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Testing for social diffusion of two novel foraging skills and conformity  
in wild redfronted lemurs (*Eulemur fulvus rufus*)

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*Für meine Eltern,*

*Angelika und Felix Schnöll*

# Contents

## Abstract

<b>1</b>	<b>Introduction</b>	1
<b>2</b>	<b>Material and methods</b>	5
2.1	Study site and subjects	5
2.2	Methods	5
2.2.1	Experimental apparatus	5
2.2.2	Experimental procedure and set-up	6
2.3	Behavioural data	9
2.4	Analysis and statistics	9
2.4.1	Modelling	11
<b>3</b>	<b>Results</b>	13
3.1	Learning behaviour	13
3.2	Conformity	15
3.3	Scrounging	18
3.4	Modelling and Social Networks	19
<b>4</b>	<b>Discussion</b>	21
<b>5</b>	<b>Acknowledgments</b>	27
<b>6</b>	<b>References</b>	28
<b>7</b>	<b>Supplements</b>	33
7.1	German Summary	33
7.2	Curriculum Vitae	34

## Abstract

Recent research revealed that traditions are not a unique feature of human culture, but that they can be found in animal societies as well. However, the underlying mechanisms and conditions leading to social diffusion of newly invented behaviours, as well as the importance of the formation of traditions for animals living in the wild, are still poorly understood. To address these questions, I conducted a social diffusion experiment with three wild groups of redfronted lemurs (*Eulemur fulvus rufus*). I used a 'two-option' feeding box, where animals could either open or push a door to get access to a fruit reward to study whether and how the trait spreads through the groups. Half of the 28 study animals were able to learn the new feeding skills and mainly kept a seeded technique (groups with training) or adjusted (group without training) their behaviour to the majority of the group. Individuals observing others more often needed fewer trials until they could successfully open the door, indicating that social learning played an important role in acquiring the task. An option bias analysis suggested that social learning was involved in the spread of the novel behaviours, whereas a network-based diffusion analysis indicated pure asocial learning. Moreover, redfronted lemurs invented a third technique for accessing the reward: scrounging. Interestingly they did not scrounge more often from kin. Thus, redfronted lemurs are able to form behavioural traditions. The results suggest that the study animals did not simply keep the first rewarded technique but showed a high flexibility in choosing between social and individual learning.

**Keywords:** *Eulemur fulvus rufus*, traditions, conformity, social diffusion experiment, scrounging

## 1. Introduction

One aim in research of animal culture is to identify the underlying mechanisms explaining the spread of traditions in animal societies (reviewed by Whiten & van Schaik 2007), as one basal requirement of culture is a set of multiple, diverse behavioural traditions. Traditions are seen by definition as distinctive behaviours that differ within or between populations, are shared among members of a group and characterized by their persistence over time and most importantly by being acquired through social learning (Fragaszy & Perry 2003; Galef 2003; Whiten & van Schaik 2007). Traditions in animals have been identified so far in food processing techniques (primates: Kawai 1965; Whiten et al 1999; van Schaik et al 2003, Perry 2009; cetaceans: Rendell & Whitehead 2001, Krützen et al. 2005; birds: Hunt & Gray 2003), in affiliative behaviours (primates: Whiten et al. 1999) and in communication (birds: Catchpole & Slater 1995; cetaceans: Janik & Slater 1997).

Animal traditions were first documented in wild Japanese macaques (*Macaca fuscata*), in which a low-ranking female began to wash sweet potatoes in salt water, a new feeding technique that subsequently spread through the group of this female (Kawai 1965). Most subsequent intra- and inter-population comparisons of animal traditions were made in wild populations of great apes, which exhibit different techniques to use tools that are thought to be acquired by social learning (Sugiyama 1997; Whiten et al. 1999; van Schaik et al. 2003; Gruber et al. 2009). Different food-processing techniques have also been documented in wild capuchin monkeys (*Cebus sp.*: Izawa & Mizuno 1977; Fernandes 1991; Panger 1998, Fragaszy & Visalberghi 2004, Perry 2009) and cetaceans (Rendell & Whitehead 2001, Krützen et al. 2005). Despite these documentations of intergroup differences, their origin as well as the underlying mechanisms leading to tradition remain unclear because it is difficult to assess by field observations alone whether a trait was acquired through social or individual learning.

Social learning is the essential mechanism for the formation of traditions, as it is necessary for diffusion and maintenance of intra-group specific behaviours. It is defined as the change of an individual's behaviour by using the information provided by others (McGrew 1998). Primates are able to learn socially, as demonstrated by experimental studies in captivity (Voelkl & Huber 2000; Whiten et al. 2005; Dindo 2008). By introducing an artificial foraging box that could be opened using two different

techniques into groups of captive chimpanzees (*Pan troglodytes*), it could be demonstrated that the introduction of a socially learned foraging technique led to social diffusion of the respective technique within groups (Whiten et al. 2005).

Such social diffusion experiments have the advantage that animals are tested on a group level, i.e., in a situation similar to the one in which social learning would normally occur in the wild (Whiten et al. 2005, Whiten and Mesoudi 2008). Whereas such experiments in captivity have the potential to reveal whether behavioural traits in groups are subject to individual modification or social transmission, field studies can provide an ecologically more valid picture and address questions about the importance of social diffusion for animals living in the wild, where they have to manage their time and energy budgets carefully to manage survival (Parker 1990). Social learning can help save energy in the sense that individuals do not have to figure out certain behaviours themselves but instead can observe and copy/imitate others. However, there is also always a risk that individuals might gather wrong information, which would increase the costs of learning considerably (Parker 1990). Thus, even species with the cognitive capacity for social learning may only do so when it provides a net benefit.

However, only a few studies have focused on the social diffusion of a new foraging skill under natural settings in birds and mammals, including pigeons (*Columbidae*; Lefebvre 1986), magpie jays (*Calocitta formosa*; Langan 1996), keas (*Nestor notabilis*; Gajdon et al. 2004), meerkats (*Suricata suricatta*; Thornton & Malapert 2009) and wild banded mongooses (*Mungos mungo*; Müller & Cant 2010). Some of these studies (Langan 1996, Gajdon et al. 2004) had to cope with practical problems, such as dominant individuals monopolizing the feeding apparatus or too difficult foraging tasks. Lefebvre (1986), who trained captive and wild pigeons to peck through paper covers, could find a higher level of social diffusion in wild compared to captive pigeons, probably due to a stronger selective pressure on the development on efficient foraging skills.

In addition to the spread of new foraging techniques, Whiten et al. (2005) documented the formation of conformity in chimpanzee groups. Conformal behaviour is defined as adoption of the group's norm despite being principally able to behave differently, i.e., in the case of the chimpanzee feeding box experiment to use an alternative technique to open the box (Whiten et al. 2005). Thus, conformity represents a strong indirect indicator for social learning. Subsequent research on Norway rats (*Rattus norvegicus*) (Galef & Whiskin 2008) showed that conformity is not unique to

chimpanzees and humans (Whiten et al. 2007). Norway rats learned by observing others to suppress their personal knowledge about toxic or safe, as well as good or bad tasting items in a food choice task (Galef & Whiskin 2008). Moreover, brown capuchins (*Cebus apella*) also exhibited conformity in using a specific technique to open a feeding box (Dindo et al. 2009). In one of the few primate field studies on this topic it was suggested that conformity in common marmosets (*Callithrix jacchus*) to a certain feeding technique could be explained by the preference of subjects for simply sticking to the first rewarded technique in a two-action feeding box task and not by adjusting to the 'group norm'. The authors argued that the underlying social and cognitive mechanism could be a rather simple one (Pesendorfer et al. 2009). This interpretation is supported by the fact that all trained groups, i.e. groups in which every individual learned one of two techniques beforehand, kept the trained technique when offered the possibility to choose freely between them, and that a control group did not show any preference at all. However, they did not take in account that conformity must not necessarily lead to homogeneity within a group – one could also imagine scenarios where more than one technique spreads through different subgroups, as the strength of relationships differs between individuals even in small family groups (Digby 1994). Relationships might influence the individual levels of motivation for learning as well as the amount of social learning opportunities due to higher tolerance towards 'friends' (de Waal 2001). Therefore it is important to consider the social network of a group when looking at social diffusion (Franz & Nunn 2009).

Moreover, Pesendorfer et al. (2009) pointed out that they would expect from 'a true conformist' to scan conspecifics regularly to gather knowledge about the current group norm. De Waal et al. (2010) found that vervet monkeys (*Chlorocebus pygerythrus*) paid more attention to female than male demonstrators and therefore found higher levels of participations as well as conformal behaviour in a social diffusion task with feeding boxes. The authors argued that this phenomenon might occur because females are the philopatric sex and therefore might have more knowledge about their habitat than males. However, vervet monkeys also exhibit strict dominance hierarchies (Struhsaker 1967), so that different dominance status could have influenced the outcome of this study as well, even though the authors claim that aggression rates did not differ between males and females. But if dominance relationships are established, the effect of dominance cannot be excluded simply due to low aggression levels.

Hence the social system of a species may play a role in the formation and spread of traditions as well as in generating conformity, as different systems may offer more or less opportunities to learn socially. Against this background, I chose a highly tolerant and egalitarian species for this study: Redfronted lemurs (*Eulemur fulvus rufus*). They are group-living and neither do they exhibit a linear dominance hierarchy nor is one sex dominant over the other (Ostner & Kappeler 2004). They exhibit high levels of social affinity (Pereira & Kappeler 1997), which allows individuals to spend time in close proximity to others, leading to learning opportunities. Males typically disperse from their natal groups, but females are sometimes expelled (Ostner & Kappeler 2004).

Even though the brain size of Malagasy lemurs is relatively smaller compared to that of Old and New World monkeys (Armstrong 1985), and despite some early doubts about their intelligence (Jolly 1966), the ability to learn socially has been demonstrated in lemurs in captive and semi-free ranging settings. For example, a group of semi-free ranging ring-tailed lemurs (*Lemur catta*) developed a new behaviour of drinking water by dipping their tails into water and sucking water from it (Hosey et al. 1997). Although the spread of this innovation has not been studied in detail, it is unlikely that 17 of 28 animals invented this behaviour independently. Furthermore, semi-free ranging ring-tailed lemurs and captive brown lemurs (*Lemur fulvus*) were able to learn to open a food box from conspecifics (Kappeler 1987; Anderson et al. 1992).

The aim of this study was to investigate the basal underlying mechanisms of the formation of traditions by examining the spread of two different handling techniques in red-fronted lemurs. I used an artificial fruit task under natural conditions. I focused on whether i) wild red-fronted lemurs can learn a new foraging technique, ii) if so, whether they learn individually or socially, and whether iii) they adapt their behaviour to the majority of the group, thereby exhibiting conformity.



## 2. Material and Methods

### 2.1 Study site and subjects

This study was conducted at the research station of the German Primate Center (Deutsches Primatenzentrum) in Kirindy Forest, Western Madagascar (Sorg et al. 2004). Kirindy is a dry deciduous forest with a pronounced annual rainy and dry season. Data collection took place between September and December 2009, which corresponds to the end of the dry season and the beginning of the rainy season.

I studied 28 individuals out of three groups of redfronted lemurs (Table 1). As part of a long-term study all subjects are individually marked with nylon collars and well habituated to human presence. Genetic relationships were known except for juveniles and for some immigrant males. Redfronted lemurs were naïve with respect to the experimental protocol and had no experience with any food not growing naturally in the forest.

**Table 1.** Composition of the study groups and corresponding conditions. The pull and push condition received a training for either pull or push, the open condition did not receive any training for neither of the two techniques.

Condition	Groups			In Total
	A	J	B	
	Pull	Push	Open	
Number of adult males	6	4	5	15
Number of adult females	3	2	2	7
Number of juvenile males	2	0	1	3
Number of juvenile females	1	2	0	3
<b>Total numbers of subjects</b>	<b>12</b>	<b>8</b>	<b>8</b>	<b>28</b>

### 2.2 Methods

#### 2.2.1 Experimental apparatus

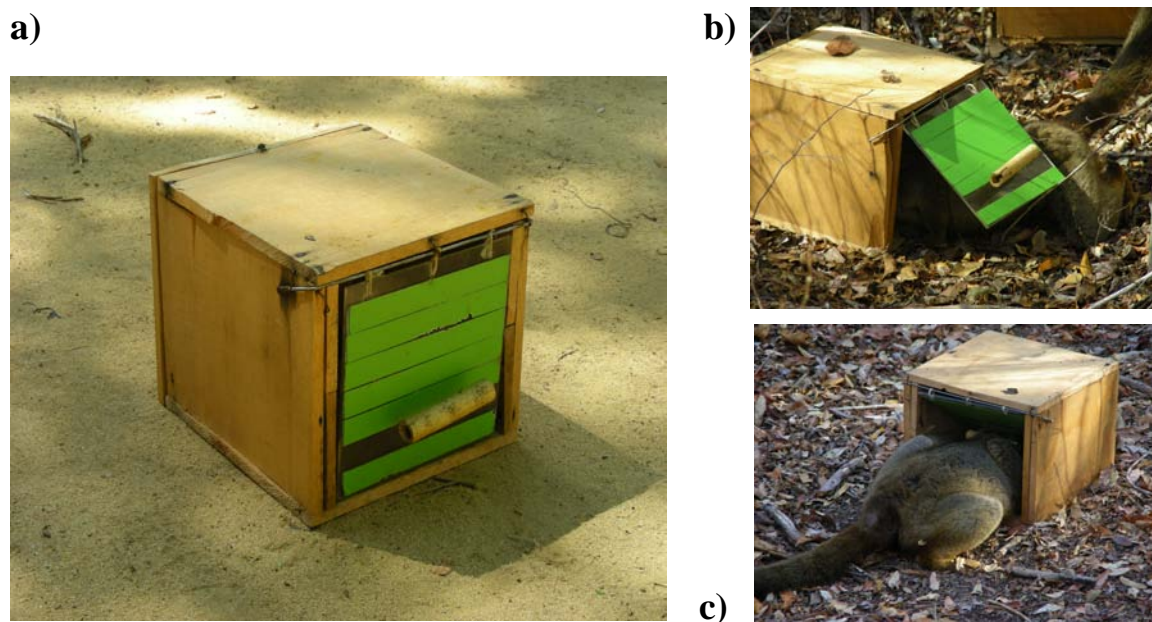
I used a feeding box similar to the one used by Bugnyar and Huber (1997) in a laboratory study with common marmosets and afterwards by Pesendorfer et al. (2009) on the same species in the field. The box was constructed of wood and measured 16 x 20 x 20 cm (Figure 1). The front side was open, but covered by a 15 x 15 cm flap door

## 2. Methods

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made of plexiglas with a handle. Additionally, the door was covered by tape, except a single narrow strip to assure, that the learning period was not influenced by the need to learn the concept of transparent materials beforehand.

The feeding box could be opened by two different techniques: by pulling or pushing the door (Figure 1). Each action requires a different movement to make sure animals learn the different movements themselves and not only how to act in a given situation (Huber et al. 2009), i.e. to just perform a movement behaviour on the door if being confronted with a feeding box. Unlike social learning, the effect of simple social influence was excluded in this way (McGrew 1998). Both actions were likely to have the same degree of difficulty to open the door. I chose relatively easy movements because of the limited dexterity of lemurs (Torigoe 1985) due to the lack of a precision grip (Holtkötter 1997) which allows opposable movements of the thumb (Napier 1961).

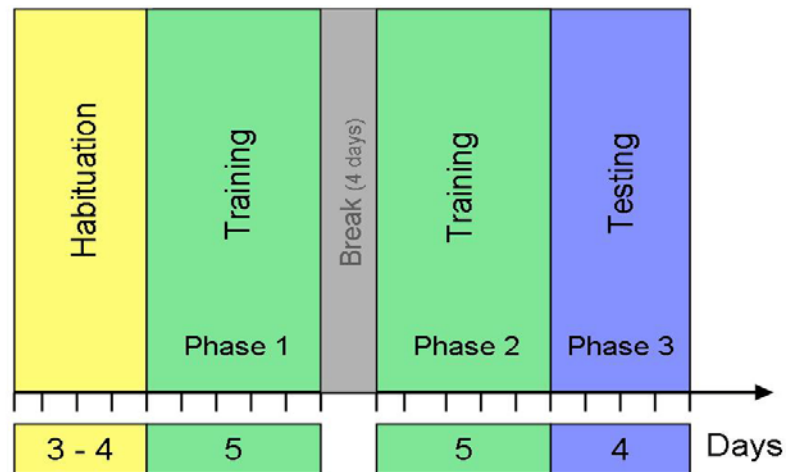


**Figure 1.** Experimental apparatus: The feeding box (a) offered two distinctive techniques for extracting reward – the door could either be pulled (b) or pushed (c).

### 2.2.3 Experimental set up and procedure

Animals were first habituated to the novel fruits (orange and mango) used as a reward and the feeding boxes during a time span of 3 to 4 days (Figure 2). Afterwards they were assigned to three different conditions for the training phase: Two groups were confronted with constrained boxes, offering either the possibility to open the door by

pulling (condition pull-group) or by pushing (condition push-group). An additional group was allowed to use both techniques from the beginning on (condition open-group).



**Figure 2.** Experimental procedure: Each group passed through habituation, training and testing. Data were collected in Phase 1, Phase 2 and Phase 3.

Because it was not possible to train specific individuals separately as demonstrators, two groups were trained group-wise to open the door by only one of the techniques (Figure 2). The third group was confronted with an unconstrained feeding box, to test whether there is a general preference for one technique over the other. All groups were trained for a maximum of 10 days, with a break of 4 days in between, but moved to testing earlier, if half of the group members were able to perform at least 5 successful operations in one session. The pull-group as well as the open-group stayed in the training phase for 10 days, whereas the push-group changed to the testing phase after 7 days. After the training phases, I confronted each group with unconstrained boxes to test whether redfronted lemurs continued opening the box with the originally learned technique or if they individually learn to open the box by the alternative technique. I conducted one session per day and group.

In each session, I presented a group with three boxes to avoid monopolization of the box (Figure 3). The boxes were filled with several pieces of oranges or mangos before approaching the group to avoid an association between the observer and food. Feeding boxes were presented when a group was resting or feeding, preferentially when

## 2. Methods

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the animals gathered on or near the ground. The three boxes were placed on open spots on the ground so that all interactions at the boxes could be video-taped (Figure 3). The experiment was started when at least one individual approached a box within a 1 meter radius. Additionally, I noted the number, position and distance of individuals gathering at a range of 10 meters around the boxes every second minute. I also noted whether individuals were looking towards another individual manipulating a box. The percentage of observation time was calculated by dividing the number of two minutes scans spent observing others by the total amount of scans. Moreover, I calculated a relative aggression score as measurement for monopolization for each individual by dividing the number of aggressive interactions (Table 2) given by the total number of aggressive interactions (number of aggressive interactions given and received) within a 1 meter radius of a box.



**Figure 3.** Experimental set-up with three boxes placed on an open space on the ground and a tripod with the video camera.

### 2.3 Behavioural data

To establish a social network, all 28 individuals were observed for one statistical day. Outside the experiments, I conducted focal animal observations on all subjects. During 30 minutes periods, I recorded predefined affiliative, affiliative and aggressive interactions (Table 2).

### 2.4 Data analyses

The videos sequences were recorded with a Sony camera (DCR-PC105E PAL) installed on a tripod. Recordings were analyzed with Adobe CS 3 Premiere Pro. I recorded the identity and sex of the individuals at the test location as well as a set of other variables describing interactions with the boxes and with conspecifics (Table 3).

To calculate the efficiency in retrieving food rewards, I divided the number of successful actions by the number of total actions performed on the door for a given individual. In order to compare whether the efficiency in retrieving food rewards changed over the experimental phases, I used a permutation test for related samples with missing values (Mundry 1999), because not all individuals manipulated the boxes in each phase.

In order to assess whether the time an individual spent in contact with the boxes is associated to its aggression score, I used correlation analysis. I used correlation analysis as well for looking at the statistical relationship between the times spent observing others and the learning efficiency as well as the latency for the first successful action. Additionally, correlation analysis was conducted to access if the latency varies with the time spent in contact with the boxes. I performed Spearman analysis because there was no normal distribution of the samples.

In order to test whether individuals exhibit a preference for one over the other technique, I first divided the number of actions in which the technique was used by all actions and then used a binomial test. For calculating the scrounge preference I again divided scrounging actions by total amount of actions, including the scrounging actions. Learning success, i.e. trials until first success, was compared between the three conditions (i.e. groups) with a Kruskal-Wallis test. The effects of age and sex on time spent observing others as well as on learning success were calculated by using a Mann-Whitney-U test. This test was also used for comparing if learner spent higher percentages of time in contact with the boxes than individuals that did not manage to learn the techniques and to compare the percentage of pull actions between the two

## 2. Methods

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constrained conditions. To access if individuals observe related individual longer than unrelated ones as well as if they make a difference in amount of scrounging according to kinship I used a Wilcoxon signed-rank test, as I calculated two values per subject – one for kins and one for nonkins. All tests were calculated with SPSS Statistic 17.0. All median values are given with interquartile range (IQR) and mean values with standard deviation.

Social networks were constructed on the basis of durations of affiliative interactions (grooming, resting in contact and resting together; definitions: Table 2). I summarized the data in an association matrix by using total durations of affiliative behaviour during the 30 min of focal observation time. The networks were constructed with Ucinet 6 and visualized with NetDraw 2.094 (Borgatti et al. 2002). For kinship data was available about maternal relatives for most individuals as well as about fatherhood for some of the males.

**Table 2.** Behavioural definition used for focal observation (modified after Pereira and Kappeler 1997).

Variable	Definition	Measure
Approach	Approaching an individual within a 1 meter radius	Frequency
Departure	Leaving the 1 meter radius of another individual	Frequency
Resting together	Resting together with at least one individual within a 1 meter radius for at least 10 seconds	Duration
Resting in contact	Resting with at least one individual in direct physical contact for at least 10 seconds	Duration
Grooming	Stroking with the tooth comb through the fur of another animal	Duration
Chasing	Running after a fleeing individual	Frequency
Biting	Biting another individual	Frequency
Hitting	Hitting another individual with one or two arms/hands	Frequency
Displaying	Sudden movement of upper body towards another individual without leaving the position	Frequency

**Table 3.** Definition of behavioural variables used in the experiment.

Variable	Definition	Measure
Within 0,5 m radius	Individual within a radius of $\leq 0,5$ m of a box	Duration
Contact with box	Manipulating the box with the hand or inspecting the box with nose within a 5 cm radius	Duration
Successful action	Opening the door to get a reward	Frequency
Unsuccessful action	moving the door for at least 5 cm without receiving a reward	Frequency
Focusing on the box	Head of individual is turned in the direction of the box	Frequency
Observing others	Head of individual is turned in the direction of the box while another individual is in contact with it.	Frequency
Aggressive interaction	All events in which a subject acts as aggressor as well as receives aggression (chasing, biting, hitting, displaying; see definition Table 2)	Frequency

### 2.4.1 Modelling

For further indications if social learning was involved, I used two statistical models: the option-bias method (Kendal et al. 2009) and the network-based diffusion analysis (Franz & Nunn 2009). For both I utilized the program R 2.8.1 (Development Core Team 2009) for calculations.

The option-bias method assumes that social learning creates a higher behavioural homogeneity in the data set than one would expect without it, if genetic and ecological differences can be excluded. Whether a trait spreads socially through a group or not gets detected by comparing the actual data set to an artificial data set created by using a null distribution. A null distribution is the probability distribution when the null hypothesis is true. The null hypothesis for the model assumes that there is no social learning involved.

As a first step, a chi-squared value for the data set was calculated as a measure for the option bias within the group. The null distribution gets generated by using randomisations. For each randomisation, individuals were assigned to groups with

group sizes corresponding to the actual data set. All simulations were run 10.000 times. The p-value was calculated as the proportion of the null distribution that was greater than or equal to the observed option bias statistics.

The network-based diffusion analysis (NBDA) tests for social learning by including the social aspect of group structure. It takes the social learning opportunities into account that a social network offers. It does so by using the order and timing in which each member of a group learns the task. These data get compared with the different amount of opportunities included in the network and it detects social learning by making use of the fact that traits spread quicker between animals with stronger bonds. In the case of this study, I used affiliative behaviour as a proxy for learning opportunity, assuming that individuals learn preferentially from conspecifics with which they spent more time in close proximity and interact affiliatively. The model detects the underlying learning mechanism by using maximum-likelihood estimation. Maximum-likelihood estimation is a common statistical procedure for fitting a model to an actual data set that determines the parameters that maximise the likelihood of the sample. For my data I used the extended version of the NBDA, which takes into account that a situation in which animals learn only socially is rather unlikely under natural conditions. It therefore compares the data to a model of social and asocial learning as well as to a model of only asocial learning. The simple NBDA compares the data to a social learning model and an asocial learning model. The calculated Akaike information criterion allows an estimation of whether the trait spread asocially or socially. This criterion (Akaike 1974) is a measurement of how good an estimated statistical model fits the data.



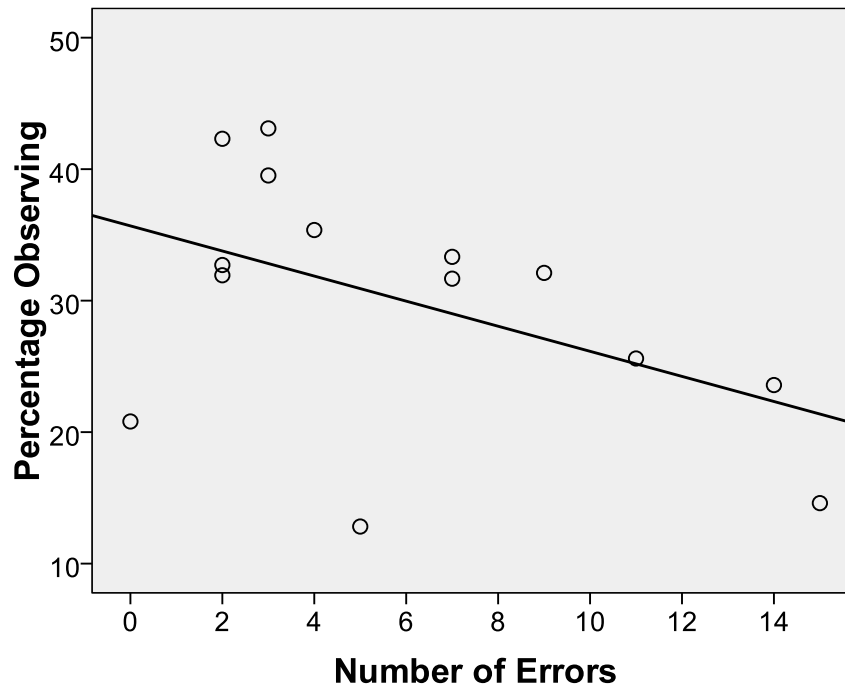
### 3. Results

#### 3.1 Learning behaviour

All 28 subjects of the three study groups explored the feeding boxes. In the group trained with the pulling technique (henceforth the pull-group) 6 out of 12 animals conducted actions at the door. Four individuals performed the task at least once with success. In the group trained with the pushing technique (henceforth the push-group) 6 out of 8 individuals managed the task and performed at least one successful action. In the group in which the feeding apparatus was not constrained (henceforth the open-group) 6 out of 8 individuals interacted with the boxes and four performed at least once with success. On average subjects needed  $6 \pm 4.8$  ( $n = 14$ ) trials until their first successful operation. Learning success did not differ across the conditions (Kruskal-Wallis test:  $df = 2$ ,  $p = 0.23$ ,  $n_{\text{pull-group}} = 4$ ,  $n_{\text{push-group}} = 6$ ,  $n_{\text{open-group}} = 4$ ;  $\text{median}_{\text{pull-group}} = 4.5$  trails,  $\text{IQR} = 3$  to  $5.5$ ;  $\text{median}_{\text{push-group}} = 7$  trials,  $\text{IQR} = 2.3$  to  $13.3$ ;  $\text{median}_{\text{open-group}} = 5$  trials,  $\text{ICR} = 2.8$  to  $7.5$ ). Interestingly, there was a sex difference in learning success with only 33.3 % of males but 80 % of females acquiring the task (Mann-Whitney-U test:  $Z = -2.32$ ,  $p = 0.03$ ,  $n = 28$ ).

Individuals that learned the task spent higher percentages of time in contact with the boxes than individuals that did not perform any successful actions (Mann-Whitney-U test:  $Z = -3.997$ ,  $p = 0.01$ ,  $n_{\text{learner}} = 14$ ,  $n_{\text{nolearner}} = 14$ ;  $\text{median}_{\text{learner}} = 22.3$  %,  $\text{IQR} = 14.3$  to  $33.2$ ;  $\text{median}_{\text{nolearner}} = 4.47$  %,  $\text{IQR} = 1.7$  to  $9.3$ ). Individuals aggressively defended the boxes and as a result more aggressive animals tended to spend longer time spans in contact with the boxes (Spearman-Rho:  $\rho = -0.38$ ,  $p = 0.05$ ,  $n = 28$ ). Females and males did not differ in the number of aggressive events (Mann-Whitney-U test:  $Z = -0.10$ ,  $p = 0.47$ ,  $n_{\text{female}} = 10$ ,  $n_{\text{male}} = 18$ ;  $\text{median}_{\text{female}} = 0.2$ ,  $\text{IQR} = 0.1$  to  $0.5$ ;  $\text{median}_{\text{male}} = 0.3$ ,  $\text{IQR} = 0.1$  to  $0.6$ ).

The percentage of time spent observing other group members performing the task was negatively correlated with learning efficiencies, i.e., number of errors before the first successful action (Fig. 3; Spearman-Rho:  $\rho = -0.72$ ,  $p = 0.00$ ,  $n = 14$ ). Thus, redfronted lemurs that observed others performing the task made fewer mistakes during their acquisition of the task. However, observing other individuals performing the task had no influence on latency of the first successful action at the box (Spearman-Rho:  $\rho = 0.35$ ,  $p = 0.11$ ,  $n = 14$ ). Latency was also not influenced by the time spent in contact with the boxes (Spearman-Rho:  $\rho = -0.04$ ,  $p = 0.45$ ,  $n = 14$ ).

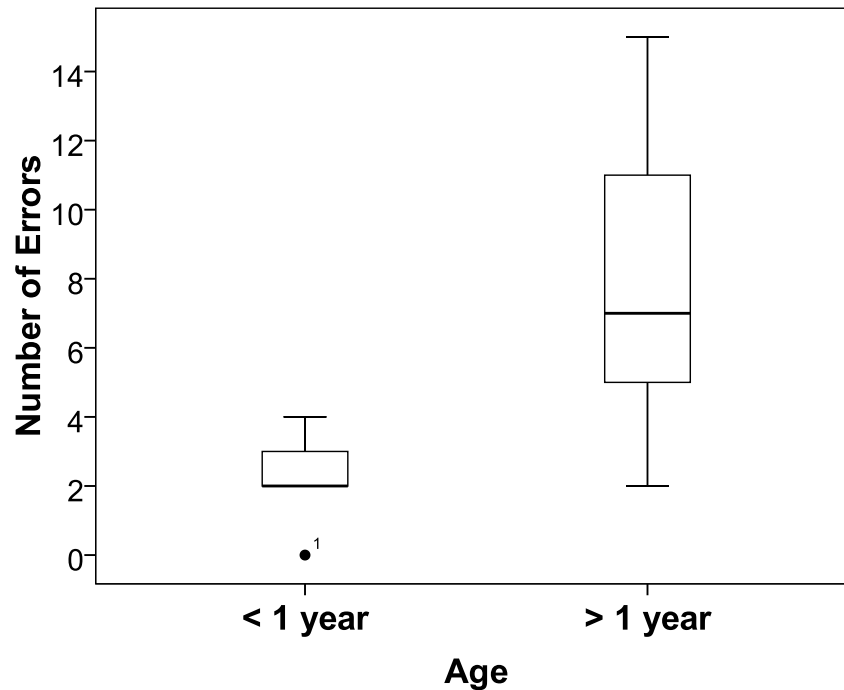


**Figure 3.** Correlation between the number of errors until first success and percentage of observing others performing the task (two-minute point samples spent observing divided by total amount of scans).

Overall, younger individuals observed more often other group members performing the task than older individuals (Mann-Whitney-U test:  $Z = -2.22$ ,  $p = 0.02$ ,  $n_{\text{young}} = 6$ ,  $n_{\text{old}} = 22$ ; median<sub>young</sub> = 35.4 %, IQR = 32.0 to 39.5; median<sub>old</sub> = 31.7 %, IQR = 23.6 to 32.7) and made consequently fewer errors (Fig. 4; Mann-Whitney-U test:  $Z = -2.42$ ,  $p = 0.01$ ; median<sub>young</sub> = 2 trails, IQR = 2 to 3; median<sub>old</sub> = 7 trails, IQR = 5 to 11).

Males observed slightly more often females performing the task (Mann-Whitney-U test:  $Z = -2.01$ ,  $p = 0.046$ ,  $n_{\text{male}} = 14$ ,  $n_{\text{female}} = 15$ ; median<sub>male</sub> = 16.0 %, IQR = 10.1 to 16.0; median<sub>female</sub> = 22.8 %, IQR = 21.2 to 40.1). This phenomenon could not be demonstrated for females (Mann-Whitney-U test:  $Z = -1.66$ ,  $p = 0.11$ ,  $n_{\text{male}} = 10$ ,  $n_{\text{female}} = 10$ ; median<sub>male</sub> = 14.7 %, IQR = 7.4 to 26.1; median<sub>female</sub> = 31.4 %, IQR = 18.1 to 53.3). Moreover, redfronted lemurs observed more often individuals with which they are closely related (siblings, mother, father; Wilcoxon test:  $Z = -2.040$ ,  $p = 0.04$ ,  $n = 14$ ; median<sub>noKin</sub> = 15.8 %, IQR = 3.9 to 23.1; median<sub>kin</sub> = 32.4 %, IQR = 15.0 to 46.1) than non-kin.

Efficiency of performing the task did not change over the three experimental phases including all animals that succeeded in handling the task (Mundry's permutation test:  $p = 0.749$ ,  $n = 14$ ).



**Figure 4.** Age difference in learning efficiency (number of errors made until first success). Black bars represent medians, white boxes upper and lower quartiles and whisker's ends represent maximum and minimum values. Data point number 1 describes an outlier.

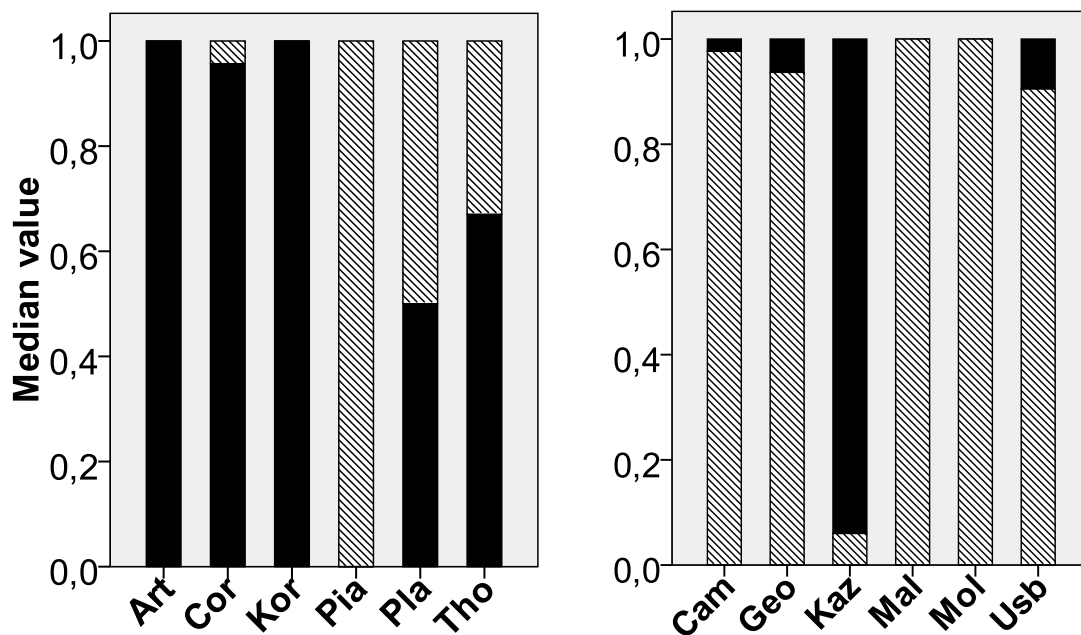
### 3.2 Conformity

In the third phase of the experiment, all groups were confronted with unconstrained boxes. Six animals in the pull-group performed actions at the boxes. Four of them used the pulling technique more often than the pushing technique (mean pull preference = pull action in total amount of actions =  $90.7 \pm 15.9$  %), whereas one individual switched to the push technique (pull preference: 0%) and one animal did not show any preference at all (pull preference = 50 %). In the push-group five animals kept the originally learned technique (mean push preference = push actions in total amount of actions =  $91.0 \pm 9.6$  %), whereas one additional individual learned the task successfully and mainly used the pulling technique (push preference = 6 %). Individuals of both groups showed a preference for the seeded technique (binomial test:  $n = 11$ , exp. proportion = 0.5,  $p = 0.03$ ).

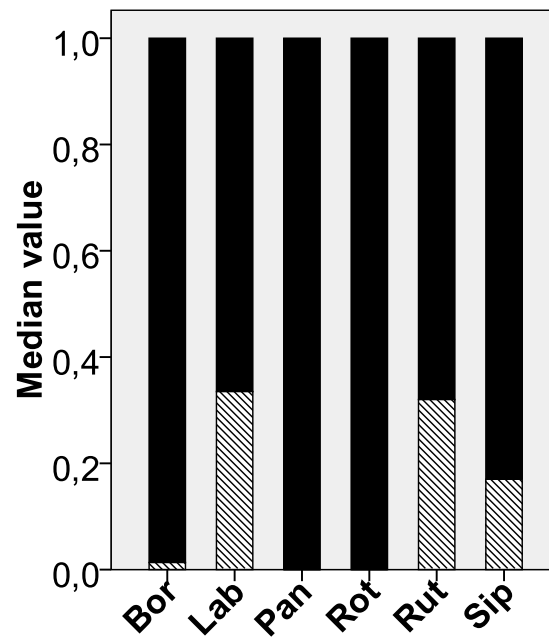
The six subjects of the open-group performed mostly pull actions (mean pull preference =  $86.0 \pm 15.9$  %). Therefore in the open-group individuals preferred the pulling over the pushing technique (Fig. 6; binomial test:  $n = 6$ , exp. proportion = 0.5,  $p = 0.03$ ).

Eleven out of the 14 individuals that successfully opened the boxes discovered both methods. On average, however, they preferred the technique that was used by the majority of their group (binomial test:  $n = 11$ , ex. proportion = 0.5,  $p = 0.02$ ; median<sub>same</sub> = 65.0 actions, IQR = 4.0 to 81.0; median<sub>contra</sub> = 5.0 actions, IQR = 1.5 to 13.5).

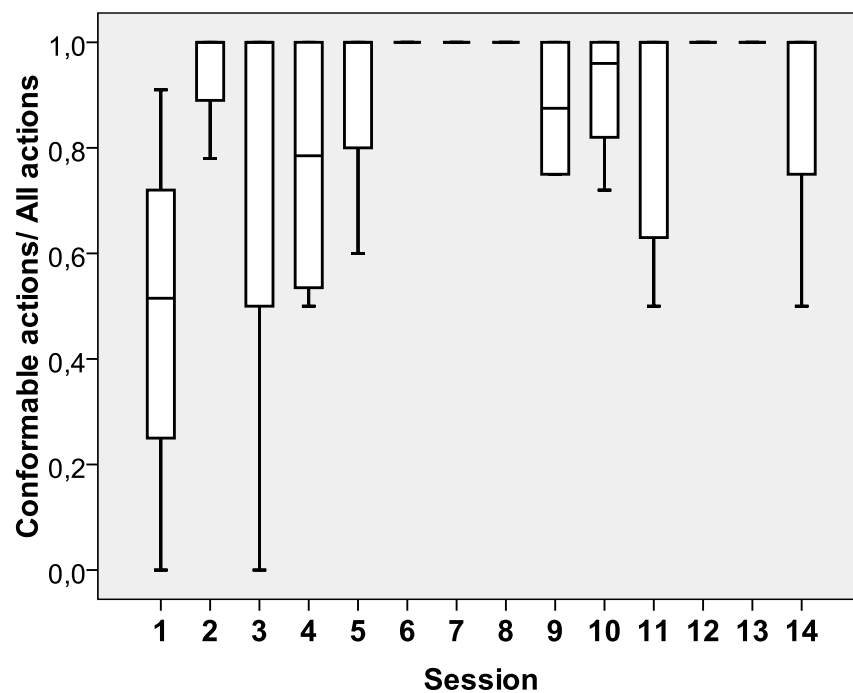
In order to analyse whether conformity may change over time, I compared rates of pulling over all sessions in the open condition group. Individuals already showed strong conformity from the first 1-2 session on, but conformity did not change over time (Fig. 7; Mundry's permutation test:  $p = 0.30$ ,  $n = 6$ ).



**Figure 5.** Difference of pulling (black) and pushing (striped) frequencies in the third phase with unconstrained boxes and with a previous training for one of two techniques. (a) Pull-group and (b) push-group.



**Figure 6.** Difference of pulling (black) and pushing (striped) frequencies in the third phase with unconstrained boxes and without any former training for one of the techniques (open-group).



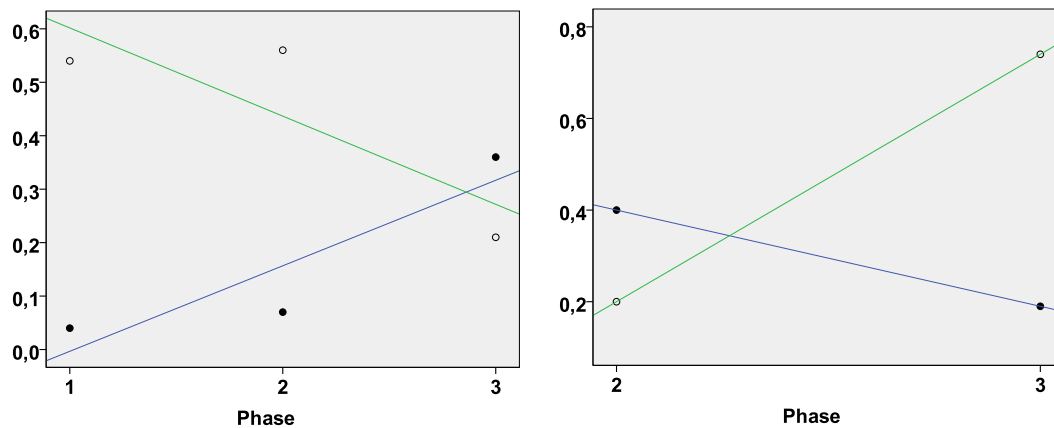
**Figure 7.** Conformity: Changes in percentage of conformable actions, i.e. pulling actions, in all actions over the sessions in the open-group. Black bars represent medians, white boxes upper and lower quartiles and whisker's ends represent maximum and minimum values.

### 3.3 Scrounging

An unexpected side-effect during the experiment was the spread of a new strategy to get access to a reward: scrounging, i.e., exploiting food others made available by opening the door. The scrounger waited until another individual opened the door to slip into the box to get access to the food without performing any actions at the box. In the pull-group five individuals scrounged at least once (mean scrounge preference = scrounging actions in all actions with scrounging actions included =  $39.2 \pm 46.2$  %), in the push-group six animals (mean scrounge preference =  $29.7 \pm 28.1$  %) and in the open-group six animals (mean scrounge preference =  $23.4 \pm 32.1$  %).

Redfronted lemurs did not scrounge more often from close relatives than they did from unrelated group members (Wilcoxon test:  $Z = -0.94$ ,  $p = 0.35$ ,  $n = 14$ ; median<sub>kin</sub> = 10 scrounging events, IQR = 8.8 to 12; median<sub>nokin</sub> = 3.5 scrounging events, IQR = 2 to 6.75).

In order to test whether individuals switched strategies, I compared rates of scrounging actions with rates of successfully actions. Scroungers operated the boxes less often successfully (Fig. 8; Spearman-Rho:  $\rho = -0.71$ ,  $p = 0.00$ ,  $n = 17$ ).



**Figure 8.** Examples for two individuals (Mol: left diagram, Mal: right diagram) of the negative correlation between scrounging rate (blue line: % of scrounging actions) and rate of successful actions (green line: % of successful pull and push actions).

### 3.4 Modelling and social networks

In order to test whether the techniques were learned socially, I used two modelling approaches: ‘the option bias method’ and ‘the extended network-biased analysis’. The option bias method revealed no evidence for social learning when considering successful actions only (*option bias*:  $\chi^2 = 107.25$ ,  $p = 0.11$ ; LLM = 95.10,  $p = 0.11$ ). However, also including unsuccessful actions into the model, the results indicate that the foraging techniques were learned socially (*option bias*:  $\chi^2 = 171.34$ ,  $p = 0.01$ ; LLM = 152.42,  $p = 0.01$ ).

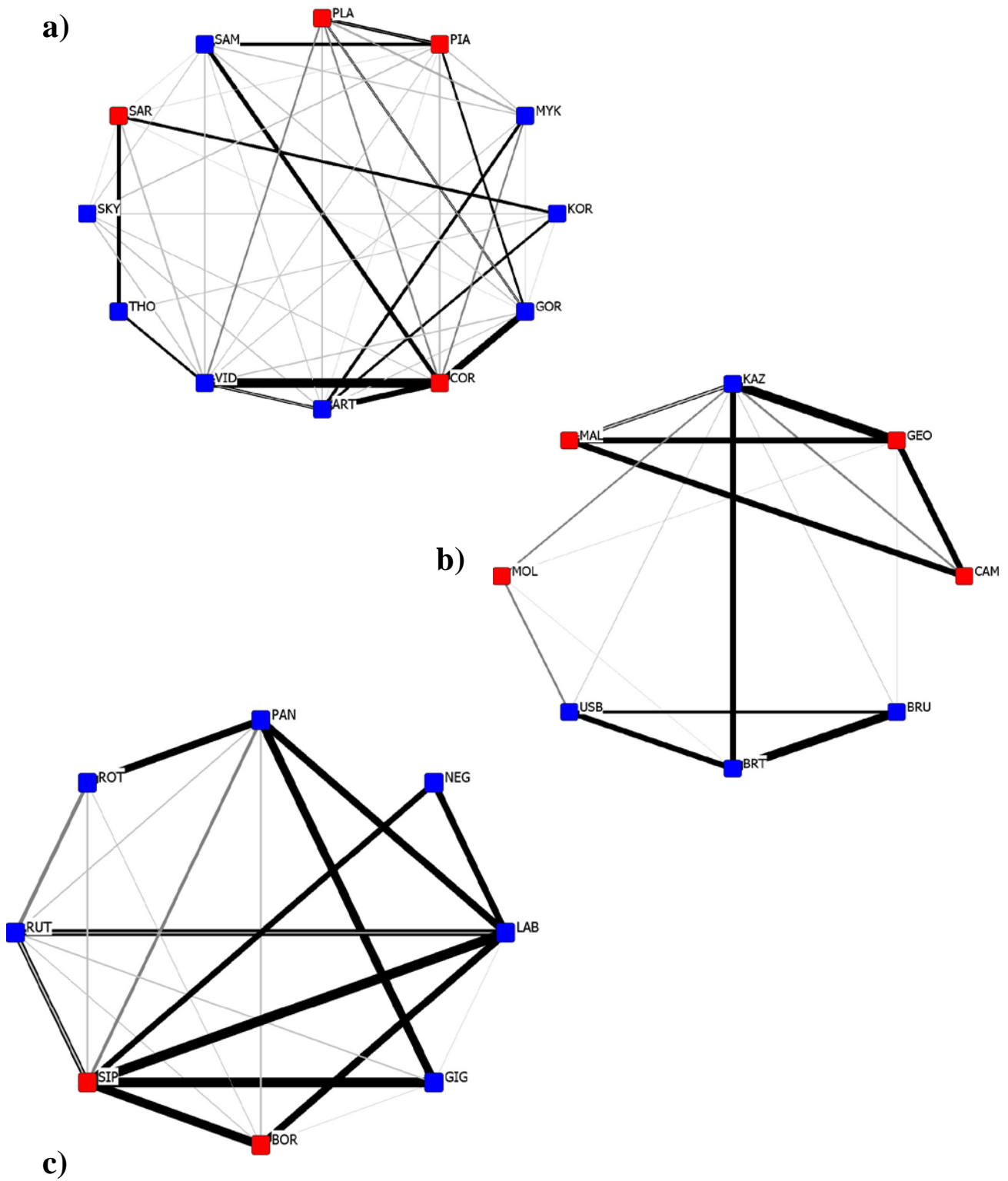
To apply the network-biased diffusion analysis social networks for each study group were calculated in advance, which revealed differently strong bonds between individuals (Figure 9). The simple network-biased analysis (asocial versus social model) indicated only in the open-group that opening techniques were propagated by social learning (Table 4). The extended version of the analysis (asocial versus asocial and social model) did not reveal a better fit with the data for any group than a pure asocial learning model (Table 5).

**Table 4.** Results of the simple net-work biased analysis. Listed AICs are calculated by fitting the data to an asocial model (left column) or to a social model (right column). The model could not calculate an AIC in two cases (n.v. = no value). Grey shading indicates significant results.

	Asocial model		Social model	
	AIC	Akaike probability (%)	AIC	Akaike probability (%)
<b>Pull group</b>	38.211	100	n.v.	0
<b>Push group</b>	24.314	100	n.v.	0
<b>Open group</b>	9.348	23.61	7.000	76.40

**Table 5.** The results of the extended net-work biased analysis. Listed AICs are calculated by fitting the data to an asocial model (left column) or to a social and asocial model (right column).

	Asocial model		Social & Asocial model	
	AIC	Akaike probability (%)	AIC	Akaike probability (%)
<b>Pull group</b>	38.211	73.10	40.211	26.90
<b>Push group</b>	24.314	69.60	25.970	30.40
<b>Open group</b>	9.348	45.66	9.000	54.34



**Figure 9.** Social networks of the three experimental groups: Pull-Group (a), Push-Group (b) and Open-Group (c). Colour of the nodes gives animal's sex (blue represents males, red represents females) and thickness of the lines indicates the strength of the social bond (durations of affiliative interactions per half an hour).



#### 4. Discussion

With the present study I aimed to contribute to a better understanding of the necessary conditions and underlying mechanisms for social learning and traditions in feral animals and to help to close the gap between captive and field data. In studying the spread of two different behavioural traits in redfronted lemurs, I investigated whether wild redfronted lemurs would learn a new foraging technique, whether they would acquire it by social or individual learning, and whether they would adapt their behaviour to that of the majority of the group and therefore show conformity.

Because half of the subjects successfully learned to perform the task throughout my experiment, redfronted lemurs are clearly able to learn new behaviours in a field setting. Additionally, I could observe a high level of motivation to explore the boxes: All individuals got at least in contact with them, suggesting an actual pressure on finding and exploiting new food sources. The reasons behind this motivation for exploitation as well as learning might have to do with the fact that I conducted the experiment during the dry season when food and water are rare (Scholz & Kappeler 2004). Offering not only sweet but also juicy fruits may have provided a big stimulus. The seasonal limitation of water and food may also explain why a relatively short phase of habituation was enough for the animals to overcome neophobia and to accept the new food items.

Interestingly, I found that a larger proportion of females learned the task. This result goes along with the first study of acquisition behaviour in lemurs. Kappeler (1987) found that in ringtailed lemurs (*Lemur catta*) only adult females and none of the adult males acquired a new behavioural trait. This result may have reflected the outcome of female dominance in *L. catta*. Because redfronted lemurs lack dominance of one sex over the other (Pereira & Kappeler 1997), a different explanation is required. One possibility is that females had an even higher motivation than males to learn the task because some of them carried babies, and lactation is known to be costly (Randolph et al. 1977).

Redfronted lemurs exhibited individual variation in aggressiveness during the experiments. There was not general pattern in one sex being more aggressive, which is consistent with the concept of egalitarian dominance relationships in this species (Pereira & Kappeler 1997). However, I found that some individuals were dominant over

others during the experiment, and more aggressive individuals were able to monopolise the boxes.

It was impossible to determine the exact learning mechanism in this sort of experimental setting, but some inferences about the relative importance of social learning are possible. One indirect indicator for the occurrence of social learning was the fact that redfronted lemurs required fewer trials before succeeding for the first time if they observed others for a higher percentage of time. This relationship suggests that they do use the information available from conspecifics performing at the box for making their own behaviour more efficient. Young animals spent more time observing others than older ones and therefore made fewer errors. The phenomenon that young animals show more interest in learning new behaviours is quite common in primates, for instance it is known that juveniles exhibit higher levels of explorative behaviour (Welles 1976; cited in Holtkötter 1997). During an acquisition task in ringtailed lemurs most of the individuals that learned the new behaviour were juveniles and infants (Kappeler 1987). Moreover, juveniles often receive more tolerance from conspecifics; e.g. Dindo et al. (2009) found that other than the highest-ranking capuchin monkeys the young ones were allowed to observe the demonstration of a new task from a close distance. Even though a longer observation duration increased learning efficiency, it did not influence the latency until the first successful manipulation, presumably as a result of monopolisation of the boxes by a few individuals.

I found that males spent looking more time at females, whereas females did not exhibit such a preference. Because females learned in higher percentages, they may be better models. However, this preference for female demonstrators could also be consistent with an explanation suggested for wild vervet monkeys (de Wall et al. 2010): Female philopatry. In redfronted lemurs, males emigrate from their natal group, whereas only some females are expelled under specific circumstances (Ostner & Kappeler 2004). Females may therefore be more ecologically knowledgeable in redfronted lemurs as well. Moreover, the lemurs seemed to favour related individuals over unrelated ones as demonstrators. This result is consistent with a study on ravens (*Corvus corax*), which found enhanced social learning between siblings: Raven showed more interest in the task if a sibling served as model (Schwab et al. 2008). Thus, the risk of receiving wrong information from kin may generally be lower.

Redfronted lemurs in the constrained conditions tend to keep their respective seeded method more often than switching to the other one. Even though I found that more than half of the individuals performed actions that were adjusted to the group norm, and it therefore seems that the animals use information gathered by observing others, the effect was not as high as in the studies on chimpanzees (Whiten 2005) and capuchin monkeys (Dindo et al. 2009). Maybe the task's low level of difficulty in this study allowed the individuals to use individual learning as well and therefore a greater flexibility in switching between the two possibilities. However, this result also suggests that primates might not be as constrained as suggested by Pesendorfer et al. (2009) because redfronted lemurs did not stay with the first rewarded technique. Interestingly, redfronted lemurs tended to adjust their behaviour to a group norm even without any previous training phase, which suggests that social learning was involved in generating conformity.

The option bias analysis (Kendal et al. 2009) did not point in the direction of social learning when focussing only on successful actions. However, after adding unsuccessful action, the social learning model explained the actual data set better than the asocial one. The negative outcome in the first case might occur because of the model's focus on homogeneity. The model wrongly assumes that there is no effect of social learning if more than one trait spreads in a group, for instance one in every subgroup or matriline. Even though there were biases for one technique in the redfronted lemur groups, both techniques were still present in all of them. Adding the unsuccessful actions permitted an increase in sample size and made it possible to detect social learning.

The NBDA (Franz & Nunn 2009) could be applied to the data in two different ways: The simple analysis is based on the hypothesis that learning either happens only socially or only individually. In this case, it showed a better fit of the social learning model only for the open-group. The alternative way of conducting an option-bias analysis is the extended analysis, which assumes that a trait spreads either through individual learning or through a combination of social and asocial learning. A situation in which pure social learning triggers the spread is rather unlikely, and especially in field settings a clear separation between these two forms of learning is not possible. Therefore the extended version tests the data set in a more relevant and more meaningful way. The outcome of this analysis pointed in the direction of the asocial model for all groups.

Redfronted lemurs seemed to be able to flexibly use asocial as well as social information. This may explain why individuals that encountered both techniques decided to stick to the one most of their conspecifics used. When additional social information is available, it might be more efficient to use it and show conformal behaviour rather than ignoring it. Thus, conformity might simply arise as a by-product of social learning. An observation supporting this hypothesis is that the animals in the open-group adjusted their behaviour very quickly at the beginning of the experiment, i.e. when the learning process took place.

An alternative method the redfronted lemurs invented additionally to pulling and pushing was scrounging, i.e. exploiting food others have made available (Bugnyar & Kotrschal 2002). I could observe scrounging in every experimental group, suggesting that its occurrence was not related to a single condition but a more general phenomenon. Ecological factors might facilitate the rather large number of individuals at least temporarily scrounging: The modified producer-scrounger model by Beauchamp (2008) predicts that scrounging is expected to increase with a decrease in food patch encounter rates. The study was conducted at a time when food and water were rare, which may have increased the motivation to try every possible way to access rewards.

There was a strong negative correlation between the rate of scrounging and the rate of successful actions. There are two possible explanations for this pattern: either scrounging was easier and more beneficial for animals, so they scrounged whenever they had the opportunity, or individuals switched from being a producer to being a scrounger because they somehow did not manage to perform successful actions on the box. Certain individuals might not be able to perform successfully because they did not manage to learn one of the regular techniques or because they simply did not have the opportunity to act as a producer. As both techniques represent rather simple movements and changes between being producer and being scrounger occurred for several individuals in both directions, differences in learning ability should not play a dominant role in explaining this pattern. Instead, animals may have scrounged because of limited opportunities to perform the task themselves as a result of monopolization by more aggressive individuals. In both cases a high flexibility in adjusting the feeding strategy exists, which has already been documented for birds (Beauchamp 2001).

Redfronted lemurs did not exhibit a kin preference when deciding which producer to scrounge from. They equally chose related and unrelated producers. This is

contrary to the common phenomenon across the animal kingdom of sharing resources with kin (Ha et al. 2003). This lack of kin bias represents another example for the high level of social tolerance found in this species. The strength of social bonds may predict scrounging. The networks showed that many strong bonds existed between related animals, but also commonly between groups of unrelated males and between females and unrelated males (cf. *Perreira & Kappeler 1997*). Therefore strong affiliative relationships may facilitate scrounging in redfronted lemurs, an idea consistent with the biological markets concept, according to which grooming could be exchanged for tolerance (*Barrett et al. 1999*).

My study suggests that redfronted lemurs principally have the ability to form behavioural traditions. This ability could be favoured in the seasonal habitat they live in and/or by their rather opportunistic feeding strategy (*Parker 1973*). In this sense, traditions can be seen as a mechanism of niche construction favoured by natural selection (*Fragaszy & Perry 2003*). This hypothesis raises the question whether the existence of traditions is a good predictor for animal culture and not simply a phenomenon of niche adaptation, which the great diversity of species where traditions were documented in the field would predict.

As mentioned before, conformity might simply be a side-effect of social learning: An animal that observes others performing in a certain manner, might start behaving in the same way due to social learning and maybe sticks to it not because it is not able to learn alternative ways, but because it is already more effective in performing a behaviour in one way. This idea would explain why I found a bias in the seeded techniques, but also subjects that showed other preferences than the group norm. Moreover, it would explain the higher biases in the more difficult task in the chimpanzees study (*Whiten et al. 2005*) compared to this rather simple feeding box – maybe the chimpanzees just kept the seeded technique in higher numbers despite discovering the alternative one because they were already more efficient in performing the seeded method. This efficiency could have occurred due to a longer time span of experience in performing it or to more available information due to observing others, i.e. due to social learning. The major problem with the concept of conformity in animals is that we cannot see an obvious ‘social pressure’ that could force the animals to behave in a certain way like we can in humans. Especially in the circumstances of feeding it might be primarily important to be as efficient as possible and the question is whether

an animal would face any consequences of behaving differently than the majority. It would therefore be interesting to study traditions in contexts other than feeding, i.e., context where the focus lies on social interactions, which is, however, experimentally much more difficult to investigate.

An aspect that seems to play a major role in the emergence of traditions is the social system a species lives in. This aspect can be illustrated by comparing egalitarian redfronted lemurs to ringtailed lemurs (Kendal et al. 2010), that are known to have ‘despotic hierarchies’ and female dominance over males (Engelhard et al. 2000). Kendal et al. (2010) also conducted a social diffusion experiment in which animals were confronted with a feeding apparatus offering two handling techniques. They found higher levels of homogeneity for the utilized technique in ringtailed lemurs assigned to the experimental than in the control group, but only if analysing the data on the level of sub-groups. They did neither find any influence on the bias for one method due to the presence of a demonstrator for one technique, nor a positive relationship between latency until first success and number of observed successful manipulations, both of which suggest individual learning processes. It therefore looks like the hierarchal organisation of ringtailed lemur societies limits the possibilities to learn socially and those for social diffusion. One reason for this effect might be the restricted social tolerance towards close kin (Jolly & Pride 1999). Thus, social tolerance may be a key factor for the spread of traditions because it facilitates social learning.

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## 7 Supplements

### 7.1 German Summary

Neuste Studien haben gezeigt, dass Traditionen keine Besonderheit der menschlichen Kultur sind, sondern auch in Tiergesellschaften vorkommen können. Jedoch ist noch nicht viel über die zugrunde liegenden Mechanismen sowie die Wichtigkeit von Traditionen für wildlebende Tiere bekannt. Um auf diese Fragen einzugehen, führte ich ein Experiment zur sozialen Ausbreitung neuer Verhaltensweisen in drei Gruppen von wildlebenden Rotstirnmakis (*Eulemur fulvus rufus*) durch. Dazu verwendete ich eine Futterbox mit zwei verschiedenen Möglichkeiten der Handhabung (Ziehen oder drücken einer Tür). Die Hälfte der 28 Versuchstiere war imstande diese neuen Fertigkeiten des Futtererwerbs zu erlernen und behielten in den Gruppen mit vorangehenden Training für eine der zwei Techniken die eingeführte Methode bei bzw. passten sich in der Gruppe ohne Training dem Verhalten der Mehrheit an. Individuen, die mehr Zeit damit verbrachten andere zu beobachten, benötigten weniger Versuche um die Tür das erste Mal erfolgreich zu öffnen, was dafür spricht, dass soziales Lernen eine wichtige Rolle im Erwerb dieser neuen Fähigkeiten gespielt hat. Eine ‚option bias‘ Analyse deutete ebenfalls darauf hin, dass soziales Lernen in der Ausbreitung involviert war, wogegen die Ergebnisse einer ‚network-based diffusion‘ Analyse für alleiniges individuelles Lernen sprechen. Außerdem fanden die Rotstirnmakis eine dritte Technik um an die Belohnung zu gelangen: Schnorren. Interessanter Weise schnorrteten sie nicht öfter bei verwandten Tieren. Dementsprechend ist es Rotstirnmakis möglich Traditionen zu bilden. Die Ergebnisse deuten darauf hin, dass die Versuchstiere nicht einfach die erste belohnte Technik beibehielten, sondern flexibel soziales sowie individuelles Lernen nutzten.

### 7.2 Curriculum vitae

#### Personal Information

First names/ Surname	Anna Viktoria SCHNOELL
Date of birth	16.05.1986 in Salzburg, Austria

#### Education

October 2004 – August 2010	University of Vienna, Austria <b>Diploma studies of biology/zoology</b>
September 2008 – July 2009	Georg- August University, Göttingen, Germany <b>Exchange year</b>
1996 to 2004	Bundesgymnasium Zaunergasse, Salzburg, Austria

#### Work Experience

September 2009 – December 2009	Kirindy Research Station, Madagascar <b>Field research</b> (Diploma thesis)
May 2009 – July 2009	Department of Behaviour Ecology and Sociobiology, German Primate Centre, Kellnerweg 4, 37073 Göttingen, Germany <b>Research assistant and animal training</b> Clicker training of ruffed lemurs and literature research
April 2009	Alfred- Wegner Institut, Sylt, Germany <b>Practical field course</b>
March 2009 – May 2009	Max-Planck Institute for biophysical Chemistry, Fassberg 11, 37077 Göttingen, Germany <b>Research assistant</b> Conducting DNA- Alignments

August 2008 and  
September 2006

Schönbrunner Tiergarten GmbH, Maxingstrasse  
13 b, 1130 Vienna, Austria

**Animal caretaker**

March 2008 – June 2008

Department of Neurobiology and Cognitive  
Biology, University Vienna, Austria

**Practical laboratory course, data analysis**

In this project we investigated the choice behaviour  
of common marmosets via string pulling  
experiments

- Supervised by Dr. Bugnyar and Dr. Huber

March 2008 – June 2008

Konrad Lorenz Institute of Ethology,  
Savoyenstrasse 1a, 1160 Vienna, Austria

**Practical laboratory course, hormone analysis**

We investigated costs of polygamy in chlid fish  
focussing on stress levels

- Supervised by Dr. Schädelin and Dr. Wagner

August – September 2007

Fethije, Turkey; Department of Marine Biology  
and Evolutionary Biology, University Vienna

**Practical field course and environmental  
education**

Measuring and marking of wild loggerhead sea  
turtles, controlling nests, handling and  
measurements of eggs as well as hatchlings,  
informing tourist via an information desk.