

Evidence for social learning in wild lemurs (*Lemur catta*)

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Interest in social learning has been fueled 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 with laboratory-based research, the study of social learning in natural contexts is in its infancy. Here, for the first time, we apply two new statistical methods, option-bias analysis and network-based diffusion analysis, to data from the wild, complemented by standard inferential statistics. Contrary to common thought regarding the cognitive abilities of prosimian primates, our evidence is consistent with social learning within subgroups in the ring-tailed lemur (*Lemur catta*), supporting the theory of directed social learning (Coussi-Korbel & Fragaszy, 1995). We also caution that, as the toolbox for capturing social learning in natural contexts grows, care is required in ensuring that the methods employed are appropriate—in particular, regarding social dynamics among study subjects. Supplemental materials for this article may be downloaded from <http://lb.psychonomic-journals.org/content/supplemental>.

Social learning, or learning from others, is currently of widespread 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, interpopulation variation in behavior, and cultural traditions in animals from fishes to apes (Lefebvre & Palameta, 1988; Rendell & Whitehead, 2001; Warner, 1988; Whiten, 2009). Interest in animal social learning has also been fueled by reports of intra- and interpopulation 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, Kendal, & Kendal, 2009), despite innovative work in captivity (e.g., Whiten et al., 2007). Moreover, since 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, in contrast to the controlled laboratory study of social learning, and despite pioneering work with apes and cetaceans (see Sargeant & Mann, 2009; Whitehead, 2009; Whiten et al., 1999), there is a dearth of tools for capturing compelling evidence of social learning in natural contexts, either in the wild or in captivity.

Recently, however, several statistical methods have been created to aid in the task of identifying social learning in naturalistic contexts (e.g., Boogert, Reader, Hoppitt, & Laland, 2008; Franz & Nunn, 2009; Hoppitt, Boogert, & Laland, 2010; J. R. Kendal, Kendal, & Laland, 2007; R. L. Kendal, Kendal, Hoppitt, & Laland, 2009; Mat-

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thews, 2009). We presented a solution to the problem in the form of a method known as *option-bias analysis* (R. L. Kendal, Kendal, et al., 2009). The method is based on the well-established premise of social learning research—that is, when ecological and genetic differences are accounted for, social learning can generate greater homogeneity in behavior between animals than would be 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, 2010). If this behavior is socially learned, a given population may disproportionately use one method, whereas, if it is asocially learned, one might expect the use of both methods in proportion to their opportunity and profitability. Thus, if alternative forms of bias can be ruled out (e.g., genetic, 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 with 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 available¹ for free for others to apply this method, which can be deployed within controlled experimental and captive animal settings, as well as to natural data sets. 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 its application to data from groups of callitrichid monkeys provided with novel, two-option, extractive foraging tasks, producing evidence that social learning could be distinguished from unlearned processes and asocial learning and that the monkeys only employed social learning for the more difficult tasks (R. L. Kendal, Kendal, et al., 2009). The method was further validated against published data sets, using standard statistics to show social learning, and through simulation, and exhibited higher statistical power than is exhibited by conventional inferential statistics (R. L. Kendal, Kendal, et al., 2009).

An alternative technique recently developed by Franz and Nunn (2009, 2010) and extended by Hoppitt and

colleagues (Hoppitt, Boogert, & Laland, 2010; Hoppitt, Kandler, Kendal, & Laland, 2010) is network-based diffusion analysis (NBDA). Here, rather than focusing on homogeneity of behavior, one uses the social network of a group to 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 & Frigaszy, 1995)—that is, that information is transmitted or directed through subsections 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 others' connections to them. The approach requires the following as inputs: (1) a social network, which may be *asymmetrical*—for example, grooming—or *symmetrical*—for example, proximity; and (2) diffusion data represented as either the order of acquisition (OADA; Hoppitt, Boogert, & Laland, 2010) or the timing of acquisition (TADA; Franz & Nunn, 2010) 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 of 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 (1973) information criterion. Franz and Nunn (2009, 2010) designed the method as a more reliable alternative to the use of diffusion-curve analysis (the reliability of which has been questioned by Hoppitt, Kandler, et al., 2010, and by Reader, 2004) for assessing evidence for social learning in free-living animals. Franz and Nunn made the R code available for free alongside their article (2009) and have assessed its utility in the field (2010). Although the method requires more substantial data than the option-bias method does, it has the potential to be used for assessing the evidence for social learning strategies (Laland, 2004), especially regarding from whom individuals learn. The development of empirical investigation of social learning strategies (R. L. Kendal, Coolen, & Laland, 2009; R. L. Kendal, Coolen, van Bergen, & Laland, 2005) 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, in an analysis of an extensive long-term data set, Perry (2009) 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, during development, the technique most frequently observed for accessing seeds from *Luehea candida* fruits 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 (i.e., the latency between first contact and first success) and the latency of first contact (Boogert et al., 2008; Day, 2003). Here a negative relationship is assumed to indicate social learning because those who contact 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 alternative 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, 2010). Here we introduce artificial extractive foraging tasks and monitor the spread of the novel behavior pattern. This has the advantage of allowing us to observe the inception of the novel trait, test for social learning of how to solve the task, and identify the preference for extraction variants afforded by the task's design. Also, because transmission of information may occur only when the task is in place, we can be sure not to miss any transmission events, a common worry with more opportunistic data collection regarding naturally occurring tasks (e.g., termite fishing) in the field (see Franz & Nunn, 2010).

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), adult females are dominant over males (Jolly, 1966), and, although rank order in both sexes is usually linear, it can occasionally be triangular (Koyama, Ichino, Nakamichi, & Takahata, 2005). Unlike in 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 researchers reporting minimal comprehension when presented with novel foraging tasks (Anderson, Fornasieri, Ludes, & Roeder, 1992; Fornasieri, Anderson, & Roeder, 1990) or objects (Jolly, 1966), and with other researchers suggesting that lemurs learn to use tools as quickly as haplorhine species do and, in some cases, more flexibly (Santos, Mahajan, & Barnes, 2005). Lemur species are, however, understudied in the field of social learning.

Describing possible patterns of innovation and social transmission in an early open-diffusion (OD) study of a single captive group of *Lemur catta* faced with a novel foraging task, Kappeler (1987) did not attempt to assess the learning mechanisms (social or asocial) involved. Likewise, a study (Hosey, Jacques, & Pitts, 1997) 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 because it was already well established in the group. Several studies (Anderson et al., 1992; Fornasieri et al., 1990; Kappeler, 1987) of the introduction of novel foraging tasks in lemurs have, however, reported a strong influence of social rank on access to novel tasks and on consequent expression of the novel trait in individuals, whether through social or asocial learning.

In this article, we aim to apply the option-bias and NBDA methods to data from the wild for the first time, 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.

METHOD

Subjects and Study Site

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 is a 200-hectare area of natural gallery forest, transitional scrub, and spiny desert (Budnitz & Dainis, 1975). The home ranges of the selected lemur troops overlap with tourist accommodation, so the lemurs were very well habituated to humans. In addition, the demographic histories of most troop members were known because they have been studied on a regular basis since the 1990s (Nakamichi et al., 1997).

Two study troops that were given the letter and number codes YF and T1B by Koyama et al. (2005) will henceforth be labeled Group 1 and Group 2, respectively. Group 1 comprised 13 lemurs: 6 adult females (3 or more years old), 2 unweaned infants, 1 juvenile female (1–2 years old), and 4 adult males. Group 2 comprised 15 lemurs: 6 adult females, 3 unweaned infants, 1 juvenile female, and 5 adult males. The ages, dominance ranks (as indicated by Nakamichi et al., 1997), and kin relationships are illustrated in Figure 1.

Materials

The lemurs were presented with a two-action puzzle feeder (Figure 2). The feeder was an 8-cm-long × 8-cm-wide transparent Perspex or Plexiglas tube enclosed at each end by 1-cm-thick pieces of wood. A plastic food cup was inserted into a 4-cm-diameter hole cut halfway down the length of the tube. A hinged aluminum flap (6 cm wide × 7 cm high) was attached to the tube. The flap was curved to fit snugly against the tube. A 2-cm-high × 1-cm-wide aluminum rod was fixed just above the flap's hinge. The rod ensured that the flap would fall back into place over the food cup unless it was being held up. The flap had a 4-cm-diameter hole cut into it, which was aligned with the food cup. A 0.5-cm-thick aluminum disk 5 cm in diameter was fixed to the flap just above the hole with a metal pin. A lug nut was fitted to the top right of the disk so it would swivel only 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 swiveling the disk to the left or lifting/flipping the flap (Figures 2A and 2B).

To prevent monopolization of a single task by dominant individuals, four to six tubes were presented simultaneously during each day

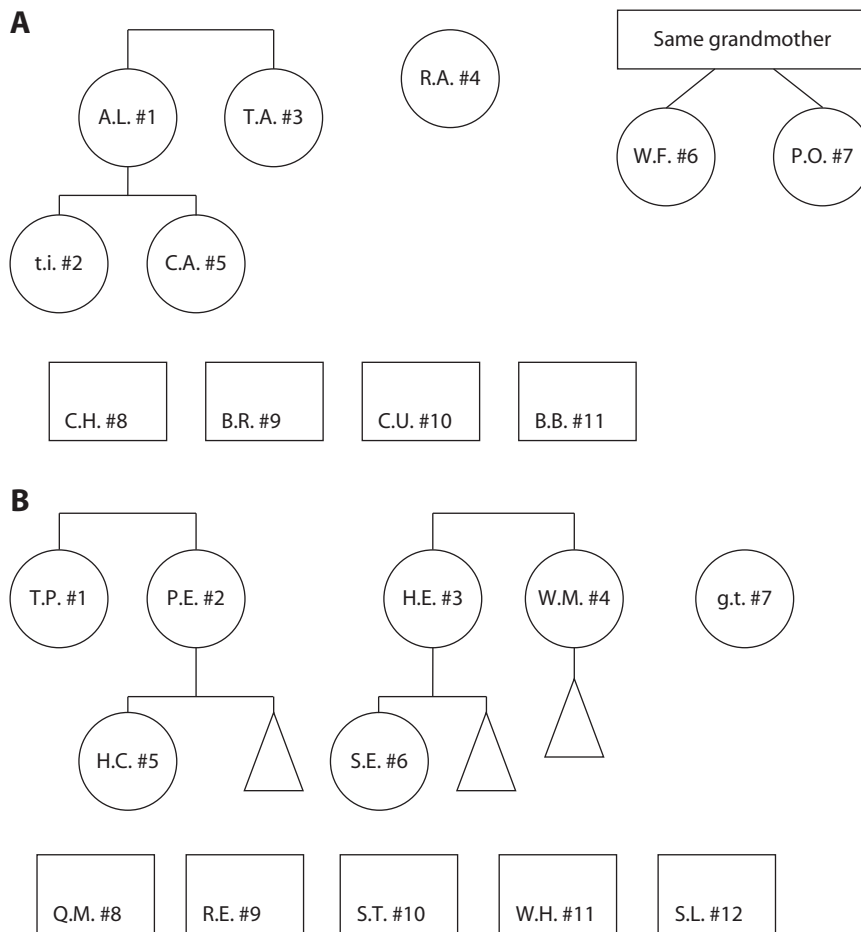


Figure 1. Kin relations and dominance ranks of (A) Group 1 and (B) Group 2. Females are indicated by circles, males by rectangles, and unweaned infants by triangles. Dominance ranks are indicated by numbers preceded by #. Juveniles (1–2 years of age) are indicated by lowercase letters.

of testing. The tubes were positioned approximately 30 cm 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, 1 or 2 high-ranking lemurs would monopolize access. Thus, the tubes were presented at two sites 10 to 15 m apart. At each site, the tubes were placed 3 to 4 m apart from each other (Figure 2C). The lemurs' behavior was recorded using two Sony camcorders fixed to tripods.

Procedure

Group 1 was tested first (October 4–14, 2006). Testing commenced at 7:00 a.m. on each of 10 consecutive days. Each testing session lasted 30 min. There were two experimenters, each of whom stood by one of the two camcorders and called out the name of each lemur that approached the tubes. The tubes were removed, refilled with food, and replaced after 15 min of testing.

After the completion of testing with Group 1, testing commenced with Group 2 (October 21–November 7, 2006). Since Group 1 showed a preponderance of flipping over swiveling, Group 2 was seeded with swiveling demonstrators to ascertain whether they would learn a relatively nonpreferred method. Two tubes that could only be swiveled (since the flaps were screwed shut) were placed into position. The 2 highest ranking females (T.P. and P.E.) monopolized these tubes during the demonstration phase and quickly learned to

swivel. The tubes were presented in this manner for 15 min on each of 8 consecutive days. During that time, only 1 other female (H.C., the 3-year-old daughter of P.E.) managed to gain access on one occasion and swiveled the disk twice. She was counted as a demonstrator thereafter.

Throughout the demonstration phase, only H.C., P.E., and T.P. approached the tubes. Most of the other lemurs sat 5 to 10 m away; if they approached any closer, they were chased away by T.P. or P.E.; therefore, we are confident that nondemonstrators only observed task manipulations (i.e., did not interact with the task) during this phase.

After the demonstration phase, tubes that could be opened by either swiveling or flipping were placed in the same configuration as for Group 1 for 30 min on each of 10 consecutive days (Figure 2). The same procedure used for testing Group 1 was followed, except for 1 day. On Day 6, a subgroup of 3 males was located approximately 30 m from the usual testing area. Since males were habitually chased away by females when they approached a tube, we took this opportunity to give the males 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 recordings of the testing sessions. The latency since session start, the subject's letter code, its action upon the tube (Table 1), the tube part manipulated (disk, right side of flap, left side

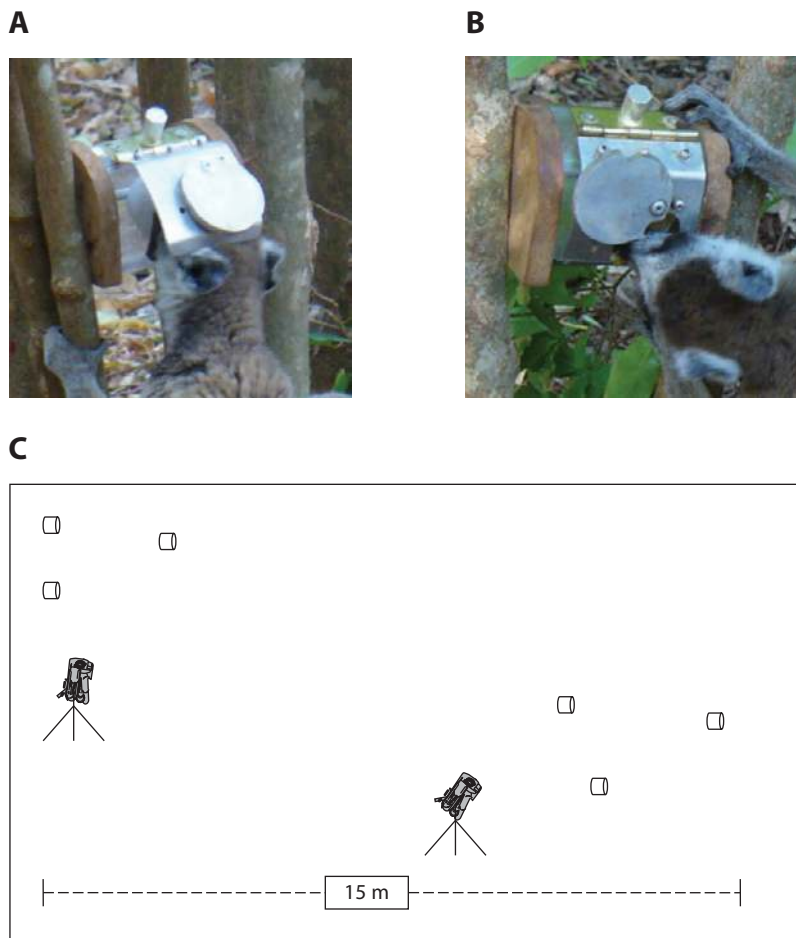


Figure 2. A lemur (A) flipping the flap and holding it open with the top of her head and (B) swiveling the disk to the left using her nose. (C) The layout of the testing sites (as used with each group), with the positions of the tubes and cameras indicated.

of flap, bottom of flap), the body part used (nose, left hand, 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 0–1 m and >1 m to 3 m), and whether they were observing (the face being oriented toward the task) during a conspecific’s task manipulation were noted. There was very good (Altman, 1991) interobserver reliability, according to Cohen κ scores, for two sessions from one site (5% of total testing with 273 separate task manipulations) for the action (.85) and body part used (.94), as well as for proximity (<1 m and >1 m to 3 m) of conspecifics to the task (.92) and whether they were observing during manipulations (.83).

Baseline data were collected in the mornings and afternoons after testing in order to determine social dynamics outside of testing sessions. Proximity data were collected using focal subject sampling. Each focal session was 3 min long; data were taken as point samples each minute. The identification of each lemur that was within 1 m of the focal subject was noted. Sixty such focals were collected per lemur between September 30 and November 23, 2006. The subjects were sampled in a randomized order.

Asocial Learning Controls

The control subjects were 4 adult male ring-tailed lemurs (6–7 years old) 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 five 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 min (for four of six sessions) or after

Table 1
Definitions of Actions Performed on the Extractive Foraging Apparatus

Task Actions	Definition
Flip (F)	Flap was lifted sufficiently to allow feeding.
Partial flip (PF)	Flap was lifted, but not sufficiently to allow feeding.
Swivel	Disk was swiveled sufficiently to allow feeding.
Partial swivel	Disk was swiveled, but not sufficiently to allow feeding.
Forward (F)	Lemur approached the tube from the front and manipulated the flap or disk (e.g., FF = forward flip).
Over the top (OTT)	Lemur climbed up behind the tube and leaned over the top of it to manipulate the disk or flap (e.g., OTTPF = over-the-top partial flip).
Up and under (UU)	Lemur approached from behind the tube, lay on the ground, and reached up to manipulate the task (e.g., UUF = up-and-under flip).

10 min of no interaction with the device (for two of six 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° angle was used to record all of the interactions with the device, and data on (1) latency of and method used (swivel, flip), (2) body part used (nose, left hand, right hand), and (3) success/no success in obtaining a food reward were extracted from the video recording.

Statistical Methods

Assessing social dynamics. During testing of each group, author D.M.C. made qualitative estimates of any apparent subgroupings. 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 & Girvan, 2004; see also Kasper & Voelkl, 2009) in a directed social network within each group, where the strength of the connection (edge weighting) between any 2 individuals was measured by the number of times the 2 individuals were within 1 m of each other during the baseline data collection sessions, in which we used the modularity function in the R (Version 2.10.1) package “igraph” (Version 0.5.3) 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) was excluded, with the exception of task manipulations produced by the demonstrators and observed by conspecifics, which were incorporated into analyses of the predictive power of observational opportunities on behavior. Nonparametric tests were used when parametric assumptions were not met. When multiple tests were conducted, the familywise error rate was controlled for by modifying the significance level of α , designated in the text as α^* . For each family of tests, $\alpha^* = \alpha/c$, where $\alpha = .05$ 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), which was developed with the more egalitarian callitrichid species. Thus, we calculated a total time at 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, since this assumes that later contactors will have observed more task manipulations than earlier contactors (Boogert et al., 2008; Day, 2003). Instead, we investigated the relationship between learning time and the number of successful manipulations observed prior to success because the latter provides a direct measure of observational opportunities.

Option-bias analysis. As emphasized by R. L. Kendal, Kendal, et al. (2009), the underlying assumption of the method—namely, that social learning leads to homogeneity of behavior—calls for researchers to assess whether homogeneity is expected in their context, to account for other factors (e.g., 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

subgroups, only within which the close proximity of members was tolerated, the option-bias analyses were conducted at the level of group and subgroup. The options used were categorized, and the analyses were conducted accordingly, into two broad options (flip/swivel); three options related to the subjects' approach to flip [forward flip (FF), over-the-top flip (OTTF), and up-and-under flip (UUF) (see Table 1)], and six body-part options [flip vs. swivel \times body part used (left hand, right hand, nose)]. Because the disk's left-turn-only movement restricted the variability in the methods used, swivel was not broken down into further options.

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 (R. L. Kendal, Kendal, et al., 2009), 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 \times group contingency table, rather than assuming an equal probability of each option for the expected value, as was used in R. L. Kendal, Kendal, et al. (2009) (for the new function code, see the supplemental materials).

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 for the use of flip versus the use of swivel using the asocial learning controls (from Zoo Atlanta) and overall option use in the two ODs. 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 resulting from social learning.

Of the 4 asocial learning control individuals, 1 did not interact with the task, and 3 did. Of these, 1 showed no clear preference (flip:swivel [f:s] = 3:4), and 2 showed some preference for flip (f:s = 10:3, 5:2), yielding an average of flip use being 2.9 times more likely than swivel use. Excluding demonstrators, the overall option use in the two OD groups (flip = 3,237, swivel = 437) indicated that flip use was 7.4 times more likely than swivel use. The average of these preference values (for the controls and ODs) gives an underlying ratio for each option of 5:1 (f:s), which may be input as an underlying bias in option use.

We also conducted 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 α at .5. Here, we used the 3 asocial learning controls and the innovator from the unseeded OD. All 4 individuals used the same option in their first and second manipulation, giving a strength of association (α) causing return to the same option of 1.0 [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 parameterization of both the underlying bias and uncertainty in α because the asocial learning controls did not provide useful data: Due to task placement, they were restricted to approaching the tube from the front and forward flipping and were unable to conduct manipulations requiring them to approach the task from behind and over the top or from behind and underneath. However, excluding demonstrators, the overall flip option use in the two OD groups gave an estimated underlying bias for FF:OTTF:UUF of 94:4:1. All simulations were repeated 10,000 times.

NBDA. 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 that were based on the time of acquisition (first successful task manipulation), coded using 20-sec time intervals, for each individual. Two social networks were used in this analysis. (1) We were interested in the role of rank-related directed social learning, so the social network we used in the analysis was a matrix of absolute rank differences among individuals (rank being indicated by Nakamichi et al., 1997). We used two symmetrical

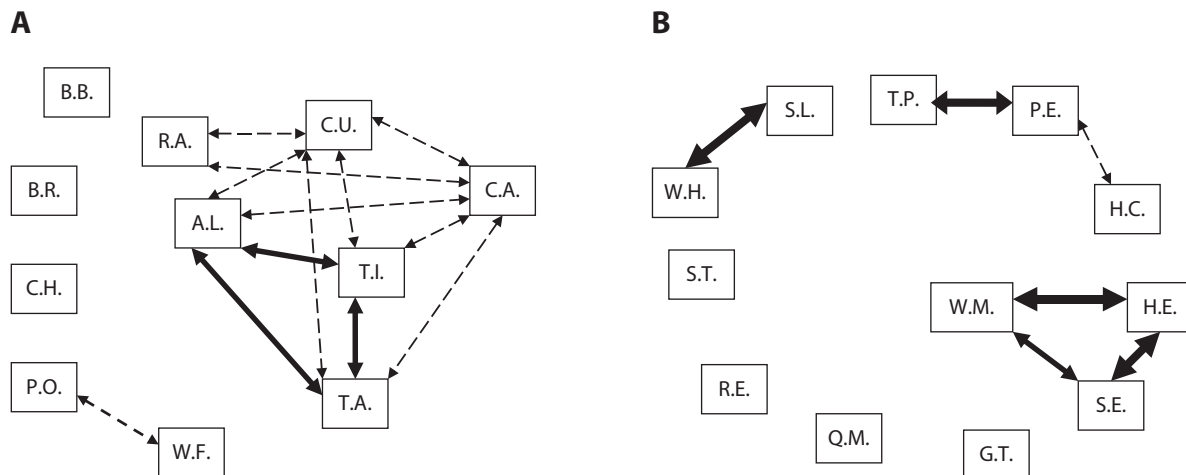


Figure 3. Sociograms in which the frequency data from focal samples were converted to percentages of total proximity across (A) Group 1 and (B) Group 2. For example, in Group 1, A.L. and T.A. were within 1 m of each other for 8.97% of the total number of proximity counts for the whole group. No line, 0%–3%; dashed line, >3%–6%; bold line, >6%–9%; thick line, >9%.

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 were more likely to learn from (and follow in the diffusion) individuals that had a large rank difference to themselves or a very similar rank, respectively. (2) Within-group structuring is strong in *Lemur catta*, so 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 1 m of each other during baseline data collection. Because all matrices had a high average connection strength, analyses began with the parameter τ (which determines the probability of social learning at each time step, given the connection strengths between naive and experienced individuals) bounded between 0 and 1, and the asocial learning parameter set at .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 subgroupings apparent to D.M.C. during testing—within Group 1, T.A.–T.I.–A.L., C.A.–C.U.–R.A., the remainder being singletons; within Group 2, H.E.–S.E.–W.M., W.H.–R.E., T.P.–P.E.–H.C. (demonstrators), the remainder being singletons—were reflected to an extent in the sociograms constructed from the baseline data (Figure 3). Using these baseline proximity data, the permutation tests (Newman & Girvan, 2004) indicated that, in both groups, the observed modularity was very low (Group 1, .033; Group 2, .186), possibly due to a lack of data. However, the observed subgroup structures gave modularity scores that lay at the 100th and 99.98th percentiles of the simulated distribution, based on the baseline data, for Groups 1 and 2, respectively. Thus, our assignment of individuals to subgroups gives a significantly

higher modularity than would be expected by chance. The proximities of individuals outside of the testing sessions correspond to the subgroupings observed during task presentations, so we may be reasonably confident in our assignment of individuals to subgroups.

Standard Inferential Social Learning Statistics

Group comparisons of option use. The possible existence of traditions in each of the OD 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 or up-and-under flip because the subjects could not approach the task from behind; the ability to approach only from the front resulted in forward flips.

There was no significant difference between the two OD groups in the percentage of swivel manipulations ($[\text{number of swivels}/(\text{number of swivels} + \text{flips})] \times 100$) produced (median: Group 1 = 10.2%, Group 2 =

Table 2
Response of Asocial Learning Controls to the Extractive Foraging Apparatus

Subject	Contact Latency	Unsuccessful Manipulation		Successful Manipulation	
		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

Note—The actions (including body part used) and latency (in seconds) of the first contact and the first unsuccessful and successful task manipulations by each of the 4 control individuals (including the innovator) in the unseeded open-diffusion (OD) group. *This individual produced a successful manipulation prior to the first unsuccessful one.

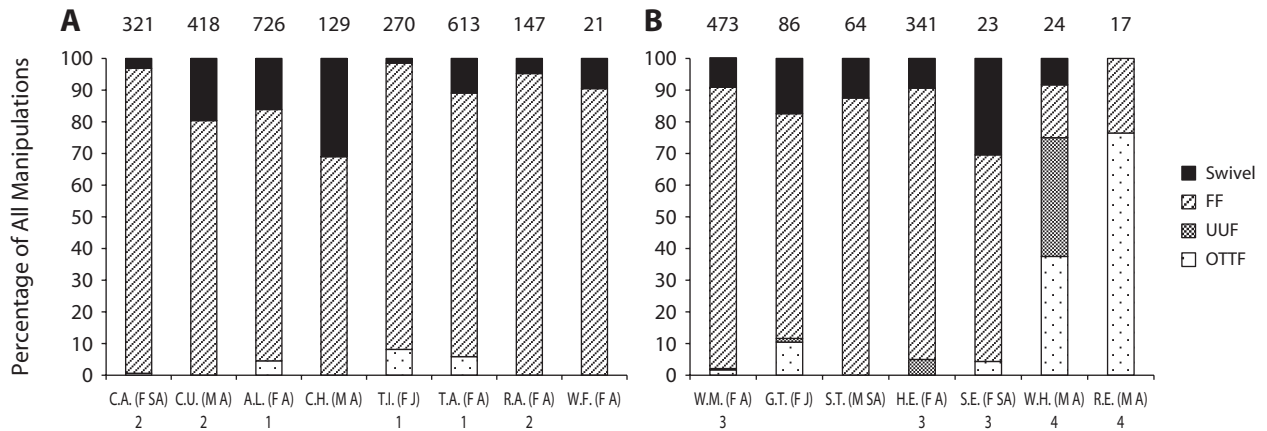


Figure 4. The percentages of all task manipulations (unsuccessful and successful) per individual, represented in order of first successful manipulation, that involved each option of swivel, forward flip (FF), up-and-under flip (UUF), and over-the-top flip (OTTF) for (A) Group 1 and (B) Group 2. Values at the tops of the bars give the total number of manipulations produced by individuals, who are represented on the x-axis by their initials. The letters within the parentheses indicate the individual's sex (F, female; M, male) and age category (A, adult; SA, subadult; J, juvenile). The values 1 through 4 under individuals' initials indicate subgroup membership.

9.4%; two-tailed Mann–Whitney U test: $U = 27$, $N_1 = 8$, $N_2 = 7$, $p = .9$), despite the fact that Group 2 was seeded with swivel-trained demonstrators. When the flip category was broken down into OTTF, UUF, and FF (with swivel), a Kruskal–Wallis analysis indicated a significant difference between the groups in the use of the UUF option only ($\chi^2_1 = 5.65$, $p = .017$), with Group 2 (median = .42) producing more than Group 1 (median = 0) (see Figure 4); however, the result should not be treated as valid, because it treats multiple manipulations from the same individuals as independent data points. As can be seen in Figure 4, Group 2 produced more OTTFs (median = 4.35%; 5 of 7 individuals exhibiting them) than did Group 1 (0.311%; 3 of 8 individuals). This is despite the fact that, ecologically, OTTF manipulations were at least twice as likely in Group 1 than in Group 2 (there were four trees at which OTTF was possible for Group 1 and only one or two 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 hand, right hand, or nose.

Influence of observation opportunities on 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 using. Full details may be seen in the supplemental materials, but, in summary, there was no indication that observation opportunities, either of actual manipulation type (e.g., flip vs. swivel / FF vs. OTTF vs. UUF / flip vs. swivel \times 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 success-

ful manipulations observed (from a zone of within 3 m 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: $t(1,12) = 6.36$, $p < .0001$]. 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 $\rho(13) = 264.66$, $p = .043$, 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 task is more representative of task monopolization than of learning, and that those monopolizing the task are tolerated in proximity to conspecifics at the task and can observe more task manipulations than less dominant individuals can.

Investigating the role of rank. LMMs with group as a random variable failed to find relationships fitting success order to either rank or total time at task prior to success. When nonsolvers are included in the analysis by giving them a ceiling success order value, however, there is a positive relationship between success order and rank [$t(1,18) = 2.74$, $p = .01$], suggesting that subordinate individuals are prevented from solving the task by dominant individuals (see Figure 5).

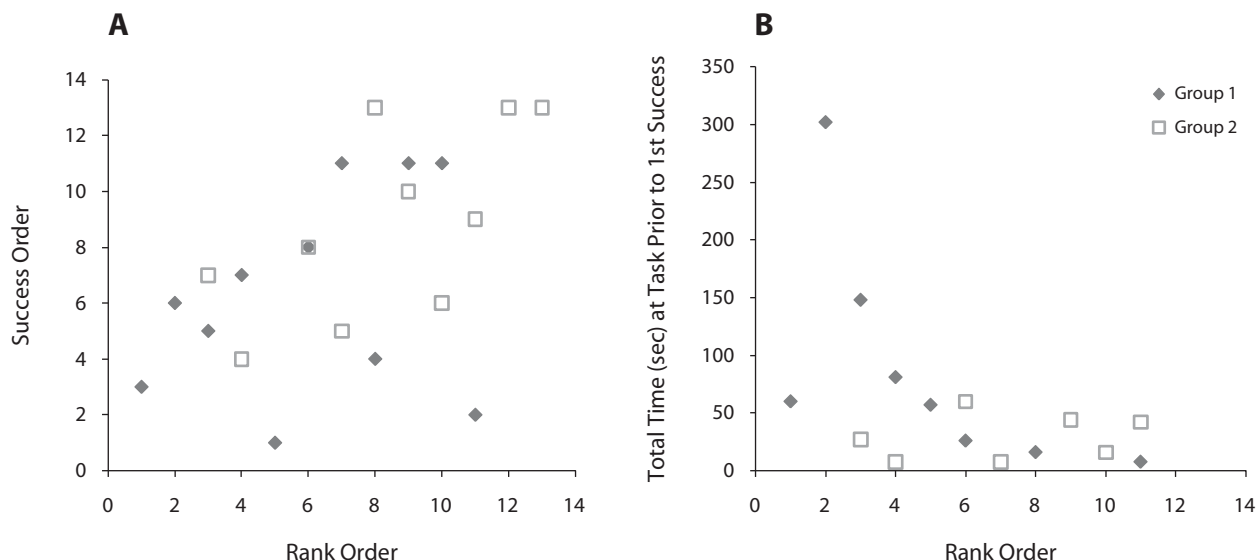


Figure 5. Significant relationships of (A) success order (with ceiling values of nonsolvers set at group sizes of 11 and 13 for Groups 1 and 2, respectively), as a function of rank order, and (B) total time at the task prior to first successful manipulation, as a function of rank order.

Of those individuals that did solve the task, there was a significant negative effect of rank on the total time needed to solve the task [$t(1,12) = -2.16, p = .05$]. In other words, subordinate individuals that gained sufficient access to solve the task learned the solution more quickly than dominant individuals did (see Figure 5). There was, however, no significant correlation between the proportion of successful manipulations [successful/(successful + unsuccessful)] produced by individuals and their rank. Thus, there is no hint that more-dominant individuals have an extended trial-and-error period (represented by a greater proportion of unsuccessful to successful manipulations), as compared with subordinate individuals, during their greater total time at the task prior to success. Thus, total time at task prior to success may have more to do with monopolization than with learning.

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 nonsolvers: $t(1,10) = 4.3976, p = .0013$] and no main effect of rank, but there was a significant interaction of successful manipulations observed and rank [$t(1,10) = -2.4612, p = .0336$]. Thus, as can be seen in Figure 6, more-dominant individuals tended to observe many successful manipulations and have a relatively long total latency to task solution, whereas more subordinate individuals tended to observe little and have short latencies to task solution. Since Ranks 1, 2, and 5 in Group 2 were trained demonstrators (and were therefore excluded), it was only in Group 1 that the top-ranking individuals featured in the data. Therefore, extreme caution is required in the interpretation of any rank-related results.

Option-Bias Analysis

The option-bias analysis was conducted at the level of flip versus swivel and, since flip could be broken down into three options, at the level of OTTF versus UUF versus FF, as well. Likewise, one can consider body part used for each manipulation, giving six options (left hand, right hand, or nose for flip or swivel). All details can be found in the supplemental materials, but, in summary, the majority of option-bias analyses (across the two groups or four subgroups, for all manipulations or successful manipulations only) yielded nonsignificant results, despite high power. However, one option-bias analysis, conducted on all manipulations of FF versus OTTF versus UUF across the four subgroups, yielded significant results (option bias: $\chi^2 = 591.278, p = .0001$; log linear model = 292.6169, $p = .0001$; see Figure 7A).

Where social learning (s) was set to zero and the asocial learning rate (α) was set to .5, with an underlying bias of 94 (FF) to 4 (OTTF) to 1 (UUF), the Type I error rates at $p = .0001$ were $<.0001$ for both methods. The familywise error rate does not need to be taken into account here because 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 was previously mentioned, such an analysis with regard to swivel was not conducted because the subjects appeared largely restricted to approaching the task from the front when swiveling.

As can be seen in Figure 7B, it was largely the proportion of option use in Subgroup 4 that resulted in the significant difference between the observed and simulated null distributions, although Subgroups 1, 2, and 3 also deviated from the global proportions. As is highlighted above,

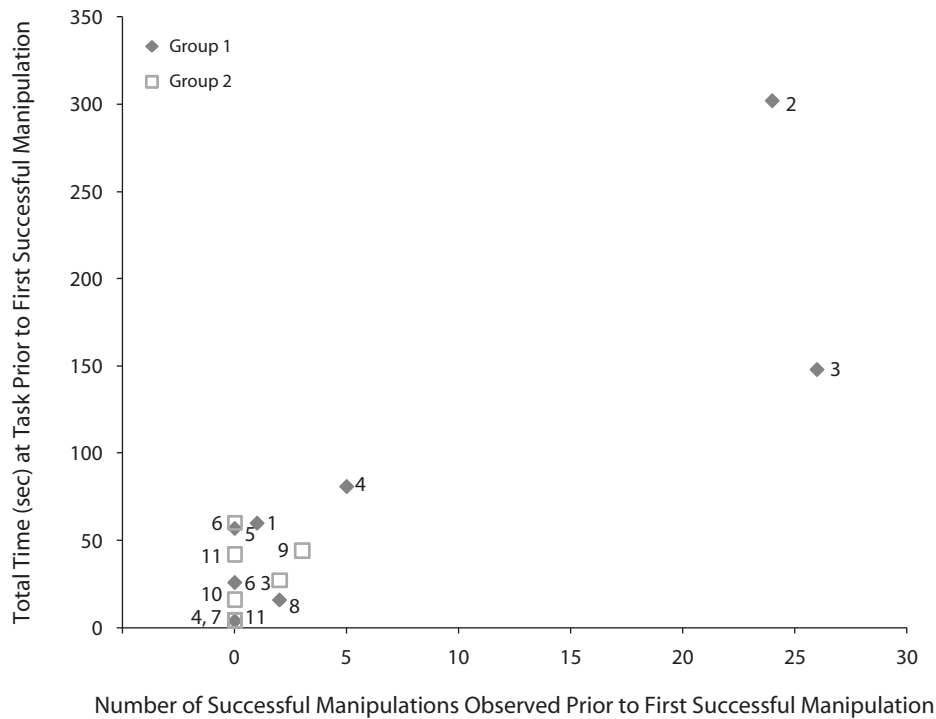


Figure 6. The significant predictive relationship between the number of successful manipulations observed prior to first success and the total time at the task prior to first success. The numbers next to the data points (to the left for Group 2 and to the right for Group 1) indicate the rank of the individual, highlighting the significant interaction of successful manipulations observed and rank on the cumulative time to solve the task. The relationship is interpreted with caution, since it is only in Group 1 that the top-ranking individuals feature in the data; the three top-ranking individuals in Group 2 were trained demonstrators.

the biases for OTTF and UUF in Subgroup 4 (of Group 2) cannot be accounted for by ecological differences since there were actually more tasks available in which these options were possible for Group 1 than for Group 2. It should also be noted that subgroups were not restricted to the use of particular tasks (of the four to six that were simultaneously presented) and, thus, differing possibilities of flip options afforded by each task's position cannot account for the significant option-bias result.

NBDA

When conducting extended NBDA—or *TADA*, as reclassified by Franz and Nunn (2010)—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 that includes both social and asocial learning (Akaike probabilities around 73%; see the supplemental materials). Thus, the difference in rank between Individuals A and B does not give any indication about the likelihood that B will produce a successful manipulation given that A has already done so. When using interindividual proximity levels (outside of testing sessions) as an indicator of the social network, for both groups, neither the so-

cial and asocial learning model nor the pure asocial learning model is favored (see the supplemental materials).

DISCUSSION

We applied the option-bias and NBDA methods to data from wild animals for the first time and 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 found a significant level of homogeneity of behavior, indicative of social learning, in the option-bias analysis of subgroups' use of options within flip. We believe this finding to be robust because it is supported by a particularly low Type I error rate of $<.0001$. In addition, as detailed below, there are many methodological and biological reasons 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 on 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

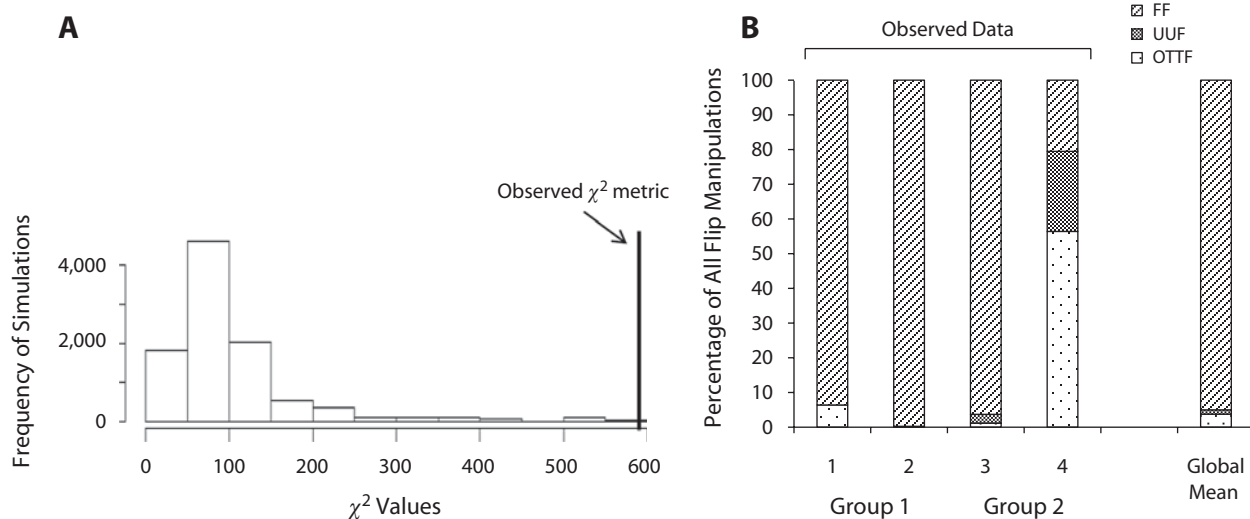


Figure 7. Results of the significant option-bias analysis (chi-square method only) of flip manipulations broken down into their component options—namely, forward flip (FF), up-and-under flip (UUF), and over-the-top flip (OTTF)—across the four subgroups. Panel A shows that the observed chi-square metric value (bold vertical line) falls in the upper tail of the null distribution of chi-square values created by the randomized simulation. Panel B depicts the observed percentages of flip options used for Subgroups 1 through 4 and the global mean percentage 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 percentages from which the simulated (randomized) data were sampled.

Fragaszy (1995)—that is, that tolerance of proximity may be required for the transmission of social information—our only evidence for social learning is within subgroups, 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 (Bonnie & de Waal, 2006; Nahallage & Huffman, 2007; Swaney, Kendal, Capon, Brown, & Laland, 2001), we 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, p. 1444) or by tolerance of proximity within subgroups, 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 to suggest only 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 (as defined by 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 subgroup, was not due to social learning. Although it appears that there was homogeneity of option use (toward flip vs. swivel) in both

groups (see Figure 2), the option-bias analysis indicates that this apparent bias may be accounted for by chance and/or by asocial learning alone. The fact that the 3 asocial learning controls and the innovator in the unseeded OD group all solved it several times within the first 10 min of exposure—exhibiting only 3, 10, 0, and 1 (OD) unsuccessful manipulations prior to first success, which occurred at an average of 71 sec—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 OD groups. Caution is, however, required because all of the controls were captive, rather than wild, adult males, and the OD innovator was a subadult 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 (R. L. Kendal, 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 (2010) with the presentation of three two-option, extractive foraging tasks to groups of captive ruffed lemurs (*Varecia variegata* spp.).

In support of the above argument (i.e., that social learning was not required for the 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 since, 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 task prior to success and the proportion of successful manipulations produced. Were the time at task to be used for trial-and-error learning, one would expect those with a low proportion of success to have had a long total time at task prior to success. Thus, the total time at 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 that is achieved by both female aggression toward 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 1 (an adult female) were low-ranking adults—often, peripheral males. This corresponds to the report of Kappeler (1987), in an early OD 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 exhibited significantly less observation of the prior successes of others, likely out of a lack of opportunity to remain within 3 m of the task when a conspecific was manipulating it (Anderson et al., 1992), as compared with dominants. This did not, however, impede their success with the task; they exhibited a significantly reduced total time at task prior to first success, as compared with dominants. This tentative finding cannot, however, be taken as conflicting with the hypothesis that cognitive ability (i.e., learning time) is positively correlated with social dominance (see Boogert, Reader, & Laland, 2006), because (1) the total time to success, as discussed above, may not be indicative of learning time, but rather of resource monopolization by dominants; and (2) 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 subgroup in the lemur

groups’ response to the extractive foraging task. Although the option-bias analysis found evidence for social learning, this was at the subgroup level and for option use, whereas the NBDA analysis used 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 OD 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 learning model nor the social and asocial learning model was favored over the other. Thus, it remains possible that there was an effect of directed social learning along pathways specified by proximity within these lemur groups that the NBDA method did not detect, due to the low power caused by small group sizes (Franz & Nunn, 2010; Hoppitt, Boogert, & Laland, 2010).

Methodological Considerations

Our analyses have highlighted several methodological considerations for the use of inferential statistical methods, option-bias analysis, and NBDA 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 was highlighted by R. L. Kendal, Kendal, et al. (2009), the researcher using option-bias analysis must independently identify the populations for which homogeneity of behavior is expected. In the present study, it was apparent that the choice of an appropriate level of population analysis (here, group or subgroup) was key.

Similarly, a new method (Matthews, 2009) developed for the study of social transmission in intermediately despotic wild capuchins used a randomization method to indicate that cliques within groups showed more evidence of social learning than did groups as a whole. Likewise, with 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 indicative of tolerance of proximity between individuals during routine foraging (i.e., a co-feeding network; Franz & Nunn, 2010). 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, 2010), this remains to be explored using real data.

We originally planned to apply J. R. Kendal et al.’s (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 de-

tect social learning. Similarly, as is emphasized by Hoppitt, Kandler, et al. (2010), the displacement of individuals from tasks by conspecifics has implications for the interpretation of NBDA, as well as of diffusion-curve analysis.

As is detailed in our Method 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 (developed for callitrichids; Day, 2003). The measure of learning time (total time at task prior to first success) was adapted to take into account the 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 task prior to first success as an indicator of cognitive learning time was flawed because time at task in dominant individuals might have had everything to do with resource monopolization and nothing to do with learning (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, the present 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 subgroup 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, swivel), but the lemurs themselves invented three different ways of flipping, necessitating analysis at this level as well. 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. This has also been suggested for New Caledonian crows' manufacture of wide *Pandanus* leaf tools (Holzhaider et al., 2010). Our finding also shows that the approach should be suitable when there is only one action (or motor pattern) required to solve a task and variation in the option choice within that action (Horner & Whiten, 2005).

When considering the application of the method to data in which there was an underlying bias for option use, we used a slightly different code for the chi-square randomization method from that used previously (R. L. Kendal, Kendal, et al., 2009). Here, the chi-square method used 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; but since the method incorporates bias, we may still be confident in the evidence we found for social learning.

Thus, the method may be used to overcome the issue faced by many studies, where groups are seeded with different techniques for task solution, one of which is considered more salient or easier than the other (see Flynn & Whiten, 2010; Hopper et al., 2007). For example, Hopper et al. were forced to be cautious in their interpretation of social learning's 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 consequently the possibility that the bias for poke in the poke-seeded group was asocially learned could not be ruled out.

Conclusion

Contrary to the common belief that lemurs are cognitively lacking, as compared with haplorhine primates (see, e.g., Jolly, 1966), we found evidence consistent with social learning in the despotic *Lemur catta* that supports the theory of directed social learning (Coussi-Korbel & Fragazy, 1995). To validate this finding, it would be useful to directly examine social learning processes with regard to 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 OD scenario with a more egalitarian lemur species, such as the red-fronted brown lemur (*Eulemur rufifrons*). We predict that we would find greater evidence for socially learned traditions in more egalitarian than in more despotic species, which, in turn, would have implications for the evolution of our own unique cultural capacities. Also, to identify the role of rank on learning, future studies should conduct OD studies and individual learning tests simultaneously with the same subjects (see, e.g., Boogert et al., 2008; Boogert et al., 2006; Hoppitt, Kandler, et al., 2010).

Finally, as the toolbox 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, with regard to the social dynamics of the subjects. The onus is thus on the creators of methods to clearly state their assumptions and constraints, whereas the researcher is responsible for deploying the appropriate method for examining putative cases of social learning.

AUTHOR NOTE

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NOTE

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

SUPPLEMENTAL MATERIALS

An R function for calculating chi-square from contingency table values and a discussion of additional results may be downloaded from <http://lb.psychonomic-journals.org/content/supplemental>.

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