

Influence of social tolerance on social learning

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SUMMARY

One outstanding feature of modern human societies is the complex cultural behaviour they exhibit. Although we do not find comparable capacities for culture in other species, some elements of culture are present in the animal kingdom as well. Recent research has described behavioural traditions in primates, cetaceans, other mammals, birds and fish. Because these traditions tend to be simpler than the ones we find in humans, research on animal traditions can provide new insights into the evolution of human culture.

However, the origin of traditions in animals is still poorly understood. It has been suggested that there are several steps that have to be passed through on the way towards a tradition. The raw materials for a tradition are innovations, thus new behavioural variants that are not present yet in the repertoire of a species. We still lack information on the frequency of innovative behaviour in different populations of animals in the wild, because reports on them are rare. In this thesis I describe an incident of a potential feeding innovation in redfronted lemurs (*Eulemur rufifrons*).

Social learning is the key mechanism for the formation of traditions, because it allows the spread of new behaviours within groups. However, the social environment of a group, in which an innovation occurs, can either facilitate or constrain the transmission via social learning. High social tolerance levels in egalitarian societies are suggested to favour the homogenous and quick spread of new information. In despotic societies, in contrast, the transmission is proposed to be limited to subgroups, because social tolerance is restricted to certain dyads within the group, like kin or friends. Social tolerance is described as the probability that individuals can stay in close proximity during a competitive situation with little or no aggression. Although there are theoretical models on the influence of social tolerance on the pattern and speed of social transmission, we still lack comparable empirical data. Therefore, in the main part of my thesis, I investigate the influence of social tolerance on social learning by comparing two lemur species: rather egalitarian redfronted lemurs and hierarchical structured ringtailed lemurs (*Lemur catta*).

In a first step, I measure the social tolerance level of both species by using a co-feeding experiment, in which wild groups of lemurs were confronted with a clumped food resource within an experimental arena. Afterwards the results of the experiment were validated by observational data. During the experiment I found that more redfronted lemurs were feeding simultaneously and were able to stay in close proximity during a competitive

situation than ringtailed lemurs, suggesting that redfronted lemurs are more socially tolerant. During the observational study, redfronted lemurs spent more time in close proximity than ringtailed lemurs, but I did not find a species difference in co-feeding. Additionally, both approaches yielded the same species difference in the outcome of aggression, with fewer agonistic interactions being decided between redfronted lemurs than between ringtailed lemurs. I therefore conclude that close proximity as well as outcome of aggression can serve as consistent measures of social tolerance.

Subsequently, I conducted a social diffusion experiment with redfronted lemurs and ringtailed lemurs to study possible differences in the pattern and speed of learning. Therefore, I confronted the study groups with feeding boxes that could be opened with two alternative techniques (“lifting” or “sliding”) and a knowledgeable demonstrator for one of the techniques. The results of the experiment revealed faster learning as well as a further spread of the new skills in the more tolerant species compared to the less tolerant species. These results suggest that social tolerance indeed influences the amount of learning opportunities. This phenomenon is probably caused by closer proximity between individuals, which allows them to observe in greater detail. There was no species difference in the homogeneity of the transmission, but I find a generally positive influence of the number of contacts an individual had with the demonstrator on the possibility of learning, again highlighting the importance of proximity in this context. Affiliative relationships in contrast did not promote learning.

I was only able to find weak evidence for social learning during the experiment: the subjects did not imitate the technique used by the demonstrator but they might have learned that the feeding boxes contain food and can be opened. In this case simple learning mechanisms might be at work, like observational conditioning or emulation. Additionally, the tolerant species was able to scrounge from a more diverse set of producers, which might have facilitated learning.

Another aspect that is still poorly understood is the longevity of traditions over time. Although we know that some animal traditions, like the famous sweet potato washing in Japanese macaques, can persist over more than 50 years, we lack information on the underlying mechanisms leading to stable behavioural patterns. Especially experimental research in this area can help to identify them. To this end, I investigated in my thesis the stability of an experimentally introduced tradition over time in wild redfronted lemurs. I

conducted an additional social diffusion experiment over three experimental years with feeding boxes that could be opened in two different ways (“pushing” or “pulling”). Less than half of the participants preferred one technique to the other one in this time interval. The remaining individuals exhibited fluctuating preferences. The low level of difficulty and/or the low object specificity of the task might have caused this instability. The majority of lemurs additionally scrounged. Thus, redfronted lemurs appear to use the two techniques flexibly but also scrounged opportunistically to get access to the rewards, indicating that traditions might be stabilized by multiple factors.

The results of my thesis indicate that these two species of group-living lemurs are able to innovate and information can spread within their groups. However, they are either unable to form long-lasting traditions or there is simply no need for them in the wild. Furthermore my study suggests a facilitating effect of social tolerance levels on learning. High levels of social tolerance seem to result in further spread of new behaviours as well as increased speed of learning.

My thesis is the first comparative study on the influence of social tolerance on social learning and intends to contribute to a better understanding of the development of traditions in animals, and possibly also in humans. However, more comparative studies with other species are needed to get a full comprehension of the influence of the social environment on social learning.

ZUSAMMENFASSUNG

Ein hervorstechendes Merkmal von modernen menschlichen Gesellschaften ist, dass sie sehr komplexes kulturelles Verhalten aufweisen. Obwohl keine vergleichbaren Fähigkeiten für eine derartig komplexe, kultivierte Lebensweise in anderen Spezien gefunden werden können, sind manche Elemente, die Kultur auszeichnen auch im Tierreich vorhanden. So wurden verhaltensbezogene Traditionen ebenfalls bei Primaten, Walen, anderen Säugetieren, Vögeln und Fischen beschrieben. Da diese Traditionen jedoch in der Regel asketischer sind, als die, die wir bei Menschen finden, kann uns die Forschung an Tieren in diesem Zusammenhang neue Einblicke in die Evolution der menschlichen Kultur ermöglichen.

Allerdings ist die Entstehung von Traditionen bei Tieren immer noch wenig erschlossen. Theoretische Arbeiten demonstrieren, dass mehrere Stufen zur Etablierung einer Tradition durchwandert werden müssen. Den Ausgangspunkt bilden dabei Innovationen, also neue Verhaltensweisen, die noch nicht im Repertoire einer Art vorhanden sind. Es ist jedoch schwer abzuschätzen, wie häufig Innovationen in verschiedenen Tierpopulationen auftauchen, da Berichte über innovatives Verhalten in freier Wildbahn selten sind. In dieser Arbeit beschreibe ich eine mögliche Innovation im Bereich der Ernährung bei wild lebenden Rotstirnmakis (*Eulemur rufifrons*).

Soziales Lernen ist der Schlüsselmechanismus für die Ausbildung von Traditionen, da es die Vermittlung der neuen Verhaltensweise innerhalb einer Gruppe ermöglicht. Doch das soziale Gefüge der Gruppe kann die Weiterverbreitung durch soziales Lernen entweder begünstigen oder hemmen. Eine hohe soziale Toleranz in egalitären Gruppen scheint zu einer homogenen und schnellen Verbreitung neuer Informationen beizutragen. Im Gegensatz dazu scheint die Verbreitung in despotischen Gruppen auf Untergruppen innerhalb der Gemeinschaft beschränkt zu sein, da hohe soziale Toleranz auf bestimmte Dyaden, beispielsweise auf Freunde oder Verwandte, beschränkt ist. Soziale Toleranz meint in diesem Sinne die Wahrscheinlichkeit, dass Individuen sich während einer kompetitiven Situation mit wenig oder keiner Aggression in unmittelbarer Nähe zueinander aufhalten können. Zwar gibt es theoretische Modelle, die den Einfluss des sozialen Umfeldes auf die Geschwindigkeit und das Muster der sozialen Verbreitung beschreiben, jedoch fehlt es an vergleichbaren Studien zu diesem Themenbereich. Daher habe ich mich in dem Hauptteil meiner Arbeit mit der Untersuchung des Einflusses von sozialer Toleranz auf soziales Lernen

beschäftigt und diesbezüglich zwei Lemurenarten verglichen: zum einen eher egalitäre Rotstirnmakis, zum anderen hierarchisch strukturierte Kattas (*Lemur catta*).

In einem ersten Schritt habe ich dafür die soziale Toleranz der beiden Arten mit Hilfe eines Fressversuches evaluiert, in welchem freilebende Gruppen dieser Lemuren mit einer zentral positionierten Nahrungsressource innerhalb einer Versuchsarena konfrontiert wurden. Anschließend habe ich die Ergebnisse des Experiments durch Verhaltensbeobachtungen validiert. Innerhalb der Versuchsarena konnten sich mehr Rotstirnmakis als Kattas in unmittelbarer Nähe zueinander aufhalten und gleichzeitig fressen, was darauf hindeutet, dass Rotstirnmakis sozial toleranter sind. Während der Verhaltensbeobachtungen, verbrachten Rotstirnmakis im Vergleich zu Kattas mehr Zeit in der Nähe anderer Individuen, jedoch konnte kein Artunterschied im gemeinsamen Fressen von mir festgestellt werden. Zusätzlich zeigten beide Forschungsansätze einen Artunterschied in den Resultaten von Aggression. Diesbezüglich wurden bei Rotstirnmakis weniger agonistische Interaktionen eindeutig entschieden. Aufgrund dieser Ergebnisse konnte ich zwei verlässliche Maße für soziale Toleranz identifizieren: zum einen die Anzahl von Individuen in unmittelbarer Nähe, zum anderen das Resultat von Aggression.

Darauffolgend habe ich, um mögliche Unterschiede im Muster und in der Geschwindigkeit des Lernens bei Rotstirnmakis im Vergleich zu Kattas festzustellen, ein soziales Diffusionsexperiment durchgeführt. Dementsprechend habe ich die Studiengruppen mit Futterboxen, welche durch zwei alternativen Techniken geöffnet werden konnten („heben“ und „schieben“) sowie einem Demonstrator konfrontiert, der für eine der Techniken trainiert wurde. Das Experiment zeigte schnelleres Erlernen sowie eine höhere Anzahl von lernenden Individuen bei der toleranteren Art. Diese Ergebnisse deuten darauf hin, dass soziale Toleranz tatsächlich einen Einfluss auf die Menge von Lernmöglichkeiten hat. Dieser Sachverhalt ist wahrscheinlich auf die Möglichkeit von Individuen, sich in der Nähe von anderen aufzuhalten und dadurch genauer beobachten zu können, zurückzuführen. Es gab jedoch keinen Artunterschied in der Homogenität der Verbreitung der neuen Techniken. Jedoch war zu beobachten, dass die Anzahl der Kontakte eines Individuums mit dem Demonstrator, einen generellen positiven Einfluss auf die Wahrscheinlichkeit des Erlernens der Techniken ausübte. Dieses Ergebnis deutet wiederum auf die Bedeutung von Nähe und Distanz im Zusammenhang mit Lernen hin. Im Gegensatz dazu scheinen affiliative Beziehungen in den zwei Lemurenarten Lernen nicht zu fördern.

Allerdings konnte ich nur schwache Hinweise für soziales Lernen in dem Experiment feststellen: einerseits imitierten die Individuen zwar nicht die Technik des Demonstrators, allerdings könnten sie durch beobachten gelernt haben, dass die Futterbox Nahrung enthält und geöffnet werden kann. In diesem Fall wirkten vermutlich einfache Lernmechanismen, wie beispielsweise Konditionierung durch Beobachtung oder Emulation. Andererseits schnorren, neben dem selbstständigen Öffnen der Boxen, Individuen beider Arten bei anderen. Die tolerantere Art war unterdessen in der Lage, bei einer größeren Auswahl von Gruppenmitgliedern zu schnorren, was eventuell ebenfalls einen Lerneffekt begünstigt hat.

Ein weiterer Aspekt von Traditionen, der nicht hinreichend geklärt wurde, ist deren Langlebigkeit. Wir wissen zwar, dass manche Traditionen bei Tieren, so wie im Falle des berühmten Süßkartoffel-Waschens bei Japanmakaken, mehr als 50 Jahre und über mehrere Generationen bestehen bleiben können. Dennoch bleiben die Mechanismen der Etablierung solcher stabilen Verhaltensmuster umstritten. Vor allem experimentelle Forschung kann dazu beitragen, diese Mechanismen zu identifizieren. Deswegen habe ich in meiner Arbeit auch die Stabilität über die Zeit von experimentell eingeführten Traditionen in freilebenden Rotstirnmakis untersucht. Ich habe ein weiteres soziales Diffusionsexperiment über drei Versuchsjahre durchgeführt und dabei ebenfalls Futterboxen verwendet, die mit zwei Techniken geöffnet werden konnten („drücken“ und „ziehen“). Weniger als die Hälfte der teilnehmenden Tiere favorisierte in dieser Periode eine der Techniken. Demgegenüber gab es Individuen, die in der Anwendung der Techniken variant agierten. Diese Variabilität wurde möglicherweise durch ein niedriges Schwierigkeitsniveau der Aufgabe und/oder der geringen Objektspezifität der zwei Techniken hervorgerufen. Viele Tiere nutzten wiederum schnorren als Alternative, um an das Futter zu kommen. Rotstirnmakis schienen daher flexibel beide Öffnungstechniken zu nutzen und opportunistisch zu schnorren. Diese Resultate deuten ferner darauf hin, dass Traditionen durch mehrere Faktoren stabilisiert werden.

Die Ergebnisse meiner Arbeit zeigen, dass beide gruppenlebenden Lemurenarten in der Lage sind, Innovationen hervorzubringen und eine Verbreitung von Informationen innerhalb ihrer Gruppen stattfinden kann. Sie scheinen aber entweder nicht in der Lage zu sein, stabile und langlebige Traditionen auszubilden oder es besteht schlichtweg keine Notwendigkeit in freier Wildbahn dafür. Außerdem weißt meine Studie auf einen fördernden Effekt von sozialer Toleranz auf Lernen hin. Ein hohes Level

von sozialer Toleranz scheint zu einer weiteren Verbreitung neuer Verhaltensweisen sowie zu einer erhöhten Lerngeschwindigkeit zu führen.

Meine Arbeit ist die erste vergleichende Studie über den Einfluss von sozialer Toleranz auf soziales Lernen und soll dazu beitragen, ein besseres Verständnis über die Entwicklung von Traditionen bei Tieren sowie eventuell bei Menschen zu erlangen. Es sind jedoch weitere vergleichende Studien mit anderen Arten notwendig, um eine umfassendere Erkenntnis des Einflusses der sozialen Umwelt auf soziales Lernen zu erhalten.

GENERAL INTRODUCTION

*“A people without the knowledge of their past history,
origin and culture is like a tree without roots.”
(Burrow 1994)*

This quote by Marcus Garvey illustrates the importance that is attached to culture in humans. Culture gives humans access to past and present events experienced by their conspecifics and thereby allows them to accumulate information (Boyd and Richerson 1985; Alvard 2003; Muthukrishna et al. 2014). In this way, culture enables humans to inhabit a wide range of habitats as well as to cope with variable environments by making use of, for instance, agriculture and different housing types (Alvard 2003; Fragaszy 2003). But where does culture come from? The investigation of animal traditions has proven successful in adding important information on the evolution and origin of human culture, because some elements of culture are present in the animal kingdom as well (labelled “protoculture” or “pre-culture” in non-human primates: Kawai 1965; Menzel et al. 1972; Thierry 1994), although other elements lack and therefore seem to be unique for humans.

In this general introduction, I will first give a short overview about the significance of traditions and will then discuss them as a product of niche construction. Subsequently, I will summarize the different steps that lead to a tradition and, in doing so, I will point out the aspects that are still poorly understood. I will describe the different approaches that are used to investigate traditions in animals in the following. Finally, I will introduce my study species and will outline the aims and approaches of my thesis.

1.1. What are traditions good for?

In humans it is generally assumed that culture is adaptive and that it helps humans to create their own ecological niche (labelled “the cultural niche”: Boyd et al. 2011). Culture is thereby defined as all information that individuals acquire from others and that generate customs and traditions, which crucially affects human lives (Whiten et al. 2011). However, humans are not the only species that is able to modify their surrounding environment and thereby buffer out natural selection to a certain extent. Niche construction, that can be defined as “activities, choices and metabolic processes of organisms through which they define, choose

and modify and partly create their own niche” (Laland et al. 2000), can be found in a big variety of animal species as well as plants. Many mammals, for instance, construct complex borrow systems for safety and temperature regulation (Nowak 1991) and insects, like *Drosophila* (Jaenike 1982), influence the environment of their offspring by selecting particular plants as sites to deposit their eggs. An example for plants actively influencing their environment are *Eucalyptus* trees that gather oil or litter to promote forest fires (Mount 1964), probably to facilitate seed germination.

Niche construction is likely to occur if its effects remain locally, so that the animals paying the cost for constructing a niche also benefit from it directly or that at least their offspring receive the benefits (Fragaszy 2003). As niche construction may also change selection pressures, individuals do not only inherit genes from their parents, but potentially also selection pressures modified by their ancestors, a phenomenon entitled “ecological inheritance” (Olding-Smee 1988; Laland et al. 2000; Sinha 2005). Ecological inheritance, in contrast to genetic inheritance, does not occur solely from parent to offspring but from a multiple set of individuals to the next generation (Laland et al. 2000).

By constructing niches it is possible for a species to keep a higher flexibility because a greater level of genetic variation is kept within a population that otherwise would have been erased by selection (Laland et al. 2000). Social learning can facilitate niche construction by increasing the feedback potential in natural selection (Fragaszy 2003). It can help to maintain adaptive practises among conspecifics, like the homing routes in pigeons (*Columba livia*; Pettit et al. 2012). In addition, in blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) the foraging niche represent a tradition and cross-fostered chicks shift their foraging sites via early social learning towards the one of their foster parents (Slagsvold and Wiebe 2011). Black rats (*Rattus rattus*) were able to increase the width of their ecological niche by establishing a tradition of an efficient handling technique of pinecones, which allowed them to invade Israeli pine forests, a habitat that would have been closed otherwise (Terkel 1996). Hence, traditions can admit access to ecological niches that are not exploited by other species but only available through social learning from conspecifics (Nishida 1987; Thierry 1994).

The definition and operationalization of culture is highly debated (Hoppit and Laland 2013; Ramsey 2013). An important feature of culture is its cumulative nature and therefore the number of traditions seems to matter (Thierry 1994). Although culture is an outstanding

feature of humans and we do not find comparable capacities for culture in other species, it is important to keep in mind that it still derives from a relatively common mechanism, niche construction, and that many other species also modify natural selection pressures in their surroundings (Laland et al. 2000).

1.2. How do traditions emerge?

The word “culture” has long been solely used for humans and therefore some biologists suggested the use of the term “tradition” for cultural behaviour in animals (van Schaik 2010). Traditions are defined as behavioural practices that are shared among all or some members of a social unit, which are performed repeatedly over time, and acquired, at least partially, through social learning (Fragaszy and Perry 2003). Famous examples for traditions in animals are sweet potato washing in Japanese macaques (*Macaca fuscata*; Kawai 1965), milk bottle opening in blue tits (Hinde and Fisher 1951), handclasp grooming in chimpanzees (*Pan troglodytes*; Nakamura and Nishida 2013) and the different techniques of pine stripping in Israeli black rats (Terkel 1996). There are several stages that have to be passed through in the development of a tradition, the starting point being innovations and the ability to learn socially (Huffman and Quiatt 1986; Huffman and Hirata 2003; Galef 2004).

1.2.1. Innovation

Innovations are the raw material for traditions. They represent new or modified behaviours that were not previously present in the behavioural repertoire of a population (Kummer and Goodall 1985; Reader and Laland 2003). Innovations can occur either in stable environments or as a response to changes in the environment and they can enable individuals to cope with environmental challenges (Boogert et al. 2008). Therefore, they crucially affect behavioural plasticity (Reader and Laland 2003).

The time available to explore can affect the likelihood of innovations to arise, which might be the reason why we find more reports of innovations in captive populations than in wild ones (Lehner et al. 2010). The mechanisms that lead to the discovery of new behaviours seem to be trial-and-error learning as well as coincidence (Thierry 1994). Additionally, some characteristics of an individual can increase the probability of an innovation, like age and life period (Kummer and Goodall 1985; Biro et al. 2003), sex (Cadieu et al. 2010) or personality (Drent et al. 2003).

Research on innovations has mainly focused on anthropoid primates in the past (chimpanzees: Whiten et al. 1999; orangutans (*Pongo pygmaeus*): van Schaik et al. 2003b; Japanese macaques: Kawai 1965; capuchin monkeys (*Cebus apella*): Perry et al. 2003). There is only a small body of reports on innovations in the wild populations of other non-human primates and even a smaller number of descriptions in strepsirrhines (Hosey et al. 1997; Fichtel and van Schaik 2006, Fichtel and Kappeler 2011). In general, innovations rarely seem to spread to other individuals in non-human primates (Nishida et al. 2009). A literature research found that only 16% of 606 cases of innovations were found to have propagated to at least one additional individual (Ramsey et al. 2007). However, as the data especially for wild settings is so little, it is of great importance to make field observations of potential innovations available to the scientific community. This would make it easier to estimate the frequency of appearance as well as spread of these innovations more precisely and to significantly describe differences in these traits between different species of primates.

1.2.2. Social learning

The necessary mechanism for an innovation to spread to other members of a group is social learning. Social learning is defined as “learning facilitated by observation of, or interaction with, another animal (typically a conspecific) or its product” (Hoppit and Laland 2013). Thereby, it allows a greater flexibility than it would be possible only with species-typical behaviour or through individual learning, so learning through one’s own efforts alone (Whiten 2012).

In general, individuals should prefer to use social information over individual learning if learning is dangerous, for instance in the case of poisonous food, and if events occur so rarely that there are no possibilities to learn individually (Kummer 1971; Thierry 1994). Young Norway rats (*Rattus rattus*) for instance use social learning to avoid poisonous food and therefore very costly individual learning. They do so by only ingesting food to which adults have introduced them (Galef and Clark 1971).

Individuals should only favour social learning if the environment changes on a medium speed (Alvard 2003); in case changes happen very slowly, a transmission on the genetic level is less expensive than social learning. If the environment changes too quickly, potential models, in other words other individuals from whom they could learn from, are unlikely to possess relevant information for the current conditions. In this case, individuals

are expected to prefer individual learning.

Generally, there is always a risk of gathering incorrect or out-dated information by using public information, which would increase the costs of social learning considerably (Giraldeau et al. 2002; Laland et al. 2005). Sticklebacks (*Pungitius pungitius*; Van Bergen et al. 2004) for instance do not use social information about the quality of a food patch if they possess personal information about it. However, if they lack this personal information, they will rely on social learning. If animals are using social learning, they should choose carefully from whom to learn from and there are several strategies that can be applied to secure the quality of the gathered information (Laland 2004). They can, for instance, preferentially select the most successful or knowledgeable individuals as demonstrators. Evening bats (*Nycticeius humeralis*) apply this strategy and individuals that were unsuccessful in foraging were described to follow the next time successful individuals from their roosting site (Wilkinson 1992). Vervet monkeys (*Chlorocebus pygerythrus*) pay more attention to female than male demonstrators in a social learning experiment, probably because females are the philopatric sex and may have more detailed knowledge about the distribution of food resources in their territory (Van de Waal et al. 2010). Another strategy is to copy positively associated individuals, like kin or friends. Common ravens (*Corvus corax*), for instance, show enhanced social learning when confronted with a sibling as demonstrator (Schwab et al. 2008).

Individuals could also copy the behaviour that the majority of other individuals are showing (Laland 2004) and therefore show some form of 'conformity' (Chou and Richerson 1992). Conformity thereby describes a "positive, frequency dependent social learning in which the probability to acquiring a trait increases disproportionately with the number of demonstrators" (Laland 2004). There is even some evidence for conformity closer to the definition anthropologists would use, that is, that personal information would be abandoned in favour of a group norm (van de Waal et al. 2013): groups of vervet monkeys were trained to associate one of two colours with a bitter taste when confronted with a new source of food (i.e. corn). Interestingly, males that migrated to other groups, switched their preference to the norm of the new group.

1.2.3. Effects of the social environment on social learning

Generally, the social environment of a group can facilitate or constrain social learning by influencing the access to information (Coussi-Korbel and Frigaszy 1995; Van Schaik et al 1999). Social tolerance is defined as a “concept that captures the probability that individuals will be in proximity to conspecifics around valuable resources with little or no aggression” (Cronin and Sánchez 2012). Higher levels of social tolerance seem to increase the opportunities for social learning because animals can stay in closer proximity to each other and therefore are able to observe in greater detail. Additionally high social tolerance allows individuals to choose from a wider range of models. In contrast, in groups with lower tolerance, learning opportunities as well as model selection seem to be restricted to friends or kin. Therefore, social tolerance might affect the pattern and speed of social learning. Indeed, a simulation study on 30 different primate groups suggests that social tolerance influences the speed of propagation of new information within a social unit, with higher speed in more tolerant compared to less tolerant groups (Voelkl and Noe 2010). Chimpanzees and orang-utans for instance showed a bigger cultural repertoire if they spent more time in association to others (Van Schaik et al. 2003a).

If animals live in intolerant groups with strict hierarchies, a high status of a model can inhibit others to observe the demonstration and/or to perform the behaviour because of the fear of provoking aggression (Fragaszy and Visalberghi 1990; Anderson et al. 1999). In rhesus macaques (*Macaca mulatta*) subdominant individuals “played dumb” in an experiment, when being in a test group with dominant individuals, but were able to perform the task when they were in a group of subdominants (Drea and Wallen 199).

However, there are also contradicting results. The spread of new foraging techniques in starlings (*Sturnus vulgaris*) was not affected by differences in the social tolerance levels between certain dyads of individuals (Boogert et al. 2008). Additionally, Chacma baboons (*Papio ursinus*) showed higher levels of social learning than more tolerant vervet monkeys (Cambefort 1981). The authors of this comparative study suggest that baboons monitor other group members more intensely and that this might be the reason for this contradictory result. However, the two species differ in so many other characteristics, like body size, brain size, diet and group composition (Napier and Napier 1972), that a comparison is generally rather difficult.

More empirical information is needed to fully understand the effects of the social environment on social learning. A first step is to conduct more and comparable studies on social tolerance and its effect on social learning in primates and non-primates. So far there are only a few studies that measured the social tolerance level of social units experimentally and all of them are restricted to a single order: primates. Social tolerance has been measured in apes by using dyadic co-feeding tasks (Melis et al. 2006; Hare et al. 2007; Wobber et al. 2010), in rhesus macaques by investigating water sharing behaviour (de Waal and Luttrell 1986) and in a battery of primate species by looking experimentally at the reparation of food monopolisation within a group (Burkart and van Schaik 2013). Although these studies yielded consistent results, with more tolerant species sharing more with others and being less aggressive, it is difficult to compare the results due to different experimental set-ups and different measurements. The second step is to conduct social learning experiments with these species with known social tolerance levels and look for differences as well as similarities in their learning behaviour.

1.2.4. Social learning mechanisms

For a long time the ability to imitate was seen as the mechanism that enables some species to propagate new information within social groups. Imitation is defined as a faithful form of copying, in which the observer copies all actions of the demonstrator, no matter if they are necessary or not (Horner and Whiten 2005) and has been associated with more advanced cognitive skills (Dindo 2009).

A famous example for imitation in non-human primates is sweet potato washing in Japanese monkeys (Kawai 1965). However, since the novel behaviour spread rather slowly through the population, it has been recently suggested that more simple social learning processes might have caused the propagation of the new foraging behaviour. Probably the behaviour spread through associative learning of food and water, or local enhancement by following demonstrators to a location and interacting with the objects present at the location (Thopre 1963; Galef 1990). Another characteristic of this transmission, in contrary to the expected imitation paradigm, is, that the rate of acquisition of potato washing did not increase as the number of knowledgeable individuals increases (Alvard 2003).

The assumption that imitation is the mechanism for the spread of new behaviour in non-human primates has been questioned also through experimental research (Tennie et al.

2006; Tennie et al. 2009). These studies showed that simple learning mechanisms, like stimulus enhancement or social facilitation, might be efficient enough to lead to diffusion of behavioural patterns, as they potentially increase the probability of individual learning (Thierry 1994; Alvard 2003; Matthews et al. 2010). Stimulus enhancement is defined as a form of social influence in which an individual is attracted to a stimulus due to the behaviour or the by-products of the behaviour of a conspecific (Spence 1937; Dindo 2009). Social facilitation describes processes in which only the presence of another individual enhances the observer's behaviour (Thorpe 1963; Dindo 2009). So far it has been shown only in captive animals that imitation is important for the propagation of behaviours (Whiten et al. 2004).

1.2.5. Social transmission

Social transmission is an incidence of social learning or enhancement leading to a bigger homogeneity in behaviour even after the interaction between subject and model already ended (Galef 1988). It describes the spreading of behaviour within a group (Huffman and Quiatt 1986). There are different modes of transmission, which differ in the dyads of individuals involved: vertical transmission describes the spread from parents to offspring, horizontally transmitted behaviours spread within one generation and in the case of oblique transmission the new behaviour spreads from non-parental adults towards young individuals (Cavalli-Sforza et al. 1982; van Schaik 2010). Different social structures favour different modes: Vertical transmission is thought to be dominant in groups in which individuals form strict hierarchies and oblique as well as horizontal transmission in more tolerant groups (Hoppit and Laland 2008).

An aspect that seems to influence whether social transmission of a behaviour takes place at all and how quickly it does so, is the complexity and frequency of a new pattern, the social status of the innovator and the ability of the observer to recognize that the pattern is useful and brings adaptive advantages (Thierry 1994). Most of the traditions described in animals are connected to the selection, acquisition and processing of food (Nishida 1987) and therefore these behaviours get a direct positive reinforcement, e.g. ingestion of food (Thierry 1994). However, there are also examples in which the utility is not so clear, for instance in the case of stone handling in Japanese macaques (Huffmann and Quiatt 1986; Leca et al. 2007). Stone handling consists of various behaviours, such as putting stones into

piles, clacking stones together or tapping stones on the floor (Huffman 1984). This behaviour most likely presents a form of solitary object play and seems to be not directly adaptive (Huffman 1984; Leca et al. 2007).

1.2.6. Longevity of traditions

Not every behavioural pattern that spreads within a social unit develops into a stable tradition that is transmitted over generations. Most of them are highly vulnerable to extinction and can disappear from a group's repertoire again (Thierry 1994). Other traditions can last for a long time, for instance the already mentioned potato washing in Japanese macaques, which persists already for over 50 years (Kawai 1965). It has been assumed that only adaptive patterns develop to fixed traditions whereas non-adaptive ones vanish (Lumsden and Wilson 1981).

Stability of behavioural patterns is favoured if changing the behaviour is not beneficial (Thornton and Clutton-Brock 2011). Also the costs, determined by time and effort an individual already invested in acquiring a pattern, might positively affect the persistency (Thornton and Clutton-Brock 2011). The main mechanisms that keep traditions stable seem to be individual conservatism and the formation of response habits. Individual conservatism is defined as a tendency to keep learned behaviour over time (Marshall-Pescini and Whiten 2008) and a response habit is an action that gets repeated over time because an individual got rewards for it in the past (Pesendorfer et al. 2009; Crast et al. 2010).

The experimental data on the persistency of traditions are inconsistent: captive capuchin monkeys were able to keep an experimentally introduced tradition over two years (Crast et al. 2010) and wild vervet monkey for longer than one year (van de Waal et al. 2012). Meerkats (*Suricatta suricatta*), however, failed to maintain their preferences in feeding at one of two artificial feeding sights (Thornton and Malapert 2009). Therefore further studies on a more longitudinal scale are needed to understand the parameters that favour long lasting traditions.

1.2.7. Modification of traditions

The last step in the development of a long-term tradition is the transformation of the behavioural pattern to improve it and to make it more efficient. Therefore, modifications can either occur due to innovative improvements but also due to copying errors and both can lead to tradition drifts (Huffman and Quiatt 1986; Thierry 1994; Huffman and Hirata 2003). The pattern of imitation, modification and transmission seems to be one feature that sets culture in humans apart from the traditions we see in animals (Alvard 2003) and was labelled “ratchet effect” (Tomasello 1999). It allows humans to accumulate modifications over time (Tinnie et al. 2009) and a balance between individual variation of behaviour and social conformism seems to be the key to a stable culture (Boyd and Richerson 1985).

However, again detailed data is lacking to make clear predictions about the ability of non-human animals to modify traditions. The small body of reports does not permit to break down the phenomenon in “guided variation”, therefore transformations due to improvements (Boyd and Richerson 1985), or coincidences.

1.3. How to study traditions in animals?

The classic way to study traditions in animals is the “ethnographic method” (labelled by Wrangham 1994). Researchers using this model compare the behaviour of two groups with each other; they look at the genetic and behavioural exchanges between groups and contrast the environmental conditions of the habitats of different groups (Fragaszy 2003). The idea behind it is that if two groups do not differ in their genetics or in their habitats, but show unique behavioural pattern only present in a subset of the population, this represents a tradition. By using this method Whiten et al. (1999), for instance, was able to identify 39 behavioural patterns that were distinct for some chimpanzee communities but absent in others. Although the group comparison model is feasible in wild populations, if long-term data are available, it also has its flaws.

The first problem is that behavioural differences cannot be labelled “tradition” until it is clear that social learning was involved in producing this pattern (Fragaszy 2003). New Caledonian crows (*Corvus moneduloides*), for instance, produce tools to extract insects and this has been claimed to represent a tradition (Hunt and Gray 2003), but they were shown to exhibit tool production even if they were hand-reared and prohibited to observe conspecifics manufacturing tools (Kenward et al. 2005). This species therefore seems to

possess an innate bias towards tool-manufacture and social learning does not seem to be the driving force. Also the famous example of dipping with sticks for ants in chimpanzees has been recently questioned as a true tradition: chimpanzees have been described to use a long stick in East Africa and a short stick in West Africa to collect ants (Whiten et al. 2001). However, this pattern seems to be mainly driven by a difference in the behaviour of the prey, with the usage of a long stick for more aggressive ants and a short stick for less aggressive ones, rather than by social learning (Humble and Matsuzawa 2002). Observational studies are therefore constrained in the implications they can draw about the learning mechanisms and might lead to a misinterpretation of the observed pattern.

Additionally, the ethnographic approach restricts the search for traditions, because it only identifies one possible outcome of social transmission, which is a difference in behaviour. Therefore, field observations alone cannot provide the essential data to reliably identify behavioural traditions.

As an alternative, social learning can be identified more clearly by using experimental approaches. The usual set-up in the laboratory consists of one condition, which allows social learning, and another one, in which social learning is not possible. In such experiments, typically two individuals are included, one individual serving as knowledgeable demonstrator and one as naïve observer (Whiten and Mesoudi 2008). Although this approach makes it easy to identify different forms of social learning, it lacks ecological validity. In the wild, traditions are rarely transmitted via dyads, but require a multitude of transmission episodes (Whiten and Mesoudi 2008). An experimental approach that tests animals in a more natural setting is the “group diffusion experiment” that tests the spread of experimentally introduced novel behaviours on a group-level. Combined with a two-option methodology these experiments allow inferences about the involvement of social learning in the propagation process (Whiten et al. 2005). Groups of animals are thereby confronted with a problem, for instance obtaining food from a feeding box, which can be solved by using two different methods and with a demonstrator that was trained for a single method in advance. If social learning is at work, individuals are expected to predominately use the method of the demonstrator. Due to its characteristic to test groups of animals on a group-level, this experimental approach is also suitable for field settings (reviewed in Reader and Biro 2010; van de Waal and Bshary 2011; Schnoell and Fichtel 2012; van de Waal et al. 2013).

1.4. The lemur model

The primate lineage is regularly used to draw inferences about the cultural evolution in humans (Fichtel and Kappeler 2010). The idea is that if there is a trait or a characteristic present in a non-human primate species and in humans then it should have been already present in their most recent common ancestor (Fichtel and Kappeler 2010). Due to their close relatedness to humans, apes, like chimpanzees (Mikkelsen et al. 2005) or orang-utans (van Schaik et al. 2003), are regularly used for contrasting behaviour. However, some characteristic might be evolutionary much older (Fichtel and Kappeler 2010) and therefore it potentially quilts interesting results to increase the search radius and to include other primate species that are less closely related to humans. Research on haplorrhines provided many interesting insights about the cognitive and cultural evolution (reviewed in Whiten and van Schaik 2007): capuchin monkeys, for instance, also exhibit cultural traditions in the wild (Perry and Manson 2003).

In this sense, the Malagasy lemurs (*Lemuriformes*) are interesting models, because the last common ancestor with primates outside of Madagascar lived in the Eocene and, therefore, even further back in time (Karanth et al. 2005; Tattersall 2007). Another interesting characteristic is that lemurs possess a relative smaller brain size than haplorrhines (Armstrong 1985; Dunbar 1998) but some of them still evolved group living, although group sizes are on average smaller than in haplorrhines (Kappeler and Heymann 1996). Brain sizes are thought to correlate with social complexity (labelled “Machiavellian Intelligence Hypothesis”; Byrne 1997); therefore it is worthwhile to investigate the strategies group-living lemurs apply to manage their social life.

For this study, I collected data on two species of lemurs, on the redfronted lemur (*Eulemur rufifrons*) and on the ringtailed lemur (*Lemur catta*). Both species share many similarities in their social organization. They both live in multi-male, multi-female groups in which females are usually related while males leave their natal group when reaching sexual maturation (Wilson and Hanlon 2010; Kappeler and Fichtel 2012a). Additionally, they have comparable diet, body size and brain size (Johnson 2007; Isler et al. 2008; Wilson and Hanlon 2010). In social learning tests, ringtailed lemurs (Kendal et al. 2010a) and redfronted lemurs (Schnoell and Fichtel 2012) seem to rely on social information when confronted with an experimental task. However, the two species differ in their social structure (Pereira and Kappeler 1997), which makes them excellent study models. In ringtailed lemurs, groups have

linear dominance hierarchies and females are dominant over males (i.e. female dominance; Pereira and Kappeler 1997). In redfronted lemurs, in contrast, females are rather egalitarian, without dominance hierarchies, no female dominance, and only one dominant male in each group (Pereira et al. 1990; Ostner and Kappeler 2004). These two species therefore constitute a well-suited model to investigate the effect of the social environment on social learning and on the diffusion of new behaviour within social groups.

1.5. Aims and approaches

The general aim of my thesis was to contribute to the growing body of knowledge on behavioural traditions in non-human primates. I thereby focused on an aspect for which information is still rare, which is the influence of social tolerance on social learning. I conducted a social diffusion experiment with two lemur species that differ in their social tolerance level to study the differences in the speed and pattern of propagation of new information within the study groups. Additionally, I operationalized social tolerance and looked into the longevity of behavioural habits within social groups. The ordinance of the different chapters of my thesis follows the steps of the development of a tradition:

In **Chapter 1** I report on a potential innovation in redfronted lemurs, namely the appearance of a new feeding behaviour that was not described in the study population yet.

In **Chapter 2** I operationalize social tolerance by establishing a co-feeding experiment to obtain comparable measurements of social tolerance across species. Additionally, I validate the outcome of the experiment by using observational data and look for a captivity effect by comparing the results of the experiment conducted in the wild to the ones conducted in captivity. In this study, I measured the social tolerance levels of redfronted lemurs as well as of ringtailed lemurs.

In **Chapter 3** I focus on differences in social transmission between the two species by investigating the number of learners, speed of propagation and homogeneity in the spread as well as in the behaviour. To do so, I conducted group diffusion experiments by using feeding boxes that can be opened in two different ways (by “sliding” or “lifting”) and trained demonstrators that were knowledgeable in one of the two methods. I tested both lemur species with exactly the same experimental set-up to make the comparison of the results possible.

In **Chapter 4** I investigate the persistence over time of experimentally introduced traditions in redfronted lemurs, a species that is able to use social information (Schnoell and Fichtel 2012), but has not been reported to exhibit traditions in the wild. I analyse individual preferences in the opening technique of a feeding box over three consecutive years.

Although the two following chapters do not tackle the main question of the thesis, I decided to include them, to give a broader overview about the work I conducted during my PhD:

In **Chapter 5** I present data on the pattern of handedness in wild redfronted lemurs by using an observational and an experimental approach. I discuss the results in the light of several theories that were proposed to explain variation in limb preferences in primates.

In **Chapter 6** I review the cognitive abilities of one of my study species, the ringtailed lemur, and give an overview about studies in the technical and social domain.

CHAPTER 2

A NOVEL FEEDING BEHAVIOUR IN WILD REDFRONTED LEMURS (*EULEMUR RUFIFRONS*): DEPLETION OF SPIDER NESTS

with Claudia Fichtel

Primates 54: 371-375 (2013)

Abstract

Reports on behavioural innovations in wild primate populations as well as on their transmission are rare. Here, we report observations suggesting that redfronted lemurs (*Eulemur rufifrons*) invent new behaviours in the wild. We observed a novel feeding behaviour in redfronted lemurs in Kirindy Forest, western Madagascar. The feeding behaviour consisted of depletion of nests of a social spider species (*Stegodyphus* sp.). The behaviour was observed in only one out of four study groups, although spider nests were present in the home ranges of all four groups. The behaviour was exhibited in three different years (2009, 2011, 2012) and appears to be re-invented from time to time. Interestingly, in 2011 this behaviour was shown by four individuals and probably spread within the group. This feeding behaviour has only been observed between the middle of June and early August (i.e. the early dry season), and nests were found to be empty later on, suggesting that these nests are available as a food source only seasonally. Our observation contributes a rare case of behavioural innovations in a wild primate population.

Keywords: Innovation; Traditions; *Eulemur rufifrons*; *Stegodyphus* sp.; Feeding behaviour; Social transmission

Introduction

An innovation is defined as “a process resulting in a new or modified learned behaviour and in introduction of novel behavioural variants into a population’s repertoire” (Reader and Laland 2003). Innovations allow animals to react to changes in their environment as well as to environmental challenges (Boogert et al. 2008) and are, therefore, an important component of behavioural plasticity (Reader and Laland 2003). Individual characteristics like age, life period and personality of individuals as well as food deprivation may make innovations more likely (Cadieu et al. 2010). Innovations are also interesting because they represent, together with the transmission of the behaviour, the initial step to develop traditions (Huffman and Quiatt 1986; Galef 2004). However, little is known about how often behavioural innovations occur in the wild, how often they do not spread within groups, or how often they do spread and develop into a tradition (Nishida et al. 2009). Evidence for the occurrence of behavioural traditions has been documented mainly in anthropoid primates (Kawai 1965; Whiten et al. 1999; Perry et al. 2003; Van Schaik et al. 2003), whereas reports on innovations as well as social transmission in strepsirrhines are rare (Hosey et al. 1997; Fichtel and van Schaik 2006; Fichtel and Kappeler 2011). Here, we report observations on a novel feeding behaviour in wild redfronted lemurs (*Eulemur rufifrons*). Redfronted lemurs live in a seasonal environment, which ought to promote behavioural flexibility (Perry et al. 2003). Moreover, they use social learning in the wild (Schnoell and Fichtel 2012) and are characterised by high levels of social tolerance (Pareira and Kappeler 1997; Ostner and Kappeler 2004), which in turn facilitates social learning (Coussi-Korbél and Fragaszy 1995; Bonnie and de Waal 2006).

Methods

As part of a long-term study, a population of redfronted lemurs in Kirindy Forest has been regularly monitored since 1996 (Kappeler and Fichtel 2012a) and there are no records of the new feeding behaviour before 2009. The study area is characterised by pronounced seasonality with an annual dry season between May and November (Kappeler and Fichtel 2012b). Between mid-March and mid-August 2011, AVS conducted regular behavioural observations on four groups of wild redfronted lemurs ($N_{\text{total}} = 33$), but the new behaviour was only observed in group A ($N_A = 11$ individuals: 3 adult females, 5 adult males, 1 subadult female, 2 subadult males). Focal behavioural sampling (Altmann 1974) was conducted

between 6:00 and 18:00 h, and the average total observation duration per individual in group A was 11.9 ± 2.1 h (mean \pm SD). Individuals in the three other study groups (B, F, J) were observed on average for 12.5 ± 2.1 h (mean \pm SD). Rates (s/h) of grooming and resting in body contact were used as measurements of social bonds, and a social network was constructed using Ucinet 6 and Net-Draw (Borgatti et al. 2002). To assess whether social bonds and the proportion of time (s/h) spent in close proximity (within a 1 m radius) differed between dyads of individuals that both exhibited the novel feeding behaviour and dyads of spider nest-feeding and other individuals, we calculated a generalized linear mixed model (GLMM; Table 1). An additional 6 weeks of observations were conducted by AVS in August and September 2012 on two of the original four study groups ($N_{\text{total}} = 12$ individuals; NA = 6 individuals: 3 adult females, 2 adult males, 1 subadult female).

Table 1 Parameters estimated for the generalized linear mixed model (GLMM) on the difference of social bonds and proximity between pairs of depleting individuals and pairs of depleting and non-depleting individuals.

Response variable	Random factors	Fixed factors	Estimate	SE	P value
Depleting (yes, no)	Individual identity, partner identity	Intercept	-1.342	0.622	0.031
		Grooming	-0.017	0.018	n.s.
		Proximity	0.003	0.006	n.s.

n.s. not significant

Results

The observed novel feeding behaviour consisted of depleting spider nests of social spiders of the genus *Stegodyphus*. Nests had a diameter of approximately 10 – 20 cm with a dense and opaque structure (Figure 1). They can be found in trees and bushes at a height of 0.5 – 1.5 m and multiple, relatively small (≤ 1 cm) spiders share one nest. The novel feeding behaviour consisted of opening the nest, breaking into the central part where the spiders live and store their prey, and removing food items from it (Figure 1a). In the process of removing the food items the nests were completely destroyed (Figure 1b). A nest opened by CF in April 2012 contained a large number of spiders as well as prey items (Figure 2). We could not

determine whether the food items were dead insects stored by the spiders or whether the lemurs were feeding on the spiders themselves, or both.



Figure 1 A nest of social spiders (Genus *Stegodyphus*) in Kirindy Forest (picture taken by CF).

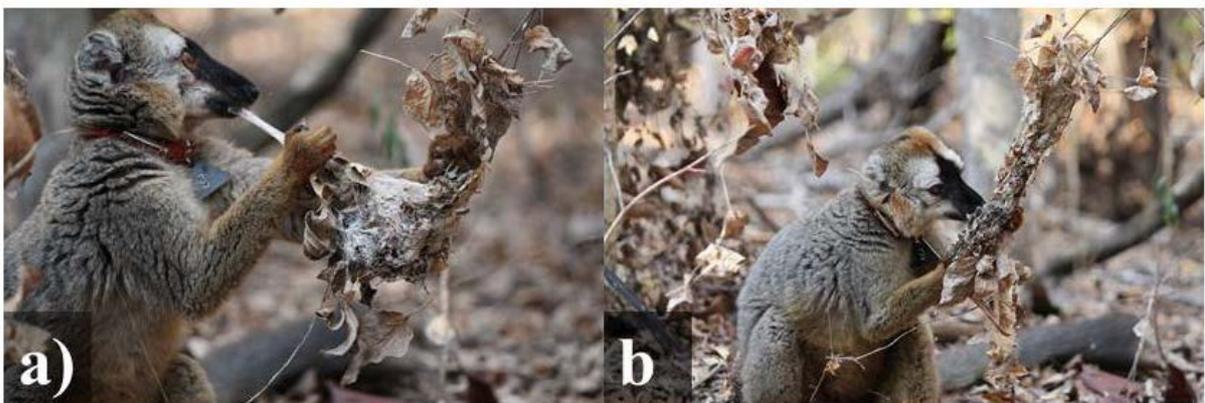


Figure 2 AMTho removing food items from a spider nest (a) and destroying the nest in the process of feeding (b; pictures taken by AS).

The novel feeding behaviour could be observed in one of four study groups (group A) in 3 years (2009, 2011, 2012; Table 2), even though there were spider nests present in the home ranges of all groups. In 2009, adult female AFCor depleted a nest once (Table 2). Unfortunately, this observation was recorded during daily census as an additional observation by a field assistant and, therefore, lacks a detailed description. AFCor was still present in 2011 and 2012, but was not observed to deplete spider nests. In 2011, four individuals (AMPax, AMTho, AMKor, AFPla; Table 2) depleted spider nests between mid June until early August. The first individual observed to perform the new feeding behaviour was adult male AMPax (Table 2). AMPax was a member of group A before (between 15 April 2009 and 21 September 2009) and re-immigrated into group A on 09 June 2011. He was observed to deplete a spider nest while the group was feeding on the ground, and one additional time during a group movement on the ground (Table 2). During the following 7 weeks the behaviour was performed each once by three additional members of group A: by adult male AMTho, juvenile male AMKor and juvenile female AFPla. AMTho and AMKor were observed to perform the new feeding behaviour while the group was feeding on the ground.

Table 2 Date, time as well as observer of single events of depletion of spider nests and identity of individuals exploiting them.

Date	Time	Individual	Observer
Dry season 2009		AFCor	Tianasoa Andrianjanahary
Middle of June 2011		AMPax	Anna Schnoell
29 June 2011	09:25	AMPax	Anna Schnoell
05 July 2011	15:30	AMTho	Anna Schnoell
22 July 2011	14:45	AMKor	Anna Schnoell
03 August 2011		AFPla	Mamy Solohery Razafindrasamba
16 June 2012	09:40	AMNeg	Roberta Aralla

First letter name of group, *second letter* sex (*F* female, *M* male), *last three letter* first three letters of the individual's name

We could not find any indications that the strength of social bonds or proximity between individuals facilitates the acquisition of the behaviour. Maximum distance between group members while feeding on the ground was 10 m. Pairs of individuals observed to deplete spider nests in 2011 did differ neither in the strength of social bonds between each other (Figure 3; depleting: mean \pm SD = 11.7 ± 24.9 , N = 6 dyads; non-depleting: mean \pm SD = 71.7 ± 126.4 , N = 28 dyads), nor in the time spent together within a 1 m radius (depleting: mean \pm SD = 69.6 ± 70.2 s/h, N = 6 dyads; non-depleting: mean \pm SD = 75.4 ± 87.5 s/h, N = 28 dyads) from pairs of depleting and non-depleting individuals (Table 2; GLMM: $\chi^2 = 2.598$, $p = 0.3$). The behaviour was last seen in August and stopped most likely because of the decreasing availability of spider nests. In August 2011, AVS opened one nest, but it was empty, suggesting that the spiders had left their nest or died during the advancing dry season (Bodasing et al. 2002). In 2012, adult male AMNeg, who was also present in 2011, was observed to deplete a spider nest once. Three of the four individuals (AMPax, AMTho, AMKor) that were observed to feed on spider nests in 2011 were not present anymore in 2012.

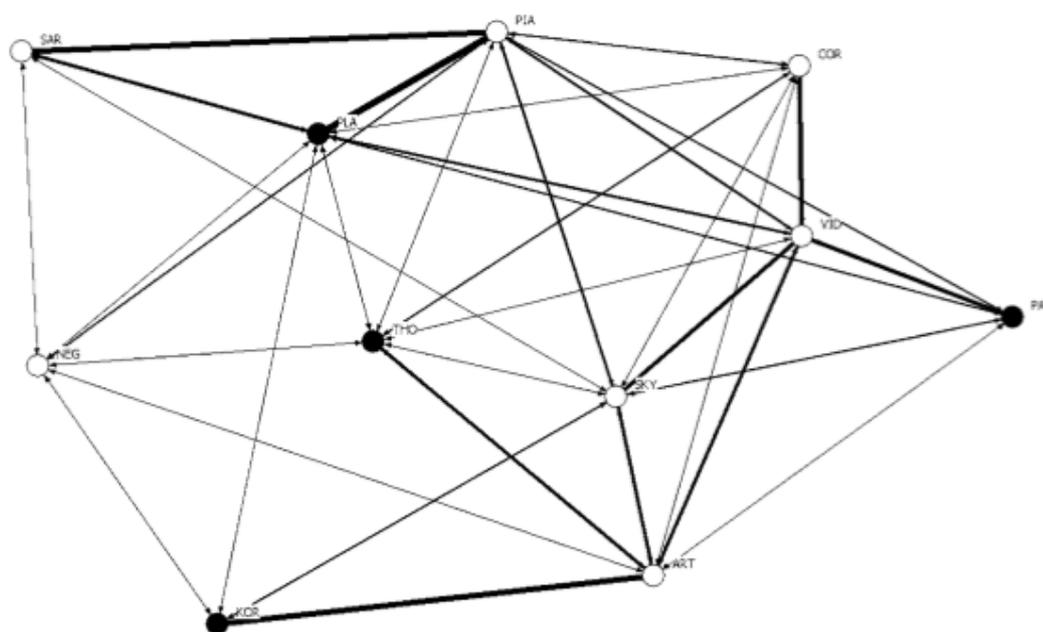


Figure 3 Schematic depiction of the social network of group A in 2011. *Circles* represent individuals; *filled circles* represent individuals depleting spider nests. Line widths are proportional to the strength of the social bond. The network is based on observed frequencies of grooming and resting in contact of 11 redfronted lemurs.

Discussion

Depletion of spider nests fulfils several characteristics of an innovation (Ramsey et al. 2007). First, it is not a common feeding behaviour in redfronted lemurs. In 3 years of observations it was performed by only some individuals in group A but was never observed in the other three study groups despite the same observation effort. We also checked the literature and could not find any description of *Eulemur* sp. in other study sites feeding on spider nests (Overdorff 1993; Tarnaud 2004; Donati et al. 2011), though they were described to include other invertebrates in their diet (Overdorff 1993; Donati et al. 2011). Second, depleting a spider nest was not an accidental behaviour (see also Reader and Laland 2003) because it was observed five times and twice in the same individual in 2011. Third, one should not find a particular trait that characterises innovators, such as age or genotype (see also McGrew 1998; Laland and Janik 2006). In redfronted lemurs, the new behaviour cannot be explained by relatedness because males migrate between groups, and two of the three inventors were males. However, there might be a bias towards adult individuals as inventors. This has also been shown in canaries (*Serinus canaria*: Cadieu et al. 2010) and chimpanzees (*Pan troglodytes*: Reader and Laland 2001; Nishida et al. 2009), suggesting that not only young individuals can serve as innovators in birds and primates (Nishida et al. 2009).

The novel feeding technique was seasonally short-lived. Since the availability of spider nests decreased with the advancing dry season, the persistence of the behaviour might have been constrained by prey availability. Depletion of spider nests occurred in the dry season, when food is generally rare. Therefore, food deprivation might have facilitated this innovation (Cadieu et al. 2010).

In 2011, after the innovation of nest depletion by adult male AMPax, one adult and two juvenile lemurs also fed on spider nests, supporting the notion that young primates appear to show more interest in learning new behaviours (for example: Kappeler 1987). Depletion of spider nests mostly occurred while the group was feeding on the ground within an inter-individual distance allowing observations of others and facilitating social learning. Nevertheless, we could not find a facilitating effect of the strength of social bonds and/or the time individuals spent in close proximity on the pattern of acquisition of the task, which would be an indirect indicator of social transmission (Coussi-Korbel and Frigaszy 1995). Thus, these preliminary data do not allow us to conclude whether the new feeding behaviour spread via social transmission or whether it was invented four times

independently in 2011.

Thus, depletion of spider nests is a behaviour that might occasionally be invented from time to time. The pattern of this new feeding behaviour in redfronted lemurs resembles the pattern of similar innovations in chimpanzees, which were limited to one or several individuals and disappeared after some time (Nishida et al. 2009). Our observations, therefore, add to the small pool of knowledge on how often behavioural innovations emerge in the wild without human interference (Ramsey et al. 2007; Nishida et al. 2009).

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CHAPTER 3

MEASURING SOCIAL TOLERANCE – AN EXPERIMENTAL APPROACH WITH TWO LEMUR SPECIES

with Claudia Fichtel and Peter M. Kappeler

Animal Behaviour: submitted

Abstract

Social tolerance crucially affects the life of group-living animals as it can influence, for instance, competitive regimes, access to food, learning behaviour and recruitment. However, it has proven difficult to operationalize social tolerance in the past. One purpose of this study was therefore to establish a co-feeding experiment that would yield comparable and straightforward measurements of social tolerance across species. Furthermore, we wanted to validate the results of this experiment by using behavioural observations. To this end, we tested the social tolerance level of two lemurid primates, redfronted lemurs (*Eulemur rufifrons*, 4 wild groups, 1 captive group) and ringtailed lemur (*Lemur catta*, 3 wild groups, 3 captive groups), by presenting them a clumped food resource in an experimental arena. We found that more redfronted lemurs were feeding simultaneously and able to stay in close proximity during a competitive situation than in ringtailed lemurs, suggesting that redfronted lemurs are more socially tolerant. During the observational study, redfronted lemurs spent more time in close proximity than ringtailed lemurs, but we did not find a species difference in co-feeding. Additionally, both approaches yielded the same species difference in the outcome of aggression, with much fewer aggressive events being decided in redfronted lemurs than in ringtailed lemurs. We therefore conclude that close proximity as well as outcome of aggression can serve as consistent measures of social tolerance; two variables that can be easily measured with this experiment in other species as well.

Keywords: Social tolerance; Co-feeding; Proximity; Lemurs; Sociality

Introduction

Social tolerance is defined as the “concept that captures the probability that individuals will be in proximity to conspecifics around valuable resources with little or no aggression” (Cronin and Sánchez 2012). It is thought to influence several aspects of the social life of group-living animals, including patterns of aggression and affiliation (Thierry 1985; Petit et al. 1997; Ciani et al. 2012), access to food and water (de Waal and Luttrell 1989; Melis et al. 2006), patterns of recruitment (Sueur and Petit 2010) and the spread of knowledge within social groups (Coussi-Korbel and Fragaszy 1995; van Schaik et al. 1999). Living in a socially more tolerant society has advantages and disadvantages, but species exhibiting higher levels of social tolerance seem to be behaviourally more flexible: they interact more often with novel objects and are therefore less neophobic (Bergman and Kitchen 2009), they learn quicker in group-settings (Lonsdorf et al. 2009), and they reach higher levels of cooperation in experiments with food rewards (Hare et al. 2007), even when interacting with strangers (Tan and Hare 2013). However, higher tolerance is also associated with delays in the development of some cognitive skills, like inhibitory control (Wobber et al. 2010; Hare et al. 2012). Moreover, living in a more tolerant society might be associated with greater health risks, because having more close and diverse social contacts with others influences the probability of parasite transmission (Anderson and May 1982). Social tolerance is thought to be associated with the social structure of a species, that describes the pattern and nature of social relationship between individuals within a group (Kappeler and van Schaik 2002), and varies from tolerant/egalitarian to intolerant/despotic (de Waal and Luttrell 1989; Matsumura 1999; Thierry 2000; van Schaik 2003; Thierry 2013).

Social tolerance can be measured with two different approaches (van Schaik et al. 1999; van Schaik 2003): the identification of the underlying behavioural traits or the investigation of the outcomes of social tolerance. The former is done by observational studies: members of tolerant societies have more diverse contacts within the group, despite rank and kinship (Aureli et al. 1997; Thierry 1990; Matsumura 1999), more grooming partners, closer proximity to other individuals as well as less directed and less intense aggression compared to members of less tolerant societies (Thierry 1985; de Waal and Luttrell 1989; Duboscq et al. 2013).

The second approach quantifies the outcome of different social tolerance levels by confronting individuals with an experimentally induced competitive situation, such as co-

feeding tasks (Melis et al. 2006; Hare et al. 2007; Wobber et al. 2010), water sharing (de Waal and Luttrell 1986), or the repartition of food monopolization within a group (Burkart and van Schaik 2013). More tolerant species were found to share more with others and exhibited less aggression than less tolerant species. However, comparisons between studies and species are difficult because different sets of measurements of co-drinking or co-feeding as well as aggression were measured. For example: the proportion of trials with and without co-feeding (Melis et al. 2006; Wobber et al. 2010), proportion of interactions with and without co-drinking (de Waal, 1986), or the evenness of distribution of food rewards within a group (Burkart and van Schaik 2013). In addition, some studies were conducted in a group setting whereas as others tested pairs of animals.

Moreover, other species than primates are affected by differences in social tolerance towards unknown individuals: Laying hens (*Gallus gallus domesticus*), for instance, show slower social learning when confronted with a demonstrator they did not know (Nicol and Pope 1994). Similarly, ravens prefer familiar individuals as well as models, like siblings and friends in social learning tasks (Schwab et al. 2008; Schied et al. 2007). However, outside the primate lineage, we lack experimental studies on social tolerance.

Almost all previous studies were conducted in captive settings, in which individuals might be more tolerant in co-feeding tasks because they are not exposed to the same intensity of feeding competition as wild animals. Thus, a validation of the usefulness of co-feeding tasks to operationalize social tolerance in wild animals is lacking. We therefore designed a simple co-feeding experiment to measure the outcomes of social tolerance to obtain a comparable measurement across species and to establish an easy test to operationalize social tolerance in field settings. Co-feeding tasks were repeated after an interval of several weeks to control for repeatability over time. In addition, we conducted focal animal observations to examine whether the two different approaches yield corresponding results. Finally, we repeated the co-feeding experiments in captive populations to examine in how far the intensity of feeding competition influences the outcome of social tolerance, assuming that captive populations experience less intense feeding competition.

We collected experimental and observational data on two species of lemurs – ringtailed (*Lemur catta*) and redfronted lemurs (*Eulemur rufifrons*). Both live in multi-male, multi-females groups with related females, unrelated males and their offspring. In both

species males leave their natal group when they are sexually mature (Wilson and Hanlon 2010; Kappeler and Fichtel 2012a). Both species are medium-sized lemurs and mainly feed on fruits and leaves (Johnson 2007; Wilson and Hanlon 2010). However, they differ in their social structure (Pereira and Kappeler 1997), which makes them well suited for this study. Ringtailed lemurs exhibit a linear dominance hierarchy, with all females dominating all males (Pereira and Kappeler 1997). In contrast, redfronted lemurs are rather egalitarian, with no clear-cut decided and stable dominance relations among females and between the sexes; only one adult male tends to dominate all other males (Pereira et al. 1990; Ostner and Kappeler 2004).

We therefore predicted that during the co-feeding experiment more redfronted lemurs would co-feed than ringtailed lemurs. During the behavioural observations we expected to find a comparable pattern to the one during the experiment, with higher proximity and more co-feeding in the redfronted lemurs. Since the intensity of feeding competition may influence social tolerance in this task, we additionally conducted the same co-feeding experiment in captive redfronted and ringtailed lemurs, predicting that animals in captivity may show higher levels of social tolerance than their wild counterparts.

Methods

Species, study sites and subjects

Wild redfronted lemurs were studied in Kirindy Forest, Western Madagascar, where the German Primate Center has maintained a research station since 1993 (Kappeler and Fichtel 2012b). We collected data on four groups (groups A, B, F and J) with a size of three to 11 individuals (group composition in Table 1). Group members are individually marked by nylon collars and well habituated to the presence of human observers (Kappeler and Fichtel 2012a). All groups have participated in other feeding experiments before (Schnoell and Fichtel 2012; Pyritz et al. 2013; Schnoell et al. 2014). One captive group of four redfronted lemurs was studied in the Lakeland Wildlife Oasis, UK (group WO; Table 1).

Wild ringtailed lemurs were studied in Berenty Private Reserve, Southern Madagascar. They were not individually marked but can be easily identified by unique facial patterns. This population has been regularly studied since 1966 (Jolly 1966; Koyama et al. 2005) and is therefore also well habituated to the presence of humans. Two of the three study groups (C1 and YF) have already participated in other feeding experiments before

(Kendal et al. 2010a). The group sizes of the three study groups (group C1, C2A and YF) varied between 11 to 12 individuals during the co-feeding experiment (Table 1). Additionally, we studied 3 captive groups of ringtailed lemurs, one group at the German Primate Center (group DPZ) and two groups at the Erlebnispark Straußberg, Germany (group OB and UN), with group sizes of 6 and 15 individuals (Table 1).

Table 1 Group composition of the study groups during the co-feeding experiment (species: *ER* = *Eulemur rufifrons*; *LC* = *Lemur catta*; setting: *W* = wild, *C* = captive; age: *adult* > 2.5 years; *juvenile* < 2.5 years; if two numbers are given: the *first number* corresponds to test block 1 and the *second number* to test block 2).

Species	Setting	Group	Adult females	Adult males	Juvenile females	Juvenile males	Total
ER	W	A	4	7/5	0	0	11/9
ER	W	B	2 /1	2	0	0	4/3
ER	W	F	3	6	2	0	11
ER	W	J	3	3	1	0	7
ER	C	WO	1	3	0	0	4
LC	W	C1	5	5	0	1	11
LC	W	C2A	5	4	1	2	12
LC	W	YF	4	4	2	2	12
LC	C	DPZ	5	1	0	0	6
LC	C	OB	5	6	2	2	15
LC	C	UN	4	7	0	0	11

Co-feeding experiment: training, set-up, procedure and sample sizes

We first trained the groups to respond to an auditory signal by approaching the location from which the signal was presented to obtain a food reward. We used a clicker used for animal training to generate the auditory signal. This procedure allowed us to set-up the experiments in some distance from the animals to avoid an association between humans and food.

The experimental set-up consisted of one or two arenas and one food bowl per arena (Figure 1). To control for differences in group size, we used one arena and one food bowl for group sizes of ≤ 8 individuals and two arenas and two bowls for groups of ≥ 9 individuals. An arena was constructed out of rope and tent pegs. It measured 1 x 0.5 meter, which corresponds to about 4 times x 2 times the average body length of the study species. The food bowls had a size of 15 x 15 x 3 cm (15 cm = 3 times the average head width of the study species) and were filled with pieces of oranges and raisins. In experiments with two arenas, we set them up with the narrow sides next to each other. All experiments were videotaped with a Sony HDR-XR350 and a Sony DCR-SR75E camcorder.

We confronted the groups with the experimental set-up over 8 sessions in the wild setting (except redfronted lemur group A with 7 sessions). We conducted four sessions on successive days and after a pause of 93 days for redfronted lemurs and 38 to 39 days for ringtailed lemurs another four sessions on successive days to test the repeatability of the social tolerance task over time. Groups in captivity were tested over 4 sessions. If less than half of the group members participated in the experiment, i.e. entered the arena at least once, or if there was a major disturbance during the experiment, such as the occurrence of alarm calls, we discarded the session and retested the group on the following day. In total, we repeated one session in redfronted lemurs (group A) and four sessions in the ringtailed lemurs (each one session in group C1, C2A, DPZ and UN).

The co-feeding experiments with the four groups of redfronted lemurs in the wild were conducted in 2011. Thirty individuals participated in the experiments, i.e. were inside the arena at least once, (group A = 10 individuals, group B = 4 individuals, group F = 9 individuals, group J = 7 individuals). Ringtailed lemur group C1 was tested in 2011 and the groups C2A and YF in 2012. A total of 32 individuals participated (group C1 = 11 individuals, group C2A = 11 individuals, group YF = 10 individuals). All captive groups were tested in 2013 and all individuals participated in the experiment.



Figure 1 Experimental set-up consisting of one arena and one food bowl.

Data analyses

Video recordings were analysed by AVS. A session started when the first animal entered the arena (starting point: the individual had at least both front legs within the arena) and ended after the last individual left the arena. From the onset, each video was divided into 15-s observation slots for which the following response variables for each arena were quantified: number of individuals inside the arena and number of individuals feeding within the arena. Being inside the arena was defined as spending a total of at least 10 s within the arena (independent of the division by the observation slots) and co-feeding was defined as incidence of feeding within the arena. The session ended after the last slot of the video in which an individual was inside the arena. To assess inter-observer reliability, another observer unfamiliar with the study scored 10% of the sessions ($N = 8$ sessions). The inter-observer reliability was extremely high (99.9%; Kolmogorov-Smirnov-test: $Z = 0.460$, $P = 0.98$).

Furthermore, the frequency of agonistic interactions was recorded as well as their constituent species-specific aggressive (threaten, chase, grab, hit, bite, wave tail, stare),

submissive (leave, flee, spat call) and non-agonistic elements (ignore, turn; Table 2; Perreira and Kappeler 1997). To compare the outcome of agonistic interactions between species we summarized the exchange of aggressive (A), submissive (S) or no agonistic behaviour (O) for each dyadic agonistic interaction (Perreira and Kappeler 1997), allowing comparison between species that differ in details of their behavioural repertoire. Dyadic agonistic interactions in which only one individual exhibited only submissive behaviour (A-S, O-S) were scored as decided. An interaction in which only one individual showed aggressive behaviour (A-O) was classified as ignored conflicts with no response, whereas all other agonistic bouts were classified as counter-aggression (A-A, A-AS, AS-AS). Ignored interactions and interactions with counter aggression were combined as undecided agonistic interactions. The correct assignment of spontaneous spat calls to single individuals during the experiments with the captive ringtailed lemurs was not always possible because the individuals were feeding closely to each other with the head turned down. Therefore, we excluded interactions including spontaneous spat calls for the comparison of agonistic bouts between captive and wild ringtailed lemurs.

The average session length (*mean* + *SD*) of a co-feeding experiment was shorter in wild redfronted lemurs (6.4 + 3.2 min; $N = 31$ sessions) than in wild ring-tailed lemurs (21.2 + 13.2 min; $N = 24$ sessions; Mann-Whitney U test: $Z = -6.112$, $N_1 = 31$, $N_2 = 24$, $P < 0.001$). Therefore, we compared only the first 6.5 minutes of the experiments between species, which correspond to the first 26 observation slots. We excluded observation slots from the analysis in which no animals were present in the arena (zero values) because social tolerance can only displayed if at least one other individual is present. We compared the average and maximum number of individuals within the arena and co-feeding per session between species. In the case of two arenas, we calculated the average and maximum number for each arena separately.

To assess whether the average and maximum number of individuals present and co-feeding differ between species, we constructed linear mixed models (*LMM*) by using the square-root transformed average and maximum number of individuals present in the arena or co-feeding as dependent variable, species and number of arenas as fixed factors and group identity as random factor. We included test block as an additional fixed factor in the wild setting. To compare the average and maximum numbers of animals within the arena and co-feeding between the captive and the wild setting, we calculated another *LMM* with

species, setting, number of arenas and the interactions between species and setting as fixed factors and group identity as random factor. Data were square-root transformed before running the models. We used Kolmogorov-Smirnov tests to analyse whether the average curves of number of individuals within the arena and co-feeding over the first 6.5 minutes differ between redfronted lemurs and ringtailed lemurs. For these tests we calculated one average value of animals within the arena and one for co-feeding per observation slot and per arena. We compared the proportion of decided agonistic interactions and undecided agonistic interactions between the two species by using a proportion test and compared spat rates per session between captive and wild setting in the ringtailed lemurs with a Mann-Whitney *U* test.

The proportion tests and the *LMMs* were calculated in R (R Development Core Team 2010). The models were fitted using the R package lme4 (Bates and Maechler 2010). The full model was compared to the null model by using a likelihood ratio test (Anova function with argument test set to " χ^2 "). We used the Markov Chain Monte Carlo sampling (Baayen 2008) to get *P* values for the individual effects. The Kolmogorov-Smirnov tests and the Mann-Whitney *U* test were calculated with IBM SPSS 21 (SPSS Inc., Chicago, IL, USA).

Behavioural observations

We used continuous focal sampling and scan sampling to collect observational data on the wild groups (Altmann 1974), focusing on adult individuals for comparison between the two species. The length of a focal animal observation was 30 min and included a group scan every 10 min, resulting in 4 scans per focal animal observation. For the continuous observations, we used a standard protocol (modified after Pereira and Kappeler 1997; Table 2). We recorded durations of affiliative behaviours as grooming, resting in contact and resting within a 1-m radius (Table 2). We also recorded the duration of co-feeding events (Table 2) as well as the frequency and outcome of agonistic interactions (Table 2). We collected observational data on four groups of redfronted lemurs (groups A, B, F and J) between 2011 and 2013. Ringtailed lemurs were observed in 2011 (group C1) and in 2012 (groups C2A and YF). We collected a total of 413 hours ($N = 36$ subjects: 13 females and 23 males) of observation for redfronted lemurs and of 579 hours ($N = 27$ subjects: 14 females and 13 males) for ringtailed lemurs. During scans, we recorded proximity in two distance

classes between the focal animal and all other group members (class 1: 0-1 m, class 2: 1-2 m).

We used *LMMs* to examine species differences in the rates of different behaviours. We calculated *LMMs* by using the average rate per individual (seconds per hour) as dependent variable (rates of resting in contact, of grooming and of co-feeding), species and the individual's sex as fixed factors and group identity as random factor. Data were square-root transformed before calculating the models. Rates of resting within 1 m and cohesiveness were compared with Mann-Whitney *U* tests. The proportion of decided and undecided agonistic interactions was tested with proportion tests.

Table 2 Definitions of social interactions used during focal observations (modified after Pereira and Kappeler 1997; Species: *ER* = *Eulemur rufifrons*, *LC* = *Lemur catta*).

Variable	Definition	Species	Measure
<i>1. Affiliative Interactions</i>			
Grooming	Licking with tongue and stroking with the tooth comb through the fur of another animal	ER, LC	Duration
Resting in contact	Resting with another individual in direct body contact for at least 10 seconds	ER, LC	Duration
Resting within a 1-m radius	Resting with another individual within a 1-m radius for at least 10 seconds	ER, LC	Duration
Co-Feeding	Feeding or searching for food with another individuals within a 1-meter radius for at least 10 seconds	ER, LC	Duration
<i>2. Agonistic interactions</i>			
<i>2.1. Aggressive</i>			
Chasing	Running after a fleeing individual	ER, LC	Frequency
Biting	To grab another individual orally	ER, LC	Frequency
Hitting	Strike another individual with one or two hands	ER, LC	Frequency

Grabbing	Grabbing the fur or body parts of another individual	ER, LC	Frequency
Threatening	Sudden movement of upper body towards another individual without leaving the position	ER, LC	Frequency
Wave tail	Flicking the tail over head while looking towards the partner (in male-male dyads)	LC	Frequency
Stare	Gazing with widened eyes at partner	LC	Frequency

2.2. Submissive

Leaving	Receiver of aggression leaves the position	ER, LC	Frequency
Flee	Receiver runs away	ER, LC	Frequency
Spat call	Submissive call	LC	Frequency

2.3. Non-agonistic

Ignoring	Receiver shows no reaction towards aggressor	ER, LC	Frequency
Turning	Receiver turns away from aggressor without leaving the position	ER, LC	Frequency

Ethical note

This study was approved by the Department of Zoology (Département de Biologie Animale) of the University of Antananarivo and the CAFF/CORE of the Direction des Eaux and Forêts de Madagascar. Research on redfronted lemurs was authorized by the CNFEREF Morondava, Madagascar, and the Lakeland Wildlife Oasis, United Kingdom. Research on ringtailed lemurs was authorized by the family de Heaulme, the owners of Berenty Private Reserve, and the Erlebnispark Straußberg, Germany. Additionally, the Animal Welfare Body of the German Primate Center confirmed that the experiments are in accordance with the legal and ethical

requirements of appropriate animal procedures using nonhuman primates in Germany (No. 14-E-2). Although our experiments involved some feeding competition, we tried to keep it to a minimum by presenting the groups with a multiple set of feeding boxes. The study groups were tested only once per day and a break of four to five days between experiments reduced the impact of the feeding experiment on the natural behaviour of the groups to a minimum.

Results

Co-feeding experiment in the wild

More individuals were present in the arena and co-feeding in redfronted lemurs than in ringtailed lemurs (Figure 2a and Table 3a, b; within arena: *LMM*: $\chi^2 = 16.758$, $F = 3$, $N = 55$ sessions, $P < 0.001$; co-feeding: *LMM*: $\chi^2 = 12.188$, $F = 3$, $N = 55$ sessions, $P = 0.001$). The maximum number of individuals within the arena was larger in redfronted lemurs than in ringtailed lemurs (Figure 2b and Table 3c; *LMM*: $\chi^2 = 9.4665$, $F = 3$, $N = 55$ sessions, $P = 0.01$). Similarly, more individuals were co-feeding in redfronted lemurs than in ringtailed lemurs (Figure 2b and Table 3d; *LMM*: $\chi^2 = 8.859$, $F = 3$, $N = 55$ sessions, $P = 0.01$).

The two species also differed in the way they interacted with the experimental set-up over time (Figure 3). In the beginning of the experiment more redfronted lemurs joined the arena and co-fed than at the end of the experiment, when the food bowl was already empty. In contrast, in ringtailed lemurs the number of individuals in the arena or co-feeding did not change significantly over the course of the experiment (within arena: Kolmogorov-Smirnov test: $Z = 5.700$, $N = 55$ sessions, $P < 0.001$; co-feeding: Kolmogorov-Smirnov test: $Z = 4.799$, $N = 55$, $P < 0.001$).

Redfronted lemurs showed on average higher rates of agonistic conflicts than ringtailed lemurs (redfronted lemurs: ($X + SD$) $28.8 + 19.1$ conflicts per hour, ringtailed lemurs: $16.2+6.4$ conflicts per hour). In redfronted lemurs, more aggression was ignored compared to ringtailed lemurs (42.3% vs. 0%; proportion test: $\chi^2 = 22.43$, $F = 1$, $P < 0.001$; Table 4a) and accordingly fewer conflicts were decided in redfronted lemurs (53.9% vs. 95.2%; $\chi^2 = 19.74$, $F = 1$, $P < 0.001$; Table 4a). Aggressive behaviours were rarely met with counter-aggression in both species (redfronted lemurs: 4.3%, ringtailed lemurs: 4.8%).

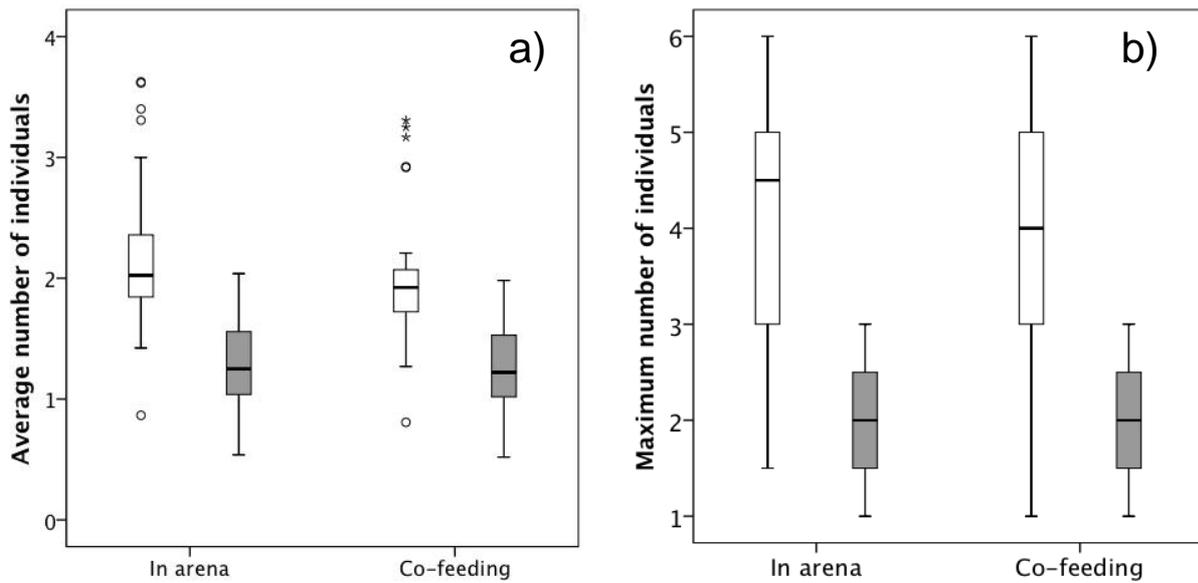


Figure 2 In a controlled co-feeding task in the wild setting more redfronted lemurs (*white*) than ringtailed lemurs (*grey*) were within an arena or co-feeding. Figure a) depicts the average number and figure b) maximum number of individuals within the arena or co-feeding. *Boxplots* indicate median, upper and lower quartiles, outliers are indicated by *circles* and *stars*.

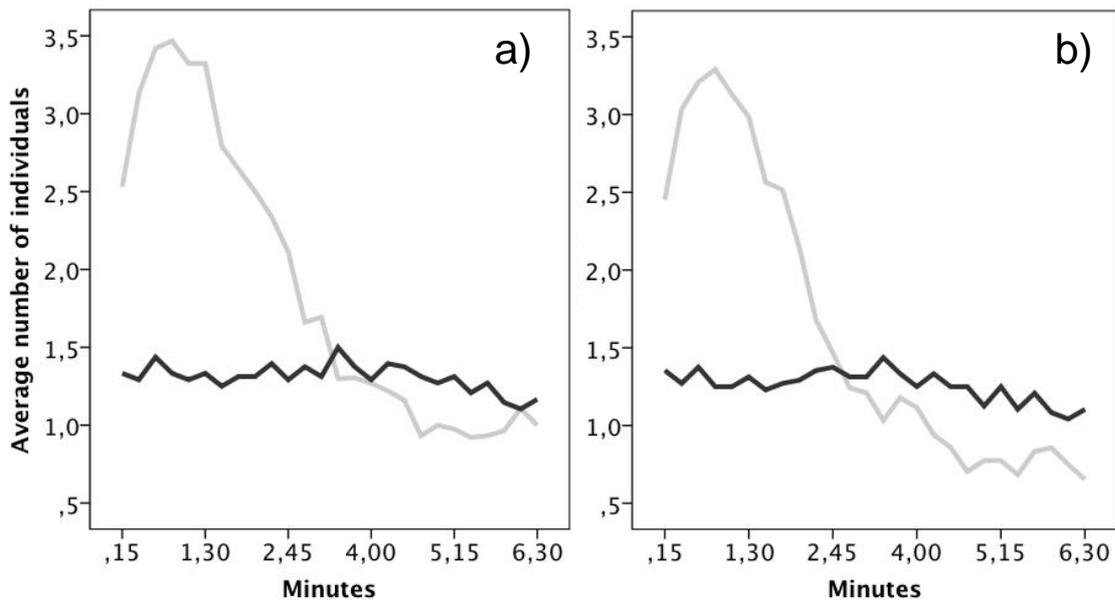


Figure 3 The course over time of the average number of individuals a) within the arena and b) co-feeding differed between wild redfronted lemurs (*grey line*; $N = 31$ sessions) and wild ringtailed lemurs (*black line*; $N = 24$ sessions).

Table 3 Parameter estimated for the Linear Mixed Models (*LMM*) on the difference of the average number of individuals within the arena (a) and co-feeding feeding (b) and the maximum number of individuals within the arena (c) and co-feeding (d) between the two species in the wild setting (*NS* = not significant).

Model	Response variable	Random factors	Fixed factors	Estimate	SE	<i>P</i> -value
<i>a LMM</i>	Average number of individuals within the arena	Group identity	Intercept	1.96	0.14	<0.001
			Species	-0.21	0.06	0.011
			Test block	-0.04	0.03	NS
			Number of arenas	-0.06	0.08	NS
<i>b LMM</i>	Average number of individuals co-feeding	Group identity	Intercept	1.88	0.14	<0.001
			Species	-0.19	0.07	0.009
			Test block	-0.03	0.02	NS
			Number of arenas	-0.04	0.09	NS
<i>c LMM</i>	Maximum number of individuals within the arena	Group identity	Intercept	2.18	0.33	<0.001
			Species	-0.57	0.18	0.003
			Test block	0.03	0.05	NS
			Number of arenas	0.07	0.20	NS
<i>d LMM</i>	Maximum number of individuals co-feeding	Group identity	Intercept	2.21	0.31	<0.001
			Species	-0.51	0.17	0.003
			Test block	0.01	0.05	NS
			Number of arenas	0.04	0.19	NS

Table 4 Rates and outcome of aggressive events during a) the co-feeding experiment and b) the behavioural observations for redfronted lemurs (ER = *Eulemur rufifrons*) and ringtailed lemurs (LC = *Lemur catta*; Setting: W = wild, C = captivity; + = data without Spat-calls).

	Species	Setting	Number of conflicts		Percentages		
			Total	Average per group/hour	Decided interactions	No response	Aggression returned
a)	ER	W	78	29	54	42	4
	LC	W	42	16	95	0	5
	LC+	W	31	12	94	0	6
	ER	C	8	22	50	50	0
	LC+	C	45	36	91	7	2
b)	ER	W	82	0.2	60	26	14
	LC	W	2455	3.9	99	1	0
	ER*	C	680		37	51	7
	LC*	C	1871		92	3	1

* Data by Perea and Kappeler 1997

Behavioural observations

We found that redfronted lemurs spent more time resting in body contact than ringtailed lemurs (Table 5 and Table 6a; *LMM*: $\chi^2 = 14.77$, $F = 2$, $N = 63$ individuals, $P < 0.001$). In redfronted lemurs, we did not find a sex difference in the time individuals rested in body contact (females: $X + SD = 95.8 + 56.5$ s/h, $N = 13$ individuals; males: $X + SD = 72.0 + 54.1$ s/h, $N = 23$; Mann-Whitney U test: $U = -1.27$, $N_1 = 13$, $N_2 = 23$, $P = 0.21$). However, in ringtailed lemurs females rested more often in body contact than males (females: $X + SD = 28.9 + 16.0$ s/h, $N = 14$ individuals; males: $X + SD = 14.6 + 10.7$, $N = 13$; Mann-Whitney U test: $U = -2.23$, $N_1 = 14$, $N_2 = 13$, $P = 0.03$). Redfronted lemurs also rested for more time within a 1-meter radius with other group members than ringtailed lemurs (Table 5; Mann-Whitney U test: $U = -2.99$, $N_1 = 36$ individuals, $N_2 = 27$, $P = 0.003$), with ringtailed lemur females spending more time within a 1-meter radius than males (redfronted lemurs: females: $X + SD = 101.9 + 48.9$ seconds per hour, $N = 13$ individuals; males: $X + SD = 76.4 + 60.9$, $N = 23$; Mann-Whitney U test: $U = -1.13$, $N_1 = 13$, $N_2 = 23$, $P = 0.13$; ringtailed lemur: females: $X + SD = 57.3 + 13.5$, $N = 14$; males: $X + SD = 33.8 + 16.8$, $N = 13$; Mann-Whitney U test: $U = -3.20$, $N_1 = 14$ individuals,

$N_2 = 13$, $P = 0.001$). In contrast, the two species and sexes did not differ in the time spent grooming (Table 5 and Table 6b; LMM: $\chi^2 = 0.47$, $F = 2$, $N = 63$ individuals, $P > 0.05$) and in the duration of co-feeding (Table 5 and Table 6c; LMM: $\chi^2 = 3.05$, $F = 2$, $N = 63$ individuals, $P > 0.05$).

Redfronted lemur groups exhibited an average rate of ($X + SD$) $0.2 + 0.04$ and ringtailed lemurs of $3.9 + 4.2$ agonistic interactions/h. Redfronted lemurs showed a smaller proportion of decided conflicts than ringtailed lemurs (60.0% vs. 99.0%; Table 4b; Proportion test: $\chi^2 = 518.04$, $F = 1$, $P < 0.001$). In redfronted lemurs more conflicts were ignored compared to ringtailed lemurs (26.3% vs. 0.9%; Proportion test: $\chi^2 = 291.25$, $F = 1$, $P < 0.001$). Aggressive behaviours were more often returned in redfronted lemurs than in ringtailed lemurs (13.8% vs. 0.1%; Proportion test: $\chi^2 = 237.76$, $F = 1$, $P < 0.001$).

Groups of redfronted lemurs were more cohesive than ringtailed lemur groups in close proximity (Mann-Whitney U tests: distance 0-1 meter: $U = -2.70$, $N_1 = 36$ individuals, $N_2 = 27$, $P = 0.01$; Table 5). However, in the distance-class of 1-2 meter radius ringtailed lemur groups showed higher cohesiveness (Mann-Whitney U test: $U = -5.13$, $N_1 = 36$ individuals, $N_2 = 27$, $P < 0.001$; Table 5).

Table 5 Comparison of several aspects of the social behavior of redfronted lemurs (*Eulemur rufifrons*) and ringtailed lemurs (*Lemur catta*; Results are listed as $X + SD$).

	<i>Redfronted lemur</i>	<i>Ringtailed lemur</i>
<i>Affiliative behaviors – Rates (seconds/ hour)</i>		
Grooming rate	5.36 + 4.43	5.11 + 3.34
Resting in contact	80.59 + 55.34	22.02 + 15.30
Resting within 1 meter radius	85.60 + 57.46	45.98 + 19.12
Percentage of affiliations with physical contact	47.96 + 14.13	31.73 + 12.92
Rate of co-feeding (seconds/hour)	10.52 + 7.21	10.53 + 6.28
<i>Group Cohesion</i>		
Number of individuals within 1 meter radius	0.41 + 0.16	0.29 + 0.15
Number of individuals in a 1-2 meter radius	0.25 + 0.15	0.56 + 0.23

Table 6 Parameter estimated for the Linear Mixed Models (*LMM*) a) on the difference between the rates of resting in body contact, b) between the grooming rates and c) between co-feeding rates (*NS* = not significant).

Model	Response variable	Random factor	Fixed factors	Estimate	SE	<i>P</i> -value
<i>a LMM</i>	Resting in body contact rates	Group identity	Intercept	9.86	1.02	<0.001
			Species	-4.65	1.57	0.004
			Sex	-1.48	0.50	0.004
<i>b LMM</i>	Grooming rates	Group identity	Intercept	2.55	0.35	<0.001
			Species	-0.13	0.54	<i>NS</i>
			Sex	-0.10	0.13	<i>NS</i>
<i>c LMM</i>	Co-feeding rates	Group identity	Intercept	3.58	0.32	<0.001
			Species	-0.09	0.45	<i>NS</i>
			Sex	-0.40	0.22	<i>NS</i>

Comparison of the co-feeding experiment with wild and captive lemurs

There was no effect of species and setting (captive vs. wild groups) on the average and maximum number of individuals within the arena and the average and maximum number of individuals co-feeding (average number of individuals with the arena: Table 7a, *LMM*: $\chi^2 = 16.84$, $F = 4$, $N = 71$ sessions, $P = 0.001$, maximum number of individuals with the arena: Table 7c, *LMM*: $\chi^2 = 9.64$, $F = 4$, $N = 71$ sessions, $P = 0.05$, average number of individuals co-feeding: Table 7b, *LMM*: $\chi^2 = 7.95$, $F = 4$, $N = 71$ sessions, $P = 0.05$, maximum number of individuals co-feeding: Table 7d; *LMM*: $\chi^2 = 8.35$, $F = 4$, $N = 71$ sessions, $P = 0.1$). However, there was a significant interaction between species and setting in the average number of individuals within the arena (Table 7a, *LMM*: $\chi^2 = 16.84$, $F = 4$, $N = 71$ sessions, $P = 0.001$), indicating that captive ringtailed lemurs tolerated more individuals in close proximity during the co-feeding task.

Redfronted lemurs did not differ in the way they interacted with the experimental set-up in captivity and in the wild; more individuals were within the arena and co-fed in the beginning than in the end of the experiment in both settings (within arena: Figure 4, Kolmogorov-Smirnov test: $Z = 0.69$, $N = 47$ sessions, $P = 0.72$; co-feeding: Kolmogorov-

Smirnov test: $Z = 0.91$, $N = 47$, $P = 0.38$). In contrast, ringtailed lemurs showed a different pattern of interaction, with a stable average number over time in the wild setting, but a peak in the average numbers in the beginning of the sessions in the captive setting (within arena: Figure 4, Kolmogorov-Smirnov test: $Z = 5.53$, $N = 40$ sessions, $P < 0.001$; co-feeding: Kolmogorov-Smirnov test: $Z = 5.65$, $N = 40$, $P < 0.001$).

Redfronted lemurs had a comparable rate of agonistic interactions in the wild setting and captive setting (22.07 conflicts/h). Ringtailed lemurs, in contrast, were more often aggressive in captivity ($X + SD = 35.7 + 23.0$ conflicts/h) and exhibited a higher rate of spat calling (wild: $X + SD = 4.6 + 6.1$ spat calls/h; captivity: $X + SD = 138.5 + 179.5$; Mann-Whitney U tests: $U = -4.75$, $N_1 = 12$ sessions, $N_2 = 24$, $P < 0.001$). Both species did not differ in the proportion of decided and undecided agonistic interactions between wild and captive populations (Table 4; Proportion tests: redfronted lemurs: decided: $\chi^2 = 0$, $Df = 1$, $P = 1.0$; undecided conflicts: $\chi^2 < 0.001$, $Df = 1$, $P = 0.97$; ringtailed lemurs: decided: $\chi^2 < 0.001$, $Df = 1$, $P = 1.0$; undecided conflicts: $\chi^2 = 0.75$, $Df = 1$, $P = 0.39$).

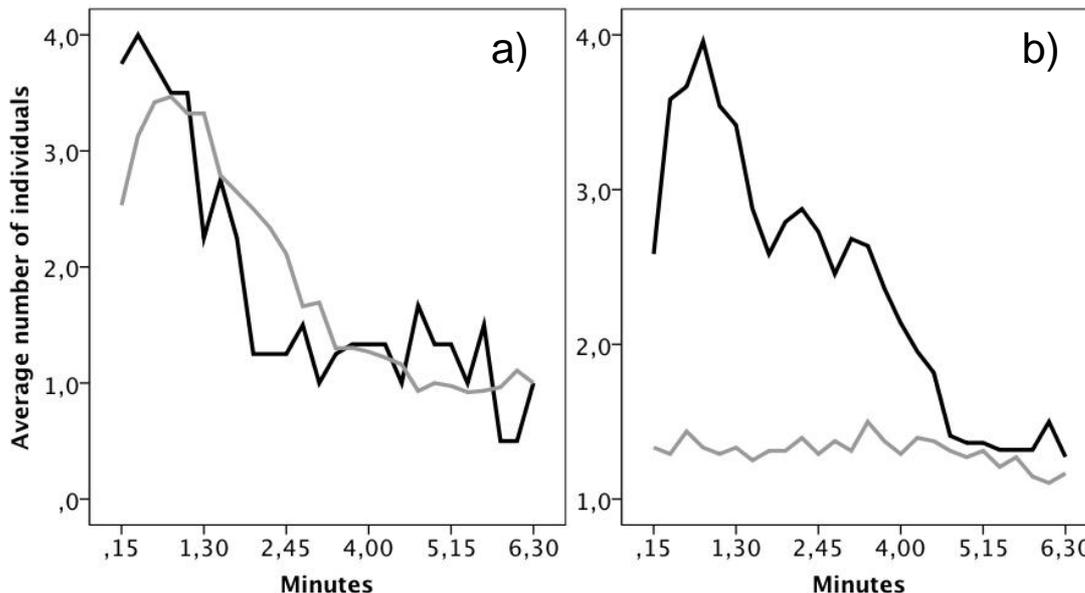


Figure 4 The course over time of the average number of individuals within the arena for a) redfronted lemurs and b) ringtailed lemurs in the wild (*grey line*) and in captivity (*black line*).

Table 7 Parameter estimated for the Linear Mixed Models (*LMM*) on the difference of the average number of individuals within the arena (a) and co-feeding (b) and the maximum number of individuals within the arena (c) and co-feeding (d) between the two species and between the wild and captive setting (*NS* = not significant).

	Model	Response variable	Random factors	Fixed factors	Estimate	SE	<i>P</i> - value
<i>a</i>	<i>LMM</i>	Average number of individuals within the arena	Group identity	Intercept	1.86	0.15	<0.001
				Species	0.23	0.15	NS
				Number of arenas	-0.12	0.08	NS
				Setting	0.14	0.14	NS
				Species:setting	-0.42	0.16	0.008
<i>b</i>	<i>LMM</i>	Average number of individuals co-feeding	Group identity	Intercept	1.96	0.24	<0.001
				Species	-0.9	0.10	NS
				Number of arenas	-0.03	0.16	NS
				Setting	-0.05	0.33	NS
				Setting:species	-0.08	0.19	NS
<i>c</i>	<i>LMM</i>	Maximum number of individuals within the arena	Group identity	Intercept	2.17	0.33	<0.001
				Species	0.10	0.33	NS
				Number of arenas	0.06	0.19	NS
				Setting	0.07	0.31	NS
				Setting:species	-0.66	0.36	NS
<i>d</i>	<i>LMM</i>	Maximum number of individuals co-feeding	Group identity	Intercept	2.21	0.33	<0.001
				Species	0.09	0.33	NS
				Number of arenas	0.02	0.20	NS
				Setting	0.04	0.31	NS
				Setting:species	-0.58	0.36	NS

Discussion

In this study, we conducted a co-feeding experiment to study social tolerance and validated the results of this experiment by studying the underlying behavioural traits of social tolerance during non-experimental interactions of two lemur species. In addition, we investigated whether the intensity of feeding competition influences the outcome of the co-feeding experiment by comparing wild and captive lemurs. We found proximity and outcome of aggression to be the measurements of social tolerance that were most consistent between species and methodological approaches. Finally, wild and captive groups of the two species did not differ in the number of individuals co-feeding, but ringtailed lemurs were more tolerant in captivity, suggesting that the intensity of feeding competition per se does not influence the level of social tolerance.

Behavioural mechanisms of social tolerance

During the co-feeding task, more redfronted lemurs were co-feeding than ringtailed lemurs. Redfronted lemurs did not monopolize the food, whereas in ringtailed lemurs the highest-ranking female monopolized almost all of it. Redfronted lemurs therefore either lack the ability to monopolize a clumped food resource or they tolerate food theft. Since they also showed high levels of aggression during the experiment, redfronted lemurs may not share food voluntarily. In a similar vein, socially more tolerant marmosets (*Callithrix jacchus*), and bonobos (*Pan paniscus*), but also less socially tolerant chimpanzees (*Pan troglodytes*) preferred to feed alone when they had the choice between feeding alone or co-feeding with a partner (Bullinger et al. 2013). Socially tolerant lion tamarins (*Leontopithecus spp.*), which share food regularly, do so often with some resistance to the begging bouts of other group members (Rapaport 2001).

In contrast, ringtailed lemurs showed a stronger ability to monopolize food than redfronted lemurs, suggesting that co-feeding might reflect social tolerance. However, our behavioural observations revealed that the two species do not differ in co-feeding rates during non-experimental feeding events. Here, co-feeding was defined as “feeding together within a 1m range”, whereas during the co-feeding experiments, food was concentrated within a 15 x 15 cm area, suggesting that the spread of food may influence resource holding potential. In semi-free ranging ringtailed lemurs, females were not able to monopolize food completely when it was distributed within a 1m radius, and even less when it was

distributed within a 2m and a 4m radius (White et al. 2007). In this experiment the resource holding potential of dominant females was lower than in our co-feeding task. Similarly, the social tolerance level in groups of chimpanzees during co-feeding tasks was mainly shaped by the presence or absence of individuals that had the motivation or ability to exclude others from a feeding site, which led to group-level variation in tolerance (Cronin et al. 2014). Thus, rates of co-feeding in close proximity may reflect different levels of social tolerance, but within species the tolerance level or the resource holding potential of dominant individuals appears to be additionally modified by monopolization potential.

During the co-feeding task more redfronted lemurs were within the arena than ringtailed lemurs. In addition the behavioural observations revealed that redfronted lemurs spent more time in proximity to each other than ringtailed lemurs. Proximity is therefore a measure of social tolerance that differed consistently between species, independent of study method. Close proximity as a measure of social tolerance can crucially influence many types of behaviour. Proximity increases for instance the amount of social learning opportunities (Coussi-Korbel and Fragaszy 1995; van Schaik et al. 1999), and therefore the spread of knowledge within a social group, which is the first step towards behavioural traditions in animals (Huffman and Hirata 2003). Also cooperation can be affected by proximity, as chimpanzees were outperformed by more tolerant bonobos in a cooperation task because dominant chimpanzees seemed to be unable to overcome their tendency to monopolize and to tolerate others in close proximity (Hare et al. 2007).

In ringtailed lemurs females were more aggressive than males, reflecting female dominance in this species (Jolly 1966; Kappeler 1990). The two species also differed in the outcome of aggression, with most conflicts being decided in ringtailed lemurs and only about half of them in redfronted lemurs during both the co-feeding task and observations. Pereira and Kappeler (1997) found the same pattern in their comparative study on captive redfronted lemurs and ringtailed lemurs. Similarly, in socially tolerant female crested macaques (*Macaca nigra*) the outcome of aggression was often undecided (Duboscq et al. 2013) and like in other Sulawesi macaques, tonkean (*M. tonkeana*) and moor macaques (*M. maura*), the majority of conflicts in crested macaques induce protest (Thierry 2007). In macaques, more tolerant species tend to show a higher number of undecided agonistic interactions than less tolerant species (stumptail monkeys (*M. arctoides*) > rhesus macaques (*M. mulatta*), de Waal and Luttrell 1989; crested macaques > Guinea baboons (*Papio papio*) >

Japanese macaques (*M. fuscata*), Petit et al. 1997; also see Thierry 2013). The outcome of aggression therefore seems to be an additional stable difference between more tolerant and less tolerant species and next to proximity a comparable measurement of social tolerance across species.

Captivity versus Wild

We did not find any difference in the number of individuals co-feeding between captive and wild groups of lemurs. It therefore seems that the baseline energy level of individuals does not influence the motivation to monopolize food in these two species. However, captive ringtailed lemurs tolerated more individuals in close proximity than in the wild, suggesting that food availability might affect social tolerance to some extent.

Ringtailed lemurs exhibit submissive signals that allow subordinate individuals to moderate socially tense situations (Pereira and Kappeler 1997). However, captive ringtailed lemurs showed higher rates of agonistic interactions as well as higher rates of submissive signalling during the experiment compared to conspecific tested in the wild. It is known that provisioned groups show increased aggression at the time of feeding especially when fed in a restricted area or with a restricted amount of food (reviewed in Asquith 1989). Submissive signals can be used to minimize the probability of agonistic interactions in competitive situations with high spatial density (Judge and de Waal 1993). However, the increase of submissive signals in captive ringtailed lemurs did not lead to a decrease of agonistic interactions and therefore ringtailed lemurs seem to be unable to reduce the risk of aggression effectively.

Conclusions

In conclusion, the combined approach of studying social tolerance in an experimental task in combination with a validation through behavioural observation indicated that proximity, co-feeding in close proximity and the outcome of aggressive interactions are useful proxies of social tolerance. Thus, the simple to implement co-feeding experiment allows standardized comparisons of social tolerance across species in captivity as well as the wild. Proximate factors, such as reduction in feeding competition in captivity, appear to have only limited effects on species-specific levels of social tolerance, but additional studies on other species

are required to better assess flexibility in traits contributing to social tolerance (Kappeler et al. 2013).

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CHAPTER 4

ON THE EFFECTS OF SOCIAL TOLERANCE ON THE SOCIAL TRANSMISSION OF NEW FORAGING SKILLS IN TWO SPECIES OF WILD LEMURS

with Claudia Fichtel

Introduction

Many animals live in stable social groups or spend at least some periods of their life in social units. One benefit of sociality is the possibility to easily gather information from conspecifics instead of learning solely (Galef and Laland 2005). Thus, social learning takes place in a structured social context, which might influence opportunities for social learning (Coussi-Korbel and Frigaszy 1995; van Schaik et al 1999). This aspect of social learning is not studied in detail yet, although it is important for understanding the ecological and evolutionary significance of social learning (Galef and Laland 2005; Lonsdorf and Bonnie 2010).

The model of social dynamics on social learning by Coussi-Korbel and Frigaszy (1995) was the first that seized the idea that social processes influence the available information that can be learned socially. They suggested that egalitarian societies allow individuals to stay in closer proximity to each other, which facilitates social learning and supports behavioural homogeneity within a social group. In despotic societies, in contrast, proximity is limited to certain dyads, like kin or friends, which potentially restricts social learning to certain pathways and supports variability of behaviour among members of a group. Behavioural homogeneity can be found therefore only on a subgroup level.

Consequently, van Schaik et al. (1999) stated in their paper on the evolution of material culture in apes that one of the four criteria that determines the propagation of information within social groups is social tolerance, next to ecological opportunities, motor dexterity and cognitive abilities. Indeed, the number of tool-use traditions in chimpanzee communities (*Pan troglodytes*) correlates strongly with a measure of social tolerance, in this case, the percentage of time spend in parties (van Schaik et al. 2003a; van Schaik and Pradhan 2003) and more contact to other individuals in a relaxed foraging context led to more tool use in orangutans (*Pongo pygmaeus*; van Schaik 2004). The positive effect of higher levels of affiliation on learning efficiency in apes was shown experimentally in a tool use task as well; few gorillas (*Gorilla* sp.) but most chimpanzees acquired the task, with chimps being the more tolerant species (Lonsdorf et al. 2009). Contrasting to the idea that tolerant societies favour social learning is the result of a comparative study on baboons (*Papio ursinus*) and vervet monkeys (*Ceropithecus aethiops*) which could find higher levels of social learning in less tolerant baboons, which the author explained through more intense social monitoring (Cambefort 1981). However, a comparison between these two species is delicate, because

they differ in many other factors as well like in diet, body size, brain size and group composition (Napier and Napier 1972).

Not only proximity can affect social learning opportunities, but also different emphasis on who to relay on for information (Coussi-Korbel and Frigaszy 1995). It is beneficial to favour individuals that are known to be reliable or more successful, which could be indicated by status in the hierarchy or age (Laland 2004). Evening bats (*Nycticeius humeralis*), for instance, which are unsuccessful in finding food, follow more successful ones to food locations (Wilkinson 1992). But also the nature of the relationship between individuals (familiarity, kinship, social affiliation) can critically affect the likelihood of observers copying the behaviour of another individual (Coussi-Korbel and Fragasuy 1995; Henrich and Gil-White 2001; Laland 2004). Laying hens (*Gallus gallus domesticus*) need more time to solve a feeding task if they are confronted with an unfamiliar individual as demonstrator (Nicol and Pope 1994). Therefore previously developed social relationships seem to influence the visual attention to others in a social learning context. Also young male ravens (*Corvus corax*) were more likely to copy the object manipulation and catching behaviour of a sibling than of a familiar non-sibling (Schwab et al. 2008). Interestingly, ravens seem to be more selective in their choice of model and attend more strongly friends, whereas cooperatively breeding jackdaws (*Corvus monedula*) are equally attentive to conspecifics (Schied et al. 2007).

However, when relaying on dominance status for evaluating success, a high status of a particular individual could also make it less likely that others would observe and/ or perform behaviour themselves because of the fear of provoking aggression (Fragaszy and Visalberghi 1990; Anderson et al. 1992; Drea and Wallen 1999). Therefore the social setting can lead to an inhibition of knowledge expression. Subdominant rhesus macaques (*Macaca mulatta*), for instance, performed a task only in a group of subdominants, but not in a group of dominants (Drea and Wallen 1999).

A higher level of social tolerance might also increase the probability for scrounging, which is exploiting food that other individuals (producers) have made available (Bugnyar and Kotrschal 2002). The effect of scrounging on social learning has been discussed controversially. On one hand scrounging was shown to facilitate social learning for instance in common marmosets (*Callithrix jacchus*; Caldwell and Whiten 2003). This facilitating effect might occur due to reduced neophobia when interacting with the experimental task

together with another individual. Additionally, scrounging allows close observation of the skill performed by the producer (Caldwell and Whiten 2003). On the other hand scrounging was also suggested to inhibit social learning, because individuals might learn to scrounge instead of learn to perform a task (Beauchamp and Kacelnik 1991). Pigeons (*Columba livia*) for instance failed to learn a novel behaviour if they were allowed to scrounge, but easily acquired the new trait if scrounging was prevented (Giraldeau and Lefebvre 1987).

Thus, more information on the effect of social tolerance levels on social learning is needed to shed light on the basic requirements for the development of traditions and therefore on the evolution of culture. In this study we conducted a social diffusion experiment (Whiten and Mesoudi 2008) to compare the speed and pattern of social transmission in two highly comparable lemur species that differ in their level of social tolerance. Social transmission is thereby defined as “cases of social learning that result in increases homogeneity of behaviour of interactants that extends beyond the period of their interaction” (Galef 1988).

We tested wild groups of rather egalitarian redfronted lemur (*Eulemur rufifrons*; Pereira et al. 1990; Ostner and Kappeler 2004) and of hierarchical organized ringtailed lemur (*Lemur catta*; Pereira and Kappeler 1997). The two species differ in their social structure, but both live in multi-male, multi-female groups (Wilson and Hanlon 2010; Kappeler and Fichtel 2012a) and have comparable body size, brain size and diet (Johnson 2007; Isler et al. 2008; Wilson and Hanlon 2010), which makes them excellent models. We also know from previous studies that both species are capable to use social learning in field settings (redfronted lemurs: Schnoell and Fichtel 2012; ringtailed lemurs: Kendal et al. 2010a) and that redfronted lemurs exhibit higher social tolerance levels than ringtailed lemurs (Chapter 3). We predicted i) a larger number of individuals acquiring the task, ii) faster learning and iii) more behavioural homogeneity within the groups in the more tolerant redfronted lemur compared to the less tolerant ringtailed lemur.

Methods

Study site and subjects

This study was conducted in two species of lemurs, in redfronted lemurs (*Eulemur rufifrons*) at the research station of the German Primate Center in Kirindy Forest, Western Madagascar, and in ringtailed lemurs (*Lemur catta*) in Berenty Private Reserve, Southern

Madagascar. The experiments on four groups of wild redfronted lemurs (group A, B, F and J) were conducted in 2011. All groups participated in other experimental studies before (Schnoell and Fichtel 2012; Pyritz et al. 2013; Schnoell et al. 2014). Three groups of wild ringtailed lemurs were tested in 2011 (group C1) and 2012 (groups C2A and YF). One group was naïve to feeding experiments (group C2A), but the other two took part in an experimental study before (group C1 and YF; Kendal et al. 2010a). All study subjects were well habituated to human presences due to long-term studies at the two sites (Kirindy Forest: Kappeler and Fichtel 2012b; Berenty Private Reserve: Jolly 1966; Koyama et al. 2005) and could be individually identified either by their unique facial coloration (ringtailed lemurs) or by nylon collars (redfronted lemurs: Kappeler and Fichtel 2012a). Group size in redfronted lemurs ranged between 4 and 11 individuals and in ringtailed lemurs between 11 and 12 individuals. A total of 34 redfronted lemurs (20 males and 14 females) and 35 ringtailed lemurs (18 males and 17 females) participated in the experiments.

Feeding boxes and experimental procedure

Study subjects were confronted with feeding boxes that could be opened by using one of two techniques (slide or lift; Figure 1a, c) to get access to the hidden reward (raisins). To successfully open the new feeding box, animals needed to make use of both hands, one hand to keep the box opened and the other hand to reach for the reward. The feeding box consisted of a wooden board as bottom part with a size of 30 cm x 20 cm x 2 cm and a wooden box as upper part which measured 15 cm x 15 cm x 10 cm. The board had a hollow carved inside, in which the reward was placed and which ensured access to the reward (Figure 1b). The wooden box had a handle attached at the front to allow better manipulation of the box (Figure 1b). When animals opened the feeding box with the lifting technique, the box would close automatically afterwards due to the weight of the upper part. However, to ensure closing when the slide technique was applied, we installed a spring at the back of the upper part that pushed the box back in place (Figure 1d).

Before we conducted the experiment, we trained demonstrators for the lifting and for the sliding technique. In both species we had two groups with trained demonstrators. For the redfronted lemurs we had an adult male (AMTho) as demonstrator for lifting (group A) and a subadult male (FMCas) as demonstrator for sliding (group F). For the ringtailed lemurs we had the dominant female (Viv) as demonstrator for lifting (group C1) and a subadult

female (Mil), the daughter of the dominant female, as demonstrator for sliding (group YF). Additionally, two more groups served as control groups in the redfronted lemurs (group B and J) and one group in the ringtailed lemurs (group C1). It was impossible to carry out the training out of sight of other group members, because individuals rarely separated from their social group. Therefore we used an approach suggested for field settings by van de Waal et al. (2010), that is, to train the demonstrator inside the social group by offering one constrained feeding box that would allow only one opening technique. Thereby, the rest of the group receives a consistent demonstration for one of the two solutions. The training phase lasted until the demonstrator conducted at least 10 successful actions per session over four days, with one session being conducted per day. A successful action consisted of opening the box and feeding on the reward. The demonstrators need 6 to 7 sessions to reach this criterion and the rest of the group thereby received at least 40 demonstrations of the opening technique before the experiment started.



Figure 1 The feeding box could be opened either by a) lifting a wooden box or c) sliding it backwards. The bottom part of the box had b) a hollow to store the reward and the upper part of the box was fixed at the back by d) a spring to ensure closing when the slide technique was used (pictures taken by AVS).

The experiment was conducted in two test blocks (test block 1 and test block 2). Each test block consisted of 10 consecutive sessions, whereby one session was conducted per day and ended after 30 minutes or if all animals left a 10-meter radius around the feeding boxes. The two test blocks were separated by a break of 4 days, except for redfronted lemur group A that had a break of 5 days in between. In test block 1 the groups were confronted with 3 feeding boxes that were placed in a row with a distance of about 1.5 meter to each other. We used one to two cameras on tripods to record all sessions. In test block 2 the groups were confronted with five feeding boxes to increase sample size by making the access possible for a bigger part of the group. We placed three boxes in the same manner than in test block 1 and added another row with two boxes in a right angle to the first row. We used two cameras (Sony HDR-XR350 and a Sony DCR-SR75E camcorder) on tripods to record all sessions.

Feeding boxes were always baited before approaching the groups to avoid the association of human observers and food. The experimental set-up was installed in some distance to the group and the animals were attracted to the test location by using an auditory signal (Chapter 3).

Video analyses and statistics

By analysing the video recordings we recorded the time and technique of each action on the box, the identity of the individual manipulating the box and whether the opener was able to feed. Preferences for a technique were only calculated for individuals that performed ≥ 6 actions. Moreover we recorded whether the individuals used the hands, the nose or a combination of hand and nose for manipulating the boxes. With this data we calculated a diversity score, by looking for each individual separately how much variety they showed in their manipulation behaviour (for instance: hand + nose + hand and nose = diversity score of 3; hand + nose = diversity score of 2). The diversity score ranged from 1 to 3. Additionally, we noted down occurrences of scrounging events, identity of the scrounger and identity of the producer. A scrounging event was defined as an individual, the scrounger, entering a feeding box that was already opened by another individual, the producer.

To assess whether a higher proportion of individuals managed to learn the experimental task in the redfronted or the ringtailed lemurs we used a Generalized Linear Model (*GLM*) with the proportion of learners to non-learners per group as response variable

and species as fixed factor. The proportion of learners to non-learners was weighted differently in the model due to different group sizes.

We calculated a non-parametric two-tailed correlation analysis to determine if the social tolerance value of a group correlates with the number of trials that individuals needed until their first success. As social tolerance value we used the average number of individuals within close proximity (within an experimental arena) in a co-feeding task per social group (Chapter 3). In this co-feeding task, groups were confronted with a clumped food resource within an experimental arena and the average number of individuals that were allowed to stay within the arena was assessed.

To compare whether the two species differed in the number of unsuccessful actions until the first success we used a Mann-Whitney U test. We conducted additional Mann-Whitney U tests to investigate if there is a species difference in the diversity scores as well as to compare the scores between learners and non-learners. Individual preferences for an opening technique were tested by binomial tests.

We used a Generalized Linear Mixed Models (*GLMM*) to assess if the approach rate affects the probability of learning, by using learning (yes, no) as dependent variable, approach rate as well as the interaction between approach rate and species as fixed factors and group identity as random factor. We conducted another *GLMM* to test if the strength of social bonds between dyads of individuals affects the learning probability, again by using learning (yes, no) as dependent variable, social bond as well as the interaction between social bond and species as fixed factors and group identity as random factor. As an approximation for the strength of social bonds, grooming rates were utilized. Grooming data were collected by using continuous focal sampling and was defined as licking with tongue and stroking with the tooth comb though the fur of another animals (modified after Pereira and Kappeler 1997; for a more detailed description of the observation protocol see Chapter 3). This behaviour presents an active affiliative behaviour and was therefore chosen as representation of social bond.

To investigate the effect of the presence of a trained demonstrator we looked whether the proportion of group members interacting with the boxes differed between groups with a demonstrator and those without a demonstrator by using a Linear Mixed Model (*LMM*) with the square-root transformed percentage of individuals in contact per session as dependent variable, species and training (yes, no) as fixed factors and group

identity as random factor. Another *LMM* was calculated to assess if the amount of scrounging events differed between the species by using the square-root transformed number of scrounging events per scrounger-producer dyad as dependent variable, species as fixed factor and group identity as random factor.

We used a proportion test to look for a difference in kin bias in scrounging between the two species. Kinship was thereby defined as maternal kin until a coefficient of relatedness of 0.25.

The *GLMMs*, the *LMMs*, the *GLM* as well as the proportion test were calculated in R (R Development Core Team 2010). The models were fitted using the R package lme4 (Bates and Maechler 2010). The full model was compared to the null model by using a likelihood ratio test (Anova function with argument test set to “ χ^2 ”). We used the Markov Chain Monte Carlo sampling (Baayen 2008) to get *P* values for the individual effects. The correlation analysis, the binomial tests and the Mann-Whitney *U* tests were conducted in IBM SPSS 21 (SPSS Inc., Chicago, IL, USA).

Option bias diffusion analysis and network based diffusion analysis

We also conducted an option-bias diffusion analysis (*OBDA*; Kendal et al. 2009) and a network based diffusion analysis (*NBDA*; Franz and Nunn 2009; Hoppitt and Laland 2013: 105-127) to test for social learning in the task.

The *OBDA* is based on the idea that social learning will lead to a high homogeneity in the behaviour of a group. The analysis detects social learning by comparing the observed behavioural homogeneity to a sampling distribution that is generated by randomisation and other procedures. It requires the total number of actions performed by each individual as well as the number of “lifting” actions and the number of “sliding” actions. We included successful as well as unsuccessful actions into the analysis to increase the sample size.

The *NBDA* tests for social learning by taking into account that a social network offers different social learning opportunities for different dyads of individuals. The analysis detects social learning if the order (*OADA* version = order of acquisition diffusion analysis) or the time (*TADA* version = time of acquisition diffusion analysis) at which individuals learn a task matches the connections of a social network. For this study, we used the *TADA* version of the analysis and affiliative behaviour (grooming rates) as a proxy for learning opportunities. We applied the extended version of the *NBDA* (*eNBDA*), which predicts that is rather unlikely

that individuals under natural conditions will learn by social learning alone. It therefore compares the fit of a model of social and asocial learning as well as of a model of pure asocial learning to the data. We selected the best model based on the Akaike information criterion (*AIC*). Calculations were conducted with R (R Development Core Team 2010).

Results

Proportion of learners and speed of learning

A higher proportion of individuals solved the task in groups of redfronted lemurs (mean \pm SD: $47.0 \pm 20.93\%$; $N_{\text{total}} = 34$ individuals) than in the ringtailed lemurs ($28.3 \pm 4.16\%$; $N_{\text{total}} = 35$; Figure 2 and Table 1a; GLM: $Df = -1$; $N = 5$ groups, $P = 0.01$).

Additionally, redfronted lemurs needed less unsuccessful actions until the first success (0.07 ± 0.27 unsuccessful actions) than ringtailed lemurs (1.6 ± 2.07 unsuccessful actions; Figure 3; Mann-Whitney U test: $Z = -2.816$, $N_1 = 14$ individuals, $N_2 = 10$ individuals, $P = 0.02$). Learning success was negatively correlated with the social tolerance value, with individuals in more tolerant social groups needing less unsuccessful actions until the first success (Figure 4; Spearman rho: $\rho = -0.460$, $N = 24$ individuals, $P = 0.02$).

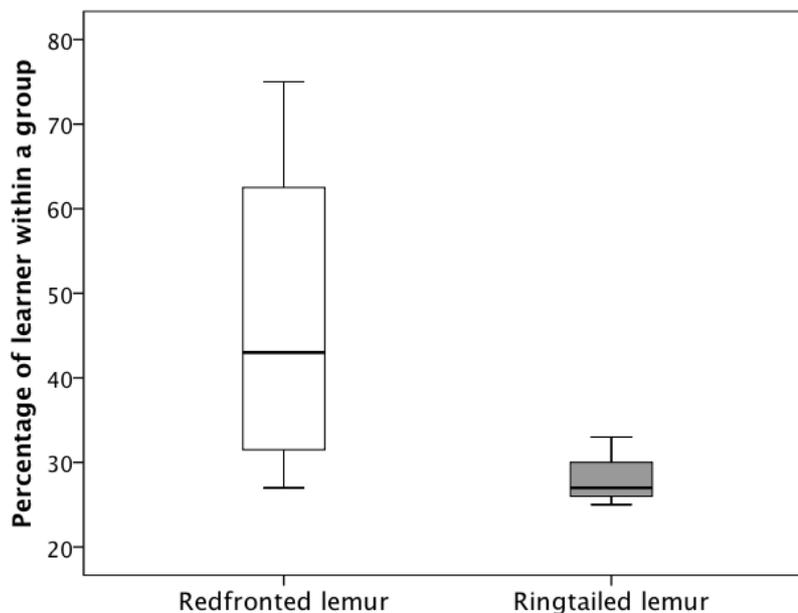


Figure 2 A higher proportion of group members learned an experimental task in redfronted lemurs ($N = 4$ groups) than in ringtailed lemurs ($N = 3$ groups).

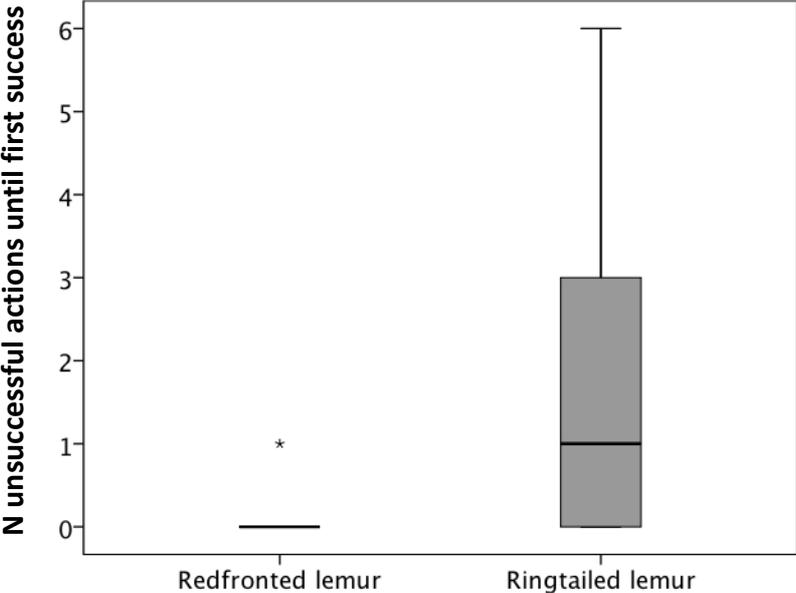


Figure 3 Redfronted lemurs ($N = 14$ individuals) needed less unsuccessful actions to solve an experimental task for the first time than ringtailed lemurs ($N = 10$ individuals).

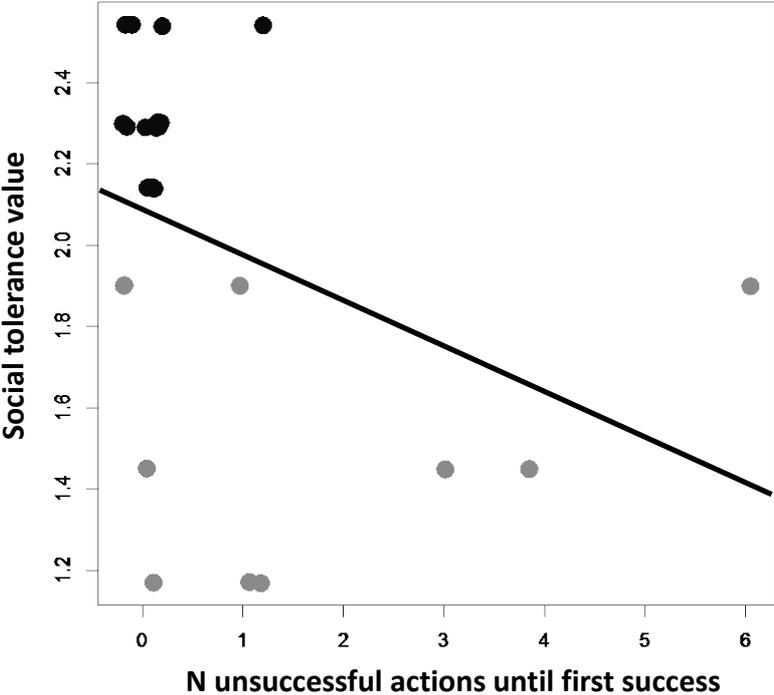


Figure 4 Individuals in a group with a higher level of social tolerance (= average number of individuals in close proximity in a co-feeding task) showed a higher learning efficiency than those in groups with a lower level ($N = 24$ individuals; *black dots* = redfronted lemurs, *grey dots* = ringtailed lemurs).

Table 1 Parameters estimated for the Generalized Linear Models (*GLM*), Generalized Linear Mixed Models (*GLMM*) and Linear Mixed Models (*LMM*) a) on the difference in the proportion of learners within groups, b) on the influence of contact rates and c) social bonds on the learning probability, d) on the effect of the presence of a trained demonstrator on the percentage of individuals in contact with the feeding boxes and d) on the number of scrounging events between the two species (*NS* = not significant).

	Model	Response variable	Random factors	Fixed factors	Estimate	SE	<i>P</i> -value
<i>a</i>	<i>GLM</i>	Proportion learners to non-learners		Intercept	-0.51	0.12	<0.001
				Species	-0.41	0.16	0.01
<i>b</i>	<i>GLMM</i>	Learning (yes, no)	Group identity	Intercept	-2.14	0.68	0.001
				Approach rate (AR)	4.11	2.04	0.01
				AR:species	-2.32	1.77	NS
<i>c</i>	<i>GLMM</i>	Learning (yes, no)	Group identity	Intercept	-1.18	0.45	0.001
				Social bond	0.03	0.04	NS
				Social bond:species	0.08	0.06	NS
<i>d</i>	<i>LMM</i>	% individuals in contact per session	Group identity	Intercept	0.97	0.05	<0.001
				Training (yes, no)	-0.24	0.07	<0.001
				Species	-0.07	0.07	NS
<i>e</i>	<i>LMM</i>	Number of scrounging events	Group identity	Intercept	0.00	0.00	NS
				Species	0.00	0.00	NS

Table 2 Preferences in the opening technique for all learners (Species: *ER* = *Eulemur rufifrons*, *LC* = *Lemur catta*; age: *adult* > 2.5 years; *juvenile* < 2.5 years; *P* value of the binomial test; n.v. = individuals did not conduct ≥ 6 actions).

Species	Group Condition	Identity	Sex	Age	Learning session	<i>N</i> actions	% Lift actions	Preference	<i>P</i> value
ER	Lift (A)	AFCor	female	adult	1	389	97.7	Lift	<0.01
ER	Lift (A)	AMSky	male	adult	9	4	75.0		n.v.
ER	Lift (A)	AMVid	male	adult	17	7	14.3	None	0.13
ER	Slide (F)	FMTri	male	adult	1	143	7.7	Slide	<0.01
ER	Slide (F)	AFAng	female	juvenil	12	2	0.0		n.v.
ER	Slide (F)	AFLuc	female	adult	14	2	100.0		n.v.
ER	Slide (F)	AFMont	female	adult	15	1	0.0		n.v.
ER	Open (B)	BMMyk	male	adult	2	599	94.7	Lift	<0.01
ER	Open (B)	BFBor	female	adult	5	289	88.9	Lift	<0.01
ER	Open (B)	BMGor	male	adult	6	94	59.6	None	0.08
ER	Open (J)	JFGeo	female	adult	1	437	90.2	Lift	<0.01
ER	Open (J)	JMKaz	male	adult	7	75	64.0	Lift	0.02
ER	Open (J)	JFCol	female	juvenil	8	123	98.4	Lift	<0.01
ER	Open (J)	JFMal	female	adult	11	68	57.4	None	0.28
LC	Lift (C1)	Fran	female	adult	1	26	92.3	Lift	<0.01
LC	Lift (C1)	Pri	female	adult	13	4	50.0		n.v.
LC	Lift (C1)	Aku	male	adult	13	3	100.0		n.v.
LC	Slide (YF)	Dav	male	juvenil	6	578	99.8	Lift	<0.01
LC	Slide (YF)	Fal	female	adult	9	187	97.8	Lift	<0.01
LC	Slide (YF)	Lol	female	adult	11	6	100.0	Lift	<0.01
LC	Slide (YF)	Lah	female	juvenil	13	12	58.3	None	0.77
LC	Open (C2A)	Sam	male	adult	1	1033	98.8	Lift	<0.01
LC	Open (C2A)	Bob	male	adult	3	39	94.9	Lift	<0.01
LC	Open (C2A)	Mar	male	adult	7	655	92.2	Lift	<0.01

Homogeneity of transmission

Concerning the homogeneity of the spread, we find in both species that those individuals that got in contact with the demonstrator more often had a higher probability of learning (frequency of approaches: redfronted lemurs: learners = 0.34 ± 0.31 , non-learners = 0.24 ± 0.16 ; ringtailed lemurs: learners = 1.76 ± 0.99 , non-learners = 0.54 ± 0.38 ; Table 1c; *GLMM*: $\chi^2 = 10.324$, $Df = 2$, $N = 41$ individuals, $P = 0.01$).

However, the strength of the social bond between the demonstrator and other group members did not affect the probability of learning neither in redfronted lemurs (learners = 8.06 ± 11.56 , non-learners = 8.49 ± 11.22) nor in ringtailed lemurs (learners = 15.23 ± 17.47 , non-learners = 3.11 ± 4.61 ; Table 1b; *GLMM*: $\chi^2 = 5.855$, $Df = 2$, $N = 41$ individuals, $P = 0.05$).

Learning mechanism

All demonstrators showed high preferences for the trained technique throughout the experiment (redfronted lemurs: lifting (AMTho) = 95.6% lifting actions, binomial test: $N = 541$ actions, $P < 0.001$; sliding (FMCas) = 73.1% sliding actions, binomial test: $N = 141$ actions, $P < 0.001$; ringtailed lemurs: lifting (Viv) = 99.0% lifting actions, binomial test: $N = 1651$ actions, $P < 0.001$; sliding (Mil) = 99.1% sliding actions, binomial test: $N = 903$ actions, $P < 0.001$). If animals use imitation as social learning mechanism, we would predict that the learner would predominantly use the same technique than the demonstrator. We do not find this pattern in the low number of learners in our experiment (Table 2). However, all learners in the control groups exhibited a preference for lifting (Table 2; redfronted lemurs: 5 x lift preferences, 2 x no preference; ringtailed lemurs: 3 x lift preference) and therefore it seems that lifting was overall the easier technique.

To test for social learning in general, we applied the option-bias diffusion analysis to our data set. The analyses did not reveal any evidence that social learning was involved in the learning of this task neither in the ringtailed lemurs (*Option bias*, $P = 0.75$) nor in the redfronted lemurs (*Option bias*, $P = 0.81$).

We additionally conducted the network based diffusion analysis. We first calculated social networks for each study group (Appendix: Figures 1 to 7) and then used the extended version of the analysis, which compares an asocial learning model to an asocial and social learning model. The analysis detected a better fit of the asocial and social model than the asocial model for one of the study groups, namely the sliding group of the ringtailed lemurs

(Table 3). In contrast, for the open group and the lifting group in the ringtailed lemurs as well as the open group J in the redfronted lemurs, the analysis showed a better fit of the asocial model than the asocial and social model (Table 3). For the additional three study groups, the analysis could not detect a better fit of one model over the other one (Table 3).

Table 3 Results of the extended network-biased analysis (*eNBDA*).

Species	Condition	Asocial model		Social and asocial model	
		<i>AIC</i>	Akaike probability (%)	<i>AIC</i>	Akaike probability (%)
<i>ER</i>	Lift	31.25	38.12	30.28	61.88
<i>ER</i>	Slide	37.85	72.92	39.83	27.08
<i>ER</i>	Open B	13.78	50.38	13.81	49.62
<i>ER</i>	Open J*	26.12	73.11	28.12	26.89
<i>LC</i>	Lift*	29.96	73.11	31.96	26.89
<i>LC</i>	Slide*	37.73	7.10	32.58	92.90
<i>LC</i>	Open*	19.67	73.11	21.67	26.89

* indicates a better fit of one model over the other one

We predict that individuals that learn socially would show less diverse exploration behaviour in interaction with the feeding boxes. Redfronted lemurs had less diverse contacts with the feeding boxes than ringtailed lemurs (Mann-Whitney *U* test: $Z = -3.868$, $N_1 = 28$ individuals, $N_2 = 31$ individuals, $P < 0.001$). Ringtailed lemurs used their nose ($54.42 \pm 35.55\%$), their hands ($35.39 \pm 36.06\%$) or a combination of hands and nose ($27.39 \pm 26.04\%$) to interact with the boxes and therefore had a mean diversity score of 2.42 ± 0.72 . Redfronted lemurs, in contrast, mainly used their noses ($91.25 \pm 10.6\%$) and rarely hand as well as nose ($8.68 \pm 10.45\%$) or hands alone ($0.11 \pm 0.42\%$) and had a mean diversity score of 1.64 ± 0.62 . However, a higher diversity of contact seems to influence the learning probability in redfronted lemurs positively, with learners exhibiting higher diversity scores (2.07 ± 0.47) than non-learners (1.21 ± 0.43 ; Mann-Whitney *U* test: $Z = -3.757$, $N_1 = 14$ individuals, $N_2 = 14$ individuals, $P < 0.001$). This pattern was absent in ringtailed lemurs (learner = 2.43 ± 0.79 , non-learner = 2.83 ± 0.39 ; Mann-Whitney *U* test: $Z = -0.425$, $N_1 = 21$ individuals, $N_2 = 10$ individuals, $P = 0.72$).

A higher percentage of group members were in contact with the feeding boxes in the untrained groups compared to the trained ones during the experiment (Figure 5, Table 1b; *LMM*: $\chi^2 = 10.345$, $Df = 2$, $N = 7$ groups, $P = 0.001$). Therefore the presence of a demonstrator seems to inhibit others group members to get in contact with the feeding boxes.

Both species did not differ in the amount of scrounging events (redfronted lemur = 452 scrounging events, ringtailed lemurs = 91 scrounging events; Table 1c; *LMM*: $\chi^2 = 1.9718$, $Df = 1$, $N = 7$ groups, $P > 0.05$). However, ringtailed lemurs scrounged mainly at their kin ($0.73 \pm 0.24\%$), which we predicted them to do with their lower level of social tolerance, whereas redfronted lemurs only chose kin as producers in $0.28 \pm 0.33\%$ of scrounging events (Proportion test: $\chi^2 = 28.2613$, $Df = 1$, $P < 0.001$).

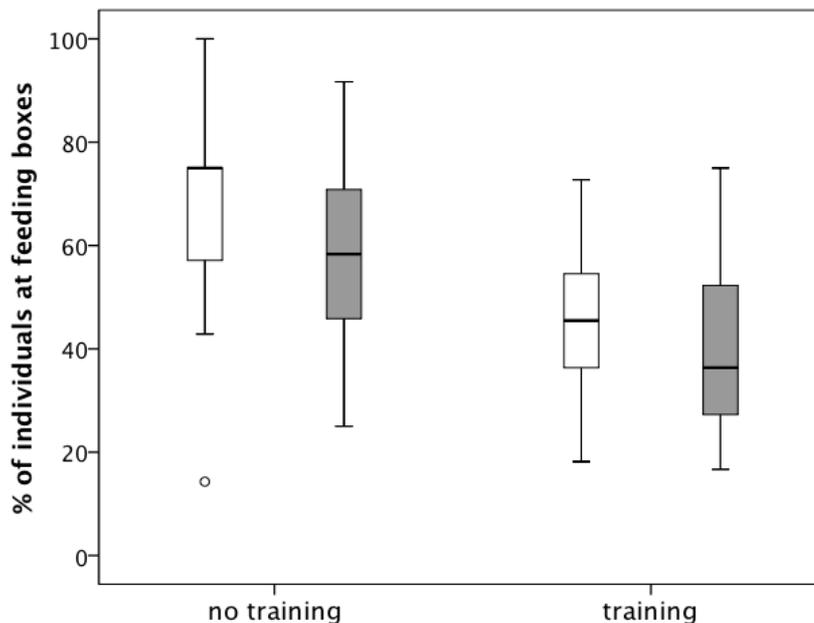


Figure 5 The percentage of individuals in contact with the feeding boxes differed between groups without training and with training (*white* = redfronted lemurs, *grey* = ringtailed lemurs).

Discussion

We presented two-option feeding boxes in the same set-up to two species of lemurs in combination with or without a demonstrator. We investigated whether these two species, which differ in their social tolerance level, would also differ in their learning behaviour. We asked whether the new behaviours would spread further, more homogeneously and quicker in the more tolerant species compared to the less tolerant species. Finally, we applied two statistical methods to test if social learning was at work in the transmission process.

Our study provides evidence that social tolerance indeed affects learning in a group setting. A higher proportion of individuals managed to learn the task in redfronted lemur, the more tolerant species, than in ringtailed lemurs, the less tolerant species. Additionally, learners in the redfronted lemurs exhibited higher learning efficiencies. We also find a general correlation between social tolerance and learning efficiency. Our social tolerance value represents a measurement of close proximity. Therefore, the reason for the observed pattern might be that individuals in a more tolerant environment have more opportunities to observe the demonstrator as well as the experimental set-up in greater detail. Another result that fits to this prediction is that we find higher diversity scores in ringtailed lemurs compared to redfronted lemurs, which could hint in the direction that individuals in less tolerant settings gather less information socially and therefore still have to explore individually in a more diverse way.

The model on the influence of social dynamics on social learning suggests a more homogeneous transmission of new information within groups in tolerant societies compared to less tolerant ones (Coussi-Korbél and Fragaszy 1995). In less tolerant species, behaviour is expected to spread in subgroups, because individuals are not likely to be close to and to observe all group members in the same probability. The transmission might be affected by factors like kinship (for instance: Schwab et al. 2008), dominance hierarchies (for instance: Pongrácz et al. 2008) and affiliative relationships (for instance: Bonnie and de Waal 2006). In our experiment, homogeneity in the spread of the behaviour in both species was affected by the frequency with which two individuals were in contact, but not by the social bond between dyads. Therefore, proximity in general seems to be the driving factor and not only proximity in the affiliative context. A possible reason for this result is that individuals might not observe others much, if they are already involved in another behaviour, in this case, in grooming. Interestingly, in chimpanzees the propagation of handclasp grooming, a unique

social custom, in a captive population was promoted by affiliative ties, but the study additionally found an even bigger effect of close proximity between dyads on the spread of the new behaviour (Bonnie and de Waal 2006).

This experiment was not primarily designed to determine the exact learning mechanism. However, by applying two statistical methods, we find only weak evidence for social transmission. The network based diffusion analysis detected social learning only in one of our seven study groups, namely the sliding group in ringtailed lemurs. Interestingly though, in the rest of the ringtailed lemur groups and in one of the redfronted lemur groups it suggests individual learning. The *NBDA* probably managed to detect social transmission in this one ringtailed lemur group, but failed to do so completely in the redfronted lemurs, because of the different social structures. It might be easier for the analysis to find evidence for social learning in hierarchical structured groups with stronger differences between social relationships than in rather egalitarian societies (Schnoell and Fichtel 2012).

The option-bias method could not detect social transmission. However, this method looks at behavioural homogeneity within a group and most individuals in our experiment, independent of the condition to which their group was signed to, preferred one of the techniques over the other one. Therefore, the generally high homogeneity that we observed during the experiment was most likely not cause by social learning, but probably by a difference in the difficulty of the two opening techniques.

Although we only have a small number of learners, it does not seem that individuals learned the technique of the demonstrator. A similar pattern was found in neotropical caracaras (*Milvago chimango*; Biondi et al. 2010); some observer birds also used different techniques than the demonstrator to reach the reward in an experimental task. It is therefore rather unlikely that contextual imitation was involved in the learning. Contextual imitation is defined as the increase in likelihood of an observer to perform an action in a specific context after observing the demonstrator performing the action in similar context (Hoppitt and Laland 2013: pp 71-72).

Instead of learning the exact technique of the demonstrator, the animals in our study seem to rather have learned that the box could be opened and contains food. Therefore, the possible underlying social learning mechanisms might be either observational conditioning or emulation. Individuals might form an association between the feeding boxes and the food by observing others manipulating the boxes, which might motivate them to find a way to get

to the reward as well. In this case observational conditioning would be at work (Hoppitt and Laland 2013: pp 68-69). Emulation, in contrast, describes the phenomenon that an observer will become more likely to perform any action leading to the same effect on an object, after having observed a demonstrator interacting with this object (Hoppitt and Laland 2013: pp 77-78). Examples for social transmission via observational conditioning are, for instance, all cases in which individuals learn where to find food by observing other individuals foraging. One example is that Burmese red junglefowls (*Gallus gallus spadecius*) are more likely to feed at the same type of feeding dishes at which they had observed the foraging of conspecifics (McQuoid and Galef 1993).

Interestingly, the presence of a demonstrator in a group had a negative effect on the participation of other group members. This result is rather striking, as one would predict that seeing a knowledgeable individual feeding on a high value food source would increase the attention of others towards the experimental set-up. However, maybe the demonstrator monopolized the feeding boxes. In tolerant redfronted lemurs, for instance, some individuals were able to exclude others aggressively from interacting with an experimental set up in a previous study (Schnoell and Fichtel 2012). Another possible explanation is that the demonstrator emptied the boxes so quickly that other individuals had little motivation to interact with the set-up.

In canaries (*Serinus cararia*) it has been shown that the most innovative individuals are not always good demonstrators (Cadieu et al. 2010). In our study we could not choose our demonstrators. Instead those individuals became demonstrators that were the most motivated ones and managed to monopolize a single feeding box during training. For the tolerant species, we had two males as demonstrators, a young male and an older central male, whereas in the less tolerant species, two female served as models, the dominant female and a young female, the daughter of the dominate female. Because of the diverse feature of the demonstrators that differed in age, sex and dominance status, it is difficult to predict what discouraged others to learn in more detail. We know from previous studies that for instance dominance can hamper the performance of learned behaviours by less dominant individuals (Drea and Wallen 1999). However, in Japanese macaques, dominant individuals tended to spread new behaviours (Kawai 1965).

Both species used scrounging as an alternative tactic to get access to the rewards, instead of opening the feeding box by themselves. Maybe the possibility to scrounge

facilitated individual learning: scrounging probably makes it easier for individuals to find the right solution, like it was shown for ravens (*Corvus corax*; Fritz and Kotrschal 1999) and for marmosets (Caldwell and Whiten 2003). In this study, both species showed the same scrounging frequency, but redfronted lemurs were able to scrounge from a bigger variety of group members, because they did not differentiate as much between kin and non-kin than ringtailed lemurs did, which might have facilitated learning as well. In guppies (*Poecilia reticulata*) it has been shown for instance that a higher number of demonstrators increases the probability that a behaviour is acquired (Sugita 1980; Laland and Williams 1997).

In conclusion, we presented the first comparative study on the effects of social tolerance on learning behaviour. High levels of social tolerance seem to result in further and a more homogenous spread of new behaviours as well as increased speed of learning, probably caused by a higher number of learning opportunities due to closer proximity between individuals in tolerant groups.

CHAPTER 5

HUMAN-INTRODUCED LONG-TERM TRADITIONS IN WILD REDFRONTED LEMURS?

with Marie T. Dittmann and Claudia Fichtel

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Abstract

Behavioural traditions have only been described for a small subset of species, and the factors responsible for the maintenance of traditions over time are unclear. Redfronted lemurs are known to learn socially but traditions have not been described in the wild. We conducted a social diffusion experiment over three experimental years with artificial feeding boxes that could be opened in two different ways (pushing or pulling a door). Six out of 14 individuals that participated in at least two years exhibited a stable preference: five lemurs maintained a pull and one lemur a push preference, suggesting that habit formation and reinforcement learning may have led to preferences over time. The remaining individuals exhibited fluctuating preferences and switched between showing a preference or no preference, but never switched between preferences. This instability might have been due to the low level of difficulty and/or the low object specificity of the task. The majority of lemurs additionally scrounged. Scrounging was not influenced by age, sex or success in manipulating the boxes. Thus, redfronted lemurs appear to use the two techniques flexibly but also scrounged opportunistically to get access to the rewards, indicating that traditions might be stabilized by multiple factors.

Keywords: Stability of traditions; Social learning; Scrounging, Long-term study; Wild lemurs; *Eulemur rufifrons*;

Introduction

Decades of experimental work, conducted in captivity as well as in the field, revealed that many animals are able to learn socially or that they at least possess the ability to use the social information provided by other individuals in the learning process (Reader and Hager 2011). Many species ranging from insects to mammals, including solitary reptiles (Wilkinson et al. 2010), are able to learn socially (Galef and Laland 2005; Leaderbeater and Chittka 2007; Laland et al. 2012). Although social learning seems to be widely spread in the animal kingdom, behavioural traditions have been documented in only a small subset of species. A tradition is a “distinctive behaviour pattern shared by two or more individuals in a social unit, which persists over time and that new practitioners acquire in part through socially aided learning” (Fragaszy and Perry 2003). Traditions have been documented in the wild in primates (Kawai 1965; Whiten et al. 1999; Perry et al. 2003; van Schaik et al. 2003b; Perry 2009; Santorelli et al. 2011), cetaceans (Rendell and Whitehead 2001; Krützen et al. 2005) and other mammals (Thornton et al. 2010), birds (Hunt and Gray 2003; Berg et al. 2012) and fish (Helfman and Schultz 1984; Warner 1988).

Traditions are classified as one of the three different stages of diffusion of new behavioural pattern within groups (Huffman and Quiatt 1986; Huffman and Hirata 2003): The first stage of diffusion is social transmission. It is an incident of social learning that leads to the diffusion of a new behaviour within groups. Traditions represent the second stage, in which the behaviour has already spread and further diffusion at this stage is mainly constrained by birth rates. The third and last stage that can follow is the one of transformation, in which the behaviour gets modified in some way, to make it, for example, more efficient. Several factors have been suggested to promote and maintain traditions over time. Behavioural patterns might be more persistent if switching between alternative behaviours is not beneficial (Thornton and Clutton-Brock 2011). For example, the stability of foraging traditions is favoured when exploration of novel food items is linked to the risk of eating incompatible and/or poisonous food, or when searching new feeding routes increases the risk of predation by leaving the safety of the social group (Thornton and Clutton-Brock 2011). However, if an already acquired technique is more costly than an alternative technique, and if the difference of costs between the two techniques exceeds a certain threshold, animals might benefit from switching between behaviours (Thornton and Clutton-Brock 2011). Costs in the form of extensive time and effort, which individuals have to invest

to acquire a certain skill can also influence the stability of foraging traditions; if the skill is difficult and time-consuming to obtain, it might be beneficial to maintain it, even if the alternative technique could be as rewarding (Thornton and Clutton-Brock 2011). Moreover, additional costs caused by conspecifics via scrounging, that is, getting access to a reward by taking advantage of the actions of other individuals, may also promote the instability of foraging traditions. Scrounging is a behaviour that might impose costs on the victims because they alone have to invest energy to obtain a reward, but then have to share it with others (McCormack et al. 2007).

High levels of individual conservatism, that is, the tendency to keep a once learned technique over time, seem to favour the stability of behavioural patterns or traditions because the behaviours can simply become habitual (Marshall-Pescini and Whiten 2008). A response habit is defined as an action that gets repeated by an animal because it was rewarded in the past (Pesendorfer et al. 2009; Crast et al. 2010). It has been suggested to be the stabilizing mechanism of the formation of a tradition in a long-term study in captive capuchins (*Cebus apella*: Crast et al. 2010) and in a short-term study of wild common marmosets (*Callithrix jacchus*: Pesendorfer et al. 2009).

The lack of social learning mechanisms that allow copying others in high fidelity, such as imitation, have been suggested to negatively influence the stability of traditions (Tomasello 1994). However, up to this date, imitation has been shown to be important for the propagation of behaviours only in captive animals (Whiten et al. 2004). Moreover, local enhancement has been suggested to be the dominant mechanism for the generation and maintenance of traditions in wild chimpanzees (*Pan troglodytes*: Inoue-Nakamura and Matsuzawa 1997) suggesting that a high level of fidelity in the copying might not be necessary for the stability of animal traditions (Caldwell and Millen 2009; Cladière and Sperber 2010).

Conformity, that is, the copying of the choice or behaviour of others even if the alternative is equally beneficial (Boyd and Richerdson 1985; Giraldeau et al. 2002), leads to higher homogeneity within groups or subgroups and therefore can have a stabilizing effect on traditions (Cladière and Sperber 2010). Conformity was proposed to explain the development of group preferences in an experiment in captive chimpanzees (Whiten et al. 2005). However, the rewarding character of behavioural traditions might be more crucial for the maintenance of traditions than the mechanism of diffusion (Galef 1995; Matthews et al.

2010). In fact, most of the behavioural traditions described for wild populations are rewarding, for instance the satisfaction of reaching and eating a food item (milk bottle opening in British tits (*Parus major*): Hinde and Fisher 1951; use of anvil and stone pounding tools in capuchins: Fragaszy et al. 2004) or the relief felt by eliminating parasites (leaf swallowing in chimpanzees: Huffman and Hirata 2004).

Although longevity of a behavioural variant is an important feature for a tradition (Whiten and van Schaik 2007), most experimental studies focused on the first stage of diffusion and examined whether different species are either able to learn socially, or whether the behaviour is transmitted within groups and/or how group preferences can develop. So far, only few experimental studies investigated the longevity of human-introduced traditions in animals (Cladière and Sperber 2010). For example, captive capuchin monkeys maintained a preference for a particular technique to open an artificial feeding box over two years (Craet et al. 2010), and wild vervet monkeys (*Chlorocebus aethiops*) maintained experimentally introduced food cleaning preferences over more than one year (van de Waal et al. 2012). In contrast, meerkats (*Suricata suricatta*), that initially shared the demonstrator's preference to forage at one of the two land marks, did not maintain this preference over time and soon fed on both land marks equally often (Thornton and Malapert 2009). The inconsistency in these findings emphasises the importance to study the development of human-introduced traditions on a more longitudinal scale, because observed patterns during a short-term study can diminish over time.

Although arbitrary traditions have been shown to persist in captive groups of animals (Craet et al. 2010), it is unclear whether they do so in the wild where nutrition is limited, where average proximity between group members is probably lower and the risk of predation might be higher (Thornton and Clutton-Brock 2011). We therefore studied the longevity of human-introduced behavioural patterns in four social groups of wild redfronted lemurs (*Eulemur rufifrons*). This species is a suitable model as it exhibits a rather egalitarian social structure (Pereira et al. 1990; Pereira and Kappeler 1997; Ostner and Kappeler 2004), suitable for social learning (Coussi-Korbel and Fragaszy 1995). Moreover, it has been demonstrated that lemurs use socially aided learning in captive and wild settings (reviewed in Fichtel and Kappeler 2010; Kendal et al. 2010a; Fichtel and Kappeler 2011; Stoinski et al. 2011). In a previous study, we introduced an artificial feeding box that could be opened by two different techniques and showed that redfronted lemurs use social information to learn

the feeding techniques and that individuals appeared to develop a group preference for one technique (Schnoell and Fichtel 2012). To examine whether redfronted lemurs maintain their individual and/or group preferences over time, we repeated these experiments over a period of three years, thereby gathering information on individual and group preferences for feeding techniques.

Methods

Study site and subjects

Experiments were conducted at the research station of the German Primate Center in Kirindy Forest, Western Madagascar (Kappeler and Fichtel 2012b). Study subjects were 42 redfronted lemurs (*Eulemur rufifrons*): 26 males and 16 females from four social groups (A, B, F and J). All subjects were individually marked with nylon collars and were well habituated to human presence (Kappeler and Fichtel 2012a, b). Experiments with feeding boxes were conducted in three consecutive years with 37 individuals in September – December 2009, with 40 individuals in August 2010 and with 32 individuals in May 2011 (Table 1). Four males switched between groups during the study period (MRot from group B to J, MNeg from B to A, MMyk from A to B and MGor from A to B).

Table 1 Number of participating individuals (≥ 3 task manipulations) and overall group size per study group and experimental year (*year 1 = 2009, year 2 = 2010, year 3 = 2011*).

Years	Group A			Group B			Group F			Group J		
	1	2	3	1	2	3	1	2	3	1	2	3
<i>N</i> participants	3	4	4	6	3	4	4	4	6	6	5	6
Group size	12	13	10	8	8	5	9	11	11	8	8	6

Experimental setup and procedure

We presented redfronted lemurs wooden feeding boxes (Schnoell and Fichtel 2012; with a size of 16 x 20 x 20 cm; Figure 1) that could either be opened by pulling or by pushing a semi-transparent door to get access to a food reward (several small pieces of orange or mango) inside the box. Feeding boxes were placed on an open spot on the forest floor to enable videotaping of all actions at the boxes. The experiment started when the first individual

entered a 1-m radius around a box and ended either when the whole group left a 10-m radius around the boxes (for more detailed description see: Schnoell and Fichtel 2012) or after a maximum of 30 min (in 2010 and 2011). Each group was usually tested once a day between 07:00 and 17:00 h, and occasionally, groups were tested every second day or twice a day.

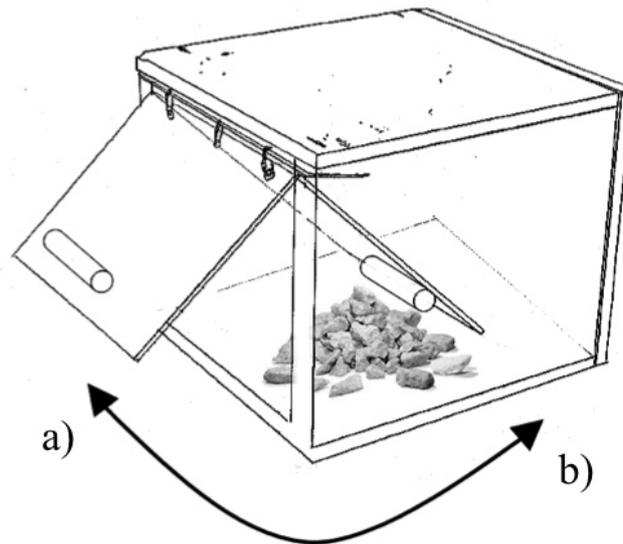


Figure 1 Experimental apparatus: the feeding box could be opened by either a) pulling or b) pushing a door to extract the reward from inside (artwork by AVS).

In the first year of the experiments (2009), two study groups (A and J) received training for one of the two opening techniques by constraining the box to a single functioning method over 7 – 10 sessions (group A: pulling; group J: pushing). Afterwards, they were confronted with unconstrained boxes in four additional test sessions. The two other study groups (B and F) did not receive any training and were tested with the unconstrained boxes over 14 sessions (Schnoell and Fichtel 2012). Preferences for one or the other technique were only determined for the last four sessions, during which all groups were confronted with unconstrained boxes.

In the second (2010) and third year (2011), we tested the four study groups with the same unconstrained feeding boxes in 12 – 14 sessions in 2010 (group A, B and J: 12 sessions; group F: 14 sessions) and 14 sessions in 2011. To increase the number of participating individuals, we presented redfronted lemurs in 2011 in the first 5 sessions with 3 boxes and

in the following 7 sessions with 6 boxes.

The interval between the end of the first experiment and the beginning of the second experiment was 36 weeks (252 days) in 2009 – 2010 and 35 weeks (247 days) in 2010 –2011.

Data Analyses

We analysed the number of successful as well as unsuccessful task manipulations and the technique used for each task manipulation from video recordings. Successful task manipulations were defined as moving the door and retrieving a reward, whereas an unsuccessful task manipulation was defined as moving the door but not gaining a reward. To compare the numbers of unsuccessful manipulations before the first successful manipulation over time, we included all individuals that managed to succeed in at least two years, regardless of how many actions they performed in total per year. Additionally, we recorded all scrounging events, that is, gaining access to the rewards by entering the feeding box which had been opened by another individual (the producer). We excluded events in which the producer left the box and a third individual scrounged from the first scrounger. Additionally, we recorded the technique the producer used to open the box.

To assess whether the number of unsuccessful task manipulations until the first success differed between years, we constructed a generalised linear mixed model (*GLMM*) by using the number of unsuccessful task manipulations until the first success as dependent variable, year as fixed factor and individual identity as random factor.

For the analysis of individual preferences for one or the other technique, we included only individuals that performed at least 6 actions at the boxes. Individual preferences for a feeding technique were analysed with a Binomial test. We also used a Binomial test to assess whether the number of individuals keeping a stable preference differed from the number of individuals with an unstable preference and to analyse whether the number of individuals exhibiting unstable preferences differed due to the technique they favoured in their first year. A stable preference was defined as keeping a preference for one technique from one year to the following year of participation. If individuals changed from one year to another, either by switching preferences or by switching from a preference to no preference or vice versa, we defined them as exhibiting an unstable preference. We constructed a *GLMM* to test whether a stable preference from one year to the other was influenced by sex, group membership, year (first: stability from 2009 to 2010, second: 2010 to 2011) or age

class (juvenile – juvenile, juvenile – adult, adult – adult; juveniles < 2.5 years, adults > 2.5 years). Individual ID was used as a random factor.

To assess whether the number of individuals performing both, scrounging and opening the box (producing) to gain rewards, differs from the number of individuals only scrounging or producing, we applied a χ^2 test. To estimate whether the frequency of scrounging events is influenced by age, sex or success in handling the task (number of successful task manipulations), we used another *GLMM*. Age, sex and the number of successful task manipulations were used as fixed factors and individual identity nested in groups as random factors.

To assess whether individuals scrounged more often when other individuals opened the box by pushing or pulling the door, we used a *GLMM*. We used technique (pull or push) as fixed factor and individual identity as random factor. In order to analyse whether the stability of individual preferences is influenced by the frequency of being scrounged, we calculated a scrounging score for each individual in 2010 and 2011 (number of actions in which other individuals scrounged by the total number of actions). We calculated a *GLMM* by using stability as response variable, scrounging scores of 2010 and 2011 as fixed factor and individual identity as random factor. All *GLMMs* were fitted in R (R Development Core Team 2010), using the R package lme4 (Bates and Maechler 2010). The significance of the full model as compared to the null model (comprising only the intercept and the random effect) was established using a likelihood ratio test (R function Anova with argument test set to " χ^2 "). P values for the individual effects were based on Markov Chain Monte Carlo sampling (Baayen 2008) of the R package language R (Baayen 2010). Binomial tests and χ^2 tests were conducted in IBM SPSS 20 (SPSS Inc., Chicago, IL, USA).

Results

Success in manipulating the box over the three experimental years

Thirty-two out of 42 members of the 4 study groups manipulated the feeding boxes (overall participation rate of 76.2%). Twenty-five individuals performed successful manipulations in at least 1 year. Eighteen individuals opened the boxes successfully in 2009. Fifteen individuals managed to retrieve rewards in 2010, and 2 of these subjects did so for the first time. In 2011, 18 individuals conducted successful task manipulations; and 5 of these 18 individuals manipulated the boxes successfully for the first time. On average, redfronted

lemurs conducted 54.4 ± 49.9 (mean \pm SD) successful task manipulations in 2009, 40.1 ± 52.1 in 2010 and 59.7 ± 38.8 in 2011.

Fifteen subjects manipulated the feeding boxes successfully in at least 2 years of the experiments. In the first year of experiment, 13% of 15 individuals were able to open the box right away, and 1 individual needed only 1 unsuccessful task manipulation before its first successful manipulation. The remaining 80% needed between 2 and 24 trials before their first successful manipulation. In the second year of participation, 40% of 15 individuals were able to open the boxes immediately with success, 13% performed only 1 unsuccessful task manipulation, whereas 47% needed between 2 and 24 trials until the first success. In the third year of participation, 45% of 11 individuals were able to successfully open the box immediately, 45% needed only 1 unsuccessful manipulation and 1 individual underwent 6 trials before the first success. The lemurs needed fewer unsuccessful task manipulations until the first successful one in the third year of participation compared to the first year of participation (Figure 2; Table 3a; *GLMM*: $\chi^2 = 6.08$, $P = 0.048$).

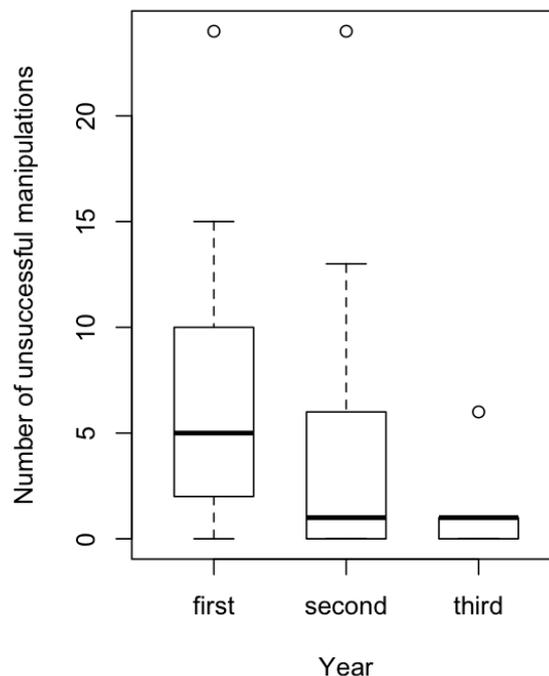


Figure 2 Number of unsuccessful task manipulations until the first success for individuals that learned the novel behaviours and participated in at least 2 years (*1st year*: $N = 15$ individuals; *2nd year*: $N = 15$ individuals; *3rd year*: $N = 11$ individuals; *boxplots* indicate median, upper and lower quartiles, outliers are indicated as *small dots*).

Table 2 Preferences of subjects that performed ≥ 6 actions per year and corresponding *P* value of the binomial test.

Group	Individual	Preference 2009	<i>P</i> value	Preference 2010	<i>P</i> value	Preference 2011	<i>P</i> value
A	FCor	Pull	<0.01	Pull	<0.01	Pull	<0.01
A	MKor	Pull	<0.01	Pull	<0.01	Pull	<0.01
B	FSip	Pull	<0.01	Pull	<0.01	Pull	<0.01
B	FBor	Pull	<0.01	Pull	<0.01	Pull	<0.01
F	MCas	Pull	<0.01	Pull	<0.01	Pull	<0.01
F	FMont	Push	0.04	No preference	0.29	Push	<0.01
F	MTri	Push	<0.01	No preference	0.21	Push	<0.01
J	FGeo	Push	<0.01	No preference	0.51	Push	<0.01
J	FMal	Push	<0.01	No preference	1.00	No preference	0.05
J	MKaz	Pull	<0.01	No preference	0.17	No preference	0.55
F	FLuc	No preference	1.00	Pull	<0.01	No preference	<0.01
J	MUsb	Push	<0.01	Push	<0.01	<i>No data</i>	
J	FCam	Push	<0.01	<i>No data</i>		No preference	0.24
A	MSky	<i>No data</i>		No preference	0.29	Pull	<0.01
A	MMil	<i>No data</i>		No preference	1.00	<i>No data</i>	
B	MLab	<i>No data</i>		No preference	0.31	<i>No data</i>	
B	MPan	Pull	0.01	<i>No data</i>		<i>No data</i>	
B, J	MRot ^a	<i>No data</i>		<i>No data</i>		Pull	<0.01
J	FMol	Push	<0.01	<i>No data</i>		<i>No data</i>	
A, B	MMyk ^a	<i>No data</i>		<i>No data</i>		Pull	<0.01
F	Fang	<i>No data</i>		<i>No data</i>		Push	<0.01
J	FCol	<i>No data</i>		<i>No data</i>		Pull	0.01

Acronyms indicate sex (1 letter) and name (2 - 4 letters)

no data individuals did not participate or did not conduct ≥ 6 actions

^a Individuals that changed groups during the years

Preferences for opening techniques over time

Twenty-two out of 32 individuals performed ≥ 6 task manipulations and were therefore included in this analysis (2009: $N = 15$ individuals; 2010: $N = 15$ individuals; 2011: $N = 17$ individuals). Eight individuals participated in one single year, 3 individuals in two years and 11 individuals conducted actions in all 3 years (Table 2). On average, they conducted 32.3 ± 22.1 (mean \pm SD) task manipulations (successful and unsuccessful) in 2009, 60.4 ± 47.6 in 2010 and 92.1 ± 52.1 in 2011.

Individual preferences were rather unstable (Table 2). Eight out of the 14 individuals participating in 2 or 3 years switched between a preference for one technique and no preference. However, 6 individuals showed a stable preference (AFCor, AMKor, BFSip, BFBor, FMCas, JMUsb; acronyms: (1) letter = group, (2) letter = sex and (3) – (5) letters = name): 5 individuals kept a preference for pulling and 1 individual a preference for pushing. There was no difference between the number of individuals exhibiting a stable or an unstable preference (Binomial test: $N = 14$, $P = 0.79$). Individuals showing a preference for pushing in their first year of participation ($N = 5$) did not switch more often between preference and no preference than individuals exhibiting a preference for pulling ($N = 1$; Binomial test: $N = 6$, $P = 0.22$). Interestingly, not a single individual switched between preferences for the two techniques. The probability of exhibiting a stable preference was not influenced by sex, age, group membership or year (Table 3b, *GLMM*: $\chi^2 = 9.16$, $P = 0.242$). Eight individuals participated only in 1 year so that no preference over the years could be identified.

On the group level, 2 individuals each of groups A and B showed a stable preference for the pulling technique over the 3 years, and only 1 individual in group A switched between a preference and no preference (Figure 3). In group F and J, however, 7 individuals showed unstable preferences, and in each group, only 1 individual exhibited a stable preference for one of the techniques (Figure 3). Although the sample size is too small for statistical analysis, individuals of former pull group A and former open group B tended to be more stable in their preferences (80% of individuals) than individuals of former open group F and former push group J (22% of individuals).

Table 3 Parameter estimated for the general linear mixed models (*GLMM*) (a) on the difference in the number of unsuccessful task manipulations until first success over the years, (b) on effects of group membership, age, sex and year on the stability of individual preferences, (c) on the difference in the number of scrounging events between individuals of different age and different sex and that performed different numbers of successful actions, (d) on the difference of task manipulation being scrounging between the two techniques and (e) on the difference in stability of individual preferences between individuals with different scrounging scores.

Model	Response variable	Random factor	Fixed factors	Estimate	SE	P value
(a) GLMM	Number of unsuccessful talks manipulations until first success	Individual identity	Intercept	6.73	1.46	<0.001
			2 nd year	-2.67	2.06	NS
			3 rd year	-2.24	2.24	0.015
(b) GLMM	Stability	Individual identity	Intercept	10.97	156.4	NS
			Juvenile-adult	0.37	244.7	NS
			Juvenile-juvenile	0.88	230.1	NS
			Sex	1.15	1.55.6	NS
			Group B	18.30	1,228,000	NS
			Group F	-24.25	234.0	NS
			Group J	-24.11	67.39	NS
(c) GLMM	Number of scrounging actions	Individual identity	Intercept	2.99	0.89	NS
			Juveniles	-0.12	0.61	NS
			Females	0.41	0.26	NS
			Males	0.03	0.89	NS
			Success	0.01	0.76	NS
(d) GLMM	Scrounging (yes, no)	Individual identity	Intercept	-2.67	0.15	<0.001
			Method	0.28	0.14	0.041
(e) GLMM	Stability	Individual identity and group	Intercept	-11.17	20.12	NS
			Scrounging score	2.34	94.6	NS

NS not significant

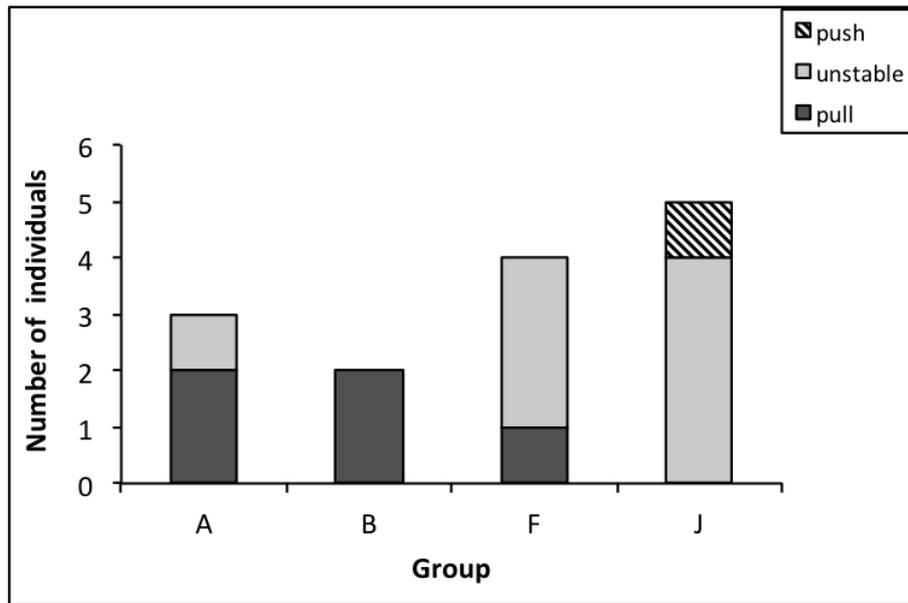


Figure 3 Number of individuals participating at least 2 years in the experiments and exhibiting a stable preference for pulling or pushing or switching between a preference and no preference.

Scrounging

Individuals scrounged in 9.1% of 4079 task manipulations. Scrounging occurred in all 4 study groups (group A: $N = 42$ events; group J: $N = 121$ events; group B: $N = 62$ events; group F: $N = 147$ events) and in all 3 years (2009: $N = 166$ events; 2010: $N = 58$ events; 2011: $N = 148$ events). During one scrounging event, the number of scroungers varied between 1 and 3 individuals (one scrounger: $N = 334$ events; two scroungers: $N = 37$ events; three scroungers: $N = 1$ events).

Twenty-two individuals performed both successful task manipulations as well as scrounging actions at the feeding boxes. Two individuals only scrounged, 3 individuals never scrounged and 5 individuals neither succeeded nor scrounged. The majority of individuals used both tactics (producing and scrounging) to get access to the rewards (χ^2 test: $\chi^2 = 10.3$, $Df = 1$, $P = 0.005$). Interestingly, the frequency of scrounging was not influenced by age, sex or by the number of successful box manipulations (Table 3c; *GLMM*: $\chi^2 = 0.58$, $P = 0.965$). Scrounging occurred more often when producers opened the feeding box by pushing (11.7%, $N = 179$ out of 1536 push actions) than by pulling the door (7.6%, $N = 193$ out of 2543 pull actions; Table 3d; *GLMM*: $\chi^2 = 3.937$, $df = 1$, $P = 0.047$, $N = 4079$ task manipulations). However, the probability of whether individuals exhibited a stable preference from 1 year to the other could not be explained by the ratio of scrounging events

(Table 3e; *GLMM*: $\chi^2 = 0.006$, $P = 0.938$). Therefore, victims of scrounging did not respond to a higher risk of scrounging events by exhibiting less stable preferences.

Discussion

The present study reveals that redfronted lemurs opened an artificial feeding box successfully more quickly over the years, indicating that they seem to remember the rewarding character of the box over time, although there were time intervals of 9 months in between the presentation of feeding boxes. However, on the population level, they did not maintain a preference for one or the other technique over the three consecutive years. Individual preferences for the pulling technique tended to be more stable than preferences for the pushing technique, but more individuals tended to switch between exhibiting a preference or no preference. Moreover, the majority of animals also scrounged, and scrounging occurred more often when individuals opened the boxes by using the less stable pushing technique. However, the stability of a preference was neither influenced by the frequency of being scrounged nor by age, sex or group membership. Interestingly, the frequency of scrounging was not influenced by age, sex or success in opening the boxes. Thus, most redfronted lemurs appear to use the two techniques to open the feeding boxes flexibly and also scrounged opportunistically to get access to rewards.

The formation of long-term traditions has been suggested to be influenced by the difficulty of the task or the costs of modifying an established, effective behaviour pattern (Gajdon et al. 2004; Hopper et al. 2007; Thornton and Clutton-Brock 2011). A behaviour, which is difficult to learn, might be discovered only by rare innovators and is unlikely to spread within groups by social learning (Gajdon et al. 2004; Thornton and Clutton-Brock 2011). However, if a behavioural trait is easy to learn, it can be discovered by (most) individuals by asocial learning (Hopper et al. 2007; Thornton and Malapert 2009). Although redfronted lemurs used social information to acquire the opening techniques (Schnoell and Fichtel 2012), they also discovered the alternative technique. Individuals might therefore have not faced high levels of costs when switching between the two techniques because they did not have to invest a lot of time and effort to acquire the alternative behaviour. Thus, the box manipulations in this study might not have been physically difficult enough to induce long-term preferences in redfronted lemurs.

Persistence of arbitrary traditions might also be influenced by whether the different

behaviours are highly option-specific, so that a generalisation from one option of the task to the other is unlikely (Hoppitt et al. 2012). Since the two options to gain a reward in this study did not differ in their difficulty to learn (Schnoell and Fichtel 2012) and could be solved by manipulating the same door, the low level of option specificity of the task may account for the fluctuation in preferences.

Nevertheless, 6 individuals exhibited a stable feeding technique preference over the 3 years. Although the sample size is rather small, neither age, sex or group membership influenced the probability of exhibiting a preference. These preferences were presumably formed by a response habit, that is, by sticking to the first rewarded technique (Craet et al. 2010). Another characteristic of habit formation is an increase in speed and accuracy in responding towards a stimulus (Neal et al. 2006), which can lead to a reinforcement of the already learned behaviour (Pesendorfer et al. 2009; Matthews et al. 2010). The individuals in this study became more efficient in manipulating the feeding boxes over the years, supporting the notion that habit formation is a likely mechanism for the formation of preferences. This is in line with other studies showing that simple learning mechanisms can explain the spread of two different pine-nut-eating traditions from mothers to offspring in wild rats (*Rattus rattus*: Terkel 1996) and novel foraging techniques in wild meerkats (Thornton 2008; Hoppitt et al. 2012), or that habit formation in combination with social facilitation and stimulus enhancement is the main mechanisms leading to a human-introduced long-term tradition in captive capuchin monkeys (Craet et al. 2010).

In addition to accessing rewards by opening the box by themselves, most redfronted lemurs also scrounged. During a single scrounging event, up to three individuals could scrounge, creating costs for the individual opening the box. Interestingly, the majority of individuals did both scrounging and manipulating boxes and did not use either tactic exclusively. Although scrounging occurred more often when individuals opened the box by pushing than by pulling the door, it did not influence whether individuals exhibited a stable preference as for example a pull-preference to avoid scrounging. Moreover, the probability of scrounging was not influenced by sex or age, suggesting that in this socially tolerant society, all group members are able and tolerated to scrounge. Since there was no relationship between scrounging and success in manipulating the boxes, redfronted lemurs appear to get access to the rewards rather opportunistically by either manipulating the boxes or scrounging.

Experiments with feeding apparatuses that can be opened in two distinctive ways are a common procedure to test for social diffusion in captive as well as field settings (reviewed by Whiten and Mesoudi 2008 and Kendal et al. 2010b). In primates, only two studies have investigated the longevity of human-introduced traditions experimentally: one in a captive population of capuchin monkeys over a period of two years (Craet et al. 2010) and one study in a wild population of vervet monkeys over one year (van de Waal et al. 2012). Our study represents an investigation over a period of three years in a field setting. Interestingly, redfronted lemurs did not maintain an experimentally introduced tradition over time. The intermediate pattern of some individuals exhibiting a clear preference over the three years and other individuals showing fluctuating preferences between a preference and no preference but not switching between preferences might have been influenced by several factors such as the formation of a response habit in some individuals, the opportunistically use of scrounging, the low levels of difficulty and/or object specificity of the task. Our results emphasise the importance of long-term studies to get a reliable picture in the area of social learning and animal traditions and to improve our understanding of the factors causing or preventing the stability of behavioural patterns over time.

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CHAPTER 6

MANUAL LATERALIZATION

IN WILD REDFRONTED LEMURS (*EULEMUR RUFIFRONS*)

DURING SPONTANEOUS ACTIONS AND IN AN EXPERIMENTAL TASK

with Franziska Huebner, Peter M. Kappeler and Claudia Fichtel

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Abstract

The dominant use of one hand is a striking feature of humans, but manual lateralization can be found in a variety of other species as well. In primates, the lateralization in hand use varies among species and several theories such as the “postural origin”, “task complexity” or “development theory” have been suggested to explain this variation. In order to contribute comparative data on this phenomenon from a basal primate, we studied manual lateralization in wild redfronted lemurs (*Eulemur rufifrons*). Data were collected on four groups at Kirindy Forest, western Madagascar, during spontaneous actions and by confronting them with artificial feeding boxes. The lemurs did not exhibit manual lateralization on a group level in either condition. More individuals showed a hand preference in the experimental task and the preferences were stronger compared to spontaneous actions. The direction of individual hand preferences was not consistent across the two conditions. The results of this study show that measuring manual laterality in different contexts can yield different results. Manual lateralization in wild redfronted lemurs therefore seems to be flexible and situation dependent and probably not ecologically relevant in their natural habitat.

Keywords: Handedness; Hand use; Strepsirrhine

Introduction

Approximately 90% of the human population is right-handed (Porac and Coren 1981; Annett 2002). Hand preference, the presence of a dominant hand or limb in unimanual actions, is not only observed in humans but also in a variety of vertebrates (fish: Bisazza et al. 2000; amphibians: Bisazza et al. 1996; reptiles: Stancher et al. 2006; birds: Rogers and Workman 1993; and mammals: McGrew and Marchant 1997; Güven et al. 2003; Quaranta et al. 2004; Papademetriou et al. 2005; Hopkins 2006), and has been a research focus for several decades. Laterality research on nonhuman primates, in particular, helps to understand the underlying mechanisms and the adaptive value of handedness in humans (McGrew and Marchant 1997; Hopkins 2006).

One possible advantage of handedness is that a preference for one limb reduces the cognitive effort for action planning as well as initiation and therefore conserves time and energy (Flowers 1975; Papademetriou et al. 2005). However, in a relatively symmetrical environment it might also be disadvantageous to constrain manual options by biasing one's manual functions (McGrew and Marchant 1997). For arboreal species especially, it might be better to be able to use both limbs in the same way. In contrast to humans, handedness exists only at the individual level in most primate species and rarely at the population or group level (McGrew and Marchant 1997). A meta-analysis on population-level handedness revealed a tendency for a left-hand bias in strepsirrhines, New World monkeys, and Old World monkeys (Papademetriou et al. 2005), whereas most studies on apes report a population level right-hand bias (Lonsdorf and Hopkins 2005; Hopkins 2006; Hopkins et al. 2007). Others studies, however, did not find population level handedness in great apes and only hand biases on an individual level (Byrne and Byrne 1991; Corp and Byrne 2004; Fletcher and Weghorst 2005; Braccini et al. 2010; Chapelain et al. 2011; McGrew and Marchant 2011).

According to the “postural origins theory” (*POT*: MacNeilage et al. 1987), hand preferences in humans evolved from functional specializations in ancestral arboreal primates. These primates used the right hand for postural support like holding on to branches, and the left hand for visually guided tasks such as reaching. In later more terrestrial species, the right hand became free for manipulating food and for other precise bimanual actions while the left hand was still used for reaching. Finally, in humans we find a population level bias for the use of the right hand (Marchant and McGrew 2013). Today,

controversial findings exist on population level handedness and there is still no strong support for POT (McGrew and Marchant 1997; Papademetriou et al. 2005). Also a review of handedness in prosimians by Ward et al. (1993) could not reveal a clear picture, with 57% of the examples being left-handed and 43% being right-handed. The existing variation might be due to the fact that handedness is influenced by various factors, for instance, sex, age, task, and experience (Fagot and Vauclair 1991; McGrew and Marchant 1997; Hopkins and Leavens 1998; Corp and Byrne 2004).

The “task complexity theory” (Fagot and Vauclair 1991) proposes that complex, high-level and novel tasks are more likely to reveal significant hand biases than are less demanding unimanual tasks like reaching. Thus, hand preferences at the population level are more likely to become apparent in complex bimanual tasks. For example, white-fronted capuchin monkeys (*Cebus apella*) showed stronger hand preferences in high-level tasks than in low-level tasks, but none of the tasks elicited a population level hand preference (Lilak and Phillips 2008). Similarly, in vervet monkeys (*Cercopithecus aethiops*: Harrison and Byrne 2000), De Brazza’s monkeys (*Cercopithecus neglectus*: Schweitzer et al. 2007) and Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*: Zhao et al. 2010) task complexity influenced handedness. In contrast, red-capped mangabeys (*Cercocebus torquatus*) and Campbell’s monkeys (*Cercopithecus campbelli*) exhibited a hand preference during spontaneous behaviour as well as in an experimental task (Chapelain et al. 2012), contradicting the “task complexity theory”. Rogers (2009) argued that it is not the complexity of a task that causes population-level handedness, but whether the task demands processing in a specialized hemisphere (also see Fagot and Vauclair 1993). In addition, Warren (1980, 1987) suggested that laterality in nonhuman primates is a learned phenomenon that develops out of routines and is highly situation dependent. Laterality is reinforced when testing animals in an experiment, and experience of the tested animals influences the measured level of laterality.

Many studies on laterality in primates have been conducted in captivity, although it has been suggested that the surrounding environment can influence the development of a hand preference. For instance, hand-rearing by highly hand-preferent humans or the rearing in a right-handed constructed environment might influence handedness in captive animals (McGrew and Marchant 1997; Hopkins and Cantalupo 2005). A study on gorillas revealed lateralization for hand use in captive-born individuals, but none in wild-born individuals (*Gorilla* sp.: Shafer 1987). However, the influence of captivity on lateralization is debated

and a study on grooming behaviour did not reveal a stronger handedness in captive compared to wild chimpanzees (*Pan troglodytes*: Hopkins et al. 2007). In most studies conducted in natural habitats, data were collected by observing animals reaching for food on the ground or on feeding platforms, which does not necessarily correspond to normal foraging (Nelson et al. 2009). Thus, more studies on handedness during spontaneous behaviour in combination with experimental approaches in wild populations are required for a more differentiated assessment of patterns of hand use.

We investigated hand preferences during spontaneous behaviour and during experimental manipulation of a feeding box (see below) in wild lemurs, which are among the most basal living primates (Fichtel and Kappeler 2010). We studied redfronted lemurs (*Eulemur rufifrons*), which are medium-sized (2 kg), cathemeral and arboreal quadrupedal primates (Kappeler and Erkert 2003; Johnson 2007). Hands are used to reach and lift branches, whereas the intake of leaves from a branch is mainly achieved orally. According to the “postural origins theory,” we predicted a left-hand bias both during spontaneous behaviour and manipulation of a feeding box. With regard to the “task complexity theory,” we predicted that redfronted lemurs exhibit either a hand preference only during manipulations of the feeding box or a stronger hand preference when manipulating the boxes than during spontaneous behaviour. According to Warren’s hypothesis, we predicted that redfronted lemurs would show different hand preferences in the two conditions.

Methods

Study site and subjects

The study was conducted at the research station of the German Primate Center in Kirindy Forest, a dry deciduous forest in Western Madagascar (Kappeler and Fichtel 2012b). The experimental data were collected in May 2011 and the data on the spontaneous actions from August 2012 to October 2012. A total number of 17 redfronted lemurs took part in the study (sex: 10 females and 7 males; age: 15 adults and 2 juveniles) living in 4 groups (group A, B, F, and J; Kappeler and Fichtel 2012a). Eleven individuals participated in both conditions and six individuals in one of the two conditions. Kin relationships were known for most individuals in the focal groups. All subjects were well habituated to the presence of humans and individually marked with unique combinations of nylon collars and pendants or radio collars.

Data collection and statistical analyses

For the analysis of manual laterality during spontaneous behaviour, focal behaviour sampling (Altmann 1974) was conducted for each individual by FH. The use of a single hand (unimanual) or both hands (bimanual) was recorded for different behavioural categories: “self-grooming,” “allogrooming,” “holding branches” while foraging, “holding food items” like fruits and leaves while moving them to the individual’s mouth, and “warding off” other individuals (Table 1). If an animal did not change its posture and repeatedly performed the same action with the same hand (e.g., reaching out for the same branch while sitting in the same position on a tree), only the first action was recorded to ensure independence of data points. A minimum of 40 unimanual actions was observed for each individual. This approach to record only a subset of hand responses (in our case the first one) has limitations. The choice of actions to be included in the analyses is somewhat subjective and additional information on hand use gets lost (also see: Hopkins 1999 and Hopkins 2013), but this drawback must be traded off against constraints of behavioural operationalization.

Table 1 Mean number of hand uses (\pm standard deviation) for each behavioural category recorded during spontaneous actions ($N = 14$ subjects with 40 unimanual hand actions per subject and all observed bimanual hand actions).

	Self-grooming	Allo-grooming	Holding branches	Holding food	Warding off others
One hand	0.5 \pm 0.91	0.07 \pm 0.26	0.36 \pm 0.61	35.86 \pm 4.58	3.14 \pm 4.56
Both hands	0.21 \pm 0.41	0	24.78 \pm 9.29	0	0

For the observation of hand preferences in the experimental condition, hand actions were observed during manipulation of artificial feeding boxes by AVS (for details, see Schnoell and Fichtel 2012; Schnoell et al. 2014). These boxes offered two distinctive opening techniques to gain access to a food reward (by either pulling or pushing a swinging door). The task of opening the box can be classified as a high-level manual task (Fagot and Vauclair 1991), which is demanding, novel and involves coordinated actions. Hand use of all door manipulations was recorded and individuals that conducted ≥ 10 actions were included in the present analysis.

Two methods were applied to characterize individual hand preferences. To determine whether animals were either left- or right-handed, we calculated a binomial z-score for each individual. The z-score determines whether the number of left- or right-hand use of an individual differed from chance, and were calculated by using the formula $z = (X - M) / \sqrt{(N \times p \times q)}$, with X = number of right-hand use of a subject, N = total number of responses of subject, $M = N/2$ and p and $q = 0.5$. Subjects could then be classified according to McGrew and Marchant (1997) as left-preferent ($z \leq -1.96$), ambipreferent ($-1.96 \leq z \leq 1.96$), i.e. with no preference or right-preferent ($z \geq 1.96$). We used binomial tests to determine significant manual lateralization at the group level.

To analyse the strength of individual hand preferences, we calculated a Handedness Index (HI) for each individual with the formula: $HI = (R - L) / (R + L)$ where R is the number of times the right hand and L the number of times the left hand was used. It varies between -1 (totally left-handed) and +1 (totally right handed) (Alonso et al. 1991).

To compare the pattern as well as the strength of hand preferences between the natural condition and the experimental condition we conducted two General Linear Mixed Models (*GLMM*; Table 3). *GLMMs* were implemented with R i386 2.15.1 (R Development Core Team 2010).

Results

During spontaneous actions, lemurs used their hands most often in feeding contexts and only rarely in the context of self-grooming or allogrooming or warding off other group members (Table 1). Foraging occurred primarily in trees and rarely on the ground. In some cases, animals used both hands simultaneously to manipulate a branch, but most often one hand was used while the other was used for postural support. Redfronted lemurs rarely brought food with hands to their mouth; more often, they pulled branches toward themselves and removed leaves or fruits orally. During spontaneous actions, only 14.3% of lemurs could be classified as exhibiting a hand preference according to their binomial z-scores, whereas 85.7% were ambipreferent ($N = 14$ individuals; Table 2). The two individuals that exhibited a significant hand bias both used the right hand predominantly (Table 2). At the group level, there was no overall hand bias, because the majority of individuals were ambipreferent (binomial test: $N = 14$, $P = 0.01$). In order to determine whether related individuals were more likely to have a hand preference, we compared hand preferences of

six mother-offspring pairs (mother-offspring: BFBor - BFAla, AFSar - AMKor, FFLuc - FMTri, JFCam - JFCol, JFCam - JFGeo, JFCam - JFMal) and three sister pairs (JFCol - JFGeo, JFMal - JFCol, JFMal - JFGeo). All subjects were determined to be ambipreferent.

Table 2 Handedness measured for each individual in the experimental task and during spontaneous actions (*left-preferent*: z-scores ≤ -1.96 ; *right-preferent*: z-scores ≥ 1.96 ; Acronyms: *first letter* = name of group, *second letter* = sex (*F* = female, *M* = male), *last three letters* = first three letters of the individual's name; *NA* = no data).

Individual	Z-scores		Handedness	
	Experiment	Spontaneous	Experiment	Spontaneous
AFCor	-8.50	2.85	Left	Right
AFSar	NA	-1.90	NA	Ambipreferent
AMKor	10.91	0.63	Right	Ambipreferent
AMSky	5.51	NA	Right	NA
BFAla	NA	-0.32	NA	Ambipreferent
BFBor	12.33	-0.63	Right	Ambipreferent
BFSip	-6.63	NA	Left	NA
BMGor	NA	-0.32	NA	Ambipreferent
BMMyk	-0.77	0.32	Ambipreferent	Ambipreferent
FFLuc	-3.00	-1.58	Left	Ambipreferent
FMCas	7.54	NA	Right	NA
FMTri	-1.26	-1.26	Ambipreferent	Ambipreferent
JFCam	-1.85	-1.26	Ambipreferent	Ambipreferent
JFCol	7.89	-1.26	Right	Ambipreferent
JFGeo	-5.43	-0.63	Left	Ambipreferent
JFMal	-2.61	1.59	Left	Ambipreferent
JMRot	-6.07	3.16	Left	Right

The mean *HI* score (\pm standard deviation, *SD*) during spontaneous actions was -0.003 ± 0.25 . The overall *HI* scores did not differ from a chance distribution with a mean of zero (one-sample *t*-test: $t_{(14)} = -0.043$, $P = 0.97$), resulting in an approximately equal distribution of left- and right-handers in the population (Figure 1).

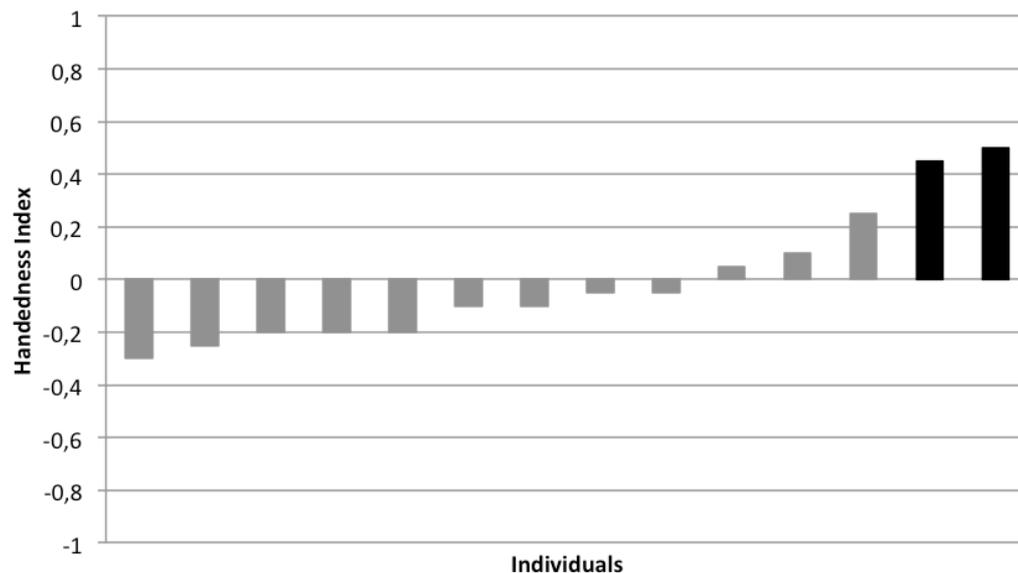


Figure 1 Hand preferences during spontaneous actions. Handedness Index at the population level for 14 individuals (-1 = fully left-preferent, 1 = fully right-preferent; *black bars* = significant hand preferences, *grey bars* = no significant hand preferences).

In the experimental task, 78.6% of the 14 subjects were classified as having a hand preference. Of those, 54.5% preferred the left hand and 45.5% the right hand (Table 2), revealing no overall hand bias (binomial test: $N = 11$ individuals, $P = 1.00$). Only three (21.4%) individuals were ambipreferent. In this condition, we found that more individuals exhibited a hand preference than were ambipreferent (binomial test: $N = 14$ individuals, $P = 0.06$). Five mother-offspring pairs participated in the experiments (FFLuc - FMTri, JFCam - JFCol, JFCam - JCGeo, JFCam - JFMal, BFSip - BFBor), but none of them showed the same lateral biases (1 x left-handed and ambipreferent, 1 x ambipreferent and right-handed, 2 x ambipreferent and left-handed and 1 x left-handed and right-handed). Only one (JFMal - JFGeo) of three maternal kin dyads (JFCol - JFGeo, JFMal - JFCol, JFMal - JFGeo) exhibited a shared left-hand preference. There was no hand bias in females (left-preferent: $N = 5$ individuals; right-preferent: $N = 2$ individuals; binomial test: $N = 7$ individuals, $P = 0.45$). Among males, one favoured the left hand and two preferred the right hand.

The mean *HI* score (\pm SD) for the experimental condition was 0.161 ± 0.717 . *HI* scores did not differ significantly from a chance distribution with a mean of zero (Figure 2; one-sample t-test: $t_{(14)} = 0.843$, $P = 0.42$).

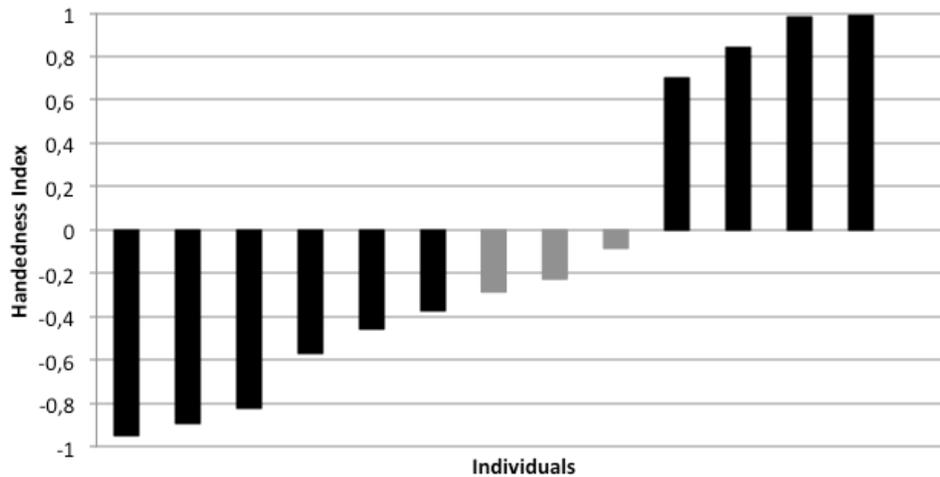


Figure 2 Hand preferences in the experimental task. Handedness Index at the population level for 14 individuals (-1 = fully left-preferent, 1 = fully right-preferent; *black bars* = significant hand preferences, *grey bars* = no significant hand preferences).

Finally, we compared the *HI* scores of the spontaneous actions with the data during manipulation of the feeding boxes. A *GLMM* revealed no significant difference of the *HI* scores between conditions (Table 3, a; *GLMM*: $\chi^2 = 2.8212$, $P > 0.05$), and only three subjects (AMKor, FFLuc and JFCol) exhibited the same direction of hand preference in both conditions. However, a comparison of the absolute *HI* scores, indicating the strength of the hand preference regardless of the direction, revealed stronger hand preferences in the experimental task (Table 3, b and Figure 3; *GLMM*: $\chi^2 = 19.031$, $P < 0.01$). Both *GLMMs* did not reveal any effect of age and sex (Table 3).

Table 3 Parameters estimated for the General Linear Mixed Model (a) on the pattern of handedness measured in the two different conditions (spontaneous actions and experimental task) and (b) on the strength of handedness in the two conditions.

<i>GLMM</i>	Response variable	Random factors	Fixed factors	Estimate	SE	<i>P</i>
a	Handedness index	Individual identity	Intercept	0.006	0.182	n.s.
			Context	0.118	0.182	n.s.
			Sex	0.141	0.236	n.s.
			Age	-0.375	0.371	n.s.
b	Absolute handedness index	Individual identity	Intercept	0.217	0.084	0.016
			Context	0.447	0.087	<0.001
			Sex	-0.041	0.100	n.s.
			Age	-0.017	0.168	n.s.

n.s. not significant

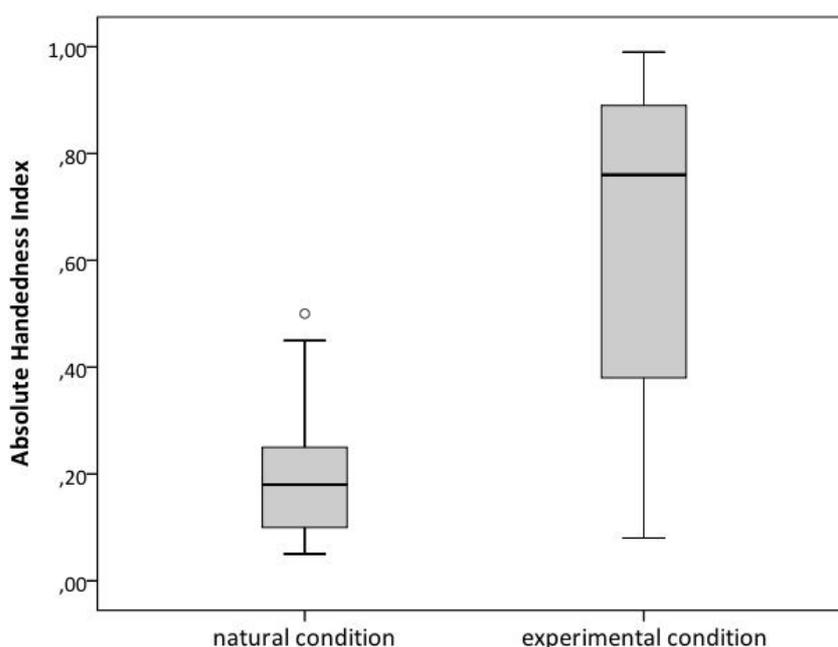


Figure 3 Strength of manual lateralization in two conditions. Wild redfronted lemurs showed a weaker strength of hand preferences during spontaneous actions compared to the experimental task (*value of 1 = strong preference for one hand, value of 0 = no hand preference; boxplots indicate median, upper and lower quartiles, the outlier is indicated as a small circle*).

Discussion

This study based on a small sample size suggests that there is no group level manual lateralization in wild redfronted lemurs, neither in an experimental task nor during spontaneous actions. This finding contradicts the “postural origin theory” (MacNeilage et al. 1987) that predicts an overall left-handedness for lemurs as very basal primates. Several other studies have failed to show any population level handedness in Garnett’s bush babies (*Otolemur garnettii*: Cantalupo and Ward 2000), ringtailed lemurs (*Lemur catta*: Shaw et al. 2004), indris (*Indri indri*: Rigamonti et al. 2005), aye-ayes (*Daubentonia madagascariensis*: Lhota et al. 2009) and in two species of mouse lemurs (*Microcebus murinus*, *M. lehilahytsara*: Leliveld et al. 2008).

At the individual level, redfronted lemurs exhibited more often and stronger hand preferences during manipulation of the feeding box than during spontaneous actions, supporting the "task complexity theory" (Fagot and Vauclair 1991; Blois-Heulin et al. 2006). The difference in the strength of the observed hand preferences between the experimental task and the spontaneous actions might be due to situational factors (Zhao et al. 2012). In our experimental condition, we presented the boxes on the ground and subjects could therefore freely decide which hand to use. In contrast, during spontaneous actions, the animals might have been constrained in their choice of hand by the position of the animal on a support or by the position of leaves or fruits when feeding in a tree (Chapelain et al. 2012). Similarly, hand preferences in gentle lemurs (*Hapalemur griseus* and *H. alaotrensis*: Stafford et al. 1993) were influenced by the position of the object that they had to reach. Interestingly, the distribution of hand preferences in the experimental condition is similar to the outcome of a food-reaching study on 11 different lemur species (Ward et al. 1990; Table 4), which found, presumably due to the larger sample size, an overall bias for the left hand.

The direction of most individuals’ hand preferences was not consistent across both conditions, findings that support Warren’s hypothesis (1980). The stronger handedness in the experimental task can be explained in the framework of this theory by the number of actions recorded in each condition. In the experimental task, we focused on one behaviour, hand use while opening the door, and thus a single task for which individuals could develop a routine. During spontaneous actions, we recorded five different actions, and thus five different situations in which the lemurs might favour different hands. Handedness in redfronted lemurs therefore seems to be situation dependent.

Table 4 Overview of the distribution of hand preferences in experimental reaching tasks in different species of prosimians.

Species	N	Left-preferent (%)	Ambipreferent (%)	Right-preferent (%)	Source
<i>Eulemur albifrons</i>	15	40.0	33.3	26.7	Ward et al. (1990)
<i>Eulemur collaris</i>	24	62.5	20.8	16.7	Ward et al. (1990)
<i>Eulemur coronatus</i>	11	54.5	9.1	36.4	Ward et al. (1990)
<i>Eulemur fulvus</i>	11	27.3	45.5	27.3	Ward et al. (1990)
<i>Eulemur monaco</i>	33	60.6	3.0	36.4	Forsythe and Ward (1988)
	29	65.5	10.3	24.1	Ward et al. (1990)
<i>Eulemur monogoz</i>	26	34.6	19.2	46.2	Ward et al. (1990)
<i>Eulemur rubriventer</i>	5	20.0	0	80.0	Ward et al. (1990)
<i>Eulemur rufifrons</i>	14	42.9	21.4	35.7	Schnoell et al. (2014)
<i>Eulemur fulvus rufus</i>	14	57.1	21.4	21.4	Ward et al. (1990)
<i>Eulemur sanfordi</i>	17	17.6	35.3	47.1	Ward et al. (1990)
<i>Galago moholi</i>	16	31.3	0	68.9	Dodson et al. (1992)
<i>Lemur catta</i>	13	46.2	30.8	23.1	Milliken et al. (1989)
	42	50.0	16.7	33.3	Ward et al. (1990)
<i>Microcebus lehilahytsara</i>	19	47.4	0	52.6	Leliveld et al. (2008)
<i>Microcebus murinus</i>	8	37.5	12.5	50.0	Dodson et al. (1992)
	44	31.8	20.5	74.7	Leliveld et al. (2008)
<i>Otolemur garnetti</i>	17	58.8	0	41.2	Hanbury et al. (2010)
	23	30.4	13.0	56.5	Milliken et al. (1991)
<i>Varecia variegata</i>	5	100	0	0	Forsythe et al. (1988)

The development of laterality might be constrained in redfronted lemurs because they spend considerable time in trees (Sussman 1974) where it might be advantageous to use both hands equally to reduce the risk of falling (Marchant and McGrew 2007). Similar to other lemurs (Ward et al. 1993; Milliken et al. 2005; Rigamonti et al. 2005), redfronted lemurs preferred oral retrieval of food after pulling a branch toward them, and were relatively flexible in their hand use while in a tree. In the grooming context, the study animals mostly used the toothcomb and only rarely their toilet claw. The establishment of a strong lateral preference may therefore not be ecologically meaningful for wild redfronted lemurs.

We did not find any effect of kinship on the strength and direction of hand preferences, which is in contrast to previous studies on chimpanzees (*Pan troglodytes*, Lonsdorf and Hopkins 2005) and humans (Annett 1985; Provins 1997). Similarly, although it has been shown that captive lemurs exhibit sex-specific handedness, with males favouring the left hand (Ward et al. 1990), our study did not reveal sex-specific handedness in both conditions. Thus, investigation of hand preferences during experimental tasks as well as

spontaneous actions in wild populations may provide more realistic insights into the evolution and importance of handedness in the animals' daily life than using only one methodological approach. We also want to emphasize the value of studies on wild populations for their ecological validity. Additionally, the usage of a combination of approaches might reveal the importance of laterality for different species living in different habitats and might provide for a better understanding of which specific manipulative challenges have an impact on laterality.

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CHAPTER 7

COGNITION IN RINGTAILED LEMURS

with Klara Kittler and Claudia Fichtel

Folia Primatologica: submitted

Abstract

In order to better understand the evolution of cognitive abilities in primates, information on cognitive traits of the most basal living primates can provide important comparative baseline data. Compared to haplorrhine primates, lemurs have relatively smaller brains and reduced abilities to solve problems in the technical and social domain. However, recent studies have suggested that some cognitive abilities of lemurs are qualitatively en par with those of haplorrhines. Here, we review studies investigating cognitive abilities in the technical and social domain of ringtailed lemurs. In the physical domain ringtailed lemurs exhibit similar qualitative cognitive skills as other lemurs but also haplorrhine primates. In the social domain, ringtailed lemurs appear to be more skilled in visual perspective taking than other lemurs. They also have among lemurs highly elaborated communicative skills. Moreover, among lemurs, within-group coalitions have only been observed in female ringtailed lemurs during rare events of female evictions. However, in several other aspects of social cognition, such as reconciliation and social learning, ringtailed lemurs cognitive abilities are en par with those of other lemurs. Thus, additional systematic comparative studies in physical and social cognition are required to understand the processes of cognitive evolution among primates.

Keywords: Ringtailed lemurs; *Lemur catta*; Physical cognition; Social cognition; Comparative research; Communication; Social structure

Introduction

Understanding the evolution of cognition has been widely regarded as a major challenge in evolutionary research. Primates stand out in this context, because they have larger brains compared to equally-sized other mammals (Isler and van Schaik 2009). These effects also increase disproportionately within the primate order from strepsirrhines to haplorrhines to hominins and humans (Dunbar 1992; Isler et al. 2008). Given that larger brains are energetically more expensive (Aiello and Wheeler 1995), the most puzzling questions in this context are how and why primates, and especially humans, have evolved such powerful and distinctive cognitive abilities requiring so much costly neural tissue (Herrmann et al. 2007; Navarrete et al. 2011).

Research on cognitive abilities of strepsirrhine primates (lemurs and lorises) is of particular interest because after their split from other primates about 60 million years ago (Yoder et al. 1996; Yoder and Yang 2004; but see Seiffert et al. 2003 for paleontological records) they retained many ancestral primate traits, making them the best living models of early primates and the link between primates and other mammals (Martin 1990; Fichtel and Kappeler 2010). Cognitive abilities of strepsirrhine primates remain understudied, and the existing studies revealed conflicting results.

Alison Jolly (1966b) established the importance of comparative studies of lemur social intelligence in the early days of primatology. She concluded that *„Lemur and Propithecus are both socially intelligent and socially dependent. They are, however, hopelessly stupid towards unknown inanimate objects. In this branch of the primates, the basic qualities of primate society have evolved without the formal inventive intelligence of true monkeys“* (Jolly 1966b: 165-166). Accordingly these older studies suggested that lemur cognitive abilities in the physical domain are inferior to those of haplorrhines (e.g. Maslow and Harlow 1932; Jolly 1964; Ehrlich et al. 1976), more recent studies, however, indicated that their cognitive abilities often match those of haplorrhines (reviewed in Fichtel and Kappeler 2010).

Here we review the cognitive abilities of ringtailed lemurs (*Lemur catta*), which live in multi-male, multi-female groups with the largest group size among lemurs and exhibiting clear dominance hierarchies (Sauther et al. 1999; Jolly et al. 2006). These aspects of their social system allows to evaluate the influence of social complexity on cognition by comparing cognitive abilities of ringtailed lemurs with other lemur species organized into

smaller groups or pairs but also makes them comparable to many haplorhines (Jolly 1966a; Kappeler 2012a), opening a window of opportunities for comparative cognition research. Because many previous studies have been hampered by very small sample sizes, we only consider studies that have tested at least 4 ringtailed lemurs in our review of physical and social cognition below.

Physical Cognition

Dealing effectively with objects and their spatial, numerical and causal relationships is critically important for everyday survival when searching for food, shelter or avoiding predators. Spatial cognition enables animals to identify their position, to remember what is located where, and to travel efficiently between sites (Gallistel 1989). A comparative study on spatial memory in four lemur species (Table 1) revealed that frugivorous lemurs showed more robust spatial memory than folivorous species, with ringtailed lemurs exhibiting intermediate spatial cognitive abilities (Rosati et al. 2014). However, wild grey mouse lemurs (*Microcebus murinus*) with an omnivorous diet also learned rapidly the spatial location of feeding sites (Lührs et al. 2009).

Regarding numerical understanding ringtailed lemurs are able to form abstract numerical ascending rules and can apply them to novel sets of numerosities (Merritt et al. 2011). Furthermore, ringtailed lemurs are as good as brown, mongoose and ruffed lemurs in understanding the outcome of simple arithmetic operations of up to three items (Table 1; Santos et al. 2005a). As in other primates, ringtailed and mongoose lemurs ability to discriminate between quantities depends on the ratio between choices being at least 1:3 or larger to successfully select the larger quantity in a spontaneous food choice task (Table 1; Jones and Brannon 2012). In addition, the precision of their approximate number system is comparable to that of rhesus monkeys (*Macaca mulatta*; Jones et al. 2014).

Ringtailed lemurs are also able to organize sequences in memory and to retrieve ordered sequences. Indeed, their accuracy and response times were similar to haplorrhine monkeys (Merritt et al. 2007). Moreover, ringtailed as well as black lemurs were able to deal efficiently with large numbers of discriminative problems in visual discrimination learning sets (Table 1; Cooper 1974; Ohta et al. 1984).

Tool use has not been reported for any strepsirrhine primate, perhaps because they have limited dexterity (Torigoe 1985) due to a lack of a precision grip (Holtkötter 1997). They

may therefore be physically unable to perform certain tasks requiring a high level of manual precision. However, recent research suggests that they nevertheless have some understanding of tool properties and functionality. Ringtailed lemurs are able chose between a functional and a non-functional tool to retrieve an inaccessible reward as quickly as capuchins, tamarins and vervet monkeys (Santos et al. 2005b). They are as black, brown and redfronted lemurs also able to acquire a novel behaviour pattern to solve simple puzzle-box problems (Table 1; Kappeler 1987; Fornasieri et al. 1990; Anderson et al. 1992; Kendal et al. 2010a; Schnoell and Fichtel 2012).

Finally, a basic problem-solving skill that is essential for an effective interaction with the environment is inhibitory control, which is the ability to control ones behaviour and impulsive reactions that would disrupt, for example, the efficient completion of a task leading to a potential food reward (Vlamings et al. 2009). Ringtailed lemurs are able to successfully use inhibitory control to acquire a reward but did not outperform other lemurs (Table 1; MacLean et al. 2013, 2014). Thus, their abilities in the physical domain are qualitatively similar to those of other lemurs but also haplorrhine primates (Fichtel and Kappeler 2010).

Social Cognition

In contrast to haplorrhine primates, brain size of lemurs does not correlate with group size (MacLean et al. 2009). However, performance in a social cognitive task did correlate with the species-typical group size, but not with brain size, suggesting the potential for cognitive evolution without concomitant changes in brain size (MacLean et al. 2013). In particular, ringtailed lemurs exhibit some similarities in social organization and social structure with haplorrhines (Kappeler 1999), suggesting convergent social-cognitive evolution (Sandel et al. 2011). Below, we will summarize the current knowledge of ringtailed lemurs' social cognition, focusing on the structure of social relationships (competition, post-conflict behaviour, coalitions), gaze following, social learning and innovations, as well as communication.

Ringtailed lemurs live in multi-male, multi-female groups with the largest group size among lemurs (Kappeler 2012a). Males and females exhibit separate linear dominance hierarchies (Jolly 1966a) but rank is not inherited maternally as in many Old World primates (Kappeler 1993a). Ringtailed lemurs are able to use transitive interference, a form of deductive reasoning that might be a cognitive mechanism by which animals can learn the

relationships within their group's dominance hierarchy (MacLean et al. 2008). Ringtailed lemurs mastered this task better than pair-living mongoose lemurs, suggesting that social complexity is an important selective force for the evolution of cognitive abilities relevant to transitive reasoning (MacLean et al. 2008).

One mechanism of post-conflict behaviour which is exhibited by many haplorrhine primates is reconciliation after aggression, and some studies suggest that ringtailed lemurs do reconcile after conflicts (Rolland and Roeder 2000; Palagi et al. 2005), whereas other studies not (Kappeler 1993b). Reconciliation has also been documented in black, brown and redfronted lemurs as well as in sifakas (Table 1; Kappeler 1993b; Roeder et al. 2002; Palagi et al. 2008). Third-party affiliation after aggression seems to be absent in this species (Kappeler 1993b). The formation of coalitions appears to be limited to specific contexts in ringtailed lemurs. Although ringtailed as well as redfronted lemurs tend to form partnerships with other males during migration, they do not actively support each other in within group conflicts (Gould 1997a; Ostner and Kappeler 2004). Female ringtailed lemurs experience high levels of competition over reproduction, resulting even in eviction of potential competitors (Vick and Pereira 1989). In contrast to males, related females occasionally form even within-group coalitions during eviction of other females (Jolly 1998). In contrast, female coalitions have not been documented in redfronted lemurs during eviction of other females (Kappeler and Fichtel 2012a).

Another benefit of group-living is to gather information about the environment, for instance about what to feed on, what to avoid, or about appropriate sex-specific behaviours, by observing conspecifics (Gould 1997b; O'Mara et al. 2012). Ringtailed lemurs as well as black and brown lemurs use gaze following to track the attention of conspecifics (Shepard and Platt 2008; Ruiz et al. 2009). In contrast to black, mongoose and red ruffed lemurs brown and ringtailed lemurs are also able to follow human gaze, however (Botting et al. 2011; Sandel et al. 2011). Ringtailed lemurs as many *Eulemur* species, red ruffed lemurs and Aye Ayes are able to learn socially (Kappeler 1987; Fornasieri et al. 1990; Anderson et al. 1992; Kendal et al. 2010a; Schnoell and Fichtel 2012). However, studies on social learning in the wild indicate that in contrast to redfronted lemurs (Schnoell and Fichtel 2012) the spread of information appears to be limited to subgroups of individuals that tolerate each other in close proximity (Kendal et al. 2010a). Although ringtailed lemurs are able to learn socially, there is only one report of a potential behavioural tradition, which describes the innovation

and spread of a novel way of drinking in a captive population (Hosey et al 1997). Behavioural traditions in the wild have also been found in Verreaux's and Coquerel's sifakas and potentially in redfronted lemurs (Fichtel and van Schaik 2006; Fichtel and Kappeler 2011; Schnoell and Fichtel 2013).

Finally, ringtailed lemurs are more skilled in using social cues in comparison to brown, black, mongoose as well as black and white ruffed lemurs and Coquerel's sifakas in a food competition task in which the experimental subject was supposed to avoid food that an experimenter was facing (Sandel et al. 2011; MacLean et al. 2013).

Thus, in the realm of social intelligence, ringtailed lemurs appear to be more skilled than other lemurs in using social cues during food competition tasks. Within-group coalitions appear to be rare and limited to rare events of female evictions, in contrast to redfronted lemur females. However, in several other aspects of social cognition, such as reconciliation and social learning, ringtailed lemurs' cognitive abilities are en par with those of other lemurs.

Although non-human primates have a limited repertoire of signals, they can provide listeners with an open-ended, highly, modifiable, and cognitively rich set of meanings (Cheney and Seyfarth 2010). Among lemurs, ringtailed lemurs have the largest vocal repertoire, produce the largest number of facial expressions and have elaborated olfactory communication (Fichtel unpubl. data). They produce functionally referential alarm calls in response to both, aerial and terrestrial predators (Pereira and Macedonia 1991), whereas sifakas and redfronted lemurs produce functionally referential alarm calls only in response to aerial predators (Fichtel and Kappeler 2002, 2011; Fichtel and van Schaik 2006). Redtailed sportive lemurs and grey mouse lemurs, however, produce no predator-specific but general alarm calls (Fichtel 2007; Rahlfs and Fichtel 2011). In the domain of visual communication produce more signals than other redfronted or ruffed lemurs (Pereira et al. 1988; Pereira and Kappeler 1997). In the domain of olfactory communication, ringtailed lemurs use various scent marks to signal individuality as well as dominance and reproductive status (Drea 2007; Charpentier et al. 2008; Crawford et al. 2010). Ringtailed lemurs are also able to recognize kin or chose mating partners by means of olfactory signals (Charpentier et al. 2010; Crawford et al. 2010). Even cross-modal recognition of individuals by means of olfactory and vocal signals has been demonstrated in ringtailed lemurs (Kuhlaci et al. 2014). Thus, ringtailed lemurs appear to have among lemurs highly elaborated communicative skills.

In summary, although only limited data are available, this review indicates that ringtailed lemurs exhibit similar qualitative cognitive skills in the physical domain as other lemurs but also haplorrhine primates (Fichtel and Kappeler 2010). In the social domain, ringtailed lemurs are better skilled in using social cues in food competition tasks than other lemurs. Coalitions have only been observed in female ringtailed lemurs during rare events of female evictions. However, in several other aspects of social cognition, such as reconciliation and social learning, ringtailed lemurs cognitive abilities are en par with those of the so far studied other lemurs. Thus, additional systematic comparative studies in physical and social cognition are required to understand the processes of cognitive evolution through comparisons such as the present one.

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Table 1 Summary of the technical (1.) and social (2.) intelligence of ringtailed lemurs (*Lemur catta*) and comparison of their abilities to the ones of other lemur species.

Categories	Species	N	Successful?	N success / mean %	Reference	
1. TECHNICAL INTELLIGENCE						
1.1 Space and objects						
- Spatial memory	<i>Lemur catta</i>	9-12	y/n*	55.0% & 95.0%	Rosati et al 2014 (* = depending on the task)	
	<i>Eulemur mongoz</i>	11	y/n*	60.6% & 77.3%		
	<i>Propithecus coquereli</i>	12-13	y/n*	56.9% & 87.3%		
	<i>Varecia sp.</i>	12-15	y	80.0% & 95.8%		
	<i>Microcebus murinus</i>	6	y	4	Lührs et al. 2009	
- Inhibitory control	<i>Lemur catta</i>	11	y	-	MacLean et al. 2013	
	<i>Eulemur fulvus</i>	10	y	-		
	<i>Eulemur macaco</i>	10	y	-		
	<i>Eulemur mongoz</i>	10	y	-		
	<i>Propithecus coquereli</i>	10	y	-		
	<i>Varecia variegata</i>	11	y	-		
1.2 Tools and causality						
- Simple box	<i>Lemur catta</i>	18	y	8 / -	Kappeler 1987	
	<i>Lemur catta</i>	28	y	-	Kendal et al. 2010a	
	<i>Eulemur macaco</i>	4	y	2 / -	Fornasieri, Anderson & Roeder 1990	
	<i>Eulemur fulvus</i>	8	y	2 / -		
	<i>Lemur catta</i>	4	y	3 / -	Anderson et al. 1992	
	<i>Eulemur fulvus</i>	12	y	8(4) / -		
		<i>Eulemur rufifrons</i>	37	y	20	Schnoell & Fichtel 2012
	- Understanding of tools	<i>Lemur catta</i>	3	y	-	Santos, Mahajan & Barnes 2005
<i>Eulemur fulvus</i>		3	y	-		
<i>Daubentonia madagascariensis</i>		6	n	0	Sterling & Povinelli 1999	
1.3 Features and categories						
- Learning sets	<i>Lemur catta</i>	5	y	5 / -	Ohta, Ishida & Matano 1984	
	<i>Eulemur macaco</i>	3	y	3	Cooper 1974	
- Serial ordering	<i>Lemur catta</i>	2	y	2 / -	Merritt et al. 2007	
1.4 Quantities						
- Estimating numerosity	<i>Lemur catta</i>	31	y	-	Jones & Brannon 2012	
	<i>Eulemur mongoz</i>	9	y	89.5%	Lewis, Jaffe & Brannon 2005	

- Simple arithmetic operations of 1+1	Lemur catta	6	y	-	
	<i>Eulemur fulvus</i>	6	y	-	Santos, Barnes & Mahajan 2005
	<i>Eulemur mongoz</i>	4	y	-	
	<i>Varecia rubra</i>	3	y	-	
- Numerical rule-learning	Lemur catta	2	y	2 / -	Merritt et al. 2011

2. SOCIAL INTELLIGENCE

2.1 Social complexity & social relationship structure

- Transitive inference	Lemur catta	3	y	-	MacLean et al. 2008
	<i>Eulemur mongoz</i>	3	y	-	
- Coalitions	Lemur catta	9 groups	y	-	Sussman 1992
	Lemur catta	12 groups	y	-	Jones 1983
	Lemur catta	10	y	-	Gould 1997a
	Lemur catta	-	y	-	Jolly 1998
	<i>Eulemur rufifrons</i> (once: <i>E. fulvus rufus</i>)	4 groups	y	-	Ostner & Kappeler 2004
	<i>Eulemur rufifrons</i> (once: <i>E. fulvus rufus</i>)		n		Kappeler & Fichtel 2012a
	- Post-conflict behaviour	Lemur catta	2 groups	n	7.2%
	<i>Eulemur fulvus</i>	2 groups	y/n	13.6%	
	Lemur catta	16	y	57.7%	Rolland & Roeder 2000
	<i>Eulemur rufifrons</i> (once: <i>E. fulvus rufus</i>)	16	y	63.7%	Roeder, Fornasieri & Gosset 2002
	<i>Eulemur macaco</i>	8	n	34.8%	
	Lemur catta	13 (2 groups)	y/n	-	Palagi, Paoli & Tarli 2005
	<i>Propithecus verreauxi</i>	16	y	44.7%	Palagi, Antonacci & Norscia 2008

2.2 Gaze following and related skills

- Gaze following	Lemur catta	2	y	2	Shepherd & Platt 2008
	<i>Eulemur fulvus</i> & <i>Lemur catta</i>	5	y	3-4 / -	Botting, Wiper & Anderson 2011
	Lemur catta	17	y	-	
	<i>Eulemur mongoz</i>	10	n	-	Sandel, MacLean & Hare 2011
	<i>Eulemur macaco</i>	8	n	-	
	<i>Varecia variegata rubra</i>	14	n	-	
	<i>Eulemur macaco</i>	4	n	0 / -	Anderson & Mitchell 1999

- Visual perspective taking	<i>Eulemur fulvus</i>	4	y	-	Ruiz et al. 2009
	<i>Eulemur macaco</i>	2	y	-	
	<i>Lemur catta</i>	10	y	4 / 75.8% & 69.2%	Sandel, MacLean & Hare 2011
	<i>Lemur catta</i>	10	y	1 / 63.3%	
	<i>Eulemur mongoz</i>	10	n	0 / 35%	Sandel, MacLean & Hare 2011
	<i>Eulemur macaco</i>	10	n	0 / 47.5%	
	<i>Varecia variegata rubra</i>	10	n	0 / 45%	
	<i>Lemur catta</i>	10	y	75%	MacLean et al. 2013
	<i>Eulemur fulvus</i>	10	y	63%	
	<i>Eulemur macaco</i>	10	y	58%	
	<i>Eulemur mongoz</i>	10	n	55%	
	<i>Propithecus coquereli</i>	10	y	64%	
	<i>Varecia variegata</i>	10	n	48%	

2.3 Social learning and innovations

- Social learning	<i>Lemur catta</i>	2 groups	y	-	Jolly & Oliver 1985	
	<i>Varecia variegata</i>	1 group	n	-		
	<i>Eulemur mongoz</i>	1 group	y	-		
	<i>Eulemur fulvus mayottensis</i>	4 groups	y	-		
	<i>Lemur catta</i>	18	y	8 / -		Kappeler 1987
	<i>Lemur catta</i>	4	y	3 / -	Fornasieri, Anderson &	
	<i>Eulemur macaco</i>	4	y	2 / -	Roeder 1990	
	<i>Eulemur fulvus</i>	8	y	2 / -		
	<i>Lemur catta</i>	28	y	-	Kendal et al. 2010a	
	<i>Eulemur fulvus</i>	6	y	-	Feldman & Klopfer 1972	
	<i>Eulemur fulvus</i>	12	y	8(4) / -	Anderson et al. 1992	
	<i>Eulemur macaco macaco</i>	8	y	-	Gosset & Roeder 2001	
	<i>Daubentonia madagascariensis</i>	6	y	-	Krakauer 2005	
	<i>Eulemur rufifrons</i>	37	y	17	Schnoell & Fichtel 2012	
	<i>Lemur catta</i>	10	y	-	Gould 1997b	
	<i>Lemur catta</i>	7 groups	y	-	O'Mara & Hickey 2012	
	- Innovations	<i>Lemur catta</i>	28	y	17 / -	Hosey, Jaques & Pitts 1997
		<i>Redfronted lemurs</i>	29	y	15	Huebner & Fichtel,

				pers. comm.
<i>Redfronted lemurs</i>	4 groups	y/n	1 group	Schnoell & Fichtel 2013

2.4 Communication

- Functionally referential alarm calls, Vocal

	<i>Lemur catta</i>	30-40	y	-	Pereira & Macedonia 1991
	<i>Lemur catta</i>	1 group	y	-	Macedonia 1990
	<i>Varecia variegata</i>	1 group	n	-	
	<i>Lemur catta</i>	13	y	-	Oda 1999
	<i>Lemur catta</i>	25	y	-	Bolt 2013
	<i>Lemur catta</i>	15	y	-	
	<i>Eulemur rufifrons</i> (once: <i>E. fulvus rufus</i>)	11	y/n	-	Pereira & Kappeler 1997
	<i>Eulemur rufifrons</i> (once: <i>E. fulvus rufus</i>)	4 groups	y	-	Fichtel & Kappeler 2002
	<i>Propithecus verreauxi</i>	4 groups	y	-	
	<i>Propithecus coquereli</i>	2 groups	y	-	Fichtel & Kappeler 2011
- Visual	<i>Lemur catta</i>	15	y	-	Pereira & Kappeler 1997
	<i>Eulemur rufifrons</i> (o: <i>E. fulvus rufus</i>)	11	y	-	
- Olfactory	<i>Lemur catta</i>	22	y	-	Drea 2007
	<i>Lemur catta</i>	19	y	-	Charpentier, Boulet & Drea 2008
	<i>Lemur catta</i>	25	y	-	Crawford, Boulet & Drea 2011
	<i>Lemur catta</i>	33	y	-	Charpentier et al. 2010
	<i>Lemur catta</i>	13	y	-	Kuhlaci et al. 2014

GENERAL DISCUSSION

In this general discussion I will briefly summarize my main results on innovation of a new feeding behaviour (**Chapter 2**), on social tolerance (**Chapter 3**) and on its effects on learning (**Chapter 4**) as well as on the persistency of behavioural patterns over time (**Chapter 5**). I will discuss these findings in relation to results of other studies. Following this, I will address factors that might hinder lemurs to exhibit traditions in the wild. The contributions this study makes to understand the evolution of culture in humans are discussed in the following. At the end, I will list the main conclusion the result of my thesis have on the understanding of the establishment of traditions and will give an outlook for future directions in this field of research.

8.1. Step by step towards a tradition

8.1.1. Innovation

Innovations are described to occur as a response to changing environments and to environmental challenges (Boogert et al. 2008). I could describe a potentially new feeding behaviour, the depletion of spider nests, in a wild population of redfronted lemurs (*Eulemur rufifrons*; **Chapter 2**). The new behaviour was observed during the annual dry season, in which water and food resources are rare (Scholz and Kappeler 2004; Kappeler and Fichtel 2012b). Therefore, it is highly beneficial for the animals to be able to include new food sources in their diet. Innovations seem to enable redfronted lemurs to cope with a changing and challenging environment and to increase their niche breadth to ensure survival. Similarly in keas (*Nestor notabilis*), food deprivation was suggested as the main reason for a new feeding behaviour, namely the opening of bins in front of restaurants (Gajdon et al. 2006).

Concerning the age class of innovators the data on redfronted lemurs are contradicting: depletion of spider nest was innovated by adult individuals, which suggests a bias towards older individuals as innovators. However, during experimental studies on redfronted lemurs we find different patterns. In one study, juveniles were the first ones to learn an experimental task (Schnoell and Fichtel 2012) and in another one, we find an intermediate pattern, with one adult and one juvenile individual as innovators (**Chapter 4**). A reason for a bias towards older individuals as innovators might be that many innovations are modifications of other behaviours and therefore require some experience and competence

(Reader and Laland 2001). Adults have been identified as main innovators for instance in canaries (*Serinus canaria*; Cadieu et al. 2010), in chimpanzees (*Pan troglodytes*; Biro et al 2003; Nishida et al. 2009) and in keas (Gajdon et al. 2006). Also a literature analysis of innovation rates in different non-human primate species revealed that innovations are overall more common in adult compared to non-adult individuals (Reader and Laland 2001). Possible reasons for juveniles as more innovative age class is decreased neophobia in young individuals and therefore more exploration behaviour (Cambefort 1981; Biondi et al. 2013; Krueger et al. 2014) or a higher motivation to gain a food reward as younger individuals might occupy weaker positions in food competition compared to adult individuals (Kummer and Goodall 1985; Hauser 1988). For instance, in Japanese macaques juveniles seem to be more innovative than adults (Kawai 1986). These two contrary results for redfronted lemurs point out the flexibility within one species concerning the age class of innovators. Additionally, they suggest an influence of the setting in which an innovation occurs, so either a natural or an experimental setting, on the observed pattern.

The new feeding behaviour was only present in one of the four study groups and in this group a total number of four individuals depleted spider nests in one observation year. By applying the ethnographic method to the data set (for explanation of the method see **Chapter 1.3**), we obtained some evidence directing towards social learning. The behaviour cannot be explained by differences in the environmental conditions, as spider nests were available in all habitats, or by genetic difference, as there is regular male migration between the study groups. However, neither affiliation nor close proximity influenced the pattern of acquisition of the feeding behaviour within the group, which is contrary to what would be expected if social learning was involved (Coussi-Korbel and Frigaszy 1995). Therefore, this solely observational study does not allow me to differentiate between a multiple set of individual innovations and a social transmission of the new behaviour.

Research on innovations in wild animal populations was neglected for some time, partially because the traditional approach requires long-term information about the behavioural repertoire of a population (for example: Nishida et al. 2009). In this study, I successfully applied an alternative approach, namely the identification key by Ramsey et al. (2007). It recognizes innovations based on the geographic and local abundance of the candidate behaviour as well as on its properties even for smaller data sets. Rare behaviours

are, for instance, likely to represent an innovation if they are very different to other behaviours.

In summary, I could show that redfronted lemurs seem to be able to innovate new behaviours in the wild. I suggest that this ability to innovate occurs due to the challenging environment this species lives in and that different age classes might innovate behaviours in different settings.

8.1.2. Social tolerance

Social tolerance can constrain or facilitate the access that each individual has to the pool of information available within a group (Coussi-Korbel and Fragasz 1995). To investigate the influence of social tolerance on learning, I first assessed the social tolerance level of two lemur species that are highly comparable but differ in their social structure (**Chapter 3**).

To get a comparable measurement for social tolerance, I conducted a co-feeding experiment with redfronted lemurs and ringtailed lemurs (*Lemur catta*). The study groups were confronted with a clumped food resource in an experimental arena and the number of individuals within the arena as well as the number of individuals co-feeding was assessed. To evaluate the reliability of the result of the experiment, I implemented a validation by comparison with observational data.

In both approaches, redfronted lemurs were more tolerant than ringtailed lemurs. Redfronted lemurs tolerated a high number of group members in close proximity and many agonistic interactions were undecided. Both are highly relevant measurements: proximity can affect a variety of behaviours, for instance it makes social learning (Coussi-Korbel and Fragasz 1995; van Schaik et al 1999) or cooperation (Hare et al. 2007) more likely. The outcome of aggression might affect how often different individuals would seek close proximity to each other; if most of agonistic interactions are decided and a group therefore has a clear dominance hierarchy, individuals might not dare to approach high ranking individuals.

Although a higher number of individuals were in close proximity in redfronted lemurs during a competitive situation, as observed in the experimental approach, I could also observe a high number of agonistic interactions. This raises the question if redfronted lemurs shared voluntarily or if they rather lack the ability to monopolize a clumped food resource efficiently. The definition of social tolerance states that social tolerance allows

individuals to be in close proximity to others around a resource “with little or no aggression” (Cronin and Sánchez 2012), which contradicts the pattern I observed in my study. Interestingly, it has been also shown for other tolerant species, that they would prefer to feed alone instead of sharing with others if they are given the option to choose (marmosets, *Callithrix jacchus* and bonobos, *Pan paniscus*; Bullinger et al 2013) and that they often share with some resistance (lion tamarins, *Leontopithecus* spp.; Rapaport 2001).

In ringtailed lemurs we find a smaller number of individuals in close proximity and therefore they seem to possess a stronger ability or motivation to monopolize the clumped food resource. It is interesting though, that also this strong ability has its limits: if the food is not presented in a clumped pattern, but instead distributed in a wider radius, the resource holding potential of the dominant female decreases (White et al 2007).

It therefore seems that proximity between group members in a competitive situation depends on the presence or absence of individuals that have the ability or motivation to monopolize a feeding site as well as on the strength of their resource holding potential. Chimpanzees for instance exhibited group-level variation in social tolerance due the tolerance of the leaders (Cronin et al 2014). The resource holding potential of high-ranking individuals seems to be affected by the distribution pattern of the food reward, with an increased number of individuals able to feed on larger food patches.

However, different species react differently to different sizes of distribution radii. In redfronted lemurs a big number of group members were able to stay in the small experimental arena whereas in ringtailed lemurs the dominant individuals start to fail to exclude others only in a bigger radius. This difference might occur due to the different social structures of the two study species as redfronted lemurs are rather egalitarian and ringtailed lemurs show clear dominance hierarchies. The socioecological model explains the differences in social relationships within a group by environmental factors and gives predictions about the level of tolerance and cooperation the individuals should exhibit to each other (Sterck et al. 1997). The model predicts that different competitive regimes cause different social structures (Kappeler 2012b). Egalitarian societies are predicted to develop if resources cannot be monopolized by a single individual, whereas clumped resources that one individual can claim, lead to stricter dominance hierarchies (de Waal and Luttrell 1989).

Taken together, I cannot determine for sure, if it is social tolerance according to the common definition that I am measuring with my co-feeding experiment. However, the

results of my experiment showed, that redfronted lemurs are able to stay in closer proximity to each other than ringtailed lemurs. Therefore, they should have more opportunities for social learning, as they are able to observe in principal the behaviour of their fellow group members in greater detail.

8.1.3. Influence of social tolerance on social transmission

Different social tolerance levels have been proposed to influence the speed and pattern of the propagation of new information within social units (Coussi-Korbel and Fragaszy 1995; van Schaik 1999). To this end, I investigate in the next step the spread of new behaviours within the two study species, to evaluate differences in the speed and pattern of their learning behaviour (**Chapter 4**).

I conducted a social diffusion experiment with exactly the same set-up and the same procedure in redfronted lemurs and ringtailed lemurs. The study groups were confronted with feeding boxes that could be opened with two alternative techniques (“sliding” and “lifting”) and a knowledgeable demonstrator for one of the techniques was present during experiments. A higher number of individuals of redfronted lemurs, the more tolerant species, than ringtailed lemurs learned to open the boxes successfully. Additionally, redfronted lemurs were more efficient learners and needed fewer trials until the first success. These findings are in line with the prediction of the model of social dynamics on social learning (Coussi-Korbel and Fragaszy 1995) that high levels of social tolerance facilitates social learning because animals can stay in closer proximity to each other.

Another prediction of the model is that the pattern of the spread is affected by social tolerance, with a more homogenous spread in egalitarian societies than in despotic societies. In despotic groups information is suggested to spread only in subgroups because social tolerance is limited to certain dyads of individuals, like for instance kin and friends. For both species I find that the propagation of the new skill was affected by the frequency of contacts that individuals had with the demonstrator. Affiliative relationship, in contrast, did not influence the pattern of transmission within groups. Therefore, it seems to be important for individuals to be able to get in proximity to knowledgeable individuals. However, maybe their ability to observe the behaviour of an individual is constrained if they are already involved in another behaviour, namely affiliative behaviour. In line with my results, close proximity had a bigger effect on the spread of a social custom in chimpanzees, although also

social affiliation seems to promote social transmission in this case (Bonnie and de Waal 2006).

The diffusion experiment also allows some conclusions about the learning mechanisms involved in the acquisition of the skills. I could find only weak evidence that social transmission was involved in the acquisition of the task in both species, as the individuals did not copy the behaviour of the demonstrator and the social network of a group could not explain the transmission pattern. Therefore it is rather unlikely that the individuals learned by contextual imitation, so by performing actions in the same context than the demonstrator did during demonstration of the behaviour (Hoppitt and Laland 2013: pp 71-72). Interestingly through, the only individual that showed a preference for the more difficult technique (sliding) was indeed a member of a group with a demonstrator trained for this technique. Although this observation is anecdotal, it still indicates that lemurs could potentially possess the ability to use some form of copying, although incidents are very rare.

However, for the majority of the study subjects, there seemed to be simpler social learning mechanisms at work and probably they only learned that the boxes could be opened and that there is food situated inside them. Possibly they learned through emulation or observational conditioning. Emulation is defined as an increase in likelihood that a demonstrator performs an action leading to the same effect on an object, after observing a demonstrator handling the same object (Hoppitt and Laland 2013: pp 77-78). Another possibility is that they simply formed an association between manipulating the object and food by observing others at the boxes, in which case observational conditioning would be at work (Hoppitt and Laland 2013: pp 68-69).

Another explanation for individuals not acquiring the preference of the demonstrator is that the demonstrators were not good ones. In my study, individuals that were most interested in the task and managed to monopolize a single feeding box during the training phase became demonstrators. However, in canaries it was shown that innovative individuals tend to be poor demonstrators (Cadieu et al. 2010). Due to the diverse set of demonstrators in my experiments, differing in age as well as sex, it is difficult to hypothesize which features would characterize a good demonstrator for redfronted and ringtailed lemurs. Other studies, however, suggest that individuals pay more attention to, for instance, high-ranking individuals (Henrich and Gil-White 2001). Additionally, the presence of a demonstrator in a group seemed to inhibit others to interact with the feeding boxes. A possible explanation

might be that the demonstrator managed to monopolize the boxes, which hindered others to interact with the task and maybe also to acquire the preference of the demonstrator. For redfronted lemurs it has been shown in a previous study that individuals are indeed able to defend feeding boxes aggressively and thereby exclude others from an experimental set-up (Schnoell and Fichtel 2012).

Potentially, the possibility of scrounging facilitated individual learning. In both species scrounging was present as an alternative tactic instead of opening the feeding box by oneself, which might have made it easier for individuals to find the right solution. This was also shown for ravens (*Corvus corax*; Fritz and Kotrschal 1999) and for marmosets (Caldwell and Whiten 2003). In my study, both species showed the same scrounging frequency, but redfronted lemurs were able to scrounge from a bigger variety of group members, because they did not differentiate as much between kin and non-kin than ringtailed lemurs, which might have facilitated learning in redfronted lemurs. In guppies (*Poecilia reticulata*) it has been shown as well that a higher number of demonstrators increases the probability that a behaviour is acquired (Sugita 1980; Laland and Williams 1997).

In summary, I find evidence that the novel behaviours spread quicker and further in the more tolerant compared to the less tolerant study species. The homogeneity of the spread did not differ between the species, but in both species the learning probability is mainly affected by the possibility to get in close contact with knowledgeable individuals. If social learning was involved in the acquisition process, I suggest rather simple mechanisms like emulation or observational conditioning. Probably also the possibility to scrounge at a bigger variety of producers contributes to more efficient learning in the more tolerant species.

8.1.4. Longevity of traditions

Experimental studies on the longevity of human-introduced traditions are rare. Most experimental studies on animal tradition rather focus on testing the ability of an animal species to learn socially or the spread of behaviour within social units. However, the aspect of longevity represents an interesting research topic, because of the discrepancy between the high number of animal species that are able to learn socially (Reader and Hager 2011) and the rarity of animal traditions in the wild.

Redfronted lemurs represents an excellent model to study the stability of behavioural patterns over time, because they are able to use social information in the wild (Schnoell and Fichtel 2012), but no traditions have been described in this species so far. By presenting feeding boxes to the study groups that could be opened in two different ways and by monitoring individual preferences over 3 consecutive years, I could show that more than half of the animals showed unstable preferences whereas the other ones exhibited stable preferences (**Chapter 5**).

Probably the instability in the preferences in my study occurred due to two main causes: a low level of difficulty of the task and of option-specificity of the behaviours. To open a swing door by pushing or pulling it might not have been a great challenge for redfronted lemurs. Therefore, it seems to be important for a behaviour to have a specific level of difficulty to become fixed as a tradition in a group. In case the behaviour is too easy, most individuals will discover the behaviour by individual learning (Hopper et al. 2007; Thornton and Malapert 2009). However, if the behaviour is too difficult, it will be rarely discovered through innovation and it is unlikely that it will spread socially within groups (Gajdon et al. 2004; Thornton and Clutton-Brock 2011). The stability of a behavioural variant within a group seems to depend on the right balance of social and individual learning (Thornton and Clutton-Brock 2011).

Additionally, both opening techniques in my study involved manipulating the same door, which might have made it easy to discover the alternative technique. Therefore a high level of option-specificity seems to favour stability, because it prevents a generalisation from one option to the other one (Hoppitt et al 2012).

However, some redfronted lemurs also exhibited stable preference over time, which might have been caused by rather simple learning mechanisms (also see: Terkel 1996; Thornton 2008; Hoppitt et al. 2012; Crast et al. 2010). Most likely these individuals kept their preferences due to the formation of a response habit, which means that they simply stucked to the first rewarded technique (Crast et al. 2010). Another result that supports the assumption that response habits led to stable preferences in redfronted lemurs is that individuals became more efficient in opening the boxes over the years. Response habits are characterised by an increased speed and accuracy in response towards the stimulus (Neal et al. 2006), which reinforces the learned behaviour (Pesendorfer et al. 2009; Matthews et al. 2010).

Additionally to opening the feeding boxes themselves, most of the lemurs also scrounged. In this tolerant lemur species all group members, independent of age and sex, are able to use scrounging as a strategy. Therefore, redfronted lemurs appear to use the active opening of the boxes as well as scrounging rather opportunistically.

Taken together, redfronted lemurs seem to be unable to keep an experimentally introduced tradition over time. They show an intermediate pattern of some individuals exhibiting stable preferences and other being rather flexible in their behaviour. The formation of a response habit might explain stable preferences in some individuals and the opportunistically use of scrounging, as well as the low levels of difficulty and/or object specificity of the task might cause the instability in the preferences of the other study subjects.

8.1.5. Traditions in lemurs?

The results of my thesis indicate that group-living lemurs seem to be able to innovate new behaviours and that information can spread within their groups. Most likely though, lemurs use simple social learning mechanisms to do so and do not imitate the behaviour of a demonstrator in great detail. Generally, a high social tolerance level facilitated social learning in lemurs probably due to closer proximity and more diverse opportunities for scrounging. Some individuals in my study were able to keep stable behavioural preferences over time whereas others were rather flexible in their behaviour, which led to unstable preferences. Concerning the steps towards a tradition, lemurs seem to reach the steps of innovation and social transmission but fail at the step of longevity of behavioural patterns; my experiments suggest that these lemurs are either unable to form stable long-term traditions or that there is simply no need for them in the wild.

So far, only two examples for potential traditions were described in wild lemurs; both were identified in the context of communication in sifakas: different populations of Coquerels sifakas (*Propithecus coquereli*; Fichtel and van Schaik 2006) use three alarm calls in the same contexts but reacted differently to one of them. Whereas captive populations connected this alarm call to the presence of a raptor, the wild populations did not associate a certain threat with it. The second example involves alarm calls towards carnivores in wild populations of Verreaux's sifakas (*Propithecus verreauxi*; Fichtel and Kappeler 2011). Again, the reaction differed and the density of these predators explained this difference. It

therefore seems that the usage and comprehension of these alarm calls are socially learned and connected with the challenges of the surrounding environment.

Another aspect that might constrain the behaviour of Malagasy lemurs is their limited manual dexterity (Torigoe 1985), which is related to a lack of a precision grip (Holtkötter 1997). This makes it more difficult for them to manually manipulate things in comparison with other species. Mountain gorillas (*Gorilla beringei beringei*), for instance, are able to exhibit 72 functionally different manipulation actions with their hands (Byrne et al. 2001). Therefore, it is very unlikely that Malagasy lemurs would develop, for instance, tool use, even if they would possess the necessary cognitive skills.

Social learning and animal traditions have been studied only rarely in strepsirrhines for some time, because it has been questioned if they possess a high intelligence (Jolly 1966b). Additionally, lemurs have relatively small brain sizes (Deaner et al. 2006). This feature does not make them a good candidate for research on traditions, because the frequency of innovation and socially learning correlates with the brain volume in non-human primates, with low frequencies in small-brained primates (Reader and Laland 2002).

Although lemurs are expected to show limited cognitive skills, I could show in my thesis that they seem to be able to innovate feeding behaviours and use social learning. Therefore they are an interesting subject for research in the domain of social cognition.

8.2. Implications for the evolution of culture in humans

It is easier to understand the general mechanisms underlying the phenomenon of traditions in animals than in humans. This gives us the possibility to identify facilitating and inhibiting factors and then to investigate whether and in which aspects human culture differs (Ramsey 2013). Additionally, this approach gives us more insights into the evolution of the phenomenon culture as well as its biological significance.

In my study, I could identify a high level of social tolerance as an aspect that facilitates social learning, the main mechanism for the development of traditions. An implication that can be drawn from this for the evolution of human culture is that culture probably evolved in rather egalitarian societies in humans too. Whiten (1999) includes egalitarianism combined with cooperation as one of the four components explaining the “deep social mind” of humans. The other three components he states as facilitating the unique interconnectedness of the human mind are theory of mind, culture and language.

The lemurs in my study did not imitate the behaviour of the demonstrator in my social diffusion task, but used the two behavioural alternatives rather flexibly. In humans, in contrast, we find that children precisely imitate all elements of a behavioural action, even if some elements are unnecessary to achieve the goal of the behaviour (Lyons et al. 2007). This phenomenon has been labelled “over-imitation” and seems to be an effective strategy as many human tasks are rather difficult to understand; an exclusion of elements of such complex tasks often leads to non-functionality (Gergely and Csibra 2005), like for instance in the case of handling electronic devices. The ability to faithfully imitate the behaviour of a demonstrator has been discussed as a cornerstone in the evolution of human culture, because it leads to uniformity within groups and also enables the accumulation of modifications over time (Tomasello 2009).

My study also hints in the direction that the number of demonstrators might facilitate learning. In general, it seems to be easier for information to spread from many to one, than from one to many (Nishida et al. 2009). Mathematical models (Magnus et al. 2010) suggest as well that the number of social learning models available crucially affects the establishment as well as the stability of a tradition and that it is rather unlikely that a stable tradition will be established with only one available demonstrator. Also stabilizing mechanisms like conformity (Whiten et al. 2005) are only able to implement if an individual monitors more than one individual (Magnus et al. 2010). In humans we usually find large population sizes, which has been discussed as being one aspect that led to the cultural complexity we find in modern humans (Henrich 2004; Powell et al. 2009). Population size further seems to lead to stable culture in humans and it has been argued that a reduction of population size can lead to cultural losses. In the case of Tasmanian aborigines it was for instance discussed that the separation from the populations at the mainland through ocean divide led to a decrease in the amount of tools (Diamond 1999).

Taken together, I could put forwards some implications my study has for the understanding of the evolution of human culture. The results of my thesis suggest that egalitarianism facilitates learning in a group setting, which probably makes the development of traditions more likely. Additionally, faithful imitation seems to be important for tradition to spread as well as to be maintained. Finally, a big number of demonstrators seem to have crucial importance for the establishment and stability of traditions.

8.3. Conclusion and outlook

Concerning the formation of traditions, I can conclude several facilitating as well as inhibiting factors based on the results of my study:

1) There seems to be an increased probability for innovations, if a species has to cope with environmental challenges, like times of food scarcity in a seasonal habitat. A new innovation in the area of feeding would therefore directly increase the chance of survival and is consequently highly adaptive.

2) The degree of social tolerance seems to affect the speed of learning as well as the number of learners, probably because group members are able to seek and stay in closer proximity to others. However, social tolerance did not influence the homogeneity of the spread.

3) Scrounging seems to facilitate learning, if animals are able to scrounge at a variety of different individuals. During scrounging, it is possible to observe the behaviour of the demonstrator as well as the experimental set-up in close proximity and therefore to collect information in greater detail. Additionally, the number of scrounging opportunities seems to matter, because a bigger set of demonstrators might increase the probability of social learning.

4) A behaviour needs to be difficult enough to develop into a tradition, because if it is too simple, most individual will acquire the skill by individual learning. Also the right level of option-specificity seems to be important to prevent generalisation from one behavioural option to the other.

5) A mechanism that can cause long lasting traditions is habit formation.

Concerning future directions in the research field of animal traditions, I propose that it is necessary to give more importance to experimental work on all levels leading to a tradition. So far studies using experiments mainly focussed on the initial spread of a new behaviour within social groups and tested whether different animal species are able to learn socially and investigated the development of group preferences. However, we lack information on the longevity of these transmitted behaviours as well as on the mechanisms leading to stability over time. Therefore I suggest conducting more long-term experiments similar to the one described in **Chapter 5**.

Further, the influence of the social environment as such on social learning is still poorly understood. A reason for this lack of information might lie in the difficulty to operationalize social tolerance. However, it is a pity that the effects of social tolerance are rarely studied, because the model of social dynamics on social learning (Coussi-Korbel and Frigaszy 1995) gives clear and straightforward predictions that can be easily evaluated by using an experimental approach. My thesis represents the first study on the effects of social tolerance on social learning by comparing two highly comparable species that differ in their social structure.

Additionally, I want to emphasise the need of comparable study species and same experimental set-ups to get a clearer picture about the underlying mechanisms. It is difficult to draw general conclusions, if the species are too different, for instance in the case of the comparison of social transmission between baboons and vervet monkeys (Cambefort 1981). This aspect is especially important in field settings, where, in contrast to laboratory studies, it is difficult to control for many confounding factors. Therefore field biologists should try to keep those factors, which they can influence, to a minimum, in this case by choosing the right study species.

Finally, more experimental fieldwork in combination with laboratory experiments as well as observational studies in the wild might be the best way for future research in animal traditions. As I pointed out, innovations are, for instance, more likely to occur in captivity, because animals are fed regularly and therefore have more time available for other activities than foraging (Lehner et al. 2010; **Chapter 1.2.1.**). This example shows that studies on captive populations can lead to wrong assumptions and field observations can provide an ecological more valid picture. However, if approaches are combined, interesting insights can be detected.

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APPENDIX

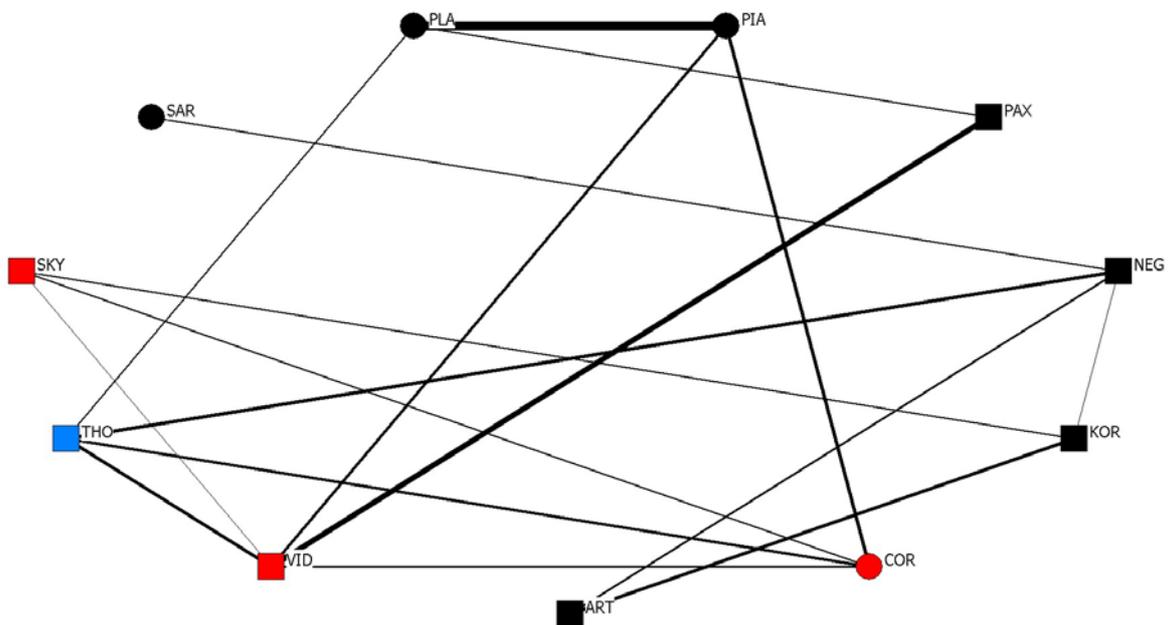


Figure 1 Schematic depiction of the social network of redfronted lemur group A (Lifting group). Symbols indicate individuals: *Circles* indicate females; *squares* indicate males. A *blue* symbol represents the demonstrator, *red* symbols represent learners and *black* symbols represent non-learners. *Line widths* are proportional to the strength of the social bond based on observed grooming rates.

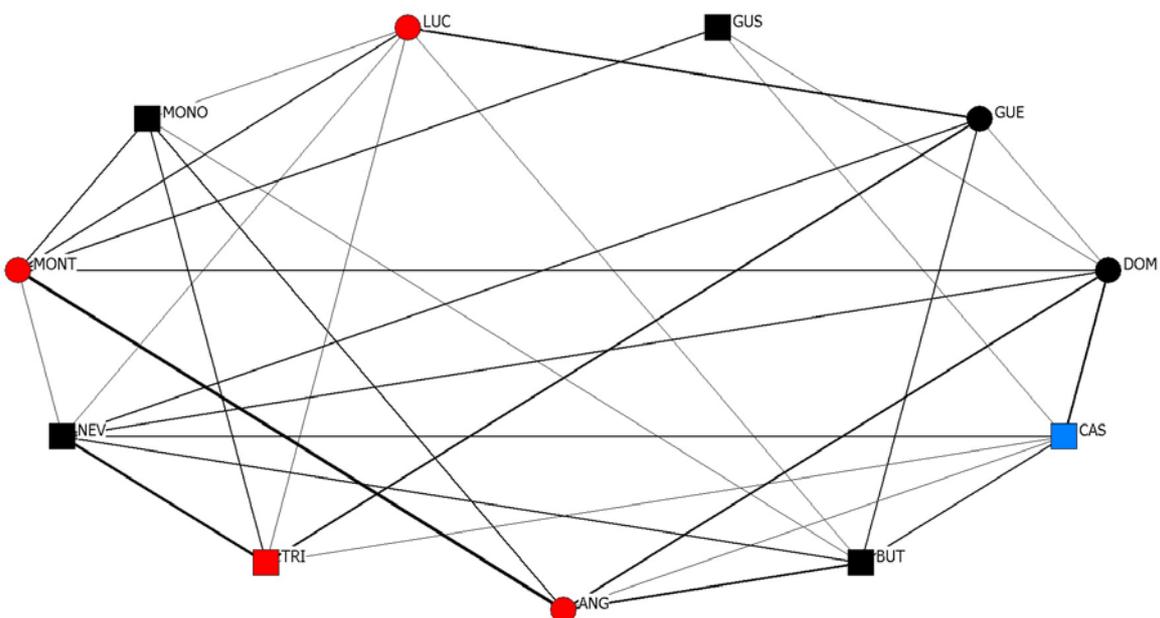


Figure 2 Schematic depiction of the social network of redfronted lemur group F (Sliding group).

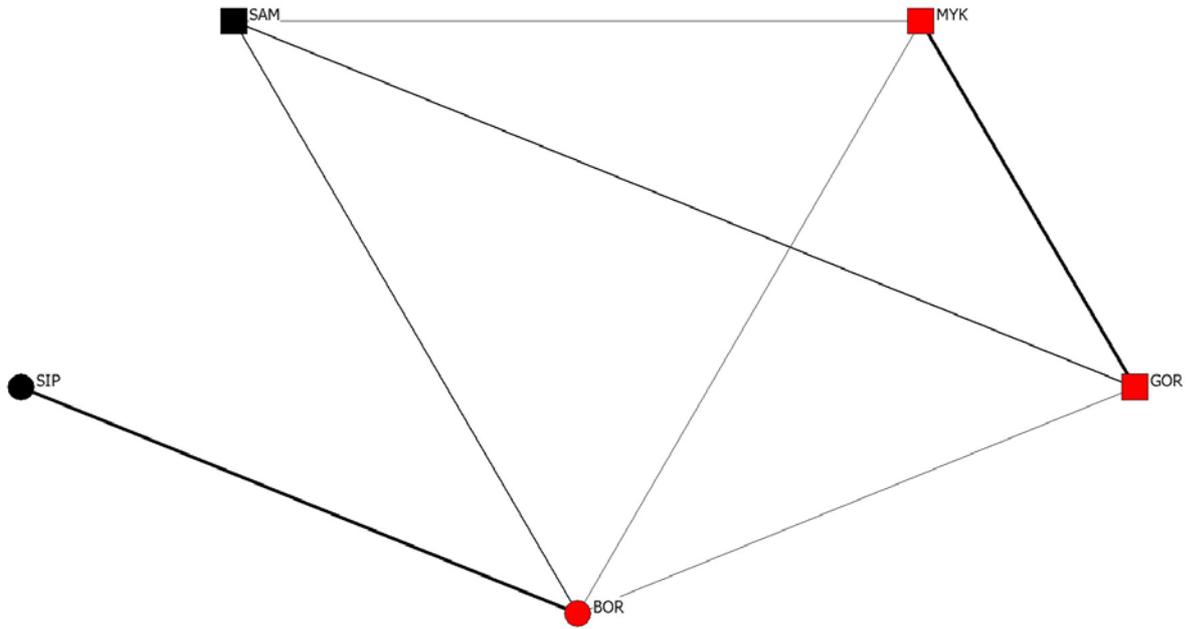


Figure 3 Schematic depiction of the social network of redfronted lemur group B (Open group).

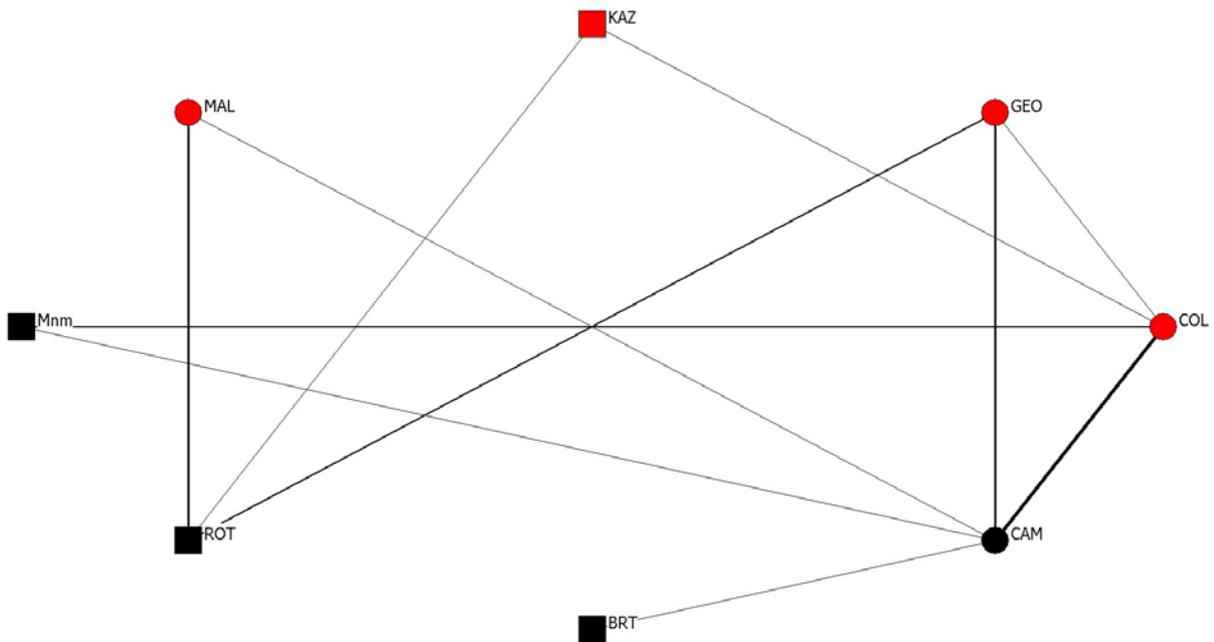


Figure 4 Schematic depiction of the social network of redfronted lemur group J (Open group).

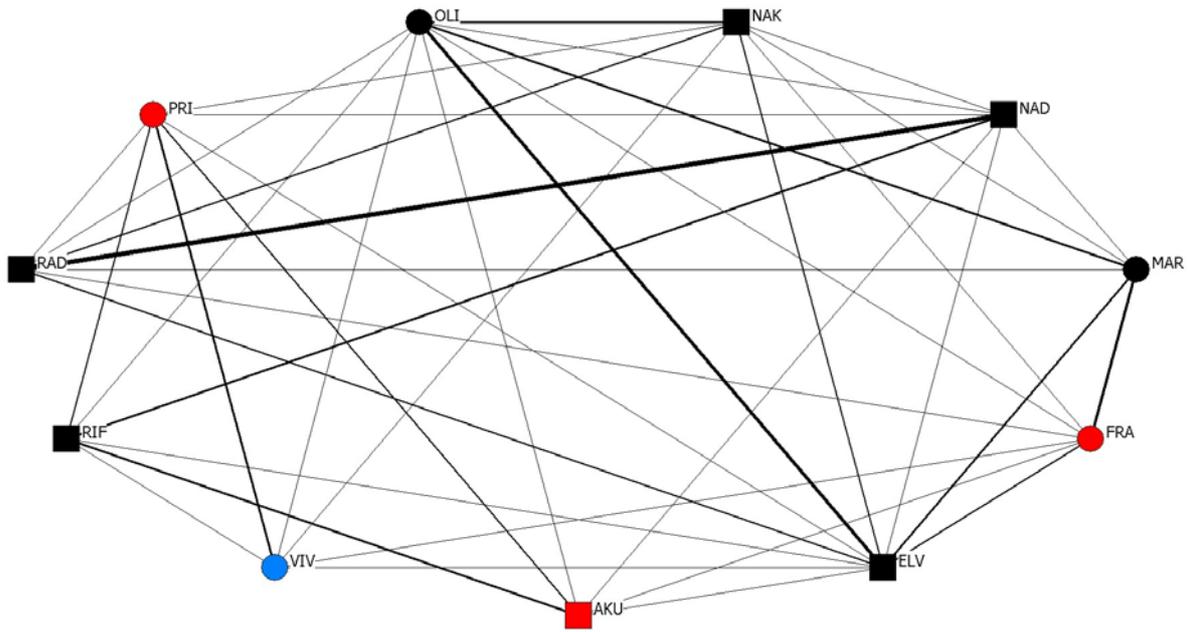


Figure 5 Schematic depiction of the social network of ringtailed lemur group C1 (Lifting group).

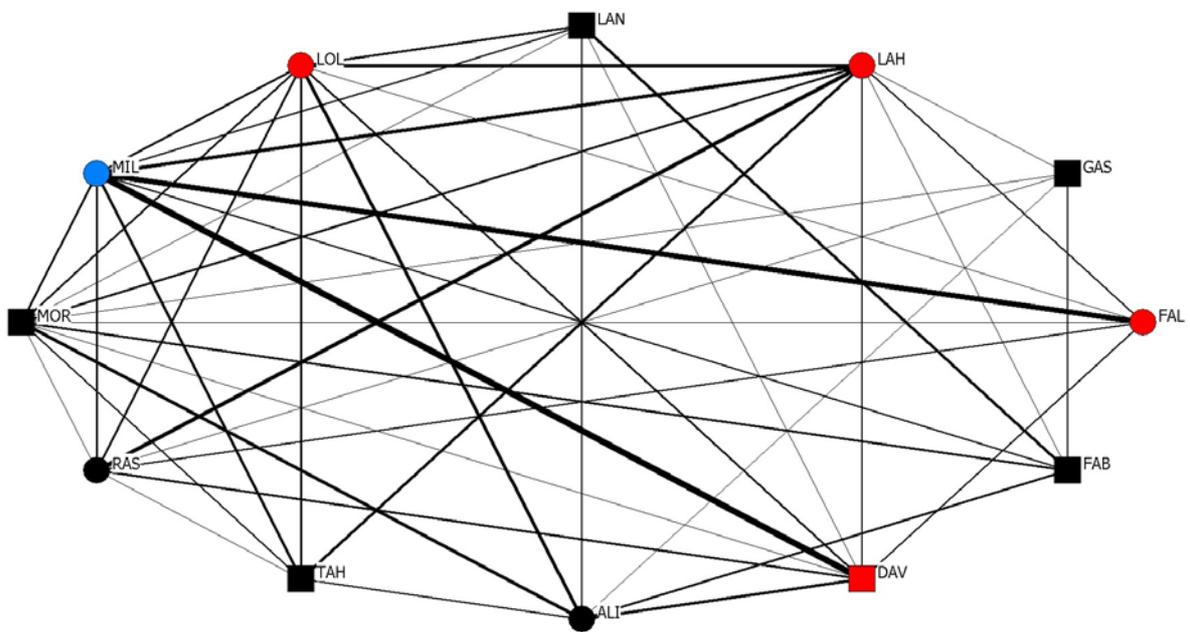


Figure 6 Schematic depiction of the social network of ringtailed lemur group YF (Sliding group).

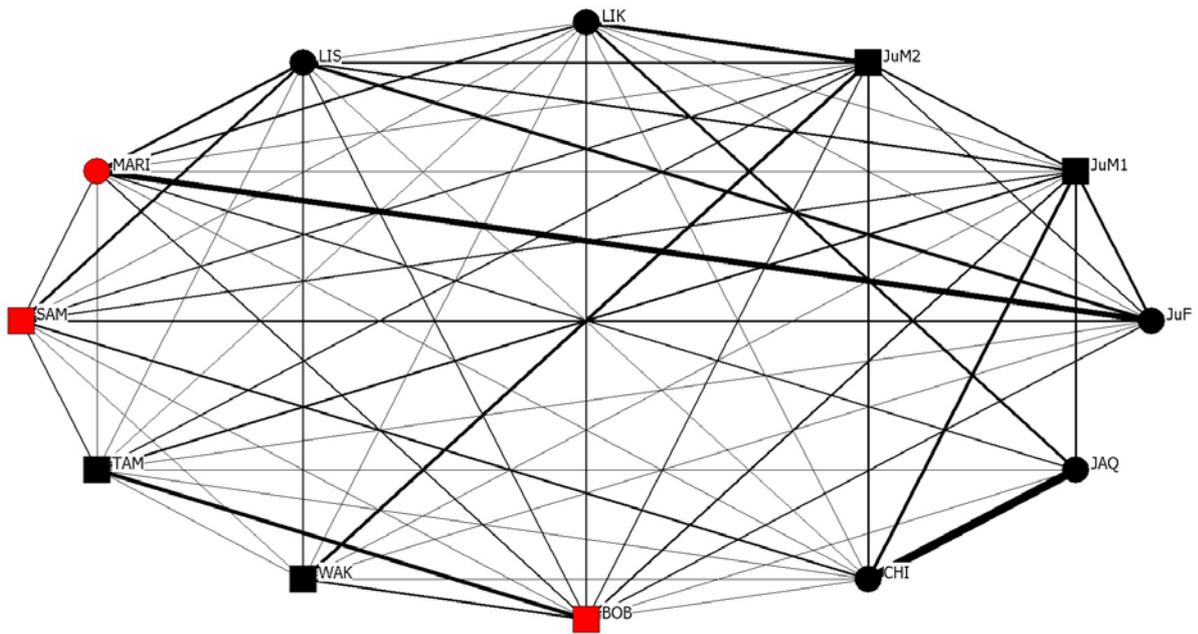


Figure 7 Schematic depiction of the social network of ringtailed lemur group C2A (Open group).

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DECLARATION

I hereby declare that I have written this thesis entitled "Influence of social tolerance on social learning" independently and with no aids or sources than quoted.

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