates, in particular lemurs (*Lemur catta*).

Social Learning in Ring-Tailed Lemurs?

We find a significant level of homogeneity of behavior, indicative of social learning, in the option-bias analysis of sub-group's use of options within flip. We believe this finding to be robust as it is supported by a particularly low Type I error rate of <0.0001. In addition, as detailed below, there are many methodological and biological reasons as to why social learning was not identified using the alternative methods applied to the data. Although this finding contrasts with that of no predictive relationship between the number of ottf, uuf and ff manipulations observed upon their subsequent use, the latter result is based on an analysis of limited power, due to small sample size. In addition, task monopolization may obscure such a relationship. In line with the theory of Coussi-Korbel and Fragaszy (1995) that tolerance of proximity may be required for the transmission of social information, our only evidence for social learning is within sub-groups, which are defined by time spent in proximity in general and tolerance of each other at proximity to the task. In a result akin to that found in fish and primates (Swaney, Kendal, Capon, Brown & Laland, 2001; Bonnie & de Waal 2006;

Nahallage & Huffman 2007 & this issue) we thus provide support for the prediction that directed social learning, “can support within group differentiations of behavior” mediated by the learning opportunities afforded by “spatial and temporal behavioral coordination,” (Coussi-Korbel & Fragaszy, 1995, pp 1444) or tolerance of proximity within sub-groups, whether mediated by age, sex, relatedness or familiarity. In addition, this finding indicates that the social learning process(es) involved in acquiring these three specific methods of using the task flap may require close observation. Such close observation was reported in the ‘drinking from tails’ documented in captive *Lemur catta* although the authors were able only to suggest that the behavior pattern may have spread through social learning (Hosey et al., 1997). We are unable to do more than speculate about the likely social learning processes involved. However, as there were three flip actions all directed at the flap of the task we may rule out local or stimulus enhancement effects (*sensu* Hoppitt & Laland 2008) alone and suggest response facilitation (Byrne 1994)

In contrast, according to the option-bias analysis, we may be confident that homogeneity in use of either the flip or swivel option, in all manipulations or for successful manipulations only, in each group, or sub-group, was not due to social learning. Although, visually, it appears that there was homogeneity of option use, towards flip versus swivel, in both groups (see figure 2) the option-bias analysis indicates that this apparent bias may be accounted for by chance and/or asocial learning alone. The fact that the three asocial learning controls and innovator in the unseeded open diffusion (OD) group, all solved it several times within the first 10 minutes of exposure (exhibiting only 3, 10, 0 and 1 (OD) unsuccessful manipulations prior to first success, which occurred at an average of 71 seconds), implies that the task was quite easy and may not, according to the ‘costly information hypothesis’ (Boyd & Richerson, 1985), have necessitated the use of social learning for many of the individuals in the open diffusion groups. Caution is, however, required as all controls were captive, rather than wild, adult males and the OD innovator a sub-adult female. Wherever possible it is advisable to acquire asocial learning controls from within the test population. The hypothesis that social learning was not required in the use of flip versus swivel is however, supported when considering the performance of callitrichids exposed to tasks of varying difficulty, where asocial learning was deemed sufficient for the ‘easy’ task and social learning for the more ‘difficult’ tasks using option-bias analysis (Kendal et al., 2009). Similarly, the finding of no evidence for social learning, at the level of two options, according to option bias analysis mirrors that of Dean, Kendal, Hoppitt and Laland (in prep.) with the presentation of three, two-option, extractive foraging tasks to groups of captive ruffed lemurs (*Varecia variegata ssp.*).

In support of the above argument, that social learning was not required for learning of flip or swivel, the lack of a predictive relationship between what was observed prior to first success and what manipulations were produced is indicative of a lack of role for social learning. Likewise the positive relationship between the 'learning time' (and the absolute latency until first success), and the number of successful manipulations observed prior to first success is contrary to evidence for social learning. This is because a negative correlation would be expected under social learning as the more successful manipulations one observes the less time one should need to be present at the task (allowing for trial and error/asocial learning) to solve it. There was also a lack of relationship between the total time at the task prior to success and the proportion of successful manipulations produced. Were the time at the task to be used for trial and error learning one would expect those with a low proportion of successes to have had a long total time at the task prior to success. Thus, the total time at the task prior to success does not appear to be a reliable proxy measure of 'learning time' in this case.

The hierarchical nature of the lemur groups would appear to be responsible for the pattern of time at the task being unrelated to the time taken to learn the task. Within *Lemur catta* "high-ranking individuals frequently and aggressively reassert their domination over the subordinate cohort" even in the absence of an overt challenge (Sapolsky, 2005 p. 648). During data collection it was apparent that the alpha females would readily interrupt their own foraging with task A in order to displace others from tasks B or C, before resuming foraging at task A. This observation is reflected in the role of rank, females above males, on success order. Although all of the rank related results are interpreted with caution, subordinate individuals, relative to dominants, tended to solve the task later in the diffusion. This corresponds to reports, of female feeding priority in lemurs, achieved by both female aggression towards males, and male deference to females (Overdorff, Erhart, & Mutschler, 2005;White et al., 2007). In our study, of the 6 individuals (3 per group) that did not interact with the task, all but one (an adult female) were low ranking adult, often peripheral, males. This corresponds to the report of Kappeler (1987), in an early open diffusion study with *Lemur catta,* that the lowest ranking individuals (peripheral males) did not acquire the novel foraging trait. Despite their later position in the diffusion subordinates exhibit significantly less observation of the prior successes of others (likely out of a lack of opportunity to remain within 3m of the task when a conspecific was manipulating it: Anderson et al., 1992) compared to dominants. This does not however impede their success with the task as they exhibit a significantly reduced total time at the task prior to first success than dominants. This tentative finding cannot, however, be taken as conflicting with the hypothesis that cognitive ability (here ‘learning time’) is positively correlated with social dominance (see Boogert, Reader, & Laland, 2006) because (i) the total time to success, as discussed above, may not be indicative of learning time but rather of resource monopolization by dominants, and (ii) learning time was not tested in individuals removed from social constraints.

The lack of evidence for social learning according to the NBDA/TADA analysis is unsurprising, despite the apparent influential role of rank and sub-groups in the lemur groups’ response to the extractive foraging task. Although the option-bias analysis found evidence for social learning, this was at the sub-group level and for option use, whereas the NBDA analysis uses as inputs learning of the task in general at the group level. Thus the transmission of information along social network pathways specified by rank or proximity is unlikely to be picked up by the NBDA analysis in this case. In accordance with the finding regarding rank, Kappeler (1987) in his open diffusion study with *Lemur catta*, reported that a direction of information propagation with respect to rank was not discernible. However, with the proximity matrix analyses, neither the asocial- nor social and asocial- learning model was favoured over the other. Thus, it remains possible that there is an effect of directed social learning, along pathways specified by proximity, within these lemur groups which the NBDA method has not detected due to the low power caused by small group sizes (Franz & Nunn, this issue; Hoppitt et al. 2010).

Methodological Considerations

Our analyses have highlighted several methodological considerations for the use of inferential statistical methods, option-bias analysis and network based diffusion analysis, in capturing social learning in natural contexts.

Primarily, the study has indicated the importance of taking the social system of the species in question into account when applying methods for the analysis of social learning. As highlighted by Kendal et al. (2009a), the researcher, using option-bias analysis must independently identify the populations for which homogeneity of behavior is expected. In this study it is apparent that the choice of an appropriate level of population analysis (here group or sub-group) is key. Similarly, a new method (Matthews, 2008) developed for the study of social transmission in intermediately despotic wild capuchins, uses a randomization method to indicate that ‘cliques’ within groups showed more evidence of social learning than groups as a whole. Likewise, with network based diffusion analysis (NBDA) the researcher should use a social network of relevance to the transmission of social information. Possibly of utmost relevance to this study, involving transmission of information regarding a novel foraging device, would have been a matrix that was indicative of tolerance of proximity between individuals during routine foraging (co-feeding network: Franz & Nunn, this issue). Unfortunately, however, these data were unavailable. Finally, although theoretically the method has utility with species that do not exhibit strong social hierarchies or variation within the social network (Franz & Nunn, this issue) this remains to be explored using real data.

We had originally planned to apply the Kendal, Kendal & Laland (2007) method of modeling social learning processes to the lemur data. However, this method was developed for use with the more egalitarian callitrichid monkeys and it was apparent that the movement and observation parameters, as developed, would be unduly affected by the social hierarchy of the lemur subjects, negating any meaningful ability to detect social learning. Similarly, as emphasized by Hoppitt et al. (this issue), the displacement of individuals from tasks by conspecifics has implications for the interpretation of network based diffusion analysis as well as diffusion curve analysis. Also, as detailed in the methods section, we a priori adapted the use of a negative correlation between contact latency and ‘learning time’ (success latency-contact latency) as an indicator of social learning (Day, 2003, developed for callitrichids). The measure of ‘learning time’ (total time at the task prior to first success) was adapted to take account of inhibited access to the task in subordinates. Also, the despotic nature of the lemur groups called for a more direct measure of observation opportunities (than latency to contact the task), such as number of task manipulations observed. However, in analyzing the results it became apparent that even using total time at the task prior to first success as an indicator of cognitive ‘learning time’ was flawed as the time at the task in dominant individuals may have nothing to do with learning but more to do with resource monopolization (White et al., 2007). This is not to say, however, that such methods cannot be used at all with more despotic species. Boogert et al. (2008), for example, did find a significant negative correlation between contact latency and ‘learning time’ in social contexts (and not individual learning contexts), in a gregarious bird with pronounced dominance hierarchies.

In addition to being the first application of the option-bias method to data from the wild, this study has also extended its use to cases where there are more than two behavioral variants for a task's solution and underlying biases in the use of each. The finding of social learning in sub-group biases for options used within flip, but not for flip versus swivel, highlights that a researcher must, to some extent, allow the study subjects to identify or define the options available to them. Our task was designed to have two options (flip versus swivel) but the lemurs themselves invented three different ways of flipping necessitating analysis at this level also. The finding also reminds us that social learning involves asocial components and social and asocial learning may variously predominate in the acquisition of different aspects of a behavior pattern (as also suggested for New Caledonian Crows', manufacture of 'wide' *Pandanus* leaf tools: Holzhaider et al., this issue) and that the approach should be suitable where there is only one action (or motor pattern) required to solve the task but variation in the 'option' choice within it (Horner & Whiten, 2005).

When considering application of the method to data in which there is an underlying bias for option use, we have used a slightly different code for the chi-square randomization method to that used previously (Kendal, et al., 2009a). Here, the chi-square method uses expected values calculated from the contingency table, rather than assuming an equal distribution of option use. This aids considerably in the interpretation of a significant option-bias result. In the analysis of options used within flip, there was a considerable bias for one option over the others, yet as the method incorporates bias, we may still be confident in evidence for social learning. Thus the method may be used to overcome the issue faced by many studies where groups are seeded with differing techniques for task solution, one of which is considered more salient or easy than the other (see Flynn & Whiten this issue; Hopper et al., 2007 and references therein). For example, Hopper et al. were forced to be cautious in their interpretation of social learning being responsible for the clear divergence in option use (lift/poke) in two demonstrator-seeded chimpanzee groups. This was because 'poke' was considered more likely than 'lift' and the possibility that the bias for poke in the poke-seeded group was asocially learnt could not be ruled out.

CONCLUSION

Contrary to common thought that lemurs are cognitively lacking compared to haplorhine primates (e.g. Jolly, 1966), we find evidence consistent with social learning in the despotic *Lemur catta* which supports the theory of directed social learning (Coussi-Korbel &

Fragaszy, 1995). To validate this finding we would look to directly examine social learning processes as regards this task in captive *Lemur catta*. In addition, to further substantiate the evidence for directed social learning, it would be fruitful, to investigate social learning, in an open diffusion scenario, with a more egalitarian lemur species such as the Red-Fronted Brown Lemur, (*Eulemur rufifrons*). We may predict that we will find greater evidence for socially learnt traditions in more egalitarian than despotic species which, in turn, has implications for the evolution of our own unique cultural capacities. Also, to tease apart the role of rank on learning, future studies could simultaneously conduct open diffusion studies and individual learning tests with the same subjects (eg. Boogert et al., 2006, 2008; Hoppitt et al. 2010). Finally, as the tool-box of statistical techniques for capturing social learning in natural contexts grows, care is required in ensuring that the methods employed are appropriate for the study in question, in particular the social dynamics of the subjects. The onus is thus on the creators of methods to clearly state their assumptions and constraints whilst the researcher is responsible for ensuring deployment of the appropriate method to examine putative cases of social learning.

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REFERENCES

Altman, D.G. (1991). *Practical Statistics for Medical Research*. London: Chapman and Hall (p. 404).

Anderson, J., Fornasieri, I., Ludes, E., & Roeder, J. (1992). Social processes and innovative behavior in changing groups of Lemur fulvus. *Behavioral processes,* **27,** 101-112.

Bonnie, K.E., de Waal, F.B.M. (2006). Affiliation promotes the transmission of a social custom: handclasp grooming among captive chimpanzees. *Primates* **47**, 27–34.

Boogert, N.J., Reader, S.M., & Laland, K.N. (2006). The relation between social rank, neophobia and individual learning in starlings. *Animal Behavior,* **72**, 1229-1239.

Boogert, N. J., Reader, S. M., Hoppitt, W., & Laland, K. N. (2008). The origins and spread of innovations in starlings. *Animal Behavior,* **75**, 1509-1518.

Boyd, R., & Richerson, P. J. (1985). *Culture and the Evolutionary Process*. The University of Chicago Press, Chicago.

Byrne, R.W. (1994). The evolution of intelligence. In (Slater, P.J.B. & Halliday, T.R., Eds.) *Behavior and Evolution*, pp. 223-265. Cambridge, Cambridge University Press.

Coussi-Korbel, S., & Fragaszy, D. M. (1995). On the relation between social dynamics and social learning. *Animal Behavior,* 50, 1441-1453.

Day, R. L. (2003). *Innovation and social learning in monkeys and fish: Empirical findings and their application to reintroduction techniques*. Unpublished doctoral dissertation, Cambridge University.

Dean, L., Kendal, R.L., Hoppitt, W. & Laland, K.N. (in prep.). Sex ratio affects sex-specific innovation and learning in captive ruffed lemurs (*Varecia variegata ssp*.).

Franz, M., & Nunn, C. L. (2009). Network-based diffusion analysis: a new method for detecting social learning. *Proceedings of the Royal Society of London: Biological Sciences*, **276**, 1829-1836.

Fornasieri, I., Anderson, J., & Roeder, J. (1990). Responses to a novel food acquisition task in three species of lemurs. *Behavioral processes*, **21,** 143-156.

Gould, L. (1997). Affiliative relationships between adult males and immature group members in naturally occurring ring-tailed lemurs. *American Journal of Physical Anthropology,* **103**, 163-171.

Hopper, L. M., Spiteri, A., Lambeth, S. P., Schapiro, S. J., Horner, V., & Whiten, A. (2007). Experimental studies of traditions and underlying transmission processes in chimpanzees. *Animal Behavior*, **73**, 1021-1032.

Hoppitt, W.J.E. & Laland, K.N. (2008). Social processes influencing learning in animals: A review of the evidence. *Advances in the Study of Behavior,* **38**, 105-165.

Hoppitt, W. J. E., Boogert, N. J., & Laland, K. N. (2010). Detecting social transmission in networks. *Journal of Theoretical Biology*, **263**(4), 544-555. oi:10.1016/j.jtbi.2010.01.004

Horner, V., & Whiten, A. (2005). Imitation and emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Animal Cognition*, **8**, 164-181.

Hosey, G., Jacques, M., & Pitts, A. (1997). Drinking from tails: Social learning of a novel behavior in a group of Ring-tailed lemurs (*Lemur catta*). *Primates* **38**, 415-422.

Jolly, A. (1966). *Lemur Behavior*. Chicago: Chicago University Press.

Jolly, A. & Pride, E. (1999). Troop histories and range inertia of *Lemur catta* at Berenty, Madagascar: A 33-year perspective. *International Journal of Primatology*, **20**, 359-373.

Kappeler, P. M. (1987). The acquisition process of a novel behavior pattern in ring tailed lemurs (*Lemur catta*). *Primates*, **28**, 225-228.

Kasper, C. & Voelkl, B. (2009). A social network analysis of primate groups. *Primates* **50**, 343-356.

Kendal, R. L., Coolen, I., van Bergen, Y., & Laland, K. N. (2005). Tradeoffs in the adaptive use of social and asocial learning. *Advances in the Study of Behavior*, **35**, 333-379.

Kendal, J. R., Kendal, R. L., & Laland, K. N. (2007). Quantifying and modelling social learning processes in monkey populations. *International Journal of Psychology and Psychological Therapy*, **7**, 123-138.

Kendal, R. L., Coolen, I., & Laland, K. N. (2009b). Adaptive Trade-offs in the use of social and personal information. In R. Dukas & J. Ratcliffe (Eds.), *Cognitive Ecology: The evolutionary ecology of learning, memory and information use* (pp. 249-271).Chicago:University of Chicago Press.

Kendal, R. L., Kendal, J. R., Hoppitt, W., & Laland, K. N. (2009a). Identifying social learning in animal populations: A new ‘option-bias’ method. *PLoS ONE* **4**(8), e6541.

Koyama, N., Ichino, S., Nakamichi, M. & Takahata, Y. (2005). Long-term changes in dominance ranks among ring-tailed lemurs at Berenty Reserve, Madagascar. *Primates* **46**, 225-234.

Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L., & Sherwin, W. B. (2005). Cultural transmission of tool use in bottlenose dolphins. Proceedings of the *National Academy of Sciences*, **102**, 8939–8943.

Laland, K. N. (2004). Social learning strategies. *Learning and Behavior*, **32**, 4–14.

Laland, K. N., & Galef, B. G. Jr. (2009). *The Question of Animal Culture*. London, England: Harvard University Press.

Laland, K. N., & Janik, V. (2006). The animal cultures debate. *Trends in Ecology & Evolution*, **21**, 542–547.

Laland, K. N., Kendal, J. R., & Kendal, R. L. (2009). Animal culture: problems and solutions. In K. N. Laland & B. G. Galef Jr. (Eds.), *The Question of Animal Culture* (pp. 174-197). Harvard: Harvard University Press.

Leca, J-B., Gunst, N., & Huffman, M. A. (2007). Japanese macaque cultures: Inter- and Intra-troop behavioral variability of stone handling patterns across 10 troops. *Behavior,* **144**, 251-281.

Lefebvre, L., & Palameta, B. (1988). Mechanisms, ecology, and population diffusion of socially learned, food-finding behavior in feral pigeons. In T. R Zentall & B. G.Galef Jr. (Eds.), *Social learning: psychological and biological perspectives* (pp.141–164). New Jersey: Lawrence Erlbaum.

Matthews, L. (2009). Intragroup behavioral variation in white-fronted capuchin monkeys (*Cebus albifrons*): Mixed evidence for social learning inferred from new and established analytical methods. *Behavior* **146**, 295-324.

McGrew, W. C. (1998). Culture in nonhuman primates. *Annual Review of Anthropology*, **27**, 301–328.

Moreno, J. L. (1960). *The Sociometry Reader*. Glencoe, Illinois: The Free Press.

Nahallage, C.A.D., Huffman, M.A. (2007). Age-specific functions of stone handling, a solitary-object play behavior, in Japanese macaques (Macaca fuscata). *American Journal of Primatoogy.* **69**, 1–15.

Nakamichi, M., Rakototiana, M. L. O. & Koyama, N. (1997). Effects of spatial proximity and alliances on dominance relations among female ring-tailed lemurs (*lemur catta*) at Berenty Reserve, Madagascar. *Primates* **38**, 331-340.

Newman, M.E.J.& Girvan, M. (2004). Finding and evaluating community structure in networks. *Physical Review* E **69**, 02611.

Overdorff, D., Erhart, E., & Mutschler, T. (2005). Does female dominance facilitate feeding priority in black-and-white ruffed lemurs (Varecia variegata) in southeastern Madagascar? *American Journal of Primatology*, **66**, 7-22.

Perry, S. (2009). Conformism in the food processing techniques of white-faced capuchin monkeys (*Cebus capucinus*). *Animal Cognition*, **12**, 705-716.

Perry, S., Baker, M., Fedigan, L., Gros-Louis, J., Jack, K., MacKinnon, K. C., Manson, J. H., Panger, M., Pyle, K., & Rose, L. (2003). Social conventions in wild white-faced capuchin monkeys. *Current Anthropology*, **44**, 241–268.

Rendell, L., & Whitehead, H. (2001). Culture in whales and dolphins. *Behavior and Brain Sciences*, **24**, 309–324.

Santos, L., Mahajan, N., & Barnes, J. (2005). How prosimian primates represent tools: experiments with two lemur species (Eulemur fulvus and Lemur catta). *Journal of Comparative Psychology*, **119,** 394-403.

Sapolsky, R.M. (2005). The influence of social hierarchy on health. *Science* **308**: 648-652.

Sargeant, B. L., & Mann, J. (2009). From social learning to culture: Intrapopulation variation in bottlenose dolphins. In K. N. Laland & B. G. Galef Jr. (Eds.), *The Question of Animal Culture* (pp. 152-173). Harvard: Harvard University Press.

Schmitt, V., Melchisedech, S., Hammerschmidt, K., & Fischer, J. (2008). Hand preferences in Barbary macaques (*Macaca sylvanus). Laterality: Asymmetries of Body, Brain and Cognition,* **13**(2), 143-157.

Swaney, W.T., Kendal, J., Capon, H., Brown C. & Laland K.N. (2001). Familiarity facilitates social learning of foraging behavior in the guppy. *Animal Behavior,* **62**, 591-598.

Thornton, A., & Malapert, A. (2009). Experimental evidence for social transmission of food acquisition techniques in wild meerkats. *Animal Behavior,* **78**, 255-264.

van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S., & Merrill, M. (2003). Orangutan cultures and the evolution of material culture. *Science,* **299**, 102–105.

Warner, R. R. (1988). Traditionality of mating-site preferences in a coral reef fish. *Nature,* **335**, 719–721.

White, F., Overdorff, D., Keith-Lucas, T., Rasmussen, M., Eddie Kallam, W., & Forward, Z. (2007). Female dominance and feeding priority in a prosimian primate: experimental manipulation of feeding competition. *American Journal of Primatology,* **69**, 295-304.

Whitehead, H. (2009). How might we study culture? A perspective from the ocean. In K. N. Laland & B. G. Galef Jr. (Eds.), *The Question of Animal Culture* (pp. 125-151). Harvard: Harvard University Press.

Whiten, A. (1999). The identification and differentiation of culture in chimpanzees and other animals: From natural history to diffusion experiments. In K. N. Laland & B. G. Galef Jr. (Eds.), *The Question of Animal Culture* (pp. 99-124). Harvard: Harvard University Press.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiama, Y., Tutin, C. E. G., Wrangham, R. W., & Boesch, C. (1999). Cultures in chimpanzees. *Nature,* **399**, 682–685.

Whiten, A., Horner, V., & de Waal, F. B. M. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature*, **437**, 737-740.

Whiten, A., Spiteri A., Horner, V., Bonnie, K.E., Lambeth, S.P., Schapiro, S.J., de Waal, F.B.M. (2007). Transmission of multiple traditions within and between chimpanzee groups. *Current Biology* **17**, 1038-1043.

FIGURE LEGENDS, TABLES & FIGURES

Figure 1
Kin relations and dominance ranks of (a) Group 1 and (b) Group 2. Females are indicated by circles, males by rectangles and unweaned infants by triangles. Dominance ranks indicated by numbers preceded by #. Juveniles (1-2 years of age) are represented with lower case lettering.

Figure 2
A lemur (a) *flipping* the flap and holding it open with the top of her head and (b) *swivelling* the disc to the left using her nose; and (c) the layout of the testing sites (as used with each group) with the positions of the tubes and cameras indicated.

Figure 3
In the above socigrams, the frequency data from focal samples were converted to percentages of total proximity across (a) group 1 and (b) group 2. For example, in group 1 AL and TA were within one metre of each other for 8.97% of the total number of proximity counts for the whole group. (no line 0-3%; dashed line >3-6%; bold line >6-9%; thick line >9%).

Figure 4
The proportion of all task manipulations (unsuccessful & successful), per individual represented in order of first successful manipulation, that involved each option of swivel, forward-flip, over the top-flip and up and under-flip for (A) group 1, and (B) group 2. Values at the top of the bars give the total number of manipulations produced by individuals who are represented on the x axis by their initials with parentheses indicating the sex (male/female) and age category (adult, sub-adult or juvenile). The values, 1-4, beneath individuals indicate sub-group membership.

Figure 5
Significant relationships of (A) success order (with ceiling values of non-solvers set at group size of 11 and 13, for group 1 and 2 respectively) and (B) total time at the task prior to first successful manipulation, as a function of rank order.

Figure 6
The significant predictive relationship of the number of successful manipulations observed prior to first success and the total time at the task prior to first success. Values next to data points (to the left for group 2 and right for group 1) indicate the rank of the individual, in order to highlight the significant interaction effect of successful manipulations observed and rank upon the cumulative time to solve the task. The relationship is, interpreted with caution as it is only in group 1 that the top ranking individuals feature in the data, the three top rankers in group 2 being trained demonstrators.

Figure 7
Results of the significant option bias analysis (chi-square method only) of flip manipulations broken down into their component options, across the four sub-groups. Part (A) shows that the observed chi-square metric value (bold vertical line) falls in the upper tail of the null distribution of chi-square values created by the randomized simulation. Part (B) depicts the observed proportion of flip options used for sub-groups 1 to 4 and the global mean proportion of options used (which includes both task constraint and social learning biases on the options used). This indicates that for the observed data, there is a significant interaction between group and option bias that is not reflected in the global option proportions from which the simulated (randomized) data are sampled.

Table 1

Task Actions	Definition
Flip (F)	Flap lifted sufficiently to allow feeding
Partial flip (PF)	Flap lifted but not sufficiently to allow feeding
Swivel (S)	Disc swivelled sufficiently to allow feeding
Partial swivel (PS)	Disc swivelled but not sufficiently to allow feeding
Forward (F)	Lemur approaches the tube from the front and manipulates the flap or disc (e.g. FF = forward flip)
Over the top (OTT)	Lemur climbs up behind the tube and leans over the top of it to manipulate the disc or flap (e.g. OTTPF = over the top partial flip)
Up and under (UU)	Lemur approaches from behind the tube, lies on the ground and reaches up to manipulate the task (e.g. UUF = up and under flip)

Definitions of actions performed upon the extractive foraging apparatus.

Table 2

	Contact	Unsuccessful Manipulation		Successful Manipulation	
Subject	**Latency**	**Action**	**Latency**	**Action**	**Latency**
1	22	Flip (nose)	31	Flip (nose)	110
2	20	Flip (nose)	148	Swivel (nose)	171
3	15	Flip (hand)	149	Swivel (nose)	22*
4 (OD)	41	Flip (hand)	63	Flip (nose)	81

The actions (including body part used) and latency (in seconds) of the *first* contact, unsuccessful and successful task manipulation by each of the four control individuals, including the innovator in the unseeded open diffusion (OD) group. *this individual produced a successful manipulation prior to the first unsuccessful one.

Figure 1

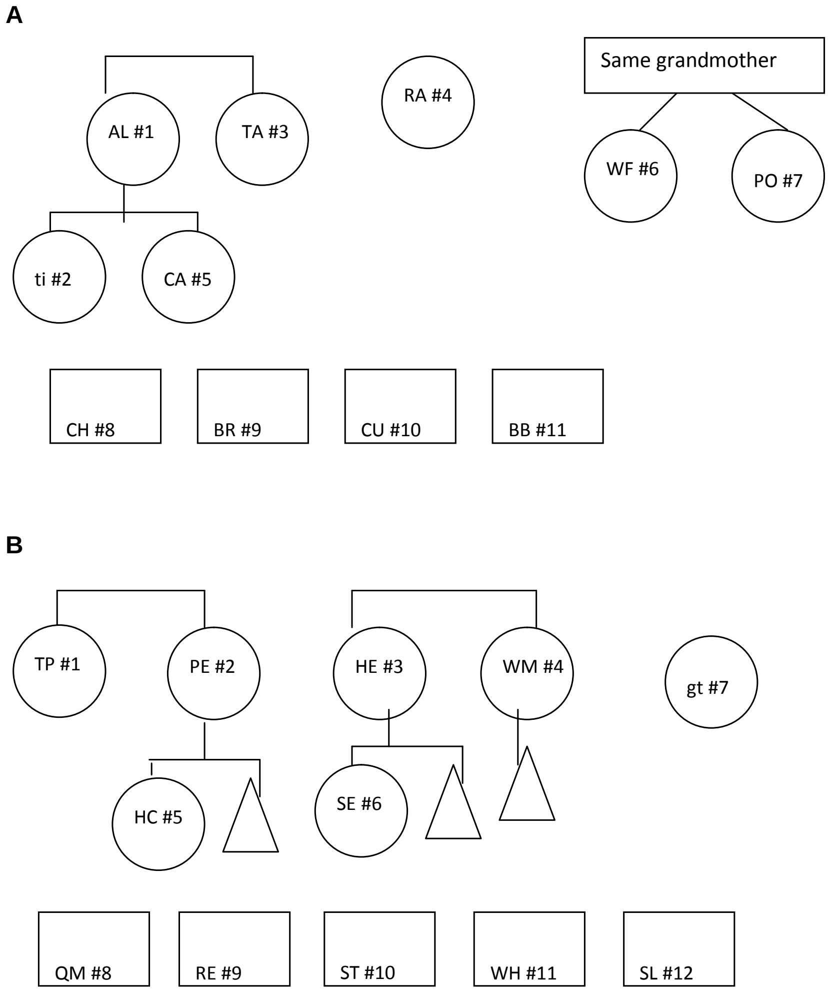

A
AL #1
TA #3
RA #4
Same grandmother
WF #6
PO #7
ti #2
CA #5
CH #8
BR #9
CU #10
BB #11
B
TP #1
PE #2
HE #3
WM #4
gt #7
HC #5
SE #6
QM #8
RE #9
ST #10
WH #11
SL #12

Figure 2

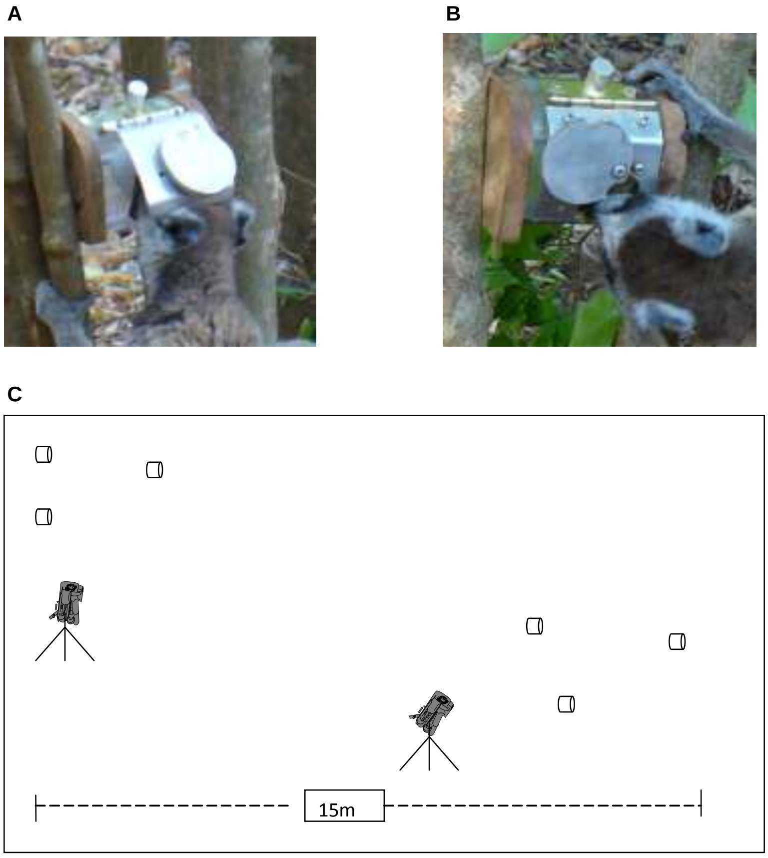


Figure 3

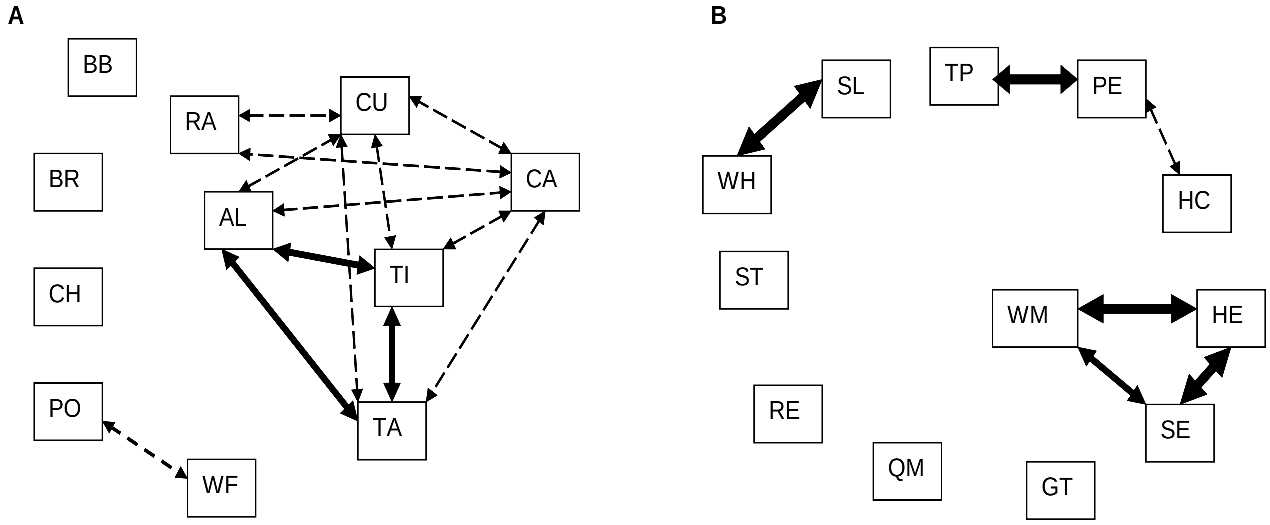


Figure 4

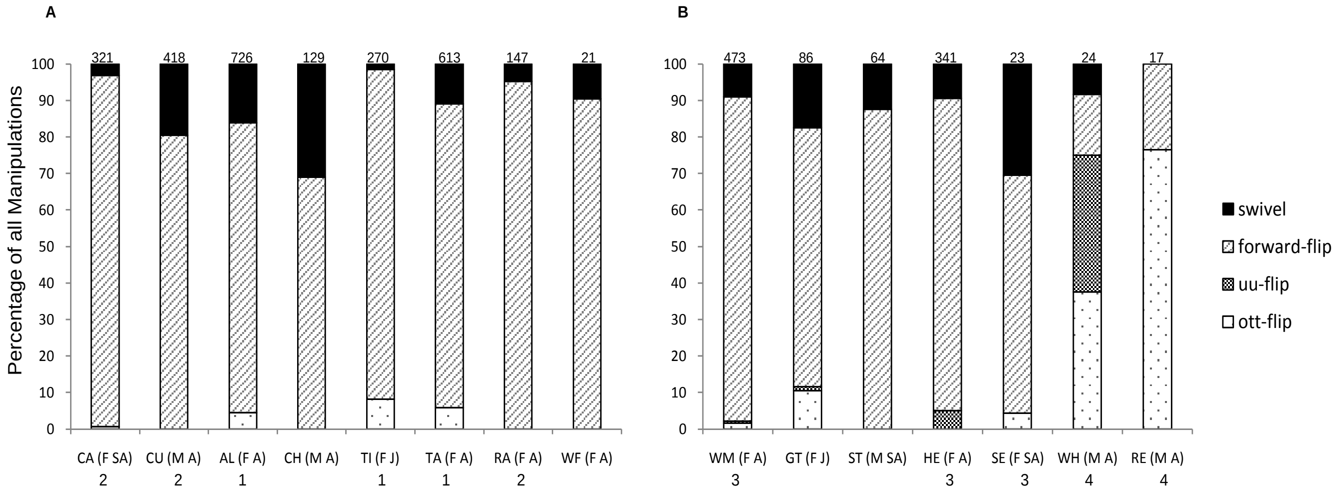

A
B
Percentage of all Manipulations
0
10
20
30
40
50
60
70
80
90
100
321
418
726
129
270
613
147
21
CA (F SA) 2
CU (M A) 2
AL (F A) 1
CH (M A)
TI (F J) 1
TA (F A) 1
RA (F A) 2
WF (F A)
473
86
64
341
23
24
17
WM (F A) 3
GT (F J)
ST (M SA)
HE (F A) 3
SE (F SA) 3
WH (M A) 4
RE (M A) 4
■ swivel
▨ forward-flip
▩ uu-flip
☐ ott-flip

Figure 5

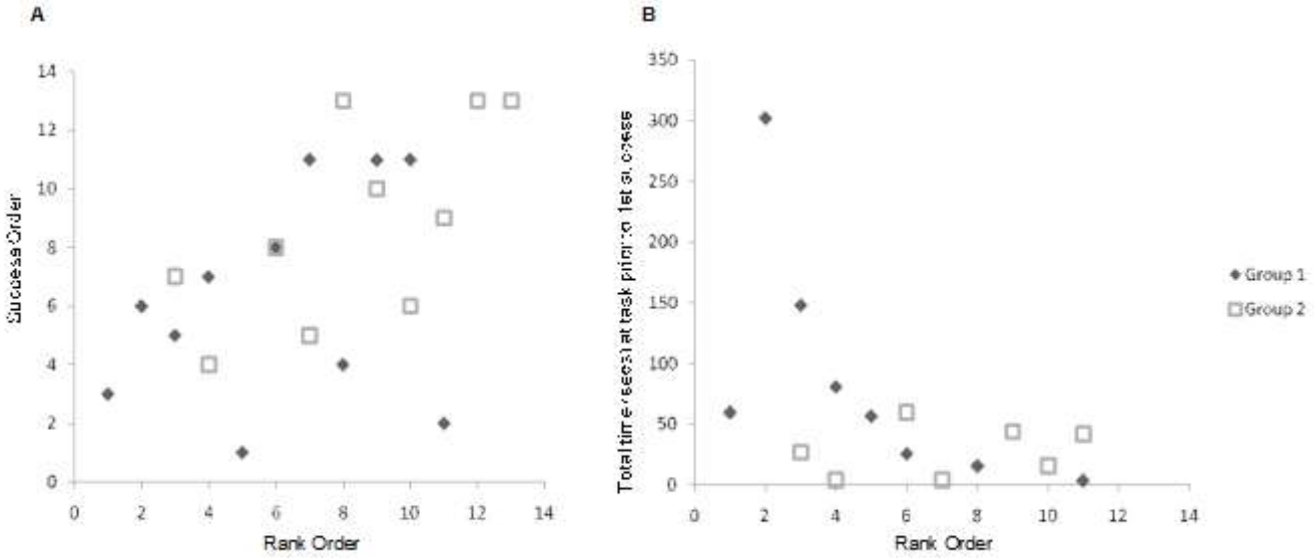

A
Success Order
Rank Order
0
2
4
6
8
10
12
14
B
Total time (secs) at task prior to 1st success
Rank Order
0
50
100
150
200
250
300
350
0
2
4
6
8
10
12
14
◆ Group 1
☐ Group 2

Figure 6

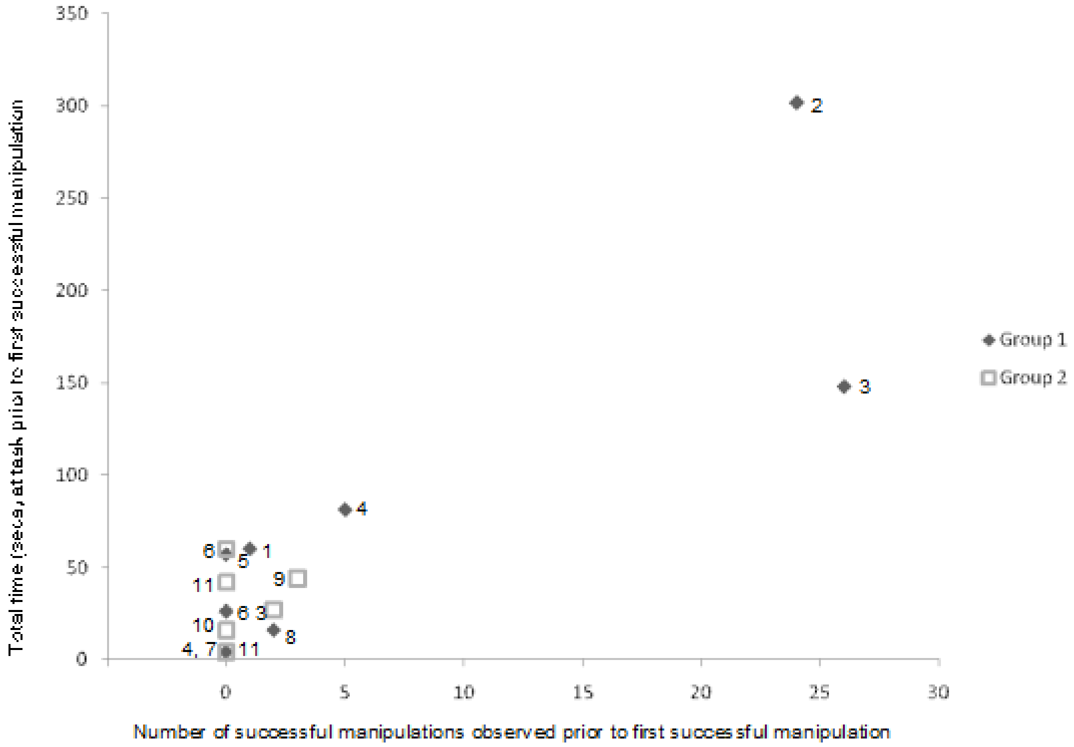
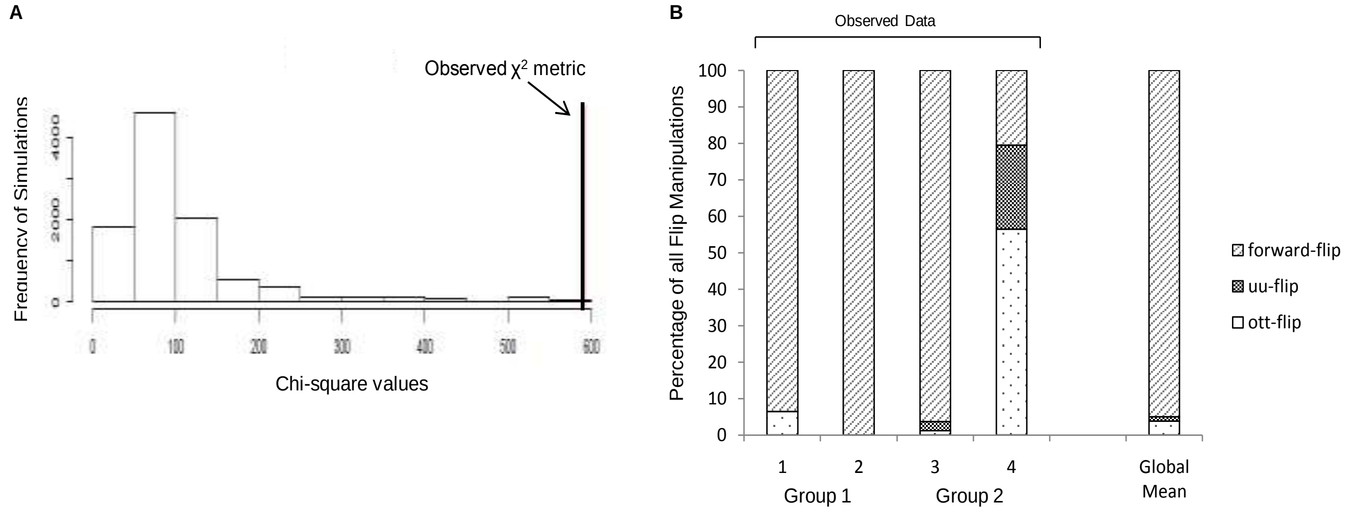

Total time (secs, at task, prior to first successful manipulation
350
300
250
200
150
100
50
0
0
5
10
15
20
25
30
Number of successful manipulations observed prior to first successful manipulation
◆ Group 1
□ Group 2
2
3
4
6
5
1
11
9
6
3
8
10
4, 7
11

Figure 7


A
Observed χ² metric
Frequency of Simulations
0
2000
4000
0
100
200
300
400
500
600
Chi-square values
B
Observed Data
Percentage of all Flip Manipulations
0
10
20
30
40
50
60
70
80
90
100
1
2
3
4
Global Mean
Group 1
Group 2
▨ forward-flip
▩ uu-flip
☐ ott-flip