ROOTS OF PRIMATE COGNITION

The Primate Cognition Test Battery applied to three species of lemurs (*Varecia variegata*, *Lemur catta* and *Microcebus murinus*)

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Summary

In comparison to other, equally-sized mammalian species, primates have relatively large brains and outstanding cognitive skills. Since brain tissue is energetically very costly, several hypotheses on possible selection pressures that might have favoured the evolution of such large brains and increased cognitive skills have been proposed. Some hypotheses focus on ecological aspects, whereas others suggest social complexity as the main factor shaping cognitive evolution. Comparative studies on cognitive abilities of multiple species are essential for answering this evolutionary puzzle. Such studies have been conducted in various haplorhine primates (great apes, Old- & New World monkeys), but systematic studies on cognitive skills in strepsirrhine primates (lemurs & lorises) were missing until now. As strepsirrhines can serve as living models of the ancestral primate state, knowledge about their cognitive abilities could help elucidate the evolution of primate cognition.

Therefore, the aim of my thesis was to first review all existing studies on cognitive skills in lemurs and then to test three species of lemurs in a systematic battery of experiments covering the physical and social cognitive domain. Subjects were black-and-white ruffed lemurs (*Varecia variegata*), ring-tailed lemurs (*Lemur catta*) and grey mouse lemurs (*Microcebus murinus*), chosen for differences in key socioecological traits. To facilitate comparisons to haplorhines, I used the experimental setup of the Primate Cognition Test Battery (PCTB) which has been tested with great apes (chimpanzees & orangutans; Herrmann et al., 2007) and Old World monkeys (baboons & macaques; Schmitt et al., 2012).

Results showed that the three lemur species did not differ significantly in performance and in general had a better understanding of the physical than the social domain. Surprisingly, an overall comparison with the four haplorhine species revealed that although lemurs performed slightly inferior in the physical domain, they were at level with haplorhines in the social domain. Specifically, lemurs were outperformed by haplorhines particularly on the scale on spatial understanding and in the active tool use task. All other scales revealed comparable results for all seven species and in the scale theory of mind lemurs even outperformed great apes. However, in several of the experimental setups results might have been influenced by confounding factors such as lemurs' limited dexterity, local enhancement or the heterospecific human demonstrator in the social tasks, and thus results have to be discussed carefully.

To investigate some of the possible influences on the performance of individuals within cognitive tasks, I incorporated two additional studies on selected tasks of the PCTB. First, I explored whether the reason for the lemurs' poor performance in the tool use task was caused by their limited dexterity. I increased the number of trials by retrieving the stick if it was lost by the subject. In contrast to the original setup in which only one ring-tailed lemur solved the task, in total 13 individuals from all three species managed to obtain the reward. In addition, lemurs performed at the same level as haplorhines in a task testing the understanding of tool properties. Thus, my results revealed that lemurs may lack the necessary fine motor skills to actively use more difficult tools, but they nevertheless appear to have an understanding of tool functionality comparable to naturally tool-using species.

The second additional study concerned the influence that different kinds of demonstrators may have on performance in gaze following tasks and in object-choice tasks using pointing cues. In the original PCTB results may have been biased by only using a human as demonstrator and thus, I additionally presented subjects with photos and videos of conspecifics. Only ring-tailed lemurs followed human gaze. Photos did not have an influence on general performance of lemurs, but videos increased performance in the gaze following task. Comparing two differently handled populations revealed that in the object-choice tasks performance was positively influenced by a high level of socialisation with humans. Thus, performance of individuals in social cognitive tasks can be influenced by the exact nature of the stimulus as well as the level of human socialisation.

The overall results of my thesis suggest that in many aspects of the physical and social domain, haplorhines and strepsirrhines do not differ substantially from each other, at least in the experiments of the PCTB. Since they differ strongly in their absolute brain sizes, my results question the notion of a clear-cut correlation between brain size and cognitive abilities, as well as assumptions of domain-general cognitive skills in primates. My thesis represents the first systematic comparative investigation of the cognitive skills of lemurs and thus provides important insights into the cognitive evolution of primates. However, further comparative studies on a wide range of species using tasks from both cognitive domains are essential to fully understand the evolutionary puzzle of cognition.

Zusammenfassung

Im Vergleich zu anderen Säugetieren haben Primaten in Bezug auf ihre Körpermasse relativ große Gehirne und herausragende kognitive Fähigkeiten. Da das Gehirn energetisch gesehen äußerst kostspielig ist, wurden bereits diverse Hypothesen zu möglichen Selektionsdrücken aufgestellt, welche die Evolution von größeren Gehirnen und erhöhter kognitiver Kompetenz beeinflusst haben könnten. Einige Hypothesen erwägen ökologische Aspekte, während andere die Komplexität des Sozialgefüges als Haupteinfluss für die kognitive Evolution vorschlagen. Um Antworten auf dieses evolutionäre Rätsel zu erlangen, sind vergleichende Analysen der kognitiven Fähigkeiten unterschiedlicher Arten unerlässlich. Diverse Haplorhini-Arten (Menschenaffen, Alt- & Neuweltaffen) wurden diesbezüglich bereits erforscht, aber systematische Untersuchungen der kognitiven Fähigkeiten von Strepsirrhini (Lemuren & Loris) fehlen bislang gänzlich. Dabei sind gerade die Strepsirrhini für die Erforschung der kognitiven Evolution von Primaten besonders geeignet, da sie zu den phylogenetisch basalsten Primaten gehören und als lebendes Modell ursprünglicher kognitiver Fähigkeiten dienen können.

Aus diesem Grund waren die Ziele meiner Doktorarbeit zunächst alle bisherigen Studien zur Kognition in Lemuren zu sichten und zusammenzufassen, sowie anschließend drei Lemurenarten in einer systematischen, experimentellen Testreihe zu untersuchen, die sowohl die technische als auch die soziale Kognition abdeckt. Aufgrund der Unterschiede in ihren sozioökologischen Merkmalen wurden schwarz-weiße Varis (*Varecia variegata*), Kattas (*Lemur catta*) und graue Mausmakis (*Microcebus murinus*) ausgewählt. Desweiteren sollte auch ein Vergleich zu Haplorhini ermöglicht werden, weshalb ich den experimentellen Aufbau der Primate Cognition Test Battery (PCTB) verwendete, welche schon mit Menschenaffen (Schimpansen & Orang-Utans; Herrmann et al., 2007) und Altweltaffen (Paviane & Makaken; Schmitt et al., 2012) durchgeführt wurde.

Die Ergebnisse weisen kaum relevante Unterschiede zwischen den drei Lemurenarten auf. Generell zeigten Lemuren ein besseres Verständnis für Aufgaben aus dem Bereich der technischen als der sozialen Kognition. Vergleiche zu den vier Haplorhini-Arten zeigten überraschenderweise, dass Lemuren im Bereich der technischen Kognition leicht unterlegen, im sozialen Bereich allerdings ebenbürtig waren. Lemuren wurden besonders beim räumlichen Verständnis und im aktiven

Werkzeuggebrauch von Haplorhini übertroffen. In allen anderen Bereichen gab es keine klaren Unterschiede zwischen den sieben Arten, mit der Ausnahme, dass Lemuren im Bereich der *theory of mind* besser abschnitten als Menschenaffen. Allerdings könnten einige der Experimente durchaus durch Faktoren wie die limitierte Fingerfertigkeit von Lemuren, *local enhancement* oder, im sozialen Bereich, durch einen artfremden menschlichen Experimentator beeinflusst worden sein, weshalb diese Ergebnisse auch mit Vorsicht diskutiert werden müssen.

Mit dem Hintergrund einige dieser möglichen Einflüsse auf das Abschneiden in kognitiven Experimenten zu untersuchen, erweiterte ich einige ausgewählte Experimente der PCTB: Zunächst untersuchte ich, ob die limitierte Fingerfertigkeit von Lemuren eine Ursache für ihr schlechtes Abschneiden im aktiven Werkzeuggebrauch sein könnte. Hierfür erhöhte ich für sie die Zahl möglicher Versuche im Vergleich zur ursprünglichen PCTB, in welcher nur ein Katta die Aufgabe lösen konnte. Durch diese Erweiterung schafften es insgesamt 13 Tiere aus allen drei Arten. Zusätzlich zeigten Lemuren ein ebenso gutes Verständnis für die Eigenschaften von Werkzeugen wie Haplorhini. Folglich scheint es Lemuren an der nötigen Fingerfertigkeit zu mangeln um kompliziertere Werkzeuge zu benutzen, jedoch weisen sie ein Verständnis für die Funktionalität von Werkzeugen auf, das vergleichbar zu Arten ist, die von Natur aus Werkzeuge verwenden.

Die zweite Unterstudie befasste sich mit dem Einfluss unterschiedlicher Arten von Stimuli auf die Leistung in Experimenten zum *gaze following* und zur Objektwahl mittels Zeigegesten. In der ursprünglichen PCTB könnten die Ergebnisse dieser Tests verfälscht worden sein, da nur mit einem menschlichen Experimentator gearbeitet wurde. Deshalb präsentierte ich zusätzlich Fotos und Videos von Artgenossen als soziale Stimuli. Nur Kattas folgten der Blickrichtung des menschlichen Experimentators, allerdings hatten auch Fotos keinen positiven Einfluss auf die Lemuren; nur Videos führten zu einer besseren Leistung im *gaze following*-Experiment. Der Vergleich von zwei Populationen mit unterschiedlich starkem Menschenkontakt zeigte, dass im Experiment zur Objektwahl die Leistung der Tiere durch ein hohes Maß an Sozialisierung zum Menschen positiv beeinflusst wurde. Folglich kann die Leistung in Experimenten zur sozialen Kognition durch die Art des Stimulus sowie das Maß an Sozialisierung zu Menschen beeinflusst werden.

Insgesamt legen meine Ergebnisse nahe, dass Haplorhini und Strepsirrhini in vielen Aspekten der technischen und sozialen Kognition nur geringfügige Unterschiede aufweisen, zumindest in den Experimenten der PCTB. Da sich beide Gruppen jedoch stark in ihren absoluten Gehirngrößen unterscheiden, stellen meine Ergebnisse die Annahmen einer eindeutigen Verbindung zwischen Gehirngröße und generellen kognitiven Fähigkeiten, sowie bereichsübergreifender kognitiver Fähigkeiten in Primaten in Frage. Meine Doktorarbeit stellt die erste systematische und vergleichende Untersuchung kognitiver Fähigkeiten von Lemuren dar und liefert dadurch wichtige Einblicke in die kognitive Evolution von Primaten. Dennoch sind weitere vergleichende Studien mit einer Vielzahl von Arten und mit einem breitgefächerten experimentellen Aufbau, welcher beide kognitiven Bereiche abdeckt, unerlässlich um das evolutionäre Rätsel der Kognition zur Gänze zu verstehen.

General Introduction

"Closeness to animals creates the desire to understand them, and not just a little piece of them, but the whole animal. It makes us wonder what goes on in their heads even though we fully realize that the answer can only be approximated."
(de Waal, 2001 p. 40)

With this statement, Frans de Waal describes the basis of the field of animal cognition, which is the study of the mental and cognitive capacities of animals. At the same time, he points out one of its main weaknesses, as cognitive mechanisms can only be studied indirectly by observing the animals' behaviour and performance in cognitive tests (Byrne, 2000). Still, the comparative investigation of the cognitive skills of animals, and especially non-human primates, allows integrating findings from morphology and behaviour (Byrne, 2000), which is of great importance for understanding how selective environmental forces have shaped cognitive abilities (Byrne, 1995; Shettleworth, 2010). Commonly accepted, Shettleworth (2010 p. 4) defined the term *cognition* as "*the mental processes by which we acquire, process, store and act on information from the environment including perception, learning, memory and decision-making*". In general, cognitive abilities are divided into skills belonging to the physical domain, which deals with the spatial-temporal-causal relations of inanimate objects, and the social domain, which encompasses intentional actions, perceptions and knowledge of conspecifics and other animate beings (Tomasello & Call, 1997).

Since the first cognitive studies in chimpanzees nearly 100 years ago (Koehler, 1925; Yerkes & Yerkes, 1929), the field of comparative cognition has grown enormously in the last decades (e.g. Rogers & Kaplan, 2004; Bentley-Condit & Smith, 2010; Shettleworth, 2010; Menzel & Fischer, 2011). The majority of studies were conducted in mammals, such as cetaceans (e.g. Marino, 1996; Smolker et al., 1997; Tschudin et al., 2001; Connor, 2007), carnivores (e.g. Holekamp et al., 2007; Benson-Amram et al., 2016), rodents (e.g. Klement et al., 2008; Schweinfurth & Taborsky, 2016), domestic animals like dogs, goats or horses (e.g. Hare et al., 2002; Kaminski et al., 2005; Maros et al., 2008) and of course various primate species (e.g. Whiten et al., 1999; Herrmann et al., 2007; Amici et al., 2010; Rosati et al., 2010; Schmitt et al., 2012; MacLean et al., 2013). However, birds, particularly corvids and parrots, have also been the focus of multiple studies, which indicated that in many aspects they may possess cognitive skills equal to those of primates (e.g. Bugnyar et al., 2004; Clayton & Emery, 2005; Seed et al., 2006; Emery & Clayton, 2009; Isler & van Schaik, 2009; Auersperg et al., 2011; Güntürkün & Bugnyar, 2016). Studies on reptiles, fish or invertebrates are still rather rare, but their numbers have been increasing in the last years as well (e.g. Wilkinson et al., 2010; Schluessel & Bleckmann, 2012; Schluessel et al., 2015; Loukola et al., 2017). However, our understanding of the cognitive evolution and the distribution of cognitive capacities between taxa and species is still incomplete and studies which systematically test cognitive abilities of multiple species are scarce. To complete this puzzle, such systematic studies are essential, as they enable comparisons of cognitive skills and brain sizes between different species, and connect these cognitive adaptations to the species-specific ecological and social environments (MacLean et al., 2012).

Throughout this general introduction, I will briefly explain why primates are of particular interest for studies on comparative cognition and review the main theories concerning the cognitive evolution in general and particularly in primates. Subsequently, I will introduce the Primate Cognition Test Battery (PCTB) and provide an overview on the species that have so far already been tested. Finally, I will shortly explain the importance of lemurs for cognitive comparisons and highlight the most crucial aspects of the three lemur species which were tested in my studies.

1.1 Why study Cognition in Primates?

Since the beginning of cognitive research, non-human primates and especially chimpanzees have been the centre of attention. The main reason is most likely their close relatedness to humans (e.g. Pruefer et al., 2012), suggesting that by investigating their cognitive abilities, implications can be drawn concerning our own cognitive evolution. Another reason for the high interest in primate cognition is that all primates have evolved larger brains and superior cognitive skills in comparison to equally-sized mammal species. Within the primate order, this effect even increases disproportionately from strepsirrhines (lemurs, lorises & galagos), to haplorhines (New- & Old World monkeys), to hominins (apes) and finally to humans, which have the largest brains and a unique set of cognitive skills (Jerison, 1973; Dunbar, 1992; Isler et al., 2008; Kappeler & Silk, 2010).

But does a bigger brain automatically imply increased cognitive skills? Opinions are still deeply divided on whether any measure of brain size, be it relative (brain/body-ratio) or absolute brain size (measured in cc or g), can predict cognitive capabilities in animals and especially non-human primates (Byrne, 1996; Reader & Laland, 2002; Emery & Clayton, 2004; Deaner et al., 2007). The fact that brain tissue is metabolically extremely expensive (Jerison, 1973; Aiello & Wheeler, 1995) raises the question about the evolutionary forces selecting for such large brains and exceptional cognitive abilities in primates, and particularly humans (Herrmann et al., 2007; Shettleworth, 2010; Navarrete et al., 2011).

1.2 How did (Primate) Cognition Evolve?

Several mutually non-exclusive hypotheses explaining the evolution of primate brain size and cognition have been suggested so far. These theories can be categorised depending on whether they see primate cognition as a more domain-general or domain-specific ability (Reader & Laland, 2002). There are two main hypotheses following the domain-general assumption. First, the *General intelligence hypothesis* (Spearman, 1904) states that humans had evolutionary advantages through their larger brains by simply being cognitively more efficient than other species, which would imply advantages in terms of faster learning and possessing more memory. This hypothesis predicts an elevation in human cognition compared to non-human primates which is uniform between the physical and social domain. Still, it remains controversial and has recently met renewed opposition (Herrmann et al., 2007).

The second domain-general hypothesis, the *Ecological intelligence hypothesis*, arose from research on non-human primates. It suggests that skills required for finding and memorizing seasonally available fruits or for tool use and extractive foraging are the driving force for brain size evolution (Clutton-Brock & Harvey, 1980; Milton, 1981; Byrne, 1996). In accordance, Aiello and Wheeler (1995) proclaimed in their expensive-tissue hypothesis that energetically costly large brains could have only evolved in species with a rich diet, such as fruits. In line with this, frugivorous primates were found to have larger brains and increased cognitive skills compared to folivorous species (e.g. Clutton-Brock & Harvey, 1980; Rosati et al., 2014). Furthermore, the *Ecological intelligence hypothesis* has recently received support by a comprehensive meta-analysis on over 140 species of primates (DeCasien et al., 2017). By including multiple socioecological variables of each species in a phylogenetic model, the results of this study mainly exclude social measures, such as group size or social system, as possible explanations for brain size variations in primates (*Social brain hypothesis*, see below). Instead, authors showed a correlation between the diet of a species and its brain size, also in favour of frugivorous species (DeCasien et al., 2017; Venditti, 2017).

As a more domain-specific hypothesis, Byrne and Whiten (1988) introduced the *Social brain hypothesis* (Jolly, 1966a; Humphrey, 1976; Dunbar, 1992; also called *Social intelligence hypothesis* or *Machiavellian Intelligence hypothesis*). It posits that the complexity of the social skills of primates, which evolved in response to the cognitive demands of constant competition and cooperation between group members, has ultimately driven the distinctive cognitive evolution of primates (Dunbar, 1998, 2003, 2009; Zuberbühler & Byrne, 2006; Byrne & Bates, 2010). This hypothesis was supported by several studies across primates, showing positive correlations between social factors, such as group size, and relative brain size (or neocortex size; e.g. Dunbar, 1992, 2003; Kudo & Dunbar, 2001; Byrne & Corp, 2004; MacLean et al., 2013). Complex fission-fusion dynamics in primate social groups have also been associated with enhanced cognitive abilities in tasks of inhibitory control (Amici et al., 2008). Interestingly, in bats and some insectivores, relative brain size also correlates with social group size (e.g. Barton et al., 1995; Dunbar & Bever, 1998; Byrne & Bates, 2010), whereas in carnivores this relationship is rather disputed (Dunbar & Bever, 1998; Dunbar & Shultz, 2007; Holekamp et al., 2007; Pérez-Barbería et al., 2007; Finarelli & Flynn, 2009; Benson-Amram et al., 2016), and no such direct correlation was found in ungulates (Shultz & Dunbar, 2006, 2007). Moreover, highly developed cognitive abilities have been described for some birds, in particular in several corvid species (Emery et al., 2007), which cannot be explained by an effect of group size since they are usually social monogamists (Byrne & Bates, 2010). Hence, the generality of the *Social brain hypothesis* across orders is still being debated and, as mentioned above, it has recently been questioned by DeCasien and colleagues (2017; see also MacLean et al., 2014).

Two additional hypotheses that derive from the *Social brain hypothesis* have also been proposed rather recently, to specifically account for the relatively large brains of primates and humans. First, based on the assumption that humans are not just social but “ultra-social” (Richerson & Boyd, 1998; Herrmann et al., 2007), the *Cultural intelligence hypothesis* suggests that culture would select for intelligence and argues that exchanging knowledge within cultural groups of humans requires some specific socio-cognitive skills, such as social learning, special forms of communication and a “theory of mind” (Herrmann et al., 2007, 2010; Burkart et al., 2007, 2009; van Schaik & Burkart, 2011). Supporting this hypothesis, in a comprehensive, comparative study on the cognitive skills of children, chimpanzees and orangutans, Herrmann and colleagues (2007) found that these species performed equally well in the physical domain, but that children outperformed great apes in the social domain. As previously mentioned, they also contradicted the *General intelligence hypothesis* with these results.

Second, the *Cooperative breeding hypothesis* states more specifically that extensive allomaternal care, i.e. care for the offspring provided by individuals other than the mother, has a positive impact on prosocial behaviour and social cognition (Hrdy, 1999, 2009; Burkart et al., 2007, 2009; Burkart & van Schaik, 2010; van Schaik & Burkart, 2011). Cooperative breeding is accompanied by psychological changes that lead to greater prosociality, which directly enhances performance in social cognition, i.e. social learning, vocal communication, teaching-like behaviours, gaze understanding and cooperative problem solving (Burkart et al., 2009, Burkart & van Schaik, 2010). Accordingly, primates exhibiting higher levels of allomaternal care should perform better in the socio-cognitive domain than primates with lower levels of allomaternal care (Burkart et al., 2009; van Schaik & Burkart, 2011).

Nevertheless, as mentioned previously, most of these hypotheses are not mutually exclusive and an increasing number of researchers agree that cognitive evolution is most likely based on several selection pressures acting together (Seyfarth & Cheney, 2002; Healy & Rowe, 2007; Burkart et al., 2016). To fully understand the evolution of primate and human cognition it seems mandatory to conduct systematic, comparative studies on the capabilities within both cognitive domains and across the entire primate order and beyond.

1.5 The Primate Cognition Test Battery (PCTB)

In the attempt to compile a comprehensive series of tests that would investigate a great variety of cognitive skills, Esther Herrmann and colleagues assembled the *Primate Cognition Test Battery* (PCTB; Herrmann et al., 2007). This systematic comparative analysis consists of 16 different experiments from the physical, as well as the social domain (for a detailed description see *Chapter 3*). The ten tasks of the physical domain can be grouped into three scales, namely space, quantities and causality. As these abilities are, for example, necessary to locate, evaluate and remember objects in space, they are essential for everyday survival when used to avoid predators or forage for food. The six tasks of the social domain of the PCTB can also be grouped into three different scales, which are social learning, communication and theory of mind. Interacting socially with other individuals, for example by following their gaze, communicating actively or understanding each other’s intentional actions, is an important way of information transfer to spot predators, locate food sources or gain social knowledge within a group (Tomasello et al., 1998; Emery, 2000; Dunbar, 2003; Zuberbühler & Byrne, 2006; Zuberbühler, 2008).

With this compilation of tasks, Herrmann et al. (2007) tested the cognitive skills of 2.5-year-old children and compared them to those of chimpanzees (*Pan troglodytes*, N=106) and orangutans (*Pongo pygmaeus*, N=32). Their results showed that children and chimpanzees had very similar cognitive skills for dealing with the physical world (both being slightly more successful than orangutans), while children had the most sophisticated cognitive skills for dealing with the social world. Hence, these results contradict the hypothesis that humans are generally more intelligent than other primates, but support the *Cultural intelligence hypothesis*.

Only a few years later, Vanessa Schmitt and colleagues ran the same test battery on olive baboons (*Papio anubis*, N=5) and long-tailed macaques (*Macaca fascicularis*, N=10-13), to compare the results of humans and great apes to those of monkeys (Schmitt et al., 2012). Surprisingly, the results of this study revealed that both Old World monkey species had cognitive abilities largely comparable to those of great apes. Specifically, chimpanzees performed better than macaques only in tasks on spatial understanding and tool use, but in none of the tasks concerning social cognition. Since chimpanzees have relatively larger brains than macaques or baboons (Jerison, 1973; reviewed in Kudo & Dunbar, 2001), the results of the same tests applied to these four primate species questioned the clear-cut relationship between cognitive performance and brain size (Schmitt et al., 2012).

In conducting some of the experiments of the PCTB with white-handed gibbons (*Hylobates lar*, N=5-8), in her dissertation Anna Yocom (2010) included another haplorhine primate species in the comprehensive species comparison. Since she did not complete the entire set of experiments of the PCTB, I did not include her results in the overall comparison of all non-human primate species (see *Chapter 3*). Still, gibbons, as lesser apes, fall in-between great apes and monkeys and therefore remain interesting for the overall comparison. Hence, I will include a brief comparison of their results with the performance of lemurs in the discussion (see *Chapter 6*). The gibbons overall performed better than the great ape and monkey species in the physical domain, but they performed inferior to all of them in the social domain. Their poor performance in the latter might originate in their social structure of very small, pair-bonded groups (Bartlett, 2007; Yocom, 2010).

However, looking at the test battery more closely, the comparison between children and non-human primates in the two domains might be biased from the beginning (Yocom, 2010; Schmitt et al., 2012). After all, all social tasks are carried out with a human as demonstrator, which implies that the children work with a conspecific, whereas the non-human primate species do not. The disadvantage of having a heterospecific demonstrator may easily lead to an underestimation of the non-human primates' cognitive abilities in the social domain (Boesch, 2007; Ruiz et al., 2009; Botting et al., 2011). Moreover, while testing children, the experimenters occasionally asked motivating questions, such as "*Where did the toy go?*", whereas non-human primates had no such additional input on the experimental setup. Accordingly, in addition to the original setup of the test battery, I modified demonstrators in two social cognitive tasks in order to quantify differences in the subjects' performance between various demonstrators (see *Chapter 5*).

In summary, this comprehensive test battery has been conducted with five haplorhine non-human primate species in the past years, while strepsirrhine primates have been neglected. Hence, the quest to understand the cognitive evolution of primates remains incomplete.

1.3 Why study Cognition in Lemurs?

"*Lemurs are […] 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 p. 165-166)

Since this quote by Allison Jolly, a variety of experiments and observations have already shown that lemurs are in physical cognitive tasks not quite as stupid as she suggested in the early days of research on strepsirrhine primates. Nevertheless, as there is still no systematic and comprehensive investigation on the cognitive skills of strepsirrhine primates, this is the next logical step on the way to understanding the evolution of primate cognition. Within the primate order, strepsirrhine primates constitute the evolutionarily most distant relatives of humans and apes (Yoder, 2007). They split from the main primate lineage approximately 60 million years ago, and retained many ancestral primate traits (Yoder et al., 1996; Martin, 1990; Yoder & Yang, 2004). As an example, strepsirrhines are not able to oppose their thumbs and have therefore a rather limited dexterity (Torigoe, 1985) since they lack a precision grip (Holtkötter, 1997). Thus, they might be physically unable to perform certain tasks of the PCTB which require a high level of manual precision. To acknowledge and at least partly quantify these constraints, I offered additional trials in one of these tasks, in order to investigate whether lemurs would be able to solve it at all (see *Chapter 4*).

Previous comparative research has already established multifold variations in relative brain size across the more than 400 species of primates (Dunbar & Shultz, 2007; Isler et al., 2008), with a significant part of the interspecific variation being explained by the shift between strepsirrhines and haplorhines (Martin, 1981). Not only do strepsirrhines have relatively smaller brains than haplorhines, but their brain size does not correlate with group size (MacLean et al., 2009). Hence, they represent the best living models of the earliest primates and the link between primates and other mammalian orders (MacLean et al., 2008; Fichtel & Kappeler, 2010) and studying their cognitive skills would certainly shed light on the evolution of cognition in primates.

However, in contrast to haplorhines, the cognitive abilities of strepsirrhine primates have only been studied fragmentarily and not in a comprehensive systematic approach (reviewed in Fichtel & Kappeler, 2010; Kittler et al., 2015; see *Chapter 2*). Therefore, a comparison of a representative range of cognitive skills across all primates is currently not possible. Moreover, the existing studies on cognitive skills in strepsirrhines and especially lemurs revealed contradicting results: For the physical domain, older studies suggest that lemurs possess cognitive abilities inferior to haplorhines' (e.g. Maslow & Harlow, 1932; Jolly, 1964; Ehrlich et al., 1976), whereas in more recent studies lemurs' physical cognitive skills often match those of haplorhines (e.g. Santos et al., 2005b; Lührs et al., 2009). Information on the social cognitive skills of strepsirrhines is even more contradictory. Some studies on lemurs have reported social cognitive skills comparable to other primates in specific aspects, such as social learning (e.g. Schnoell & Fichtel, 2012). Observations on wild lemurs indicate however, a lack of certain social cognitive skills, such as abilities of within-group coalitions or tactical deception (reviewed in Fichtel & Kappeler, 2010; Kappeler, 2012; both domains summarised in *Chapter 2*).

In summary, the existing knowledge on cognition in lemurs is still rather fragmented. Therefore, a comprehensive, systematic and most of all comparative study on the cognitive abilities of lemurs that covers multiple species and works with a sufficient number of individuals per species, seems overdue. Such a comparative investigation of lemurs' cognitive capacities would help to complete the picture of primate cognitive evolution.

1.4 The Lemur Species of my Study

Selecting species for comparison which differ in key socioecological traits (see Table 1), such as ring-tailed lemurs (*Lemur catta*), black-and-white ruffed lemurs (*Varecia variegata*) and grey mouse lemurs (*Microcebus murinus*), facilitates the testing of the hypotheses mentioned above. Thus, the most important differences between these three lemur species lie within their brain sizes, social organisation and level of allomaternal care. Absolute brain size increases from mouse lemurs to ring-tailed lemurs and to ruffed lemurs (e.g. Dunbar, 1992; Isler et al., 2008; MacLean et al., 2013), whereas mouse lemurs are solitary foragers and ring-tailed and ruffed lemurs are group-living with different average group sizes. Concerning the level of allomaternal care, in ruffed lemurs parental care is shared among all community members and even allonursing and adoption of rejected infants have been observed (Pereira et al., 1987; Morland, 1990; Sussman, 1999; Vasey, 2007; Baden et al., 2013). Mouse lemur females can form sleeping-groups during the day, in which related females care for all offspring present, including allonursing (Eberle & Kappeler, 2006). In contrast, in ring-tailed lemurs the mother is the primary caregiver for the first three weeks of life (Hosey & Jacques, 1994). Thus, the extent of allomaternal care gradually decreases from ruffed lemurs, to mouse lemurs and to ring-tailed lemurs.

Table 1 Detailed socioecological traits of the three tested lemur species.

	Ruffed lemurs (*Varecia variegata*)	**Ring-tailed lemurs** (*Lemur catta*)	**Grey mouse lemurs** (*Microcebus murinus*)
activity pattern	diurnal	diurnal	nocturnal
feeding ecology	frugivorous	omnivorous	omnivorous
main diet	fruits, nectar (leaves)	fruits, leaves, buds, insects	insects, nectar, gum, fruits
social organisation	group-living, dynamic fission-fusion system	group-living	solitary foragers, female sleeping-groups
group size[1]	5.4	15.6	1
brain size (cc)[2]	32.12	22.90	1.63
body mass (g)[2]	3512	2200	60
litter size[4]	2-3 (4)	1 (2)	2-4
nest building	yes	no	yes
parking	yes, guarded by other group members	no	yes, not guarded
infant transport[3]	by mouth between parking spaces	cling to their mothers' belly or back	by mouth between parking spaces
allomaternal care[4]	high*	low*	medium*
communal breeding	yes	no	yes (females)
indications	guarding, grooming, carrying (all group members), allonursing & adoption (related females)	grooming, occasionally carrying & allonursing (related females)	grooming, allonursing & adoption (related females)

* Level of allomaternal care among the three species; [1]MacLean et al., 2014; [2]Isler et al., 2008; [3]Ross, 2001; [4](Hosey & Jacques, 1994; Eberle & Kappeler, 2006; Vasey, 2007; Baden et al., 2013).

1.6 Objectives and Structure of this Thesis

The aim of this thesis was to systematically examine the cognitive abilities of three lemur species in a set of tasks covering many aspects of the physical and social cognitive domain and compare their results to those of previously tested great ape and monkey species. To do this I replicated the methodology of the Primate Cognition Test Battery, which was developed and tested on chimpanzees and orangutans by Herrmann et al. (2007), and later applied to baboons and macaques by Schmitt et al. (2012). To attain a meaningful dataset that allows reasonable interspecific comparisons, one of my aims was to include highest possible sample sizes for each species. Similar to both preceding studies on the PCTB, I also investigated some of the aspects that might influence the performance of the individuals in the cognitive experiments irrespective of species, such as rank level in the group, personality traits or level of inhibitory control. Finally, I adapted some of the test paradigms of the PCTB in additional experiments to make them more suitable for lemurs and to answer some specific questions.

In the chapters of my thesis I start with a review on what is already known about cognitive skills in lemurs and then present the overall results of the PCTB in comparison to the haplorhine species. I continue with two chapters on more elaborated tasks from the physical and social domain of the PCTB. In the end, I review and discuss all my results in a greater context. In detail, the chapters are ordered as follows:

Chapter 2 reviews studies reporting on the cognitive abilities of lemurs in the physical and social domain, with a special focus on ring-tailed lemurs as they are the most frequently studied lemur species. This manuscript was published in a special issue on ring-tailed lemurs of *Folia Primatologica*.

Chapter 3 summarises and compares the performance of all three lemur species in the PCTB. Their performance is also compared to the monkey and ape species, and the general implications of these results for cognitive testing and theories on the evolution of primate cognition are discussed. This manuscript was submitted to *Animal Cognition*.

Chapter 4 focusses on an aspect of physical cognition, the active usage of tools and the understanding of their crucial properties. Therefore, I elaborate on two of the tasks of the physical domain of the PCTB (*tool use* and *tool properties*) and discuss their applicability to lemurs. This manuscript was accepted for publication by the *Journal of Comparative Psychology*.

Chapter 5 investigates an important aspect of the social cognitive domain of the PCTB in more detail: The social-visual co-orientation. Additional trials were conducted for the *gaze following* task and the *comprehension* task of the PCTB, to investigate how performance varies with three kinds of demonstrators, a human experimenter, a conspecific modelled in photos and one modelled in videos. This manuscript was submitted to *Animal Cognition*.

Chapter 6 summarises and discusses various aspects of the results of my studies as well as the problems associated with a comparative cognitive approach. Possible future steps towards a comprehensive picture of the evolution of primate cognition are also proposed.

Chapter 2

Cognition in Ring-tailed Lemurs (review)

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Author Contributions

AS drafted the section on social cognition; KK drafted the abstract, the introduction and the section on physical cognition; KK assembled the summarising table for both cognitive domains; CF supervised both and participated in writing the manuscript

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 haplorhine 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 haplorhines. Here, we review studies investigating cognitive abilities in the technical and social domain of ring-tailed lemur cognition. In the physical domain, ring-tailed lemurs exhibit similar qualitative cognitive skills as other lemurs but also haplorhine primates. In the social domain, ring-tailed lemurs appear to be more skilled in visual perspective taking than other lemurs. Compared to other lemurs, they also have highly elaborated communicative skills. Moreover, within-group coalitions have been observed in female ring-tailed lemurs during rare events of female evictions but not in other lemur species. However, in several other aspects of social cognition, such as reconciliation and social learning, ring-tailed lemurs' cognitive abilities are en par with those of other lemurs. Thus, additional systematic comparative studies in physical and social cognition are required for a more comprehensive understanding of the processes of cognitive evolution among primates.

Keywords: Ring-tailed 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 & van Schaik, 2009). These effects also increase disproportionately within the primate order from strepsirrhines to haplorhines to hominins and humans (Dunbar, 1992; Isler et al., 2008). Given that larger brains are energetically more expensive (Aiello & 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 is of particular interest because after their split from other primates about 60 million years ago (Yoder et al., 1996; Yoder & 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 & Kappeler, 2010). However, cognitive abilities of strepsirrhine primates remain understudied, and the existing studies revealed conflicting results.

Alison Jolly (1966a) 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, 1966a: 165-166). Accordingly, these older studies suggested that lemur cognitive abilities in the physical domain are inferior to those of haplorhines (e.g. Maslow & Harlow, 1932; Jolly, 1964; Ehrlich et al., 1976), but more recent studies indicated that their cognitive abilities often match those of haplorhines (reviewed in Fichtel & Kappeler, 2010).

Here, we review the cognitive abilities of ring-tailed lemurs (*Lemur catta*), which live in multi-male, multi-female groups with one of the largest group sizes among lemurs and which exhibit clear dominance hierarchies (Sauther et al., 1999; Jolly et al., 2006). These aspects of their social system allow evaluation of the influence of social complexity on cognition by comparing cognitive abilities of ring-tailed lemurs with those of other lemur species organized into smaller groups. These same features make them comparable to many haplorhines (Jolly, 1966a, b; Kappeler, 2012), 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 ring-tailed 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 of spatial memory in four lemur species (Table 1) revealed that frugivorous lemurs have more robust spatial memory than folivorous species, with ring-tailed lemurs exhibiting intermediate spatial cognitive abilities (Rosati et al., 2014). However, solitary wild grey mouse lemurs with an omnivorous diet also learned the spatial location of feeding sites rapidly (Lührs et al., 2009).

Regarding numerical understanding, ring-tailed lemurs are able to form abstract numerical ascending rules and can apply them to novel sets of numerosities (Merritt et al., 2011). Furthermore, ring-tailed 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, ring-tailed 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 & Brannon, 2012). In addition, the precision of their approximate number system is comparable to that of rhesus monkeys (*Macaca mulatta;* Jones et al., 2014).

Ring-tailed lemurs are also able to organize sequences in memory and to retrieve ordered sequences. Indeed, their accuracy and response times were similar to haplorhine monkeys (Merritt et al., 2007). Moreover, ring-tailed 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).

Table 1 The cognitive abilities of *Lemur catta* and comparison with other lemur species.

a Physical/technical intelligence

Categories	Species	Common name	n	Success?	n success or mean %	Reference
Space and objects						
Spatial memory	*Lemur catta*	ring-tailed lemurs	9-12	y/n*	55.0% & 95.0%	Rosati et al., 2014
	Eulemur mongoz	mongoose lemurs	11	y/n*	60.6% & 77.3%	
	Propithecus coquereli	Coquerel's sifakas	12-13	y/n*	56.9% & 87.3%	
	Varecia sp.	ruffed lemurs	12-15	y	80.0% & 95.8%	
	Microcebus murinus	mouse lemurs	6	y	4	Lührs et al., 2009
Inhibitory control	*Lemur catta*	ring-tailed lemurs	11	y	-	MacLean et al., 2013
	Eulemur fulvus	brown lemurs	10	y	-	
	Eulemur macaco	black lemurs	10	y	-	
	Eulemur mongoz	mongoose lemurs	10	y	-	
	Propithecus coquereli	Coquerel's sifakas	10	y	-	
	Varecia variegata	ruffed lemurs	11	y	-	
Tools and causality						
Simple box	*Lemur catta*	ring-tailed lemurs	18	y	8 / -	Kappeler, 1987
	Lemur catta	ring-tailed lemurs	28	y	-	Kendal et al., 2010
	Eulemur macaco	black lemurs	4	y	2 / -	Fornasieri et al., 1990
	Eulemur fulvus	brown lemurs	8	y	2 / -	
	Lemur catta	ring-tailed lemurs	4	y	3 / -	
	Eulemur fulvus	brown lemurs	12	y	8(4) / -	Anderson et al., 1992
	Eulemur rufifrons	redfronted lemurs	37	y	20	Schnoell & Fichtel, 2012
Understanding of tools	*Lemur catta*	ring-tailed lemurs	3	y	-	Santos et al., 2005b
	Eulemur fulvus	brown lemurs	3	y	-	
	Daubentonia madagascariensis	aye-ayes	6	n	0	Sterling & Povinelli, 1999
Features and categories						
Learning sets	*Lemur catta*	ring-tailed lemurs	5	y	5 / -	Ohta et al., 1984
	Eulemur macaco	black lemurs	3	y	3	Cooper, 1974
Serial ordering	*Lemur catta*	ring-tailed lemurs	2	y	2 / -	Merritt et al., 2007
Quantities						
Estimating numerosity	*Lemur catta*	ring-tailed lemurs	31	y	-	Jones & Brannon, 2012
	Eulemur mongoz	mongoose lemurs	9	y	89.5%	Lewis et al., 2005

Simple arithmetic operations of 1+1	*Lemur catta*	ring-tailed lemurs	6	y	-	Santos et al., 2005a
	Eulemur fulvus	brown lemurs	6	y	-	
	Eulemur mongoz	mongoose lemurs	4	y	-	
	Varecia rubra	ruffed lemurs	3	y	-	
Numerical rule-learning	*Lemur catta*	ring-tailed lemurs	2	y	2 / -	Merritt et al., 2011

y=yes; n= no; *= depending on the task

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. Ring-tailed lemurs are able to choose 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; Fornasierei et al., 1990; Anderson et al., 1992; Kendal et al., 2010; Schnoell & 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., 2010). Ring-tailed 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 cognitive domain are qualitatively similar to those of other lemurs, but also to those of many haplorhine primates (Fichtel & Kappeler, 2010).

Social Cognition

In contrast to haplorhine 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, ring-tailed lemurs exhibit some similarities in social organization and social structure with haplorhines (Kappeler, 1999), suggesting convergent socio-cognitive evolution (Sandel et al., 2011). Below, we will summarize the current knowledge of ring-tailed 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.

Ring-tailed lemurs live in multi-male, multi-female groups with some of the largest group size among lemurs (Kappeler, 2012). Males and females exhibit separate linear dominance hierarchies (Jolly, 1966b), but rank is not inherited maternally as in many Old World primates (Kappeler, 1993a). Ring-tailed 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). Ring-tailed lemurs mastered transitive interference 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 social behaviour that is exhibited by many haplorhine primates is reconciliation after aggression, and some studies suggest that ring-tailed lemurs do reconcile after conflicts (Rolland & Roeder, 2000; Palagi et al., 2005), whereas other studies found no evidence for it (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 ring-tailed lemurs. Although male ring-tailed as well as redfronted lemurs tend to form partnerships during migration, they do not actively support each other in within group conflicts (Gould, 1997a, Ostner & Kappeler, 2004). Female ring-tailed lemurs experience high levels of competition over reproduction, resulting even in eviction of potential competitors (Vick & Pereira, 1989). In contrast to males, related females occasionally form within-group colations during eviction of other females (Jolly, 1998). In contrast, female coalitions have not been documented in redfronted lemurs during eviction of other females (Kappeler & Fichtel, 2012).

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 & Hickey, 2012). Ring-tailed lemurs as well as black and brown lemurs use gaze following to track the attention of conspecifics (Sheperd & Platt, 2008; Ruiz et al., 2009). In contrast to black, mongoose and red ruffed lemurs, brown and ring-tailed lemurs are also able to follow human gaze (Botting et al., 2011; Sandel et al., 2011). Ring-tailed 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., 2010; Schnoell & Fichtel, 2012). However, studies on social learning in the wild indicate that, in contrast to redfronted lemurs (Schnoell & Fichtel, 2012), the spread of information appears to be limited to subgroups of individuals that tolerate each other in close proximity (Kendal et al., 2010). Although ring-tailed 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, 1997). Behavioural traditions in the wild have also been found in Verreaux's and Coquerel's sifakas and potentially in redfronted lemurs (Fichtel & van Schaik, 2006; Fichtel & Kappeler, 2011; Schnoell & Fichtel, 2013). Finally, ring-tailed 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, ring-tailed 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. However, in several other aspects of social cognition, such as reconciliation and social learning, ring-tailed lemurs' performance is en par with those of other lemurs.

In the realm of communication, non-human primates have a limited repertoire of signals, but they can provide listeners with an open-ended, highly, modifiable, and cognitively rich set of meanings (Cheney & Seyfarth, 2010). Among lemurs, ring-tailed 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 & Macedonia, 1991), whereas sifakas and redfronted lemurs produce functionally referential alarm calls only in response to aerial predators (Fichtel & Kappeler, 2002, 2011; Fichtel & van Schaik, 2006). Redtailed sportive lemurs and grey mouse lemurs, however, produce general alarm calls instead of predator-specific ones (Fichtel, 2007; Rahlfs & Fichtel, 2011). Ring-tailed lemurs also produce more visual signals than redfronted or ruffed lemurs (Pereira et al., 1988; Pereira & Kappeler, 1997). They also use various scent marks to signal individuality as well as dominance and reproductive status (Kappeler, 1990; Drea, 2007; Charpentier et al., 2008; Crawford et al., 2011). Ring-tailed lemurs are also able to recognize kin or chose mating partners by means of olfactory signals (Charpentier et al., 2010; Crawford et al., 2011). Even cross-modal recognition of individuals by means of olfactory and vocal signals has been demonstrated in ring-tailed lemurs (Kulahci et al., 2014). Thus, ring-tailed lemurs appear to have more elaborated communicative skills than many other lemurs.

In summary, although only limited data are available, this review indicates that ring-tailed lemurs exhibit similar qualitative cognitive skills in the physical domain as other lemurs and many haplorhines primates (Fichtel & Kappeler, 2010). In the social domain, ring-tailed lemurs are better skilled in using social cues in food competition tasks than other lemurs. Coalitions have only been observed in female ring-tailed lemurs during rare events of female evictions. However, in several other aspects of social behaviour, such as reconciliation and social learning, ring-tailed lemurs' cognitive abilities are en par with those of other lemurs with the caveat that the social behaviour and cognitive abilities of other lemurs have not yet been studied in comparable detail. Thus, additional systematic comparative studies in physical and social cognition are required for a more comprehensive understanding of the processes of primate cognitive evolution.

Table 1 The cognitive abilities of *Lemur catta* and comparison with other lemur species.
b Social intelligence

Categories	Species	Common name	n	Success?	n success or mean %	Reference
Social complexity & social relationship structure						
Transitive inference	*Lemur catta*	ring-tailed lemurs	3	y	-	MacLean et al., 2008
	Eulemur mongoz	mongoose lemurs	3	y	-	
Coalitions	*Lemur catta*	ring-tailed lemurs	9 grps	y	-	Sussmann, 1992
	Lemur catta	ring-tailed lemurs	12 grps	y	-	Jones, 1983
	Lemur catta	ring-tailed lemurs	10	y	-	Gould, 1997a
	Lemur catta	ring-tailed lemurs	-	y	-	Jolly, 1998
	Eulemur rufifrons	redfronted lemurs	4 grps	y	-	Ostner & Kappeler, 2004
	Eulemur rufifrons	redfronted lemurs	5 grps	n	-	Kappeler & Fichtel, 2012
Post-conflict behaviour	*Lemur catta*	ring-tailed lemurs	2 grps	n	7.2%	Kappeler, 1993b
	Eulemur fulvus	brown lemurs	2 grps	y/n	13.6%	
	Lemur catta	ring-tailed lemurs	16	y	57.7%	Rolland & Roeder, 2000
	Eulemur rufifrons	redfronted lemurs	16	y	63.7%	Roeder et al., 2002
	Eulemur macaco	black lemurs	8	n	34.8%	
	Lemur catta	ring-tailed lemurs	2 grps	y/n	-	Palagi et al., 2005
	Propithecus verreauxi	Verreaux's sifakas	16	y	44.7%	Palagi et al., 2008
Gaze following and related skills						
Gaze following	*Lemur catta*	ring-tailed lemurs	2	y	2	Shepherd & Platt, 2008
	Eulemur fulvus and Lemur catta	brown lemurs and ring-tailed lemurs	5	y	3-4 / -	Botting et al., 2011
	Lemur catta	ring-tailed lemurs	17	y	-	Sandel et al., 2011
	Eulemur mongoz	mongoose lemurs	10	n	-	
	Eulemur macaco	black lemurs	8	n	-	
	Varecia rubra	ruffed lemurs	14	n	-	
	Eulemur macaco	black lemurs	4	n	0 / -	Anderson & Mitchell, 1999
	Eulemur fulvus	brown lemurs	4	y	-	Ruiz et al., 2009
	Eulemur macaco	black lemurs	2	y	-	
Visual perspective taking	*Lemur catta*	ring-tailed lemurs	10	y	4 / 75.8% & 69.2%	Sandel et al., 2011
	Lemur catta	ring-tailed lemurs	10	y	1 / 63.3%	Sandel et al., 2011
	Eulemur mongoz	mongoose lemurs	10	n	0 / 35%	
	Eulemur macaco	black lemurs	10	n	0 / 47.5%	

	Varecia rubra	ruffed lemurs	10	n	0 / 45%	
	Lemur catta	ring-tailed lemurs	10	y	75%	MacLean et al., 2013
	Eulemur fulvus	brown lemurs	10	y	63%	
	Eulemur macaco	black lemurs	10	y	58%	
	Eulemur mongoz	mongoose lemurs	10	n	55%	
	Propithecus coquereli	Coquerel's sifakas	10	y	64%	
	Varecia variegata	ruffed lemurs	10	n	48%	
Social learning and innovations						
Social learning	*Lemur catta*	ring-tailed lemurs	2 grps	y	-	Jolly & Oliver, 1985
	Varecia variegata	ruffed lemurs	1 grp	n	-	
	Eulemur mongoz	mongoose lemurs	1 grp	y	-	
	Eulemur fulvus	brown lemurs	4 grps	y	-	
	Lemur catta	ring-tailed lemurs	18	y	8 / -	Kappeler, 1987
	Lemur catta	ring-tailed lemurs	4	y	3 / -	Fornasieri et al., 1990
	Eulemur macaco	black lemurs	4	y	2 / -	
	Eulemur fulvus	brown lemurs	8	y	2 / -	
	Lemur catta	ring-tailed lemurs	28	y	-	Kendal et al., 2010
	Eulemur fulvus	brown lemurs	6	y	-	Feldman & Klopfer, 1972
	Eulemur fulvus	brown lemurs	12	y	8(4) / -	Anderson et al., 1992
	Eulemur macaco	black lemurs	8	y	-	Gosset & Roeder, 2001
	Daubentonia madagascariensis	aye-ayes	6	y	-	Krakauer, 2005
	Eulemur rufifrons	redfronted lemurs	37	y	17	Schnoell & Fichtel, 2012
	Lemur catta	ring-tailed lemurs	10	y	-	Gould, 1997b
	Lemur catta	ring-tailed lemurs	7 grps	y	-	O'Mara & Hickey, 2012
Innovations	*Lemur catta*	ring-tailed lemurs	28	y	17 / -	Hosey et al., 1997
	Eulemur rufifrons	redfronted lemurs	29	y	15	Hübner & Fichtel, unpubl.
	Eulemur rufifrons	redfronted lemurs	4 grps	y/n	1 group	Schnoell & Fichtel, 2013
Communication						
Functionally referential alarm calls	*Lemur catta*	ring-tailed lemurs	30-40	y		Pereira & Macedonia, 1991
	Lemur catta	ring-tailed lemurs	1 grp	y	-	Macedonia, 1990
	Varecia variegata	ruffed lemurs	1 grp	n	-	

	Lemur catta	ring-tailed lemurs	13	y	-	Oda, 1999
	Lemur catta	ring-tailed lemurs	25	y	-	Bolt, 2013
	Lemur catta	ring-tailed lemurs	15	y	-	Pereira & Kappeler, 1997
	Eulemur rufifrons	redfronted lemurs	11	y/n	-	
	Eulemur rufifrons	redfronted lemurs	4 grps	y	-	Fichtel & Kappeler, 2002
	Propithecus verreauxi	Verreaux's sifakas	4 grps	y	-	
	Propithecus coquereli	Coquerel's sifakas	2 grps	y	-	Fichtel & Kappeler, 2011

y=yes; n= no; grp/s= group/s; *= depending on the task

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Chapter 3

The Lemur Baseline: How Lemurs Compare to Monkeys and Apes in the Primate Cognition Test Battery

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Animal Cognition: submitted

Author Contributions

KK and CF designed the experiments; KK conducted the experiments, analysed the data and drafted the manuscripts; CF and PK participated in writing the manuscripts

Abstract

Primates have relatively large brains, although brain tissue is energetically costly. Thus, the evolutionary key question is which socioecological aspects selected for large brains and comparative studies on the cognitive skills of multiple species can provide answers. However, unlike haplorhine primates (great apes, Old- and New World monkeys), strepsirrhine primates (lemurs and lorises) have not yet been included in systematic comparative studies, although they may serve as living models of primate ancestral cognitive skills. To begin filling this gap, we tested members of three lemur species (*Microcebus murinus*, *Varecia variegata*, *Lemur catta*) with a comprehensive set of experiments addressing physical and social cognitive skills that has previously been used on four haplorhine species. We found no significant differences in performance among lemur species and, surprisingly, their average performance was not different from that of the haplorhines in many aspects. Specifically, lemurs' overall performance was slightly inferior in the physical domain but matched that of haplorhines in the social domain. Our results question a clear-cut link between brain size and cognitive skills suggesting a more domain-specific distribution of cognitive abilities in primates.

Key words: Cognition, Primate Cognition Test Battery, Primates, Lemurs

Introduction

One central question in comparative cognition is why primates have evolved larger brains and enhanced cognitive skills compared to other equally-sized mammalian species (Shettleworth, 2010). Among primates, this effect is paralleled by a disproportionate increase in brain size from strepsirrhines to haplorhines and humans (Jerison, 1973; Martin, 1981; Dunbar, 1992; Isler et al., 2008). Because larger brains are energetically more expensive (Aiello & Wheeler, 1995), they are assumed to confer benefits with regard to enhanced cognitive abilities (Reader & Laland, 2002; Navarrete et al., 2011; Reader et al., 2011).

Several mutually non-exclusive hypotheses on the evolution of brain size have been proposed to account for the distinctive cognitive abilities of primates (Dunbar & Shultz, 2017). According to the *General intelligence hypothesis*, humans are thought to be cognitively more efficient through their larger brains than other species, and to have an evolutionary advantage because of faster learning and larger memory capacities (Spearman, 1904). The *Ecological intelligence hypothesis* suggests that environmental and ecological challenges in food acquisition, including spatial or spatio-temporal processes to memorize seasonally available food or manipulative skills for extractive foraging, selected for larger brains (Clutton-Brock & Harvey, 1980; Milton, 1981; Byrne, 1996; Heldstab et al., 2016; Powell et al., 2017). Several versions of the *Social brain hypothesis* posit that increased cognitive skills in primates evolved in response to the constant challenges associated with complexity of social life, such as competition and cooperation within larger social groups (Jolly, 1966a; Humphrey, 1976; Byrne & Whiten, 1988; Dunbar, 1992; Kudo & Dunbar, 2001; Dunbar & Shultz, 2007). However, support for the *Social brain hypothesis* is less compelling in other taxa, with brain size correlating positively with measures of sociality in some insectivores, bats and ungulates (e.g. Barton et al., 1995; Dunbar & Bever, 1998; Shultz & Dunbar, 2006; Byrne & Bates, 2010), but not in corvids (Emery et al., 2007; Shultz & Dunbar, 2007) and it is equivocal in carnivores (Dunbar & Bever, 1998; Holekamp et al., 2007; Pérez-Barbería et al., 2007; Finarelli & Flynn, 2009; Benson-Amram et al., 2016). Moreover, recent comparative meta-analyses among primates indicated that brain size is associated with ecological factors (home range size, diet, activity period), but not with social factors (DeCasien et al., 2017; Powell et al. 2017), also challenging the social brain hypothesis.

Since these studies usually link brain size with certain life-history traits, it is essential to understand how brain size actually impacts cognitive skills. Hence, comparative analyses of cognitive abilities across the primate order and beyond are required. However, comparisons of performance in cognitive experiments across species often fail due to variation in the experimental set-up and specific methods (MacLean et al., 2012). To overcome this problem, Herrmann and colleagues (2007) assembled a systematic toolbox for comparative analysis, called the *Primate Cognition Test Battery* (PCTB), which compared 2.5-year-old children, chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus*) in their cognitive skills in various tasks in the physical and social domain. The physical domain deals with the spatial temporal-causal relations of inanimate objects, while the social domain deals with the intentional actions, perceptions, and knowledge of other animate beings (Tomasello & Call, 1997). These tests revealed that children and chimpanzees have similar cognitive skills for dealing with the physical world, but children have increased cognitive skills for dealing with the social world, particularly in the scale of social learning. These results support the *Cultural intelligence hypothesis*, a variant of the Social brain hypothesis, suggesting that exchanging knowledge within human cultural groups requires specific socio-cognitive skills, such as social learning or Theory of Mind (e.g. Boyd & Richerson, 1988; Herrmann et al., 2007; Whiten & van Schaik, 2007).

Application of the PCTB to two other haplorhine primate species, long-tailed macaques (*Macaca fascicularis*) and olive baboons (*Papio anubis*), revealed that both species performed similarly to great apes in both the physical and the social domain (Schmitt et al., 2012). Specifically, chimpanzees outperformed macaques only in tasks on spatial understanding and tool use. Since chimpanzees have relatively larger brains than macaques or baboons (Jerison, 1973; Isler et al., 2008), these results question the clear-cut relationship between cognitive performance and brain size (Schmitt et al., 2012). Therefore, further studies on additional non-human primates are required to explore the relationship between cognitive abilities, socio-ecological traits and brain size.

Strepsirrhine primates are the obvious choice for such an extended comparative approach because they represent the best living models of the earliest primates and the link between primates and other mammalian orders (MacLean et al., 2008; Fichtel & Kappeler, 2010). Strepsirrhines split off from the main primate lineage approximately 60 million years ago, and retained many ancestral primate traits (Martin, 1990; Yoder et al., 1996; Sauther et al., 1999; Yoder & Yang, 2004). Importantly, strepsirrhine primates have relatively smaller brains than haplorhines, and their brain size does not correlate with group size (MacLean et al., 2009). Although older studies suggested that strepsirrhine primates possess physical cognitive abilities that are inferior to those of haplorhines (e.g. Maslow & Harlow, 1932; Jolly, 1964; Ehrlich et al., 1976), recent studies indicated that their cognitive skills are similar to those of haplorhines (e.g. Hosey et al., 1997; Santos et al., 2005a, b; Deppe et al., 2009; Fichtel & Kappeler, 2010; Kittler et al., 2015). Hence, a comprehensive study investigating a broad variety of tasks addressing different cognitive skills in the same group of individuals, and replicating the exact same methods already used in four haplorhine primate species, seems indicated for a systematic comparison across both primate suborders.

To this end, we applied the PCTB to three species of lemur that differ in key socio-ecological traits: ring-tailed lemurs (*Lemur catta*), black-and-white ruffed lemurs (*Varecia variegata*; in the following: ruffed lemurs) and grey mouse lemurs (*Microcebus murinus*, Table 1). Specifically, mouse lemurs have one of the smallest brain sizes among primates, and absolute brain size increases from mouse lemurs over ring-tailed lemurs to ruffed lemurs (Isler et al., 2008). Ring-tailed lemurs are diurnal opportunistic omnivores that live in groups of on average 14 individuals (Jolly, 1966b; Sussman, 1991; Gould et al., 2003). Ruffed lemurs are diurnal, frugivorous and live in small groups (average 6 individuals), exhibiting a fission-fusion structure (Vasey, 2003; Baden et al., 2015; Holmes et al., 2016). Grey mouse lemurs are nocturnal, omnivorous solitary foragers that form sleeping-groups among related females (Eberle & Kappeler, 2006; Isler et al., 2008; Tecot et al., 2012).

According to the *General intelligence hypothesis*, ruffed lemurs should perform better than ring-tailed lemurs and mouse lemurs, and lemurs should be cognitively inferior to haplorhine species, because they have absolutely larger brains than lemurs (Table 1; Reader & Laland, 2002; Deaner et al., 2007; Isler et al., 2008). In accordance with the *Ecological intelligence hypothesis* we predicted that the most frugivorous ruffed lemurs should outperform both other lemur species (Table 1). However, according to the *Social intelligence hypothesis*, ring-tailed lemurs should perform better in the cognitive tasks than both other species, and ruffed better than mouse lemurs. Besides orangutans, lemurs generally live in smaller groups than monkeys and apes (Kappeler & Heymann, 1996) and should have inferior cognitive abilities than the other species according to the *Social intelligence hypothesis* (Table 1). In summary, systematic studies of lemur cognitive abilities represent a unique opportunity for testing predictions of the different hypotheses on the evolution of brain size and for investigating the existence of a functional relationship between brain size and cognitive abilities.

Table 1 Summary of the most important traits for the seven non-human primate species.

species	n	ECV (cc)	relative brain size (%)	% fruit	social system	average group size
chimpanzees (*Pan troglodytes*)	106	368.4	0.91	66	group	47.6
orangutans (*Pongo pygmaeus*)	32	377.4	0.71	64	solitary	1.5
olive baboons (*Papio anubis*)	5	167.4	0.96	62	group	69
long-tailed macaques (*Macaca fascicularis*)	10-13	64	1.63	66.9	group	26
ruffed lemurs (*Varecia variegata*)	13	32.1	0.96	92	group	6
ring-tailed lemurs (*Lemur catta*)	26-27	22.9	1.16	54	group	11
grey mouse lemurs (*Microcebus murinus*)	9-16	1.6	2.76	31.3	solitary	1

n=number of individuals, ECV=endocranial volume (absolute brain size), % fruit=percentage of fruit in the diet, allo care= level of allomaternal care; Data from: Herrmann et al., 2007; Schmitt et al., 2012; Isler et al., 2008; MacLean et al., 2014; Dammhan & Kappeler, 2008; Radespiel et al., 2006; Lahann, 2007.

Methods

Experiments were conducted with adult individuals of grey mouse lemurs (n=9-15), ring-tailed lemurs (n=26-27) and black-and-white ruffed lemurs (n=13). All individuals were born in captivity and housed in enriched or semi-natural environments, either at the German Primate Centre (DPZ, Göttingen) or the Affenwald Wildlife Park (Straußberg). The lemurs at the Affenwald range freely within a 3.5 ha natural forest enclosure. At the DPZ, ring-tailed and ruffed lemurs are offered indoor and outdoor enclosures equipped with enriching climbing materials and natural ground vegetation. The nocturnal mouse lemurs are kept indoors with an artificially reversed day-night-cycle and cages are equipped with climbing material, fresh natural branches and leaves. All individuals were tested individually in their familiar indoor enclosures and were unfamiliar with the presented tasks. Since some individuals passed away during the course of the study, not all individuals participated in every task of the test battery (Table S2, *Supplementary Material*, File *Suppl1*). To ensure comparability with the previous studies, the experimental setup was replicated after the PCTB (Herrmann et al., 2007; Schmitt et al., 2012), but adjusted in size for lemurs.

Ethical statement

All animal work followed relevant national and international guidelines. The animals were kept under conditions documented in the European Directive 2010/63/EU (directive on the protection of animals used for experimental and other scientific purposes) and the EU Recommendations 2007/526/EG (guidelines for the accommodations and care of animals used for experimental and other scientific purposes). Consultation and approval of the experimental protocols by the Animal Welfare Body of the German Primate Center isdocumented (E2-17).

General testing procedure

During the experiments, individuals were briefly separated from the group. The testing apparatus for all tasks consisted of a table with a sliding board on top that was attached to the fence of the subjects' enclosures (see Figure S2, *Supplementary Material*). In most of the tasks two or three opaque cups (ruffed- & ring-tailed lemurs: Ø 6.8 cm x 7.5 cm; mouse lemurs: Ø 2.5 cm x 3 cm), which were placed upside down in a row on the sliding board, were used to cover the food reward (other materials are reported in the *Supplementary Material*). If necessary, a cardboard occluder was put on top of the sliding board between the experimental setup and the individual to hide the baiting process from the individuals. The position of the reward was randomized and counter-balanced across all possible locations, and the reward was never put in the same place for more than two consecutive trials. Once the board was pushed into reach of an individual, the experiment began and, depending on the task, the individual had to manipulate an item or indicate its choice by pointing or reaching towards the chosen item, to obtain the reward if chosen correctly. If the choice was incorrect, the correct location of the reward was shown to the individual after each trial.

For most of the tasks at least 6 trials were conducted per individual and setup (Table S2, *Supplementary Material*). Raisins and pieces of banana served as rewards. During testing, no possible cues to where the reward was located were provided by the experimenter; she simply put her hands on her lap and her gaze was directed downwards. All experiments were videotaped and responses of the subjects to the tasks coded afterwards from the videos. A naïve second observer additionally scored 20% of all trials a second time to assess interobserver reliability. The Interclass Correlation Coefficient was excellent (ICC = 0.985).

The Primate Cognition Test Battery

All experimental setups and methods were replicated from the PCTB (Herrmann et al., 2007; Schmitt et al., 2012). Following Schmitt et al. (2012), we also doubled the number of trials for all object-choice tasks of the test battery (Table S2, File *Suppl1*) to evenly distribute objects between all possible spatial positions and combinations of manipulations. In total, the PCTB consists of 16 different experimental tasks, 10 investigating physical and 6 social cognitive skills. These tasks can be grouped into 6 different scales: space, quantity and causality for the physical and social learning, communication and Theory of Mind for the social domain. In the physical domain, the scale space examines the ability to track objects in space in four tasks: spatial memory, object permanence, rotation and transposition. The scale quantity tests the numerical understanding of individuals and consists of two tasks: relative numbers and addition numbers. The scale causality consists of four tasks: noise, shape, tool use and tool properties to examine the ability to understand spatial-causal relationships. In the social domain, the scale social learning examines in one task whether individuals use social information provided by a human demonstrator to solve a problem. The scale communication examines whether individuals are able to understand communicative cues given by humans in three tasks: comprehension, pointing cups and attentional state. Finally, in the scale Theory of Mind, individuals were confronted with two tasks: gaze following and intentions. A detailed description of the general setup and the methodology of the experiments can be found in the supplementary material (File *Suppl1*).

Temperament, inhibitory control, rank and learning effect

To assess the influence of temperament, inhibitory control and dominance rank on lemurs' performances in the test battery, individuals participated in a set of additional tests (Herrmann et al., 2007; Schmitt et al., 2012). Due to logistic reasons, the temperament and dominance rank tests could only be conducted with ring-tailed and ruffed lemurs. For temperament, we measured whether individuals would approach novel objects, people and foods (for details see *Supplementary Material*). Inhibitory control was measured during an additional session of the spatial memory task, in which out of three cups only the two outer one were baited with a reward and hence, individuals had to skip the middle one. Dominance rank (high, middle or low-ranking) was inferred by additional focal observations, using criteria proposed by Pereira and Kappeler (1997). We also controlled for potential learning effects within the trials of a task by calculating Pearson's correlations between performance in the first and second half of trials.

Data analyses

We measured the performance of individuals by the proportion of correct responses for each task. To determine whether individual performance in each task was above chance level, we conducted binomial tests using the specific chance levels. On the species level, we applied for each task and lemur species Wilcoxon tests followed by Benjamini-Hochberg corrections (for multiple testing) to examine whether they performed above chance level. Since no individual solved the social learning task and only one the tool use task, we omitted both tasks from the between species comparisons. To analyse whether the three lemur species differed in their performance in the tasks of the PCTB, we used multivariate analysis of variance (MANOVA) with species, sex, rank, age and age:species as between-subject factor and their performance in all tasks as dependent variable. Afterwards, to compare all three species' performances between the different tasks, we used univariate analysis of variance (ANOVA, for normally distributed data) or Kruskall-Wallis tests (for not normally distributed data) followed by post hoc analyses (Bonferroni correction). For significant results, we used an analysis of covariance (ANCOVA) to control for age in these tasks.

For comparisons in performance between the three lemur species and the four haplorhine species that were already tested with the PCTB, we applied on the scale level a MANOVA, followed by ANOVAs or Kruskall-Wallis tests and post hoc corrections (Bonferroni) in case of significant results. All statistical analyses were conducted in R version 3.2.2 (R Core Team, Vienna, Austria).

Results

Lemur performance in the physical domain

The chance level was at 33% in all four tasks of the scale space. The three lemur species performed significantly above chance level in the spatial memory and the rotation task (Table 2, Fig. 1). In the object permanence tasks only ruffed lemurs performed above chance level, while in the control task, all three species performed above chance level (all $p<0.05$). In the scale quantity, the three lemur species performed significantly above chance level (50%) in both tasks (Table 2, Fig. 1). In the scale causality, the tool use task was successfully solved by only one ring-tailed lemur. However, in the shape and tool properties tasks, all three lemur species performed above chance level (50%; Table 2).

Lemur performance in the social domain

No lemur could solve the social learning task using a similar technique as demonstrated by the human experimenter (Table 2, Fig. 1). In the scale communication, all three lemur species performed significantly above chance level (50%) in the comprehension task, whereas only mouse lemurs performed above chance level (50%) in the pointing cups task, and no lemur species performed above chance level in the attentional state task. In the scale Theory of Mind, none of the lemur species did follow the gaze of the human experimenter upwards significantly more often than in the control condition in which no cue was given (baseline: 20%; Table 2, Fig. 1). In contrast, all lemur species performed significantly above chance level (50%) in the intentions task (Table 2, Fig. 1).

Table 2 Summary of the mean proportions of correct responses of the three lemur species in all tasks and *scales* of the *PCTB*.

			Ruffed lemurs						Ring-tailed lemurs						Mouse lemurs					
	trials	**chance**	**n**	**M**	**adj p**	**SD**	**95% CI**	**ind**	**n**	**M**	**adj p**	**SD**	**95% CI**	**ind**	**n**	**M**	**adj p**	**SD**	**95% CI**	**ind**
Physical domain																				
Space				*46.8*		*8*	*51, 58*			*44.2*		*7*	*42, 47*			*50.8*		*7*	*47, 55*	
Spatial memory	6	33	13	**53.9**	0.017	23	42, 66	3	27	**55.6**	<0,001	17	49, 62	4	15	**66.7**	0.004	18	58, 68	6
Object permanence	18	33	13	**47.9**	0.006	12	41, 55	2	27	38.3	0.112	15	32, 44	2	12	42.1	0.074	10	36, 48	0
Rotation	18	33	13	**45.3**	0.014	10	40, 51	2	26	**41.0**	0.002	9	37, 45	1	12	**47.7**	0.008	9	43, 53	0
Transposition	18	33	13	40.2	0.052	13	33, 47	2	27	**42.2**	<0.001	11	38, 46	0	12	**41.2**	0.019	12	35, 48	1
Quantity				*66.4*		*12*	*60, 73*			*58.5*		*11*	*54, 63*			*63.9*		*6*	*60, 68*	
Relative numbers	16	50	13	**62.0**	0.006	7	58, 66	0	27	**60.4**	0.007	10	57, 64	2	9	**66.0**	0.019	11	59, 73	1
Addition numbers	14	50	13	**70.9**	0.014	20	60, 82	5	26	**60.2**	0.003	13	55, 65	2	9	**61.9**	0.019	8	57, 67	0
Causality				*51.0*		*7*	*47, 55*			*48.6*		*7*	*46, 51*			*44.0*		*4*	*42, 46*	
Noise	12	50	13	**63.5**	0.015	13	56, 71	2	27	**59.3**	0.002	10	55, 63	0	15	50.0	0.958	17	41, 59	0
Shape	12	50	13	**76.9**	0.006	15	69, 85	7	27	**72.8**	<0.001	10	69, 77	7	15	**70.6**	0.004	12	65, 77	4
Tool use	1	-	13	0.0	-	-	-	0	27	3.7	-	19	-4, 11	1	15	0.0	-	-	-	0
Tool properties	30	50	13	**63.6**	0.013	12	57, 70	4	27	**58.6**	<0.001	8	56, 62	4	15	**55.6**	0.040	9	51, 60	2
Social domain																				
Social learning	*3*	-	*13*	*0.0*	-	-	-	*0*	*26*	*0.0*		-	-	*0*	*12*	*0.0*		-	-	*0*
Communication				*53.1*		*12*	*47, 60*			*49.6*		*11*	*46, 54*			*52.1*		*9*	*47, 57*	
Comprehension	18	50	13	**70.9**	0.006	10	66, 76	5	27	**70.8**	<0.001	13	66, 76	9	13	**65.4**	0.008	11	59, 72	3
Pointing cups	8	50	13	53.9	0.220	9	49, 59	0	27	55.1	0.050	12	51, 59	1	15	**68.3**	0.008	16	60, 76	1
Attentional state	4	-	13	34.6	-	28	19, 50	0	26	21.2	-	22	13, 30	0	14	25.0	-	22	14, 36	0
Theory of mind				*43.7*		*10*	*45, 57*			*56.8*		*18*	*50, 64*			*51.4*		*11*	*39, 49*	
Gaze following	9	20 (bl)	13	23.9	0.326	17	15, 33	0	27	30.0	0.340	33	18, 42	6	15	11.1	0.713	17	2, 20	1
Intentions	12	50	13	**78.9**	0.006	13	72, 86	7	27	**83.6**	<0.001	15	78, 89	19	15	**71.1**	0.004	10	66, 76	2

Numbers in boldface: Significant deviations from chance level (Wilcoxon tests); Trials=number of trials per task; chance=chance-level for each task; n=number of participating individuals; M=medians of performance; adj=adjusted p-values (Benjamini-Hochberg-corrections); SD=standard deviation; CI=confidence interval; ind=individuals performing above chance level: bl= baseline calculated from control condition.

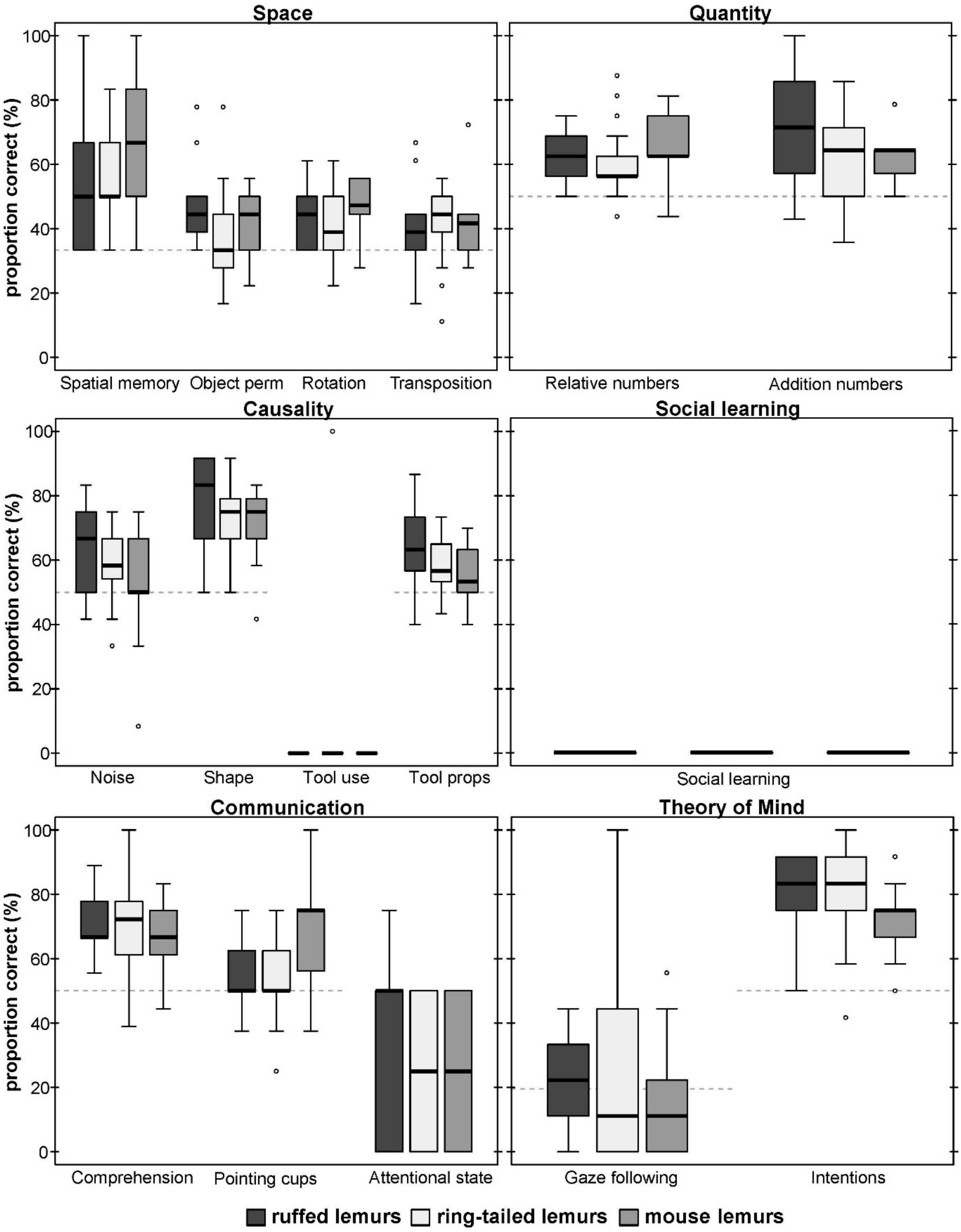

Figure 1 Average performance of the three lemur species in all tasks of the PCTB. Represented are medians (black bars), interquartile ranges (boxes), upper and lower hinges (whiskers), and outliers (circles).

Comparison of the three lemur species

Because the tool use task was solved by only one individual and the social learning task by none, the two tasks were excluded from this comparison. A multivariate analysis of variance of the 14 remaining tasks revealed no differences between the three lemur species (MANOVA; Wilk's Λ=0.498, *F*(19,14)=1.37, p=0.257). Furthermore, performance was not influenced by sex (Wilk's Λ=0.461, *F*(19,14)=1.59, p=0.173), rank (Wilk's Λ=0.273, *F*(38,28)=1.24, p=0.268), age (Wilk's Λ=0.568, *F*(19,14)=1.03, p=0.466) or age within species (age:species; Wilk's Λ=0.599, *F*(19,14)=0.91, p=0.566). Follow-up univariate analyses of each task only revealed significant differences in performance between species in the pointing cups (Kruskal-Wallis test, *χ*2=10.14, df=2, p=0.006) and the intentions task (Kruskal-Wallis test, *χ*2=9.88, df=2, p=0.007; Fig. 1). In the pointing cups task, mouse lemurs performed significantly better than ruffed (pairwise t-tests with Bonferroni corrections, p=0.007) and ring-tailed lemurs (p=0.003), while in the intentions task, ring-tailed lemurs outperformed mouse lemurs (p=0.015). These differences remained significant when we controlled for age (ANCOVA, pointing cups: mouse vs. ruffed lemurs: p=0.017, mouse vs. ring-tailed lemurs: p=0.002; intentions: ring-tailed vs. mouse lemurs: p=0.007).

Influence of personality, inhibitory control and learning effect

The three personality measures (latency, proximity and duration) of ring-tailed or ruffed lemurs did not correlate with the performance in the physical domain of the PCTB (Pearson's correlations, all p>0.05, see *Supplementary Material*), and performance of ring-tailed lemurs in the social domain. In ruffed lemurs, however, the latency to approach and proximity to a novel stimulus correlated with performance in the social domain (latency to approach: Pearson's correlation, *r*(11)=0.61, p=0.026; proximity: Pearson's correlation, *r*(11)=-0.59, p=0.032). Ruffed lemurs approaching a novel object more slowly performed better in the social domain, and individuals that came closer to the novel stimulus performed less well in the social domain. No correlation was found between time individuals spent close to the setup (duration) and performance (Pearson's correlation, *r*(11)=-0.30, p=0.323). Performance in the inhibitory control task did not differ between the three species (Kruskal-Wallis test: χ2=2.34, p=0.311) and did not correlate with performance in the physical and social domain (see Table S4, File

Suppl1). In addition, we did not find a learning effect in performance between the first and second half of trials within the tasks (Wilcoxon Signed-Rank test: V=806.5, p=0.585).

Comparison of lemurs and haplorhines in the physical and social domain

The comparison of chimpanzees, orangutans, baboons, macaques, ruffed-, ring-tailed- and mouse lemurs in their overall performance in the two domains using a MANOVA revealed differences among species (Wilk's Λ=0.383, *F*(406,12)=20.87, p<0.001). Species differed in performance in the physical domain (Kruskal-Wallis test, $\chi 2=127.26$, df=6, p<0.001; Fig. 2) but not in the social domain (Kruskal-Wallis test, $\chi 2=10.25$, df=6, p=0.115; Fig. 2). In the physical domain, only chimpanzees performed significantly better than ruffed lemurs, and chimpanzees and orangutans outperformed ring-tailed and mouse lemurs (see Table S1, File *Suppl1*).

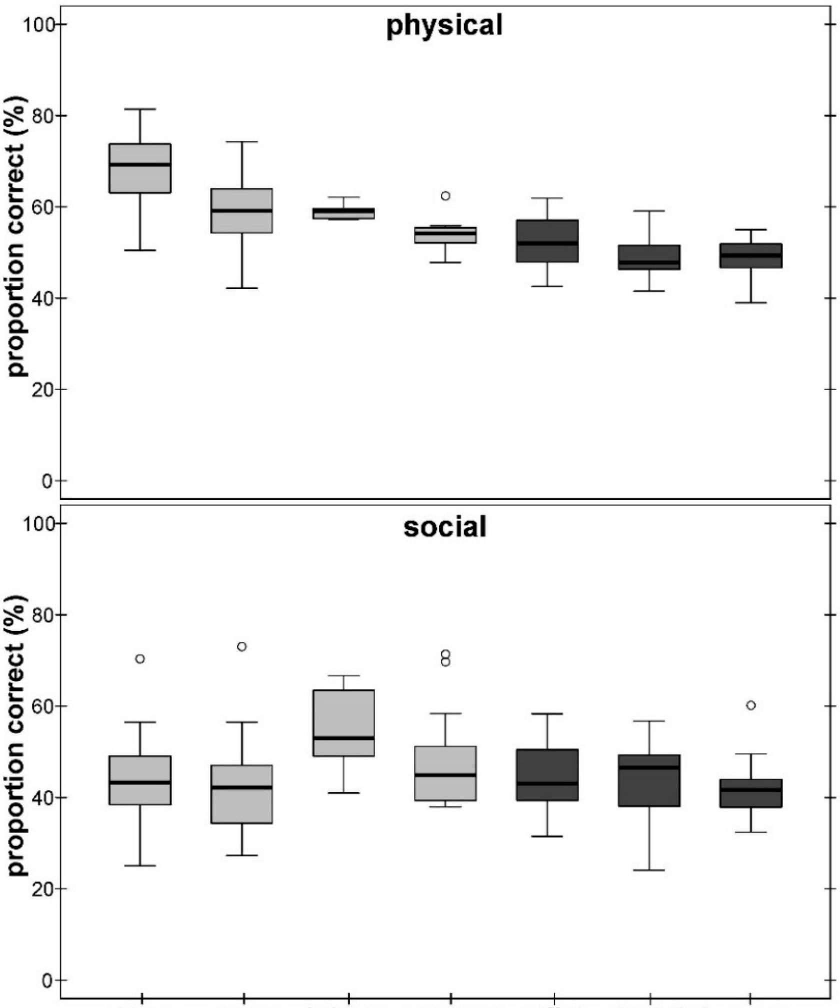

Figure 2 Average performance of the overall performance of the apes & monkeys (light grey) and the lemurs (dark grey) in the two domains. Represented are medians (black bars), interquartile ranges (boxes), upper and lower hinges (whiskers), and outliers (circles).

Comparison of lemurs and haplorhines in the different scales

For a more detailed comparison of all seven species, we conducted a MANOVA including each individuals' overall performance in all six scales, which revealed significant differences among species (Wilk's Λ=0.284, *F*(833,36)=7.68, p<0.001). Species differed in all scales except the scale communication (ANOVAs or Kruskal-Wallis tests, see Table 3; Fig. 3). In the scale space, chimpanzees outperformed all other species, except baboons. Orangutans performed better than ruffed and ring-tailed lemurs, baboons performed better than all three lemur species, and macaques performed similar to all lemur species (Table 4; Fig. 3). In the scale quantity, only chimpanzees performed better than ring-tailed lemurs (Table 4; Fig. 3), and in the scale causality, chimpanzees outperformed all other species and orangutans performed better than mouse lemurs (Table 4; Fig. 3). However, this scale was strongly biased by the results of the tool use task, which was only solved by chimpanzees, orangutans and one ring-tailed lemur. Excluding the tool use task from this comparison revealed that only chimpanzees performed better than mouse lemurs (Table 4; Fig. S1, File *Suppl1*). Except for the great apes, all other species performed poorly in the social learning task, whereas all species performed equally well in the scale communication. In the scale Theory of Mind, however, chimpanzees were outperformed by macaques and ring-tailed lemurs. Orangutans were outperformed by all other species, except mouse lemurs and macaques, as well as ring-tailed lemurs outperformed mouse lemurs (Table 4; Fig. 3).

Table 3 Univariate analyses for the species differences for the six scales.

ANOVAs	**Df**	***F*-value**	**P-value**
Quantity	6	3.49	**0.0026** **
Communication	6	2.10	0.0549
Kruskal-Wallis tests	**Df**	χ^2	**P-value**
Space	6	111.68	**<0.001** ***
Causality	6	68.59	**<0.001** ***
Social learning	6	20.17	0.0026 **
Theory of mind	6	55.08	**<0.001** ***

<0.01; *<0.001 - significance levels

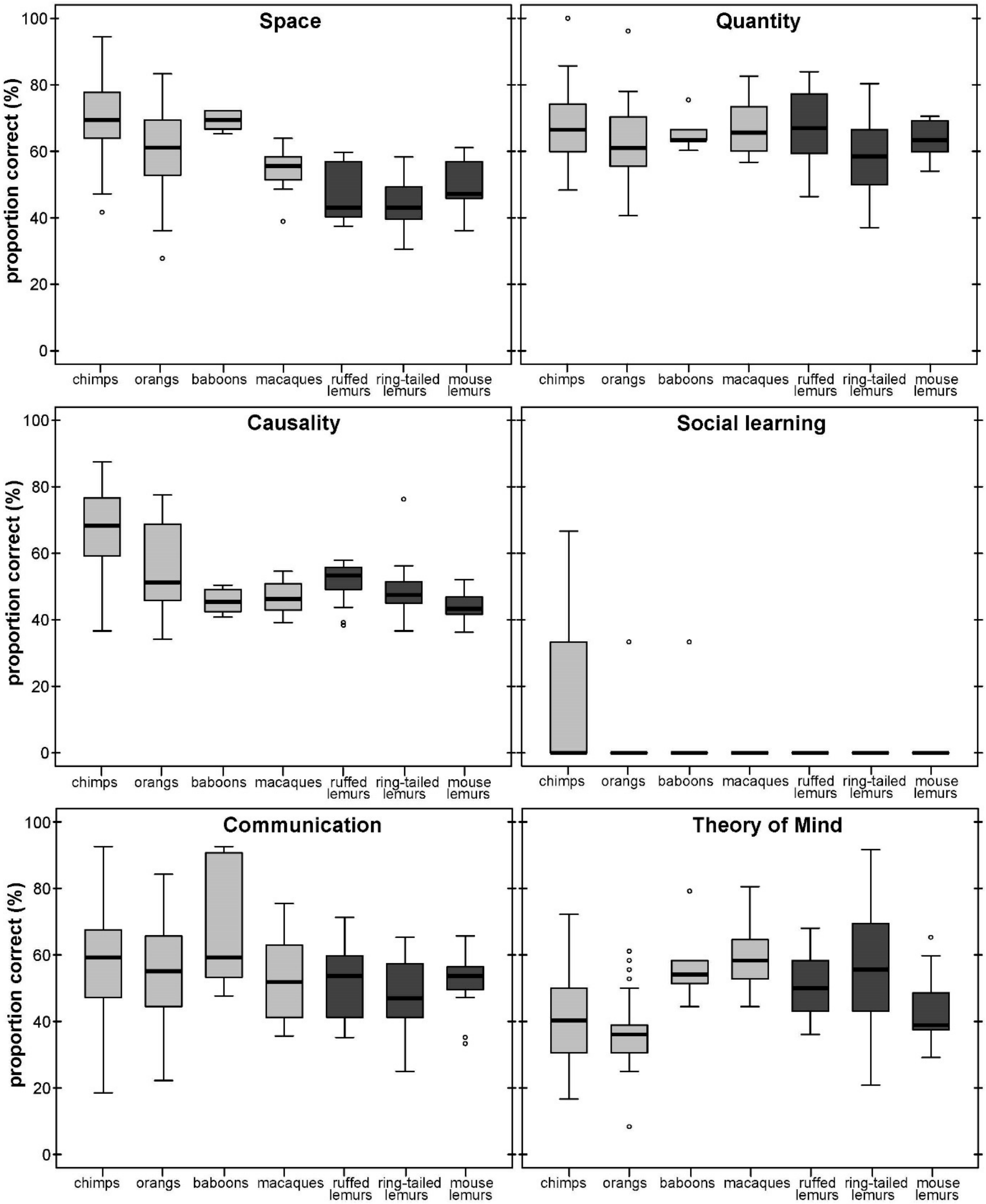

Figure 3 Average performance of the apes & monkeys (light grey) and the lemurs (dark grey) over the six scales. Represented are medians (black bars), interquartile ranges (boxes), upper and lower hinges (whiskers), and outliers (circles).

Table 4 Comparisons of performance among the seven non-human primate species for all six scales of the PCTB. Presented are the results of *post hoc* multiple comparisons (Bonferroni); significant results are in boldface. Causality II: The scale causality without the tools use task.

	Space	Quantity	Causality	Causality II	Social learning	Commun-ication	Theory of Mind
Chimp - Orang	**<0.001**	0.275	**<0.001**	1	1	1	1
Chimp - Baboon	1	1	**0.003**	1	1	1	0.082
Chimp - Macaque	**<0.001**	1	**<0.001**	1	0.699	1	**<0.001**
Chimp - Ruffed lemur	**<0.001**	1	**<0.001**	1	0.352	1	0.077
Chimp - Ring-tailed lemur	**<0.001**	**<0.001**	**<0.001**	1	**0.025**	0.29	**<0.001**
Chimp - Mouse lemur	**<0.001**	1	**<0.001**	**0.041**	0.229	1	1
Orang - Baboon	1	1	1	1	1	0.677	**0.014**
Orang - Macaque	1	1	0.433	1	1	1	**<0.001**
Orang - Ruffed lemur	**0.004**	1	1	0.560	1	1	**0.009**
Orang - Ring-tailed lemur	**<0.001**	1	0.643	1	0.919	1	**<0.001**
Orang - Mouse lemur	0.237	1	**0.046**	0.918	1	1	1
Baboon - Macaque	0.176	1	1	1	1	0.591	1
Baboon - Ruffed lemur	**0.001**	1	1	1	1	0.653	1
Baboon - Ring-tailed lemur	**<0.001**	1	1	1	1	0.094	1
Baboon - Mouse lemur	**0.023**	1	1	1	1	0.424	0.816
Macaque - Ruffed lemur	1	1	1	1	1	1	1
Macaque - Ring-tailed lemur	0.074	0.307	1	1	1	1	1
Macaque - Mouse lemur	1	1	1	1	1	1	**0.033**
Ruffed - Ring-tailed lemur	1	0.409	1	1	1	1	1
Ruffed - Mouse lemur	1	1	1	**0.008**	1	1	1
Ring-tailed - Mouse lemur	1	1	1	0.106	1	1	**0.036**

Discussion

In this study, we applied the Primate Cognition Test Battery to three lemur species differing in socioecological traits and brain size and compared lemurs' performance in these tasks with four haplorhine species tested in previous studies. Lemurs' performance did not differ in the scales of the physical cognitive domain, but in some of the social cognitive domain, with mouse lemurs performing better than ruffed lemurs in the pointing task and ring-tailed lemurs performing better than ruffed and mouse lemurs in the intention task. The comparison with the four haplorhine species revealed that lemurs performed slightly inferior in the physical domain, but at level to them in the social domain. Most interestingly, in the scale Theory of Mind, great apes were outperformed by all other species except mouse lemurs. Hence, since these species differ in relative and absolute brains size (Table 1) with a more than 200fold difference in brain size between mouse lemurs and orangutans or chimpanzees, our results do not support the notion of a clear-cut link between brain size and cognitive skills, but suggest a more domain-specific distribution of cognitive abilities in primates.

Comparison of the three lemur species

Despite differences in socioecological traits and brain size, the three lemur species performed similarly in the physical domain and differed in performance only in two tasks from the social domain. Although it has been suggested that frugivorous ruffed lemurs should have a better spatial memory than omnivorous ring-tailed and mouse lemurs (Rosati et al., 2014; Rosati, 2017), they performed similarly in these experiments. As mouse lemurs feed on gum and spend the day in tree holes, a good spatial memory might be advantageous to locate feeding and sleeping trees, as already indicated by studies in captivity and the wild (Picq, 1993; Lührs et al., 2009). In both tasks on quantities, all three lemur species showed a numerical understanding supporting results of other studies investigating numerosities and simple arithmetic operations (Santos et al., 2005a; Merritt et al., 2011; Jones & Brannon, 2012).

Within the scale causality, all three lemur species performed poorly in the tool use task. However, lemurs appeared to exhibit an understanding for the necessary functional properties of pulling tools (Santos et al., 2005b; Kittler et al., in press or see Chapter 4), although they have never been observed to use tools in the wild (Fichtel & Kappeler, 2010; Kittler et al., 2015 or see Chapter 2). In the noise task, mouse lemurs performed rather poorly, although they rely on acoustic cues when foraging for insects and are even able to discriminate prey-generated rustling sounds representing insects of different size (Goerlitz & Siemers, 2007; Siemers et al., 2007). However, food rattling in artificial metal cups might have been a too artificial stimulus for them. Among the tests in the physical domain, the three lemur species showed the best performance in the shape task, indicating that they can make use of inferential reasoning when it comes to visual discrimination.

In the social domain, all three lemur species failed in the social learning task. However, in ring-tailed lemurs the ability to learn socially has already been reported (e.g. Kappeler, 1987; Kendal et al., 2010; O’Mara & Hickey, 2012), whereas there is no support for social learning in ruffed lemurs (Jolly & Oliver, 1985; Dean et al., 2011) and it remains unstudied in mouse lemurs. Since the social learning task required the ability to grab and shake a transparent tube or insert a stick with the other hand, this task, as well as the tool use task, which also required grabbing a stick, might have been too difficult for lemurs due to their limited dexterity and the lack of precision grip (Torigoe, 1985). Therefore, an easier social learning task adapted to the limited manipulative skills of lemurs (Schnoell & Fichtel, 2012) might be more informative in future studies.

All three lemur species could make use of communicative cues given by the experimenter in object-choice tasks, whereas they were less good in inferring the attentional state of the experimenter. In the pointing cups task, mouse lemurs outperformed both other lemur species. Since in this task individuals basically had to remember under which cup the reward was hidden, this task might have rather tested spatial memory abilities than social skills. The scale Theory of Mind consisted of gaze following and understanding intentions. None of the lemur species performed above chance level in the gaze following task, despite studies showing that at least ring-tailed lemurs do follow the gaze of conspecifics (Shepherd & Platt, 2008) and are also able to follow and evaluate gaze directions of a human experimenter (Botting et al., 2011; Sandel et al., 2011; MacLean et al., 2013). In contrast, in the task of inferring the intention of a human experimenter, lemurs performed much better. Since in this task the experimenter tried in vain to reach the baited cup, lemurs might have used the movement cue as local enhancement. These results, in combination with the pointing cups task, support the notion that it is not always possible to disentangle the underlying cognitive processes in solving specific tasks (Burkart et al., 2016). In summary, no clear pattern of which lemur species performed best in the PCTB, neither in the physical nor the social domain, could be found, suggesting that variation in brain size, group size or diet do not predict performance in these tests.

Comparison of lemurs and haplorhines

The quantitative comparison between the cognitive skills of lemurs and haplorhines, revealed that in the physical domain, lemurs performed inferior than haplorhines, supporting results of a study testing two problem-solving tasks in several primate species (MacLean et al., 2014). However, in the social domain, lemurs matched the performance of haplorhines and, interestingly, ring-tailed lemurs outperformed chimpanzees as well as orangutans, and ruffed lemurs outperformed orangutans in one task of the Theory of Mind scale.

In the physical domain, lemurs were outperformed by all haplorhines in the scale of spatial reasoning, but not in the scale of quantities and causality, when the tool use task was excluded. Because in the scale of quantities all seven species performed similarly, a certain level of numerical understanding appears to be a basal cognitive trait in all primates. Indeed, a comparable numerical understanding as tested in the PCTB has already been reported for various taxa outside the primate order, including fish and insects (e.g. Chittka & Geiger, 1995; Agrillo et al., 2012; Pahl et al., 2013). In the scale causality, lemurs performed equally well as both monkey species, but all were outperformed by chimpanzees, due to their better performance in the tool use task. All other species, including natural tool users as orangutans and long-tailed macaques (van Schaik et al., 2003; Brotcorne et al., 2017), hardly solved the task (Schmitt et al., 2012). Excluding this task from the scale quantities resulted in a rather equal overall performance of all species, with ruffed lemurs exceeding all other species. An earlier meta-analysis on performances in several tasks in the physical cognitive domain among primates suggested a domain-general distinction between haplorhines and strepsirrhines (Deaner et al., 2006). However, our results do not support this domain-generality but instead suggest rather domain-specific cognitive differences.

In the social domain, species differences were less pronounced, and lemurs' overall performance was equal or even superior (Theory of Mind) to that of halporrhine primates. In the scale social learning neither lemurs, nor baboons or long-tailed macaques, which exhibit cultural variation in stone handling techniques in the wild (Brotcorne et al., 2017), solved the task. Since in this task individuals had to copy a human demonstrator, the phylogenetic distance between species and the demonstrator might have influenced learning abilities, because great apes performed better than Old World monkeys and lemurs (Schmitt et al., 2012). Hence, it remains an open question whether monkeys and lemurs would perform better when tested with conspecific demonstrators. Moreover, the task required inserting a stick into a plastic tube, which might have been too challenging for species exhibiting either a medium (baboons, macaques) or low (lemurs) level of precision grip (Torigoe, 1985).

In the scale communication, all species performed equally well. In contrast, in the scale Theory of Mind, species differences emerged, with great apes performing inferior to both monkeys and lemurs. This difference was mainly due to monkeys' and lemurs' better performance in the intentions task, in which a human observer tried to reach in vain a cup with a hidden reward. As discussed for lemurs above, baboons and monkeys may also have used the hand movement cue as local enhancement (Schmitt et al., 2012). Still, it remains puzzling why chimpanzees and orangutans did not use the hand movement as cue for the location of the hidden reward. In contrast to these results, a comparative study among seven non-human primate species examining Theory of Mind compatible learning styles in a simple dyadic game revealed that performance in these tests is correlated with brain volume but not with social group size (Devaine et al., 2017). This result supported the scaffolding hypothesis, stating that the ability to develop a sophisticated Theory of Mind is mostly determined by general cognitive capacity. Hence, additional cognitive Theory of Mind tests are required to obtain a better understanding of the relationship between brain size and cognitive abilities in the social domain.

Altogether, performances were generally not as different as it might have been expected in view of the various hypotheses on the evolution of cognitive abilities. The overall comparison does not provide support for the *General intelligence hypothesis*, since variation in brain size cannot explain the observed results. Similarly, performances of the seven species did not reflect any clear patterns concerning their feeding ecology, i.e. the percentage of fruit in the diet or dietary breadth (see Table 1); hence these results do not provide support for the *Ecological intelligence hypothesis*. In contrast, comparative studies among primates suggests that performance in two tasks of inhibitory control is best predicted by absolute brain size and dietary breadth or that variation in brain size is best predicted by ecological factors such as diet or home range size (Decasien et al., 2017; Powell et al., 2017). Moreover, our results do not provide support for the *Social intelligence hypothesis* because lemurs and especially the solitary mouse lemurs should have performed inferior compared to the haplorhine species, considering social group size as a proxy for social complexity (Dunbar & Shultz, 2017).

Earlier comparative studies among primates linking performance in a range of comparable cognitive tests of the physical or social domain or compiling information on social learning, innovation, extractive foraging and deception revealed a link between performance in these tasks and brain size (Reader & Laland, 2002; Deaner et al., 2006, 2007; Reader et al., 2011). However, studies using the exact experimental set up revealed contradictory results, with either a positive relationship between brain size and performance in inhibitory control tasks (Maclean et al., 2014), or no clear-cut relationship between brain size and cognitive abilities, such as various tests on inhibitory control and spatial memory tasks (Amici et al., 2008, 2010, 2012) or tasks of the Primate Cognition Test Battery as in this or earlier studies (Herrmann et al., 2007; Schmitt et al., 2012), highlighting the importance of using the exact experimental set up for comparisons of cognitive abilities among species.

Even though lemurs performed at level with monkeys and great apes in many of these experiments, we do not suggest that their cognitive abilities are *per se* on par with those of larger-brained primates. In the physical domain, the PCTB examines rather basal cognitive abilities, which might not be specific enough to reveal actual differences between species, as studies revealed that fish and insects possess similar basal cognitive skills in the physical domain (Fuss et al., 2014; Schluessel et al., 2015; Loukola et al., 2017). In the social domain, performance in some tasks might have been influenced by local enhancement (Schmitt et al., 2012), and individuals might also have recruited other abilities to solve the problems, as discussed for the pointing cups task.

The PCTB was designed to examine the spontaneous ability to solve the tasks and not to examine how long individuals need to learn the task. Hence, a test battery that continued testing until individuals reached a certain criterion (e.g. 80 % correct responses) or detailed analyses of applied learning strategies as in Devaine et al. (2017) may allow to compare not only species differences in their spontaneous ability to solve the task, but also species-specific learning curves as well as learning strategies, which might reveal more informative differences.

To conclude, our study generated the first systematic results on cognitive abilities in lemurs, and the comparison with haplorhines suggested that in many aspects of the physical and social domain, the average performance in these tests of members of these two clades do not differ substantially from each other. These results reject the notion of a direct correlation between brain size and cognitive abilities and question assumptions of domain general cognitive skills in primates. Overall, our results strengthen the view that when comparing cognitive abilities among species, it is of vital importance to include a diverse set of tests from both cognitive domains which are applicable to a diverse range of species and taxa (Auersperg et al., 2011; MacLean et al., 2012; Schmitt et al., 2012; Auersperg et al., 2013; Burkart et al., 2016) and to carefully consider the external validity of the specific tests.

Acknowledgements

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Supplementary Materials

1. Additional Results

Table S1 Comparisons of performances of the seven non-human primate species within the two domains. Presented are the results of *post hoc* multiple comparison analyses (Bonferroni); significant results are in boldface.

	physical domain	social domain
Chimp - Orang	**<0.001**	1
Chimp - Baboon	0.075	0.087
Chimp - Macaque	**<0.001**	0.842
Chimp - Ruffed lemur	**<0.001**	1
Chimp - Ring-tailed lemur	**<0.001**	1
Chimp - Mouse lemur	**<0.001**	1
Orang - Baboon	1	**0.032**
Orang - Macaque	0.700	0.269
Orang - Ruffed lemur	0.150	1
Orang - Ring-tailed lemur	**<0.001**	1
Orang - Mouse lemur	**<0.001**	1
Baboon - Macaque	1	1
Baboon - Ruffed lemur	1	0.291
Baboon - Ring-tailed lemur	0.070	0.207
Baboon - Mouse lemur	0.082	0.093
Macaque - Ruffed lemur	1	1
Macaque - Ring-tailed lemur	1	1
Macaque - Mouse lemur	1	0.927
Ruffed lemur - Ring-tailed lemur	1	1
Ruffed lemur - Mouse lemur	1	1
Ring-tailed lemur - Mouse lemur	1	1

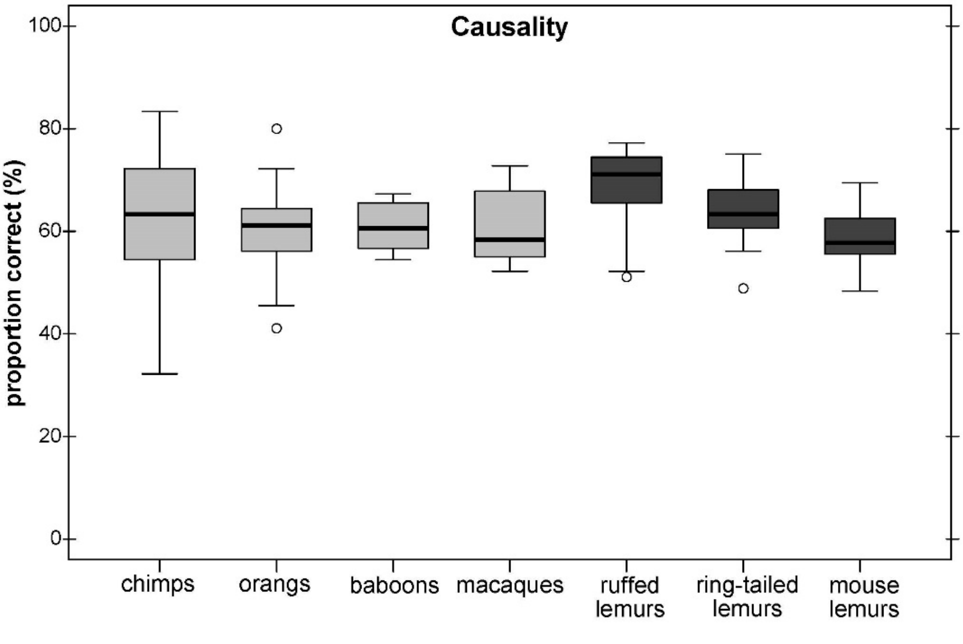

Figure S1 Average performance of apes & monkeys (light grey) and the lemurs (dark grey) in the scale causality excluding the tool use task. Represented are medians (black bars), interquartile ranges (boxes), upper and lower hinges (whiskers), and outliers (circles).

2. Detailed Methodology of the Primate Cognition Test Battery (*PCTB*)

Experimental setups were adopted from Herrmann et al. (2007) and reasonable changes in the experimental procedure, which we partly adopted from Schmitt et al. (2012), are marked in the detailed descriptions below by using parentheses. As suggested by Schmitt et al. (2012) we doubled the number of trials for all object-choice tasks from 3 to 6 (see Table S2) to include all possible locations and combinations. In addition, some of the original tasks were extended by using control conditions and the quantity combinations in experiments 5 and 6 were adopted from their methodology (2012). Otherwise the experimental setups are the same in the PCTB by Herrmann et al. (2007). To avoid confusion, we used a similar wording to describe the tasks. The size of the items and objects used was adjusted to make them operable for lemurs, especially for the small mouse lemurs. Most of the experiments were conducted by the same experimenter (E1), but for some of them (2.2.3, 2.2.4 and 2.2.6) a second person (E2) was required. Two different second persons assisted in different experiments, but the same person assisted always in one task for all trials and individuals.

Figure S2 Basic experimental setup of the PCTB (depicted here experiment 3, *Rotation*). The table with the sliding board on top is attached to the mesh of the sujects' cage and the subject is positioned in the centre of the setup using a carabiner (they have been previously trained to stay put wherever the carabiner is positioned). In this example, after watching the placement of the reward and the subsequent rotational movement, the sliding board was pushed towards the individual to choose between the three cups.

Table S2 Summary of the PCTB and the number of trials per task and individuals per species and task.

	scale	**task**	**trials**	***Lemur catta***	***Varecia variegata***	***Microcebus murinus***
physical	space	**2.1.1 *Spatial memory***	**6**	27	13	16
		2.1.2 *Object permanence*	**24**	27	13	12
		a) Single displacement	6			
		b) Double-adjacent displacement	6			
		c) Double non-adjacent displacement	6			
		d) Single displacement touch	6			
		2.1.3 *Rotation*	**18**	26	13	12
		a) 360°	6			
		b) 180° middle	6			
		c) 180° side	6			
		2.1.4 *Transposition*	**18**	27	13	12
		a) Single	6			
		b) Double unbaited	6			
		c) Double baited	6			
	quantities	**2.1.5 *Relative numbers***	**16**	27	13	9
		2.1.6 *Addition numbers*	**14**	26	13	9
	causality	**2.1.7 *Noise***	**12**	27	13	15
		a) Noise full	6			
		b) Noise empty	6			
		2.1.8 *Shape*	**12**	27	13	15
		a) Board	6			
		b) Cloth	6			
		2.1.9 *Tool use*	**1**	27	13	16
		2.1.10 *Tool properties*	**30**	27	13	15
		a) Side	6			
		b) Bridge	6			
		c) Ripped	6			
		d) Broken wool	6			
		e) Tray circle	6			
social	social learning	**2.2.1 *Social learning***	**4**	26	13	15
		a) Paper tube	1			
		b) Banana tube	1			
		c) Stick tube	1			
	communication	**2.2.2 *Comprehension***	**42**	27	13	13
		a) Head & eyes	18			
		b) Head, eyes & paw	18			
		c) Marker	6			
		2.2.3 *Pointing cups*	**8**	27	13	15
		2.2.4 *Attentional state*	**4**	26	13	15
		a) Away	1			
		b) Towards	1			
		c) Away body-facing	1			
		d) Towards body-facing	1			
	theory of mind	**2.2.5 *Gaze following***	**9**	27	13	16
		a) Head & eyes	3			
		b) Back	3			
		c) Eyes	3			
		2.2.6 *Intentions*	**12**	27	13	15
		a) Trying	6			
		b) Reaching	6			

2.1 Tasks of the physical domain

2.1.1 *Spatial memory*

On the experimental sliding board three cups were placed in a row. While the individual was watching, two rewards were first presented and then openly placed under two of three cups. After the board was moved towards the individual the individual had to choose between the three cups and point at the chosen one. The individual could choose two times consecutively, but if it chose the cup without reward first, no further choices were allowed. Individuals had to choose both cups correctly to count as a correct response.

2.1.2. *Object permanence*

Again, three cups were placed in a row. A smaller fourth cup (placed in the beginning on the far left or right side of the board) was used for displacing the reward into one of these three cups. Therefore, while the individual was watching, a reward was placed under the fourth cup and afterwards four different displacement-scenarios were conducted:

a) *Single displacement*: The fourth cup, including the reward, was moved under one of the three big cups without touching the other two cups.

b) *Double adjacent displacement*: The fourth cup was moved consecutively under two adjacent cups and the reward was left under one of these cups without touching the third.

c) *Double non-adjacent displacement:* The fourth cup was moved under the two outer cups and the reward was left under one of these cups without touching the cup in the centre.

d) *Single displacement touch*: The fourth cup was moved under one of the three cups and the reward was left there. E1 touched the other two cups in order to find out whether the individuals simply chose the cup touched last by E1 or indeed followed the small cup to the last location it was moved to.

After these displacements, the empty fourth cup was shown to the individual and the board was moved towards it. The individual was now allowed to make one choice for the single displacement and two consecutive choices for the double displacements. If it chose a cup that had not been part of the displacement-scenario no further choices were allowed. Individuals had to choose the reward-cup as first choice to count as a correct response.

2.1.3 *Rotation*

A movable tray is put on top of the board with three cups placed on it in a row. While the individual was watching, a reward was first presented and then openly placed under one of the three cups. The tray and hence the cups were then rotated in three different spatial scenarios:

a) *360°:* The reward was placed under one of the outer cups and the tray was rotated 360° in clockwise (or counter clockwise) direction. Hence, the reward was in the end again in the same position as before the rotation.
b) *180° middle:* The reward was placed under the cup in the centre and the tray was rotated 180° in clockwise (or counter-clockwise) direction. Hence, the reward was in the end still in the same position as before the rotation.
c) *180° side:* The reward was placed under one of the outer cups and the tray was rotated 180° in clockwise (or counter-clockwise) direction. Hence, the reward was in the end in the opposite position as before the rotation.

After the rotations, the board was moved towards the individual and it could choose a cup once. Individuals had to choose the reward-cup correctly to count as a correct response.

2.1.4 *Transposition*

Again, three cups were placed in a row and while the individual was watching a reward was first presented and then openly placed under one of the cups. The cups were then transpositioned in three different spatial scenarios:

a) *Single transposition:* The position of the reward-cup was switched with one of the empty cups without touching the third cup.
b) *Double unbaited transposition:* The position of the reward-cup was switched with one of the empty cups and afterwards the positions of the two empty cups were switched.
c) *Double baited transposition:* The position of the reward-cup was switched with one of the empty cups and afterwards again switched with the other empty cup.

After the transpositions, the individual could make a choice once and only the reward-cup being the first choice counted as a correct response.

2.1.5 *Relative numbers*

Two plastic plates were placed on the testing board and then hid from the view of the individual using an occluder. Both plates were then baited with different amounts of equally sized reward pieces, covered with lids and placed in the middle of the board. After removing the occluder the lids of both plates were simultaneously lifted and hence the individual could see the amounts of reward pieces in each plate for about 5 seconds. Then the plates were moved to the sides of the board, one right and one left, and the individual could make its choice. Each of the following pairs of numbers of reward pieces was trialled once per individual[2] (the order of presentation was randomized):

1:0 II 1:2 II 1:3 II 1:4 II 1:5 II 2:3 II 2:4 II 2:5 II 2:6 II 3:4 II 3:5 II 3:6 II 3:7 II 4:6 II 4:7 II 4:8

(Additional four control conditions *1:1 II 2:2 II 3:3* and *4:4* were tested to monitor any possible side biases, e.g. choosing the same side in every trial.)

The individual had to choose the larger quantity first to count as a correct response.

2.1.6 *Addition numbers*

Hidden behind the occluder, three plastic plates were baited with different amounts of reward pieces and then covered with lids and placed in the middle of the board. The occluder was removed, the lids of the outer plates were lifted simultaneously, and the individual could see them for about 5 seconds. Then they were covered again, and the lid of the middle plate was uncovered, allowing the individual to see its amount of reward pieces for 5 seconds. Afterwards the contents of the middle plate were transferred into one of the outer plates, with the individual being able to watch the transfer but not the content of the side plates. The empty middle plate was removed from the board and the individual could make its choice between the two covered outer plates. Each of the following pairs of reward pieces is trialled once per individual (the order in which they are presented is randomized):

1:0 + 3:0 = 4:0 II 6:1 + 0:2 = 6:3 II 2:1 + 2:0 = 4:1 II 4:3 + 2:0 = 6:3 II 4:0 + 0:1 = 4:1 II 2:1 + 0:2 = 2:3 and 4:3 + 0:2 = 4:5

(Each combination was presented with the resulting higher number being once on the left and once on the right side, resulting in 14 trials in total.) The individual had to choose the larger quantity first to count as a correct response.

2.1.7 *Noise*

Behind the occluder a reward was hidden in one of two opaque cups. After the occluder was removed, the cups were manipulated in the two following ways while the individual was watching, and it had to choose the reward cup first to count as a correct response:

a) *Noise full:* The reward cup was shaken three times, letting the food rattle inside and the empty one was simply lifted once without shaking (order was randomized).

b) *Noise empty:* The empty cup was shaken three times, producing no sound and the baited cup was simply lifted once without shaking (order was randomized).

2.1.8 *Shape*

Behind the occluder a reward was hidden beneath one of two identical pieces of plastic board or cloth, thereby changing the appearance of the baited piece. After removing the occluder the individuals were presented with two different situations and they could choose once between the two possibilities. The individual had to choose the reward board or cloth first to count as a correct response.

a) *Board:* The reward was hidden underneath one of two plastic boards (sized 15x10 cm; 4x3 cm for mouse lemurs). The reward plastic board was not lying flat on the surface but inclined a bit.

b) *Cloth:* The reward was hidden underneath one of two pieces of cloth (sized 15x10 cm; 4x3 cm for mouse lemurs). A visible bump in the cloth was made by the reward instead of remaining flat on the surface.

2.1.9 *Tool use*

A reward was placed on the board out of reach of the individual (about 25 cm; 8 cm for mouse lemurs). Because the reward itself was out of reach for the individual it could only gain the food item by manipulating the tool, in this case a simple wooden stick (length 30 cm; 10 cm for mouse lemurs) that was provided to the individual. It had to retrieve the reward using the tool within two minutes; otherwise the attempt was not counted as a correct response.

2.1.10 *Tool properties*

Behind the occluder two different tool setups, one intact and effectively functioning to gain the food reward and the other not, were placed on the sliding board. The individual could choose a tool once by pulling it and the first choice had to be the functioning tool to count as a correct response. Five different tool setups and objects were used:

a) *Side:* Two identical pieces of cloth (sized 15x10 cm; 4x3 cm for mouse lemurs) were placed next to each other on the board. On top of one piece a reward was placed and for the other piece it was placed directly next to the cloth, making it the ineffective tool. The individual could only gain the reward placed on top of the cloth by pulling at it.

b) *Bridge:* Again, two identical pieces of cloth (see above) were placed on the board, but this time two identical plastic bridges were placed over each of their far ends. For the ineffective tool, the reward was placed on top of the bridge and for the other underneath it. Hence the individual could obtain the reward by pulling the cloth.

c) *Ripped:* Two pieces of cloth were again used, but only one of them intact the other was ripped apart in the middle. The two broken pieces were placed on the board with a gap of 1 cm in between, making it visually obvious that they were not connected. It was important that the intact piece of cloth (sized 15x10 cm; 5x3 cm for mouse lemurs) was equally sized as the ripped pieces including the gap (2 smaller pieces sized 7x10 cm; 2x3 cm for mouse lemurs). For both cloths, the reward was placed on top of the far end, hence for the ripped cloth on the unreachable piece, making it ineffective. The individual could choose one cloth and obtain the reward by pulling at it.

d) *Broken wool:* This task was basically identical to the previous one, except that pieces of wool string were used instead of cloth. The rewards were tied to the far ends of the wool pieces, making the broken one ineffective. The individual needed to pull at the intact string in order to gain a reward.

e) *Tray circle:* Two small plastic trays (sized 6x6.5 cm; 2x2.5 cm for mouse lemurs) were placed on the board. One of them had a round hole cut in the middle (Ø 3 cm; 1 cm) and the other a u-shaped hole cut from out of its back. A reward was placed in the middle of each of the holes with the round one surrounding it effectively and the u-shaped one not holding it when pulled towards the individual. Using a string attached to the trays the individual was then allowed to pull at one of them to obtain the reward. Only the tray with the round hole would work effectively as it would push the reward towards the cage.

2.2 Tasks of the social domain

2.2.1 *Social learning*

In the three different treatments of this task there was always a piece of reward stuck inside a plastic tube and E1 demonstrated the solution of this problem to the individuals once. The observing individual was then given two minutes to solve the problem on its own. A trial counted as correct only if the individual obtained the reward successfully by using a method highly similar to the previously demonstrated one.

a) *Paper tube:* A reward was placed inside a 10 cm long transparent plastic tube with a piece of paper attached over both ends. E1 demonstrated how to open the tube: First E1 poked her finger through the paper on one end and then wiggled her finger in the tube to rip the paper further, making the hole in the paper larger (i.e. as opposed to using her mouth or hands to tear the paper off the tube). Finally, E1 tilted the tube in order to let the reward fall in her hand. After the demonstration, an identical tube was handed to the individual.

b) *Banana tube:* A small slice of banana was placed in the centre of a transparent plastic tube (15 cm) and a specific force had to be applied to get the reward out of the tube. E1 demonstrated how to get the reward by banging one end of the tube on the table (as opposed to shaking it forcefully). An identical tube with banana inside was afterwards handed to the individual.

c) *Stick tube:* An opaque plastic tube with caps on each end was baited with a reward. One of the caps had a hole in it but was glued to the tube, whereas the other cap had no hole but could be removed. E1 demonstrated how to open the tube: First E1 inserted a stick through the cap with a hole, and then she pushed the stick through the hole which forced the cap on the other end to fall off. After the successful demonstration, an identical grey tube was handed to the individual.

2.2.2 *Comprehension*

Behind the occluder a reward was hidden under one of two cups placed on the board in a row. After the occluder was removed E1 indicated the rewards' hidden location through three different possible pointing cues:

a) *Look (Head & eyes):* E1 alternated her gaze three times between the individual and the baited cup while calling the individuals' name and afterwards continuously looked towards the cup until the individual chose.

b) *Point (Head, eyes & hand):* E1 alternated her gaze three times between the individual and the baited cup while calling the individuals' name and continuously looked towards the cup and additionally pointed at it with the extended index finger of her cross-lateral hand until the individual chose.

c) *Marker:* E1 held an iconic photo marker, which depicted the reward (banana pieces), in her hand and alternated her gaze three times between the photo and the individual while calling the individuals' name. Then E1 placed the photo on top of the baited cup.

After the board was moved towards the individual it could choose between both cups. It had to choose the reward-cup first to count as a correct response.

2.2.3 *Pointing cups*

Two identical cups were placed at the far ends of the sliding board. The individual was directed to a starting point in the middle of the board and E2 (a second experimenter) entered the testing area, placed a reward under one of the two cups while the individual was watching and left again. After E2 left, E1 entered the area and centred the individual again on its starting point using a piece of food. Then E1 stood in the middle between both cups and waited for the individual to choose one of the cups. Given the individual chose the reward cup correctly within 60 seconds E1 offered it the reward and a correct response was scored.

2.2.4 *Attentional state*

In the beginning a second experimenter (E2) entered and placed a reward in front of the cage but out of reach of the individual, randomly varied either on its right or left side, and left the room again. Afterwards E1 entered but stood at the end of the room opposite of the reward and thus did not notice the reward on the floor. The attentional state of E1 varied in the different trials by looking in 4 different directions:

a) *Away:* E1 turned around and looked away from the reward. The individual had to approach from her front to gain her attention. If the individual did so within 20 sec, E1 turned around and waited for the individual to direct her attention to the reward by moving back to it. If the individual indicated the rewards' location within 20 sec, E1 handed it to the individual.
b) *Towards:* E1 looked towards the reward and waited for the individual to approach the reward and direct her attention towards it within 20 sec. If the individual indicated the rewards' location within 20 sec, E1 handed it to the individual.
c) *Away Body-facing:* This trial was identical to "*Away*", except that E1s' body faced toward the reward and only her face was turned away.
d) *Towards Body-away:* This trial was identical to "*Towards*", except that E1s' body was turned away and only her face was directed towards the reward.

Indicating the location of the hidden food item was possible by pointing to the rewards' location if it was in view of E1 or by first moving into E1s' view (i.e. gaining her attention) and then pointing to the location. To count as a correct response, the individual had to successfully gain the reward by indicating its location to E1, otherwise E1 left the room and E2 entered again and removed the reward.

2.2.5 *Gaze following*

By calling and presenting a reward the attention of the individual was attracted and once the individual looked at E1 one of three different communicative gaze cues (implemented on different days to minimize any kind of habituation) was performed by orienting in the corresponding direction:

a) *Head & eyes:* E1 called the individuals' name and showed a reward. Then she hid the food in her hand, which remained in front of her body. Afterwards she looked up with both her head and eyes for ~10 sec.
b) *Back*: E1 sat with her back facing the individual. She called the individuals' name and showed a reward. Then she hid the food in her hand, which remained in front of her body. Afterwards she looked up at the ceiling for ~10 sec. Within the ~10 sec she looked back over her shoulder at the individual three times to ensure the

individuals' attention. If it was not paying attention when E1 looked the second time, the trial was repeated.

c) *Eyes:* E1 called the individuals' name and showed a reward. Then she hid the food in her hand, which remained in front of her body. Afterwards she looked up at the ceiling for ~10 sec while her face was still facing the individual.

To count as a correct response the individual had to follow the gaze of the conspecific during the first 10 seconds after the E1 changed the gaze direction.

2.2.6 *Intentions*

Behind the occluder a reward was hidden by E1 in one of two closed metal tins placed on the board in a row. The occluder was removed and the tins were manipulated by E2 as follows:

a) *Trying:* E2 tries in vain to open the reward tin by removing the lid while looking at the tin.
b) *Reaching:* E2 tries in vain to reach for the reward tin by extending the equilateral arm and looking at the tin, but a Plexiglas barrier blocks the access to the tin. The cue is given continuously until the individual indicates its choice.

About 3 seconds after each demonstration E1 approaches again and moves it towards the individual, allowing it to make a choice. The reward tin had to be chosen first to count as a correct response.

3. <u>The Personality Study</u>

As temperament or personality of individuals can influence performance in problem solving tasks (Hare & Tomasello, 2005), study individuals were tested with respect to their reaction to 29 different items (novel objects, persons, foods; Herrmann et al., 2007; Schmitt et al., 2012). The testing situations varied depending on 1) the nature of the different items presented (humans, objects or food pieces), 2) whether the items were presented in combination or alone (e.g. non-familiar human moving a novel object), and 3) the level of activity of the items that took place during their presentation (e.g. novel object moving, also see Table S3).

The items were presented by a second, unfamiliar experimenter (E2) sitting in front of the cage (except the very first test, in which the familiar human experimenter E1 is presented to the individual). The individual was then directed to a starting point offering food and the stimuli ware each presented for 30 seconds. Each individual participated in one session per day on three consecutive days with the same order of stimuli (see Table S3). The first day all the items were presented and placed on the board by E2 and the individual was only allowed to view them (visible). Additionally, two non-social trials were also run during which the individual could either view the empty board alone or a bright red spot was placed on the board before E2 left the area. During the sessions of the second day (movement) E2 moved the different items from left to right over the board and on the third day (touch) the items were put close to the cage allowing the individual to potentially touch them if they wanted to.

Table S3 Summary of the items and methods used in the *Personality Study*.

	category	**item**	**description**
Visible	***Human***	a) Familiar (E1) b) Non-familiar (E2)	E1/E2 sits behind the board, hands on the lap facing the mesh.
	Object	a) Film roll canister b) Plastic animal c) Police car	E2 sits behind the board, hands on her lap with the object placed in the middle of the board. In the police car condition E2 holds the remote control and presses the horn button ten times.
	Food	a) Undesirable food b) Dried fruit piece c) 3 Raisins d) Banana piece	E2 sits behind the board, hands on her lap with the food placed in the middle of the board.
	Non-Human	a) Red spot b) Nothing	E2 places a red spot in the middle of the board and leaves. Nothing is on the board and E2 is out of sight.
Movement	***Human***	a) Hand b) Body	E2 sits behind the board and moves her right hand from the left side to the right side. In the body condition E2 nods up and down while seating.
	Object	a) Film roll canister b) Plastic animal c) Police car	E2 sits behind the board and moves the object from the left side to right side and back on the board. In the police car condition E2 lets the car drive to the other side of the board, left to right, two times.
	Food	a) Undesirable food b) Dried fruit piece c) 3 Raisins d) Banana piece	E2 sits behind the board and moves the food from the left side to right side and back on the board.
Touch	***Human***	Hand	E2 sits behind the board and puts her right fist on the board.
	Object	a) Film roll canister b) Plastic animal c) Police car d) Box	E2 sits behind the board, hands on her lap with the object placed on the board within reach of the individual.
	Food	a) Undesirable food b) Dried fruit piece c) 3 Raisins d) Banana piece	E2 sits behind the board, hands on her lap with the food placed on the board within reach of the individual.

All experiments were videotaped. Each individual's degree of anxiety and/or disinterest as a response to the different testing situations was scored from the video recordings. Therefore, the time it took the individual to approach the new item (latency) or whether they did it at all was noted and also whether they tried to touch it or not. In addition, the time the individual spent near the item (duration) and also how close it approached (proximity) was noted. Overall, this part of the study allows controlling for temperamental factors (anxiety-boldness/interest-disinterest) influencing cognitive abilities.

3.1 *Data analyses and detailed results*

Results for the correlations between the three personality measures (latency, proximity and duration) and the performance in the two cognitive domains of the PCTB are reported in the main article. A multivariate analysis of variance of the three personality measures revealed no differences between the ring-tailed and ruffed lemurs (Wilk's $\Lambda=0.941$, $F(3,34)=0.71$, p=0.550) and neither sex (Wilk's $\Lambda=0.828$, $F(3,34)=2.35$, p=0.090) nor the interaction between species and sex (species:sex; Wilk's $\Lambda=0.955$, $F(3,34)=0.54$, p=0.660) had an influence on individuals' performance. Univariate analyses (ANOVAs or Kruskal-Wallis-Tests) of each measure confirmed these insignificant differences between both species in all three personality measures.

4. <u>Inhibitory Control Test</u>

Testing inhibitory control of individuals (the ability to control one's impulses) might help to explain potential species differences in the physical or social domain of the tasks (Herrmann et al., 2007; Schmitt et al., 2012). It has been shown that inhibitory control can constrain apes in solving tasks in the physical (e.g. chimpanzees, Boysen & Berntson, 1995) and the social domain (e.g. chimpanzees, Melis et al., 2006b; Stevens & Hauser, 2004). The inhibitory control test of this study consisted of six additional trials of the spatial memory task of the PCTB (experiment 2.1.1), assessing whether the individuals would skip the middle one out of three cups. Therefore, while the individual was watching, rewards were placed under the two outer cups and the middle cup was left empty. The individual could then choose one of the cups, and if it chose one of the baited cups correctly, it could choose a second time. No second choice was allowed if the individual chose the middle cup first. To correctly perform this task, individuals had to inhibit their tendency to choose the empty middle cup, which was positioned closest to them. Hence, a response was only scored as correct when the individual consecutively chose the two outer cups and skipped the middle cup. We found no differences in performance between the three species (Kruskal-Wallis test: χ^2=2.34, p=0.31) and there were no correlations for inhibitory control and performance in any species, neither in the social nor the physical domain (Table S4).

Table S4 Spearman rank correlation between inhibitory control and performances in the physical and social domain.

species	domain	n	rho	p-value
Ruffed lemurs	physical	13	-0.13	0.662
	social	13	-0.09	0.772
Ring-tailed lemurs	physical	27	-0.08	0.691
	social	27	-0.06	0.765
Mouse lemurs	physical	15	-0.19	0.502
	social	15	-0.12	0.677

5. Rank

The possible influence of the individuals' rank on performance was examined as well, except for the mouse lemurs that are housed solitarily. In all lemur groups, rank was inferred through additional focal animal observations.

Chapter 4

Instrumental Problem-Solving Abilities in Three Lemur Species

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Author Contributions

KK and CF designed the experiments; KK conducted the experiments, analysed the data and drafted the manuscripts; CF and PK participated in writing the manuscripts

Abstract

Apes and some New and Old World monkeys (i.e., haplorhine primates) are known to routinely use tools. In strepsirrhine primates (i.e., lemurs & lorises), no tool use has been reported, even though they appear to have some basic understanding of spatial relations required for using a pulling-tool. To facilitate direct comparisons of the underlying abilities between haplorhine and strepsirrhine primate species, we experimentally examined instrumental problem-solving abilities in three captive lemur species (*Microcebus murinus*, *Varecia variegata*, and *Lemur catta*), using methods from previous experiments with haplorhine primates. First, lemurs were supposed to use a stick to gain access to an inaccessible food reward. Only one ring-tailed lemur solved this task spontaneously on the first attempt. After offering the stick repeatedly, 13 individuals of all three species solved it successfully. Second, lemurs had to choose between pairs of reachable objects with a food reward on or near them, where one object did not afford pulling in the food. Ring-tailed and grey mouse lemurs generally selected the correct (connected) object, thus performing comparably with haplorhine primates, and ruffed lemurs even matched chimpanzees in their performance. Thus, although strepsirrhine primates may lack the fine motor skills to use a stick as a reaching tool, they performed comparable with naturally tool-using haplorhine primates on means-end problems. Our findings suggest a dissociation in primates between the judgment of spatial relations between two objects, which appears to be roughly equivalent across species, and facility at handling sticks for instrumental purposes, which favours species with enhanced manual dexterity.

Key words: Primate cognition, lemurs, instrumental problem-solving, physical cognition, means-end reasoning

Introduction

Although tool use among animals is relatively rare, it is taxonomically widespread, including various mammals, birds, fish and invertebrates, and the number of reports of this behaviour has steadily increased in recent years (reviewed in Bentley-Condit & Smith, 2010; Fellers & Fellers, 1976; Sanz, Call & Boesch, 2013; Shumaker et al., 2011). Animals use tools mainly in foraging contexts, to deter predators, or for personal hygiene or comfort. Examples include sea otters (*Enhydra nutri nereis*) carrying rocks to the surface to crack open invertebrate prey (Fisher, 1939); baboons (*Papio ursinus*) deliberately throwing stones from elevated positions towards possible threats, such as unfamiliar observers (Hamilton, Buskirk & Buskirk, 1975); or elephants (*Elephas maximus*) using branches to chase off insects (Darwin, 1871).

Most recent reports of tool use are based on observations or experiments with birds and primates. Several passerine bird species, such as the woodpecker finch (*Cactospiza pallida*) or the New Caledonian crow (*Corvus moneduloides*), use stick-tools that are sometimes manufactured by themselves from twigs or leaves to forage for larvae in tree holes and are occasionally also cached for later use (Hunt, 1996; Klump et al., 2015; Millikan & Bowman, 1967). Among nonhuman primates, only a few haplorhine species, that is, monkeys and apes, regularly use tools spontaneously (reviewed in Bentley-Condit & Smith, 2010). One of the best-known examples is the use of stones or solid branches as pounding hammers in combination with wood or stone anvils to crack open hard-shelled foods in chimpanzees (*Pan troglodytes*; Beatty, 1951; Boesch & Boesch, 1993), long-tailed macaques (*Macaca fascicularis*; Carpenter, 1887; Malaivijitnond et al., 2007), and black-striped capuchins (*Cebus libidinosus*; Anderson, 1990; Fragaszy et al., 2004).

In strepsirrhine primates, that is, lemurs and lorises, which represent the most basal living primates (Yoder, 2007), no unequivocal observations of tool use have been reported so far, even though they comprise about 150 species with very diverse ecologies (Kappeler, 2012). Why tool use in this order is apparently absent or very rare might be due to several reasons: First, it might simply be underreported because most lemurs and lorises are nocturnal and relatively small, making behavioural observations difficult. Second, even though many strepsirrhines are exposed to seasonal resource variation, which has been suggested to be a selective pressure in some haplorhines to access energy-rich resources with the help of tools (Bentley-Condit & Smith, 2010), lemurs and lorises evolved other tactics, like torpor and hibernation, to deal with ecological bottlenecks (Schülke & Ostner, 2007). Third, strepsirrhines have relatively smaller brains than haplorhines (Isler et al., 2008) and may therefore lack the cognitive abilities to use tools, even though some of their cognitive abilities in the physical domain are on par with those of many haplorhines (reviewed in Fichtel & Kappeler, 2010). Finally, unlike some haplorhines, strepsirrhines are not able to oppose their thumbs and have therefore limited dexterity (Torigoe, 1985), which might hamper their ability to manipulate tools. Indeed, most strepsirrhine primates prefer to carry and manipulate objects or food with their mouth rather than with their hands (Jolly, 1964). Interestingly, food-grasping behaviour in lemurs appears to have coevolved with infant-carrying styles (Peckre et al., 2016). Species in which infants cling to their mothers’ fur used more unimanual grasps and less mouth grips during feeding sessions than species that carry their infants orally, suggesting that the fur-clinging ability coevolved with more precise manipulative skills (Bishop, 1962; Peckre et al., 2016).

Although lemurs apparently do not spontaneously use tools, studies with captive lemurs demonstrated that they are able to reason about spatial relations between objects: Individuals of two lemur species (*Eulemur fulvus* and *Lemur catta*) confronted with two different canes, varying in their functionality and properties, were able chose the one that allowed them to gain access to an out-of-reach food reward (Santos et al., 2005a). The lemurs solved this task as quickly as two monkey species faced with the same experimental situation (*Saguinus oedipus oedipus* and *Cercopithecus aethiops*; Hauser, 1997; Santos et al., 2005b). Because relational spatial reasoning is a cognitive requisite to solve instrumental problems and use tools, comparative studies of this ability can contribute to our understanding of its origins and elaboration (Cummins-Sebree & Fragaszy, 2005).

We therefore investigated the ability to judge spatial relations between objects in three lemurid primate species in tasks that have already been investigated in haplorhine primates (Herrmann et al., 2012). To this end, we experimentally investigated the ability to use a stick to extend the reach to get access to a reward and to solve dichotomous object-choice tasks between connected and disconnected object/reward pairs in captive populations of grey mouse lemurs (*Microcebus murinus*), black-and-white ruffed lemurs (*Varecia variegata*; hereafter called “ruffed lemurs”) and ring-tailed lemurs (*Lemur catta*). To directly compare the performance of lemurs with haplorhine primates, we performed experiments that have already been conducted with chimpanzees (*Pan troglodytes*), Sumatran orangutans (*Pongo pygmaeus*), olive baboons (*Papio anubis*) and long-tailed macaques (*Macaca fascicularis*) as part of the Primate Cognition Test Battery (PCTB; Herrmann et al., 2007; Schmitt et al., 2012). The PCTB included one so-called tool-use experiment (Experiment 1) in which individuals could use a stick to pull in an out-of-reach reward. Because this task basically requires the ability to reason about the relation between the stick and the reward, as well as the ability to manipulate the stick, but not the ability to alter the physical properties of another object an important criterion for tool-use (Beck, 1980; St Amant & Horton, 2008; page 1203), we, henceforth, refer to this task as the “stick task”. We additionally conducted experiments in which the subjects chose between a food item on a continuous support or a food item on a discontinuous support, a task thought to tap means-end reasoning (Experiment 2). In the stick-task the two great ape species, which possess a higher precision grip level, outperformed the two monkey species, which exhibit a medium precision grip level (Torigoe, 1985). In contrast, the results for the means-end reasoning tasks were indistinguishable among the four species.

Grey mouse lemurs are nocturnal, solitarily foraging primates with an omnivorous diet and carry their infants orally (Eberle & Kappeler, 2006; Ross, 2001; Tecot et al., 2012). In contrast, ring-tailed lemurs are diurnal, live in groups of 11 individuals on average, are opportunistic omnivores, and have infants who cling to the fur of the mother (Gould et al., 2003; Jolly, 1966; Ross, 2001; Sussman, 1991). Ruffed lemurs are also diurnal, live in small groups (average six individuals), mainly feed on fruits, and have infants who are carried orally (Ross, 2001).

We predicted that among lemurs the stick task would be solved only by ring-tailed lemurs because infants cling to their mothers’ fur. However, due to the lemurs’ inferior level of precision grip and dexterity (Torigoe, 1985), we predicted them to be generally less successful than the four haplorhine species. Because dexterity is irrelevant in the means-ends choice problems, and because brown and ring-tailed lemurs performed similar to haplorhine primates in a previous study using a slightly different setup (Santos et al., 2005a), we predicted that the three lemur species would perform equally and also at levels comparable with the four haplorhine primate species tested with the same experimental set-up (Herrmann et al., 2007; Schmitt et al., 2012).

Methods

This study was conducted between October 2014 and November 2015 with animals housed at the German Primate Center, Göttingen, Germany, and the Affenwald Wildlife Park, Sondershausen, Germany (www.affenwald.info/en). Both experimental setups are originally part of the PCTB and were adopted from Herrmann et al. (2007) and Schmitt et al. (2012). Only the size of the items and objects needed some adjustment to make them operable for lemurs, especially for the mouse lemurs (average body mass: Ruffed lemurs 3500 g, ring-tailed lemurs 2200 g and mouse lemurs 60 g; Isler et al., 2008).

Ethical statement

All experiments were noninvasive and based on a voluntary participation of the animals which obtained desired food as rewards, using positive reinforcement. The experiments took place without any food reductions, and water was always available *ad libitum* in both locations. This study is in accordance with the German ethical requirements of appropriate animal procedures. Consultation of the Animal Welfare Body of the German Primate Center is documented (E2-17).

Study subjects and general testing procedure

The experiments were conducted with a total of 56 adult individuals, including 15 to 16 grey mouse lemurs, 27 to 29 ring-tailed lemurs, and 13 ruffed lemurs. All study subjects were born in captivity and are housed at the German Primate Center (DPZ) or the Affenwald. In both facilities, animals are provisioned with fresh food twice a day. At the German Primate Center, ring-tailed and ruffed lemurs are offered an outdoor enclosure equipped with enriching climbing material and natural ground vegetation. At the Affenwald, both species range freely within a large natural outdoor enclosure (3.5 ha), covered mainly with beech trees (*Fagus sylvatica*). The nocturnal mouse lemurs are kept indoors at the German Primate Center, with an artificially reversed day-night cycle, and their cages are equipped with climbing material, fresh natural branches, and leaves.

All animals were individually tested in familiar surroundings and were unfamiliar with the tasks presented. The testing apparatus for all tasks consisted of a sliding board attached to the fence of the subjects' enclosure. Once pushed into reach, the subject had to either manipulate a stick (Experiment 1) or indicate its choice by pointing or reaching through the mesh wire towards the chosen item (Experiment 2; Fig. 1). The setup was identical for ruffed and ring-tailed lemurs but adapted in size for the mouse lemurs. Raisins or pieces of banana served as rewards for all species. During testing, no possible cues to the rewards' location were provided by the experimenter. Experiments were videotaped, and the subjects' responses to the tasks were coded afterwards from the videos. A naïve second observer additionally scored 20% of all trials. With an agreement of 100%, interobserver reliability was very good (Interclass Correlation Coefficient =1).

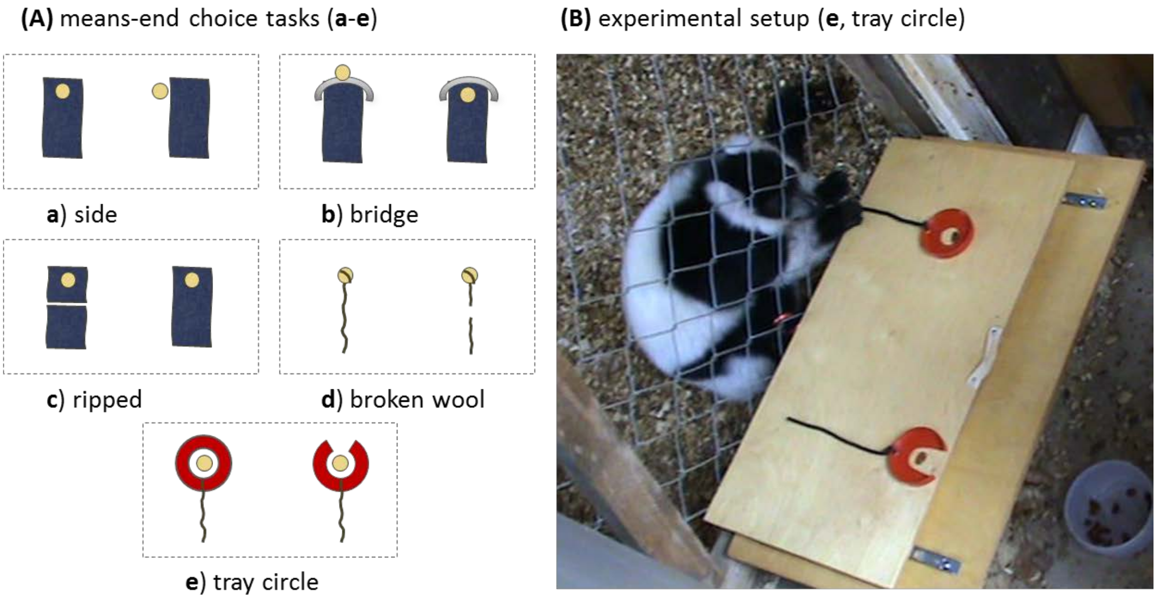
Experiment 1: The stick task

A piece of banana (ruffed and ring-tailed lemurs: about 1.5 cm thick; mouse lemurs: about 0.5x0.5 cm) was placed on the board out of reach of the test individual. The individual could only gain access to it by manipulating a straight wooden stick (length for ruffed and ring-tailed lemurs: 30 cm; for mouse lemurs: 6 cm). The stick was placed next to the banana, and the individual could retrieve the reward by using the tool in their first attempt and within two minutes; otherwise the attempt was not counted as a correct response.

Experiment 2: Means-end problems

Two different surfaces were set up on the sliding board behind an occluder, one with continuous connection or enclosure of the distal food reward with the reachable surface, and one with discontinuous connection or enclosure of the distal food reward with the reachable surface. Afterward, the individual was allowed to choose one reachable surface once by touching or pulling it, and the first choice had to be the continuous surface to count as a correct response. Five different means-end problems were tested (Fig.1):

a) *Side:* Two identical pieces of cloth (ruffed and ring-tailed lemurs: 15x10 cm; mouse lemurs: 5x2 cm) were placed next to each other. On one piece of cloth, the reward was placed on top, and for the other piece of cloth, the reward was placed directly next to it, making it the ineffective tool. The cloth with the reward placed on top was the correct choice.


(A) means-end choice tasks (**a**-**e**)

(B) experimental setup (**e**, tray circle)

Figure 1 (**A**) The different setups of the means-end choice task (a-e) and (**B**) the general experimental setup. A ruffed lemur sitting in front of the sliding table, pulling the reward towards itself using the connected object (Experiment 2e).

b) *Bridge:* Two identical pieces of cloth were placed next to each other, but this time, two identical transparent plastic bridges were placed above each of their far ends. For the incorrect choice, the reward was placed on top of the bridge, and for the correct choice the reward was placed on the cloth underneath the bridge.

c) *Ripped:* In this task two pieces of cloth were used again, but only one of them was intact; the other one was ripped apart in the middle. The two broken pieces were placed with a gap of 1 cm between them, to make it visually obvious that they were not connected. The intact piece of cloth (ruffed and ring-tailed lemurs: 15x10 cm; mouse lemurs: 5x2 cm) had the same size as the ripped pieces including the gap (two smaller pieces, ruffed and ring-tailed lemurs: 7x10 cm; mouse lemurs: 2x2 cm). For both cloths, the reward was placed on top of the far end. The individual was now allowed to choose one cloth and try to obtain the reward by pulling at it.

d) *Broken wool:* This task was basically identical to the previous one, except that pieces of wool string were used instead of cloth. The rewards were tied to the far ends of the wool pieces, making the broken one ineffective.

e) *Ring:* In this task two small plastic rings (ruffed and ring-tailed lemurs: 7 cm diameter; mouse lemurs: 3 cm) with a round hole in the middle (Ø 3 cm and 1 cm) were placed on the board. One ring had a segment (approximately 60°) removed from the back of the ring (see figure 1B). A reward was placed in the centre of each ring, and, using a string attached to the rings, the individual could pull one of them to obtain the reward. The string attached to the intact ring was the correct choice.

For each of the five problems, six trials were conducted per individual, as per Schmitt et al. (2012), who increased the number of trials, compared with the three trials per task originally conducted by Hermann et al. (2007), to use both possible spatial positions evenly (left and right). Accordingly, the position of the reward was randomized and counterbalanced across both possible locations, and the reward was never put in the same place for more than two consecutive trials.

Data analyses

For the stick task, a descriptive comparison of all species, including the great apes and monkeys (Herrmann, et al. 2007; Schmitt et al., 2012) was implemented. A Kruskall-Wallis test was conducted to compare the species in the number of sticks (or trials) needed by the successful lemurs. All analyses were conducted in R version 3.2.2 (R Core Team Vienna, Austria), and the critical *p* value was set at α = 0.05. To determine whether lemurs' overall performance in the means-ends choice problems was significantly better than expected by chance (chance-level at 50%), we used a generalized linear mixed model (GLMM; R-package "*lme4*", Bates et al., 2015). Correct responses combined with failures (c-binded) were used as binomial response variable, species as fixed factors, and individual identity as random grouping factor, and we estimated species-level specific intercept coefficients.

GLMMs were also used to test for differences in the performance in choosing the functional surface among the lemur species. Correct responses combined with failures (c-binded) were included as binomial response variable, whereas species, task, location, sex, and age were fitted as fixed factors and individual identity as random factor. To test all possible pairings among species and tasks, additional *post hoc* analyses using Tukey's multiple comparison test (R-package "*multcomp*", Hothorn et al., 2008) were implemented. All full models (including the predictors and control factors) were compared to the null model (only with the control factors) by analysis of variance (ANOVA). To test for a learning effect, we applied a Wilcoxon signed-rank test, using performances of the first three trials and the second three trials of each problem. For an overall comparison of performance in the means-end problems among lemur species, long-tailed macaques, olive baboons, chimpanzees and Sumatran orangutans, we calculated a one-way ANOVA with species as between-subject factor and performance of the species as dependent variable (data for nonlemurs from Herrmann et al., 2007 and Schmitt et al., 2012). To examine differences in performance of all possible pairings among the species, a Tukey's multiple comparison test was used.

Results

Experiment 1: The stick task

Nearly all individuals at least grabbed the stick once (ruffed lemurs: 93%, ring-tailed lemurs: 97%, mouse lemurs: 94%), and more than half of them were also able to move the food reward using the stick, albeit not within reach (ruffed lemurs: 73%, ring-tailed lemurs: 55%, mouse lemurs: 56%). Only one female ring-tailed lemur solved the stick task on the first attempt.

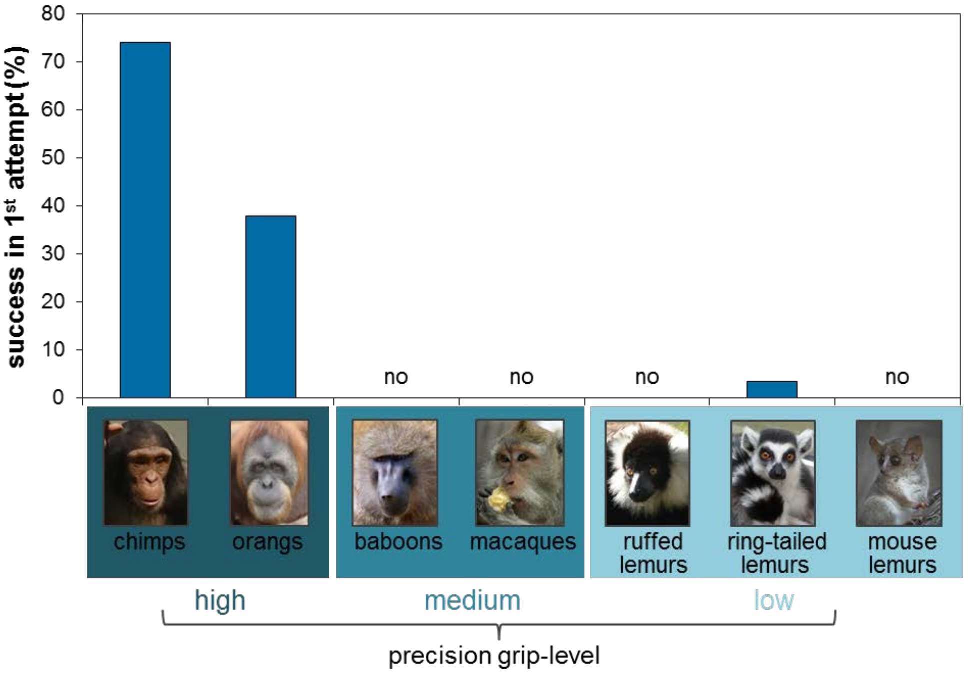


Figure 2 Proportion of success of the different primate species in the first attempt of the stick task (data for nonlemurs from Herrmann et al., 2007 and Schmitt et al., 2012); precision grip-level applied after Torigoe (1985).

Compared with lemurs, macaques and baboons performed equally poorly, with no successful subject in the first attempt, whereas in orangutans and chimpanzees, more individuals were successful (Fig. 2). In contrast to the experimental design of the original PCTB, we also put the stick back on the table after it fell down so that individuals had more trials to solve the problem. In total, 13 individuals (5 ruffed, 4 ring-tailed, and 4 mouse lemurs) used the stick to retrieve the reward during subsequent trials. Of these successful individuals, ring-tailed lemurs needed fewer trials (median: 3 trials ±1.3) to solve the task than did mouse (4.5 trials ±3.6) and ruffed lemurs (5 trials ±3.3), but this trend was not statistically significant (Kruskall-Wallis test: χ^2=4.67, p=0.097). Some individuals developed specific methods when handling the stick repeatedly, which can be mainly divided into two categories labelled "*push*" and "*pull*". In total, more than half of all individuals used one of these two methods in an attempt to obtain the reward (ruffed lemurs: 73%, ring-tailed lemurs: 59%, mouse lemurs: 50%).

Experiment 2: Means-end problems

In total, all three lemur species chose the correct object more often than expected by chance (binomial GLMM: χ^2=40.5, df=3, P<0.001; Table 1). With an average proportion of 64.6% correct responses, ruffed lemurs performed better than mouse lemurs but not better than ring-tailed lemurs (ring-tailed lemurs: 58.6%; mouse lemurs: 55.6%; see Table 2; binomial GLMM: χ^2=17.4, df=9, P=0.043; Table 3, Fig. 3).

Because the two study groups of ring-tailed and ruffed lemurs were both housed in two different facilities with different levels of enrichment, we also tested whether their housing location had an influence on their performance, which was not the case (Table 3). Furthermore, neither sex nor age influenced performance, and the performance of the lemurs did also not differ between the five different setups on means-end reasoning (Table 2, 3 and Fig. 4). In addition, we did not find a learning effect between performances in the first and second half of all trials (Wilcoxon signed-rank test: V=752.5, p=0.403).

Table 1 Results on whether the three different lemur species' performance was above chance level in the means-end choice task.

Fixed effects	Estimate	Odds ratio	SE	P-value
Ruffed lemurs	0.56	1.75	0.11	**<0.001 *****
Ring-tailed lemurs	0.35	1.42	0.07	**<0.001 *****
Mouse lemurs	0.22	1.25	0.10	**0.019 ***

*<0.05; ***<0.001 - significance levels

Table 2 Summary of the average proportions of correct responses of the three lemur species in the five different tasks of the means-end choice experiment and the overall results per species.

		Ruffed lemurs				**Ring-tailed lemurs**				**Mouse lemurs**			
	trials	n	Av	SD	ind	n	Av	SD	ind	n	Av	SD	ind
side	6	13	67.9	19	2	27	53.7	13	0	15	61.1	16	0
bridge	6	13	66.7	18	1	27	63.0	18	2	15	57.8	12	0
ripped	6	13	66.7	20	2	27	54.3	16	0	15	57.8	18	0
broken wool	6	13	57.7	18	0	27	57.4	13	0	15	51.1	15	0
tray circle	6	13	59.0	18	0	27	64.8	16	2	15	50.0	19	0
totals	30	13	**63.6**	**12**	**4**	27	**58.6**	**8**	**4**	15	**55.6**	**9**	**2**

Trials=number of trials per task; chance-level for each task: 50%; n=number of participating individuals; Av=average performance; SD=standard deviation; ind= individuals performing above chance level.

Table 3 Results on the influence of species, task, location, sex and age on the performance in the different tasks of the means-end choice experiment (p-values corrected for multiple testing, Tukey's).

Fixed effects	**Estimate**	**Odds ratio**	**SE**	**P-value**
Intercept (mouse lemurs, task a)	0.09	1.09	0.20	
Ring-tailed lemurs – mouse lemurs	0.26	1.30	0.15	0.20
Ruffed lemurs – mouse lemurs	0.60	1.82	0.18	**0.0021****
Ruffed lemurs – ring-tailed lemurs	0.33	1.40	0.15	0.06
Task b – a	0.14	1.15	0.16	0.90
Task c – a	-0.04	0.96	0.16	1.00
Task d – a	-0.14	0.87	0.16	0.91
Task e – a	0.01	1.01	0.16	1.00
Task c – b	-0.18	0.84	0.16	0.80
Task d – b	-0.28	0.76	0.16	0.41
Task e – b	-0.13	0.88	0.16	0.93
Task d – c	-0.10	0.91	0.16	0.97
Task e – c	0.05	1.05	0.16	1.00
Task e – d	0.15	1.16	0.16	0.88
Location (DPZ)	0.12	1.13	0.14	0.37
Sex (m)	-0.13	0.88	0.10	0.19
Age	-0.03	0.97	0.02	0.06

**<0.01 - significance level

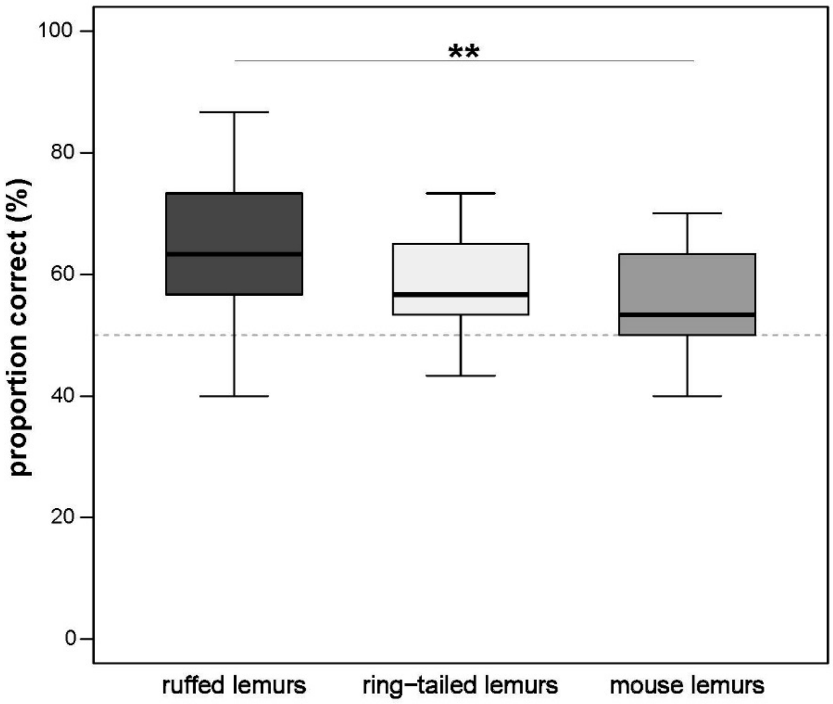


Figure 3 Comparison of the lemur species tested in the means-end choice task (**comparison ruffed vs. mouse lemurs: p=0.0021; ruffed vs. ring-tailed lemurs, ring-tailed vs. mouse lemurs: ns; binomial GLMM). Represented are medians (black bars), interquartile ranges (boxes), upper and lower hinges (whiskers), and the chance level (50%; dashed line).

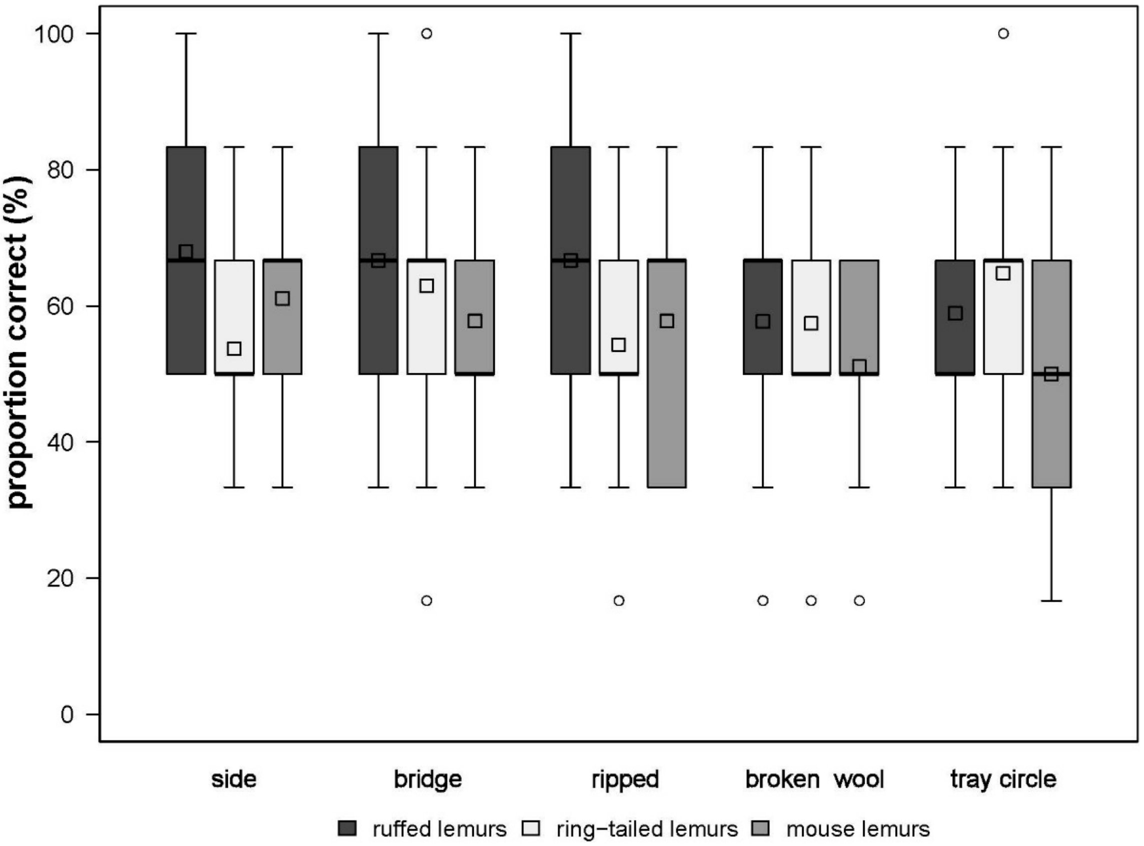


Figure 4 Comparison of the lemur species in the tasks of the means-end choice experiment. Represented are medians (black bars), interquartile ranges (boxes), upper and lower hinges (whiskers), averages (squares), and outliers (circles).

All three lemur species performed at levels comparable with the haplorhines (Fig. 5). Ruffed lemurs were even slightly better (median: 63.6% correct responses) than a natural tool user, the chimpanzees (median: 60.6% correct responses). Ring-tailed and mouse lemurs performed on average as well as the other nonhuman primates (1-way-ANOVA, *F*[6, 204]=1.45).

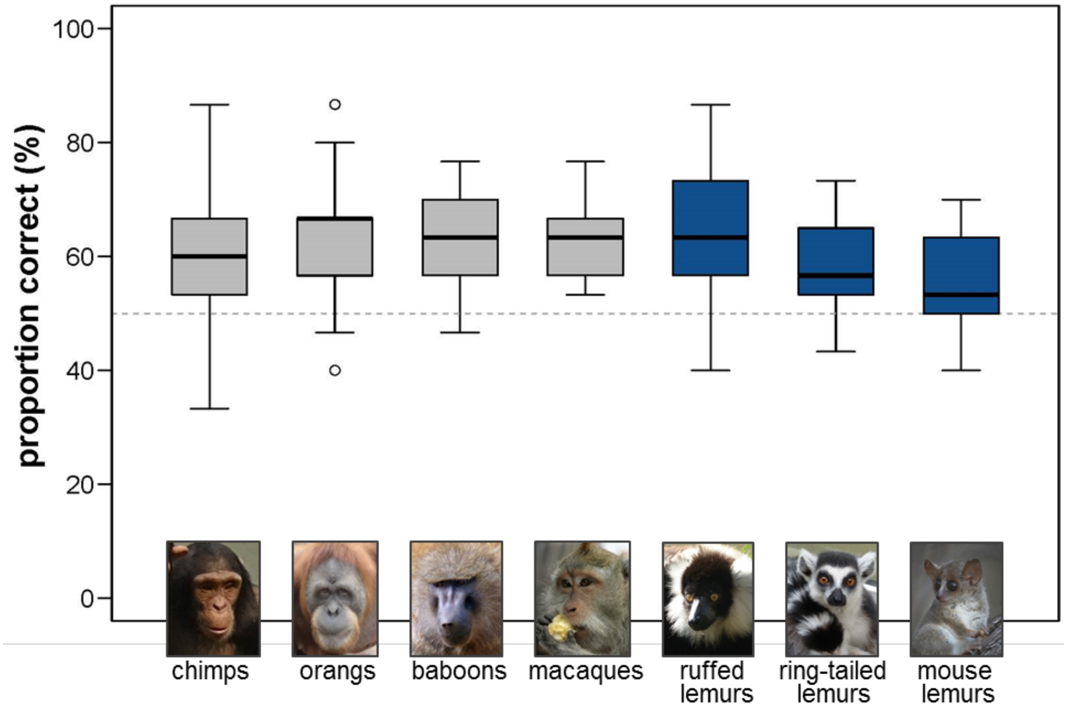


Figure 5 Comparison of all nonhuman primate species tested in the means-end choice task. Represented are medians (black bars), interquartile ranges (boxes), upper and lower hinges (whiskers), averages (squares), and outliers (circles; data for nonlemurs from Herrmann et al., 2007 and Schmitt et al., 2012).

Discussion

In the present study, 13 out of 56 individuals of three lemur species used a stick to pull a reward within reach, but only one individual managed to do so successfully in the first trial. In comparison with the haplorhine primate species, both ape species, but none of the other primate species could solve this task on the first trial. In the means-end problems examining judgments about spatial continuity between the food reward and the supporting, reachable surface, all three lemur species performed above chance level and their performance was similar to the performance of the haplorhine species. Hence, correct judgments about physical support relations do not seem to be restricted to naturally tool-using haplorhine species. These findings suggest that perceiving spatial support relations between objects appears to be a shared cognitive feature across primates.

In the stick task almost all lemurs failed in their first attempt to make use of the stick that required fine-scale motor control. Only one female ring-tailed lemur spontaneously used the tool successfully on the first attempt. Indeed, all five species exhibiting a low or medium level of precision grip (lemurs, long-tailed macaques, and olive baboons; Torigoe, 1985) that have been tested in this way were unable to use the stick to pull a reward into reach on the first attempt. However, returning the stick for additional trials, thereby giving the lemurs additional opportunities to explore and handle the stick, revealed that they tried to grab the stick but had problems handling it, although a few individuals solved the task in these subsequent trials. These findings support theoretical perspectives from ecological psychology, which suggest that animals visually perceive relevant features of spatial relations between objects and surfaces and that this visual information initially guides action (Shaw, 2003; Cummins-Sebree & Fragaszy, 2005). With regard to manipulative activity, animals may seek additional information that is not available from the visual array while manipulating objects, which provides information on the properties and consequences of acting with objects in different ways. As a consequence, animals learn from this activity which in turn guides future actions (Gibson, 1988). Hence, species-specific manipulative activities in everyday life have been suggested to predict the form and flexibility of different species in instrumental problem-solving tasks or tool-use (Cummins-Sebree & Fragaszy, 2005). For example, a comparison of the ability to manipulate objects to retrieve an out-of-reach reward between cotton-top tamarins (*Saguinus oedipus)* and tufted capuchins (*Cebus apella)*, which are extractive foragers whereas tamarins are not, revealed that capuchins discovered different ways to manipulate the objects through exploratory actions whereas tamarins did not (Cummins-Sebree & Fragaszy, 2005). Hence, the strict criterion to use the stick on the first attempt as suggested by Herrmann et al. (2007) might be too strict and too simple to investigate the abilities of solving instrumental problems across species. In addition, the experimental setup in which individuals had to reach the stick through the wire mesh might have hampered the subjects' ability to fully explore the propensities of the stick to reach the reward.

Among lemurs, which are all not extractive foragers, ring-tailed lemurs required fewer trials during subsequent opportunities to use the stick to get access to the out-of-reach reward than did members of the other two species. Because ring-tailed lemurs are the only one among the three species that cling to the fur of their mothers as infants, infant-carrying style might have facilitated the evolution of manipulative skills (Bishop, 1962; Peckre et al., 2016). Because brain size also correlates with manual dexterity (Heldstab et al., 2016), the relative importance of manual and cognitive constraints in limiting the manipulation of the stick remains unclear from these experiments.

Therefore, we also investigated the subjects‘ means-end reasoning about the continuity of contact between two objects in the second experiment, in which they had to choose between objects, but did not have to grasp an object, to obtain an out-of-reach food reward. As in a previous study (Santos et al., 2005a), members of all three lemur species tested in our study showed a similar sensitivity to the continuity of a supporting surface as the already tested haplorhines. Thus, a basic understanding of this feature of spatial relations between objects is apparently shared across the main primate lineages, irrespective of whether they use tools in the wild or not (Hauser, 1997; Hauser et al., 2002; Santos et al., 2005a).

Although it has been shown that the performance in tool using tasks can improve with practise (e.g. Cummins-Sebree & Fragaszy, 2005), we did not find an effect of experience in the tasks on means-end reasoning about spatial relations between objects. However, these experiments consisted of only six trials each, and a potential learning effect might only be evident with an increased number of trials. In addition, presenting lemurs with a series of more complex tasks with different difficulty levels concerning means-end reasoning, as well as the actual use of tools, seems now indicated. For example, we would like to investigate if lemurs would not only choose between objects to use as tools but also learn to move an object to create an appropriate interface with another object to solve the problem at hand (Cummins-Sebree & Fragaszy, 2005; Santos et al., 2005a). More information on strepsirrhine primates’ abilities to manipulate objects in instrumental tasks might ultimately contribute to a more comprehensive understanding of the evolution of tool use in primates and other orders.

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Supporting Online Material: Movies

Stick-task

The individual can only gain access to an out-of-reach food reward by manipulating a straight wooden stick that was placed next to the banana.

Movie S1

Stick-task - successful trial; ring-tailed lemur (*Lemur catta*)

Movie S2

Stick-task - problems handling the stick; ruffed lemur (*Varecia variegata*)

Means-end problems

The individual has to use means-end reasoning in order to choose between a continuous and a discontinuous surface in order to pull in a distal food reward. Mouse lemurs were attracted to the working platform by tapping on the mesh of the cage with the tweezers. In addition, individuals were usually "centred" using a small piece of food reward before pushing the board towards them to choose.

Movie S3

Means-end problems, task a) Side; mouse lemur (*Microcebus murinus*)

Movie S4

Means-end problems, task b) Bridge; ring-tailed lemur

Movie S5

Means-end problems, task c) Ripped; ruffed lemur

Movie S6

Means-end problems, task d) Broken wool; mouse lemur

Movie S7

Means-end problems, task e) Tray circle; ring-tailed lemur

Chapter 5

Use of gaze and pointing cues presented by a human demonstrator, modelled humans and conspecifics in Malagasy primates

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Animal Cognition: submitted

Author Contributions

KK and CF designed the experiments; KK conducted the experiments, analysed the data and drafted the manuscripts; CF and PK participated in writing the manuscripts

Abstract

Being able to follow the gaze and to understand gestures of other individuals is beneficial in intraspecific interactions. This ability has been studied in various animals, especially in several species of non-human primates, by conducting gaze following and object-choice experiments offering social-visual cues by human demonstrators to locate a reward. However, compared to conspecifics, humans may not be an appropriate model for this task. We therefore tested whether members of three lemur species (*Microcebus murinus*, *Lemur catta*, *Varecia variegata*) are able to follow the gaze and to locate a hidden food reward in an object-choice experiment by using social-visual cues given by either a human or by human and conspecific model-demonstrators presented as photographs or video-clips. Lemurs followed the gaze of conspecifics in videos but not on photos. They did not follow the gaze of humans in photos or videos, and only ring-tailed lemurs followed the gaze of a human. In the object-choice experiment, all lemur species made use of social-visual cues when presented by a human or a photo of conspecifics, but not when they were presented by videos or photos of humans. Since the study groups were housed under different conditions of human exposure, we examined whether the housing condition influenced performance in these tests. Lemurs performed better with a human demonstrator when they were used to regular close human contact (tourist park). Thus, lemurs can make use of social-visual cues and the exact nature of the stimulus (conspecific/human), and the level of human socialisation modulates their performance.

Key words: Primates, gaze following, pointing cues, objects-choice test, social cognition

Introduction

One advantage of living in groups is information transfer among group members. For species that rely on visual communication, it is beneficial to be able to follow the gaze of other individuals and to understand their communicative signals to spot predators, locate food sources or to obtain social knowledge from conspecifics (Emery, 2000; Tomasello et al., 1998; Zuberbühler & Byrne, 2006; Zuberbühler, 2008). Visual co-orientation has been recognized as an important behavioural mechanism in this context (Itakura, 1996, 2004; Miklósi & Soproni, 2006; Zuberbühler, 2008). In experiments on this ability, animals were either tested for their ability to visually co-orient with a human or conspecific demonstrator (i.e. gaze following: e.g. Itakura, 1996; Tomasello et al., 1998) or to use gaze-direction or pointing cues of a demonstrator to locate a hidden food reward in object-choice experiments (e.g. Anderson et al., 1995; Kaminski et al., 2005). In the latter, individuals have not only to follow the demonstrators' gaze to the target location, but they also have to infer that gazing or pointing provide salient cues.

The ability to follow human gaze has been demonstrated in ravens (Bugnyar et al. 2004) and several primate species (Amici et al., 2009; Kano & Call, 2014; Liebal & Kaminski, 2012). Studies working with a conspecific as demonstrator revealed gaze following skills in reptiles (Wilkinson et al., 2010), birds (Kehmeier et al., 2011) and primates (Kano & Call, 2014; Tomasello et al., 1998). The usage of social-visual cues presented by a human demonstrator in object-choice experiments was demonstrated in birds (Schmidt et al., 2011), mammals, such as sea lions or dolphins (Malassis & Delfour, 2015; Tschudin et al., 2001), domestic animals, like dogs, goats or pigs (Kaminski et al., 2005; Miklósi et al., 1998; Nawroth et al., 2016; Wallis et al., 2015), as well as primates (Anderson et al., 1995; Itakura, 1996). However, a human demonstrator might not be able to cross the cognitive boundary required for understanding signals from a member of another species, leading to an underestimation of the taxonomic distribution of these abilities (Botting et al., 2011; Ruiz et al., 2009).

Phylogenetic proximity to humans might be one factor explaining inter-specific variation in performance in gaze-following and object-choice experiments with human demonstrators. Among primates, haplorhines (monkeys and apes) indeed tend to perform better in such tests than strepsirrhines (lemurs and lorises; Kittler et al., 2015). Brown lemurs (*Eulemur fulvus*, N=3) and black lemurs (*Eulemur macaco*, N=4), for example, did not follow human gaze, and when pointing cues were implemented they rather looked at the demonstrator's finger than in the indicated direction (Itakura, 1996; Anderson & Mitchell, 1999). More recent studies in several lemur species indicated a certain ability to make use of human head orientations and gaze directions in tasks on competitive food choice, however (Botting et al., 2011; MacLean et al., 2013). For example, of four species of lemurs (ring-tailed lemurs, brown lemurs (*Eulemur mongoz*), black lemurs and red ruffed lemurs (*Varecia variegata rubra*)) only ring-tailed lemurs were able to avoid a human competitor by choosing between food at which the human gazed and food that was not competed for (Sandel et al., 2011). However, brown and black lemurs (N=4 and 2, respectively) were able to use visual cues of conspecifics depicted in photographs to locate a hidden food reward (Ruiz et al., 2009). Moreover, ring-tailed lemurs clearly follow conspecifics' gaze, as inferred by a telemetric gaze-tracking device (Shepherd & Platt, 2008). Hence, so far there is mixed support for social-visual co-orientation in lemurs, which might be either due to the use of different demonstrators and/or relatively small sample sizes. In addition, knowledge on solitary and nocturnal lemur species is totally missing yet.

Therefore, the objective of this study was to investigate gaze following abilities and the utilisation of pointing gestures in lemurs, by using human and conspecific demonstrators in two experimental setups on social co-orientation in three 93 lemur species differing in their levels of sociality. Grey mouse lemurs (*Microcebus murinus*) are nocturnal, solitary foragers, whereas ring-tailed (*Lemur catta*) and black-and-white ruffed lemurs (*Varecia variegata*; hereafter "ruffed lemurs") are diurnal and group-living. Specifically, we investigated whether lemurs' ability to co-orient differs between conspecific demonstrators offering a social-visual cue depicted on photographs and videos compared to a human, presented by an actual human, as well as photographs and videos. By presenting either static (photo) or moving (video) stimuli, we additionally investigated whether the nature of the stimulus influences lemurs' performance. Moreover, the level of socialisation with humans appears to influence the animal's use of socio-visual cues of humans (Maros et al., 2008; Miklósi et al., 2003), but studies using identical methods on two populations of animals with different levels of human socialisation are rare (Hare et al., 2002; Miklósi et al., 2003). Therefore, we compared the use of socio-visual cues of ring-tailed and ruffed lemurs between populations exposed to different levels of human contact (daily care-taking vs. walkable enclosure in a tourist park).

We first conducted a classical gaze following experiment in which the demonstrator, either a human or a human/conspecific model (photos or videos), looked upwards and the individuals were observed for subsequent gaze-shifts during the following 10 seconds. We predicted that lemurs follow the gaze of conspecifics more often than the gaze of humans and that they follow the gaze of conspecifics depicted in videos more often than on photos. In addition, we predicted that the two group-living lemur species make more use of socio-visual cues than the solitary mouse lemurs. In the second experiment, we investigated whether lemurs locate a hidden food reward indicated by a social-visual cue (looking and looking & pointing) given by a human or a human/conspecific model demonstrator (photo or video). We predicted that lemurs make more often use of social-visual cues given by a conspecific than a human demonstrator and when the conspecific is depicted in a video compared to the photo. Finally, ring-tailed and ruffed lemurs with more and regular exposure to humans should perform better with a human demonstrator than those that are exposed to low levels of human contact.

Methods

This study was conducted with animals housed at the German Primate Center (DPZ) and the Affenwald wildlife park (AW) between February 2014 and October 2017. Parts of the experimental setup were adopted from the *Primate Cognition Test battery* (treatments with a human demonstrator; Herrmann et al., 2007), but adjusted in size to make it operable for lemurs. Additionally, we added experiments using photos and videos of humans and conspecifics.

Ethical note

All experiments were non-invasive and based on a voluntary participation of the animals. The individuals were all trained to get used to the general experimental procedures and to being separated from the group for the short time during the experiments by rewarding them with much desired food for participation, using positive reinforcement. All experiments took place without food restrictions. In both locations, animals are provisioned with fresh food twice a day and water is available *ad libitum*. The German Primate Center is registered and authorised by the local and regional veterinary governmental authorities (Reference number: 32.22/VO Stadt Göttingen; 392001/7 Stadt Göttingen) as well as the Affenwald (Veterinäramt Sondershausen & UNB Kyffhäuserkreis; Reference number: 13 6433-04/2 SDH Kö). This study is in accordance with the German ethical requirements of appropriate animal procedures. Consultation of the Animal Welfare Body of the German Primate Center is documented (E2-17).

Study subjects and general testing procedure

The experiments were conducted with adult individuals of grey mouse lemurs (n=11-16), ring-tailed lemurs (n=20-27) and black-and-white ruffed lemurs (n=11-13). All study subjects were unfamiliar with the presented tasks, born in captivity and housed either at the German Primate Center (DPZ) in Göttingen or the Affenwald in Sondershausen (see supplementary material, Table S1). At the DPZ, ring-tailed and ruffed lemurs each inhabit an outdoor enclosure equipped with enriching climbing material and natural ground vegetation. The nocturnal mouse lemurs are kept indoors on an artificially reversed day-night-cycle, and cages are equipped with climbing material and fresh natural branches. The level of interaction between primates and humans (caretakers & scientists) is kept to a minimum at the DPZ. At the Affenwald, the lemurs range freely within a large natural outdoor forest enclosure (3.5ha). Since lemurs are handled by animal caretakers from birth on to facilitate brief veterinarian inspections, and because visitors can walk through the enclosure, lemurs at the Affenwald are used to close interaction with humans from birth on. All animals were individually tested in separated but familiar test rooms. The testing apparatus consisted of a sliding board attached to the subjects' enclosures on which the experiments were set up (Fig. 1). The experimental setup was identical for ruffed and ring-tailed lemurs but adapted in size for the smaller mouse lemurs. Raisins or pieces of banana served as food rewards.

All experiments were videotaped, and the performance of the subjects was coded afterwards from the videos. A naïve second observer additionally scored 20% of all trials for the pointing cues experiment and 100% of the gaze following experiment. The overall Interclass Correlation Coefficient was very good with ICC=0.957. In the experiments the socio-communicative gaze following and pointing cues were either given by the experimenter (E1) or by photos and video clips of humans and conspecifics. For the model conspecifics, unknown individuals were used to avoid any potential influence of familiarity. Similar photos of conspecifics were shown to the individuals before the start of the experimental trials to habituate them to photos in general. Due to methodological problems, such as taking video-recordings under dim red-light, the experiments using videos were only conducted with ring-tailed and ruffed lemurs but not with mouse lemurs.

Experiment 1: Gaze Following

The experiment was set up behind an occluder and the trial began with the removal of the occluder. Each individual participated in 16 different tasks (10 for mouse lemurs) consisting of 3 trials each and conducted on different days to minimize habituation:

a) Control condition: This task was conducted in order to establish a baseline estimate of how often the subjects look upwards in the absence of any social-visual cues. Therefore, E1 called the subjects' name and showed a reward. Then she hid the food in her hand, which remained in front of her body and looked straight at the subject's chest for 10s.

b) Head & eyes: E1 called the subjects' name and showed a reward. Then she hid the food in her hand, which remained in front of her body. Afterwards she looked up with both her head and eyes for 10s. In the modelled human and conspecific experiments, the individual (human or conspecific) in the photo or video looked up with both its head and eyes for 10s with the eyes open.

c) Back: E1 sat with her back facing the subject. She looked back over her shoulder, called the subjects' name and showed a reward. Then she hid the food in her hand, which remained in front of her body. Afterwards she turned around and 189 looked at the ceiling for 10s, during which she looked back over her shoulder at the subject twice while calling its name to ensure that it was still paying attention. In the modelled human and conspecific experiments, the individual in the photo or video sat with its back towards the subject and looked up for 10s (see supplementary material, Fig. S1B).

d) Eyes: E1 called the subjects' name and showed a reward. Then she hid the food in her hand, which remained in front of her body. Afterwards she looked up at the ceiling for 10s with her eyes only while her face was still facing the subject. In the modelled human and conspecific experiments, the individual in the photo or video glanced to the ceiling for 10s with its eyes only while the face was still oriented towards the subject.

Tasks b-d were conducted with five different demonstrator categories (human, photo human/conspecific and video human/conspecific). To count as a correct response the subject had to follow the demonstrators' gaze upwards during the 10s after the social-visual cue was presented.

Experiment 2: Pointing Cues

A reward was hidden behind an occluder under one of two cups placed next to each other on the board. When the occluder was removed, the subject was presented with communicative pointing cues towards the rewards' hidden location offered either by E1 or by photos and videos of humans and conspecifics. To this end, the photo or small video screen was placed between the two cups (Fig. 1). Each individual participated in 10 different tasks (6 for mouse lemurs) consisting of 6 trials each that were conducted on different days to minimize habituation:

a) Looking (Head & eyes): E1 alternated her gaze three times between 212 the subject and the baited cup while calling the subjects' name to assure its attention and afterwards continuously looked towards the cup until the subject made a choice. For the human and conspecific photos and videos, E1 always ensured the individuals' attention by calling its name before presenting the cue. In the photos the background was always white (see supplementary material, Fig. S1) and the depicted human or lemur oriented its head and eyes towards the baited cup. In the videos, the individual first moved its head and eyes from a central position towards the correct side and then the screen froze, showing the correct orientation until the subject made a choice.

b) Pointing (Head, eyes & hand/paw): In addition to the previous setup, E1 also pointed at the cup with the extended index finger of her cross-lateral hand until the subject made a choice. In the human and conspecific photos and videos the individual additionally also pointed/grabbed with its hand towards the baited cup (see Fig. S1C).

Similar to the gaze following experiment, both tasks were conducted with five different demonstrator categories (human, photo human/conspecific and video human/conspecific). After the cues were presented, the board was moved towards the subject and it could choose between the two cups. It had to choose the baited cup first to count as a correct response. The position of the reward was randomized, and counter balanced across both possible locations and the reward was never put in the same place for more than two consecutive trials. The insides of both cups were beforehand rubbed with a piece of reward in order to prevent any inadvertent olfactory cues, and during testing of the conspecific demonstrator conditions no possible cues were provided by E1.

Figure 1 General experimental setup. A female ring-tailed lemur sitting in front of the sliding table and choosing between the two cups after looking at the social-visual cue (video) presented on the screen between the two cups.

Data analyses

All analyses were conducted in R version 3.2.2 (R Core Team, Vienna, Austria) and the critical p-value was set to $\alpha = 0.05$. In the gaze following experiment, the control condition without any social-visual stimulus served as baseline against which we compared the performance in the other treatments. To examine whether lemurs looked more often up in response to one of the five categories (human, photo human/conspecific, video human/conspecific) than in the control condition we used a generalized linear mixed model (GLMM; R-package "*lme4*"; Bates et al., 2015). We used correct responses (looking upwards) combined with failures (c-binded) as binomial response variable, while species, category, location, sex and age were fitted as fixed factors, and individual identity as random factor. To compare species' performances in all possible combinations, we conducted additional *post hoc* analyses using Tukey's multiple comparison tests (R-package "*multcomp*"; Hothorn et al., 2008). To investigate differences between the categories for each species, we also used GLMMs separated per species, with correct responses combined with failures (c-binded) as binomial response variable, category, location, sex and age as fixed factors and individual identity as random factors. For all possible combinations of categories we conducted *post hoc* analyses (Tukey's).

For the pointing cue experiments, we used a GLMM to determine whether lemur species' overall performance was better than expected by chance (chance-level at 50%). We used correct responses combined with failures (c-binded) as binomial response variable, species as fixed factors, individual identity as random grouping factor and we estimated species-level specific intercept coefficients. For the overall comparison of the species performances between human and the photo demonstrators, we also used a GLMM, with correct responses combined with failures (c-binded) as binomial response variable, species, category, location, sex and age as fixed factors and individual identity 260 as random factor. To test all possible combinations between the species we implemented an additional *post hoc* analysis (Tukey's). For investigating whether the level of socialisation had an influence on performance we conducted GLMMs separately for the human, photo human and photo conspecific-category, as well as by species (ruffed and ring-tailed lemurs). We used correct responses combined with failures (c-binded) as binomial response variable, location as fixed factors and individual identity as random grouping factors. For analysing whether our models indeed explain more of the observed effects than just individual variation, we compared all GLMMs to their null model (a GLMM with the same response variable but simply individual identity as fixed factor) afterwards by analysis of variance (ANOVA).

Results

Experiment 1: Gaze Following

In the control condition, members of all three lemur species looked upwards without any social-visual cue given by a demonstrator in about every fifth trial (ruffed 23.9%, ring-tailed 17.3%, mouse lemurs 18.0%; Fig. 2). Only during the presentation of video conspecifics, ring-tailed and ruffed lemurs looked up more often than in the control condition. Overall, males looked up more often than females (males: 35.9% correct responses, females: 20.0%; Table 1). Species, location or age did not influence the frequency of looking up (Table 1).

Figure 2 Percentage of coorientation of lemurs in response to different demonstrators in the gaze following experiment. In comparison to the control condition, only ring-tailed lemurs looked up more often when a video of a conspecific (***p<0.001) and video of a human human (**p=0.0039 was presented (all other conditions: n.s.; see Table 2). Represented are medians (black bars), interquartile ranges (boxes), upper and lower hinges (whiskers), outliers (circles), and averages (squares).

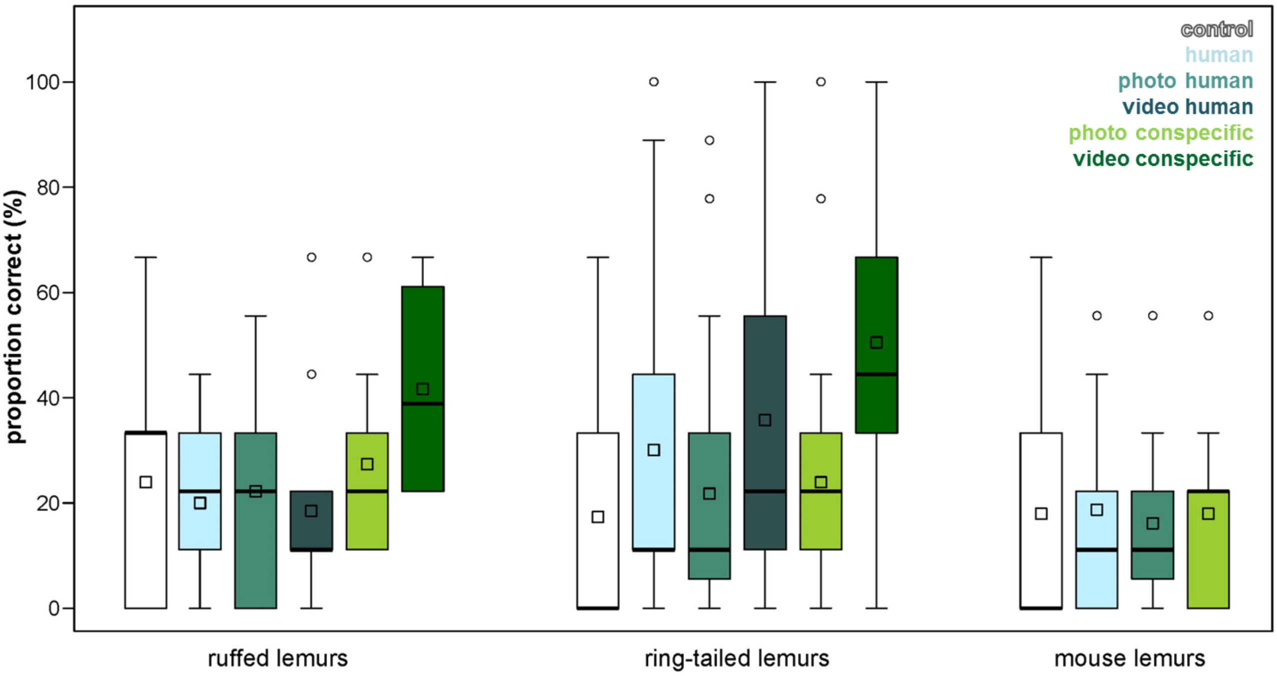

Table 1 Summary of the influence of species, category, location, sex and age on the performance in the gaze-following experiment (binomial GLMM, comparison to null model: χ2=76.15, df=10, P<0.001; p-values are adjusted for multiple testing).

Fixed effects	**Estimate**	**SE**	**P-value**
Intercept (Ring-tailed, Control condition)	-1.93	0.34	
Ruffed lemurs - Ring-tailed lemurs	-0.13	0.37	0.93
Mouse lemurs - Ring-tailed lemurs	-0.31	0.41	0.74
Ruffed lemurs - Mouse lemurs	0.18	0.45	0.92
Category: Human	0.42	0.25	0.55
Category: Photo Human	0.03	0.26	1.00
Category: Video Human	0.60	0.26	0.20
Category: Photo Conspecific	0.29	0.25	0.87
Category: Video Conspecific	1.36	0.26	**<0.001 *****
Location (DPZ)	-0.06	0.34	0.85
Sex (m)	0.79	0.27	**0.004 ****
Age	0.00	0.04	0.99

*<0.05; **<0.01; ***<0.001 - significance levels

Table 2 Results of the multiple comparisons for each species on the influence of the social cue-giver on coorientation in the gaze following tasks (Tukey's multiple comparisons).

Fixed effects	**Estimate**	**SE**	**P-value**
Ruffed lemurs			
Human - Control	-0.19	0.43	1.00
Photo Conspecific - Control	0.09	0.42	1.00
Photo Human - Control	-0.19	0.44	1.00
Video Conspecific - Control	0.68	0.42	0.58
Video Human - Control	-0.43	0.45	0.93
Photo Conspecific - Human	0.28	0.31	0.94
Photo Human - Human	-0.00	0.32	1.00
Video Conspecific - Human	0.87	0.30	**0.0380 ***
Video Human - Human	-0.23	0.34	0.98
Photo Human - Photo Conspecific	-0.28	0.31	0.94
Video Conspecific - Photo Conspecific	0.59	0.28	0.30
Video Human - Photo Conspecific	-0.51	0.33	0.61
Video Conspecific - Photo Human	0.87	0.30	**0.0456 ***
Video Human - Photo Human	-0.23	0.34	0.98
Video Human - Video Conspecific	-1.10	0.32	**0.0062 ****
Ring-tailed lemurs			
Human - Control	1.10	0.39	0.05
Photo Conspecific - Control	0.62	0.40	0.62
Photo Human - Control	0.35	0.40	0.95
Video Conspecific - Control	2.03	0.39	**<0.001 *****
Video Human - Control	1.42	0.39	**0.0039 ****
Photo Conspecific - Human	-0.49	0.24	0.33
Photo Human - Human	-0.76	0.26	0.0342 *
Video Conspecific - Human	0.93	0.23	**<0.001 *****
Video Human - Human	0.32	0.23	0.75
Photo Human - Photo Conspecific	-0.27	0.26	0.90
Video Conspecific - Photo Conspecific	1.41	0.25	**<0.001 *****
Video Human - Photo Conspecific	0.80	0.24	**0.0127 ***
Video Conspecific - Photo Human	1.69	0.26	**<0.001 *****
Video Human - Photo Human	1.07	0.26	**<0.001 *****
Video Human - Video Conspecific	-0.61	0.23	0.08
Mouse lemurs			
Human - Control	-0.02	0.49	1.00
Photo Conspecific - Control	0.00	0.49	1.00
Photo Human - Control	-0.15	0.51	0.99
Photo Conspecific - Human	0.01	0.34	1.00
Photo Human - Human	-0.13	0.37	0.99
Photo Human - Photo Conspecific	-0.15	0.38	0.98

*<0.05; **<0.01; ***<0.001 - significance levels

In comparison to the control condition ring-tailed and ruffed lemurs looked more often up in response to a conspecific video but not in response to human gaze changes or photos with a human or conspecific (Fig. 2 & Table 2). Ruffed lemurs also looked more often up in response to videos of conspecifics than to videos of humans. Interestingly, ring-tailed lemurs looked more often up in response to videos of conspecifics in comparison to photos of humans and conspecifics. They also looked more often up 284 in response to gaze changes of both, humans and videos of humans compared to photos of humans (Fig. 2, Table 2). All lemurs looked up more often to changes in human gaze directions compared to the head and back condition (Fig. S2), but not compared to the other conditions (Table S2).

Experiment 2: Pointing Cues

All three species performed above chance level (50%) in the object-choice tasks using a human demonstrator or a photo of a conspecific, and ring-tailed lemurs also performed above chance using a photo of a human (Table 3 & Fig. 3). However, ruffed and ring-tailed lemurs did not perform significantly better than chance when cues were provided

Table 3 Performance of lemurs in the object-choice experiments. Comparison with the chance level (50%) in each of the five categories (human, photo conspecific/human and video conspecific/human; binomial GLMM, comparison to null model: χ^2=146.3, df=13, P<0.001).

Fixed effects	Estimate	SE	P-value
Ruffed lemurs			
Human	1.00	0.18	**<0.001** ***
Photo Human	0.03	0.17	0.87
Video Human	0.14	0.17	0.41
Photo Conspecific	0.75	0.17	**<0.001** ***
Video Conspecific	0.20	0.17	0.24
Ring-tailed lemurs			
Human	0.85	0.12	**<0.001** ***
Photo Human	0.25	0.12	**0.0412** *
Video Human	0.03	0.12	0.81
Photo Conspecific	0.68	0.12	**<0.001** ***
Video Conspecific	0.17	0.12	0.18
Mouse lemurs			
Human	0.72	0.18	**<0.001** ***
Photo Human	0.13	0.18	0.47
Photo Conspecific	0.63	0.18	**<0.001** ***

*<0.05; ***<0.001 - significance levels

by videos of humans or conspecifics (Table 3). The frequency of correct choices was higher when a photo of a conspecific served as demonstrator in comparison to a human photo (Table 4). However, lemurs inferred more often the correct location when a human presented the cues compared to a human photo.

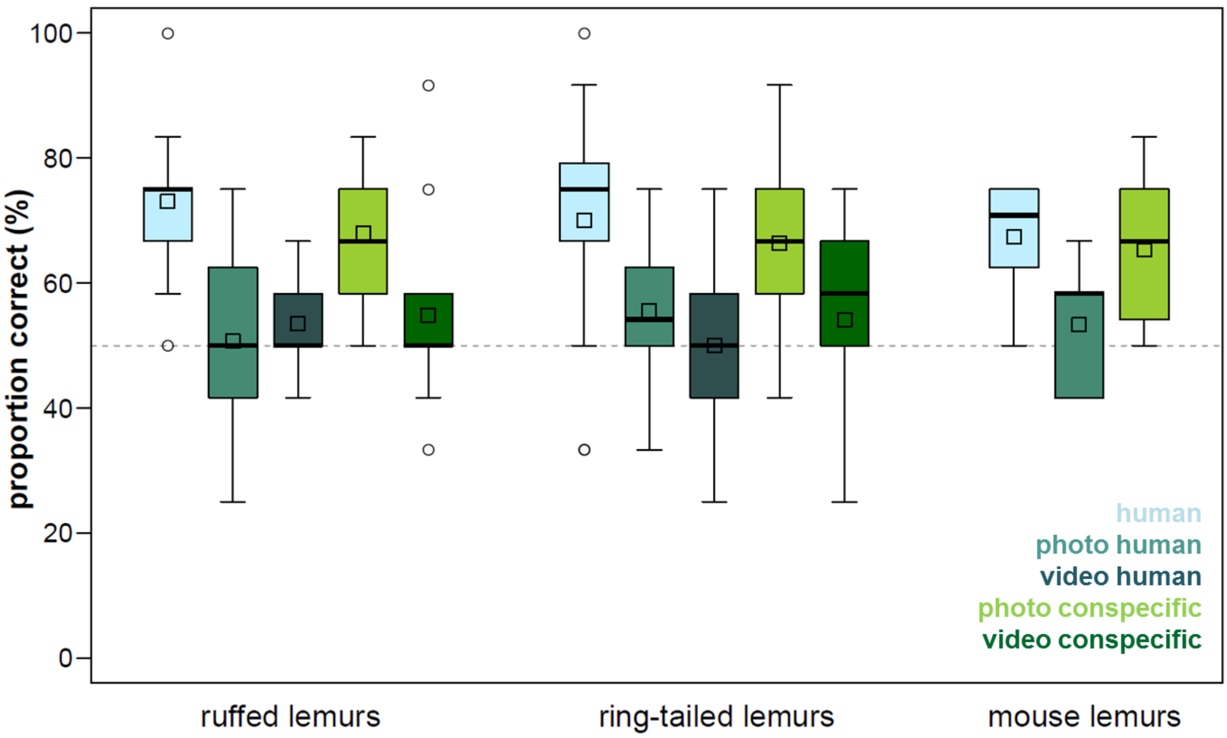

Figure 3 Percentage of correct choices of lemurs in the object-choice experiment with the five different demonstrators (video demonstrators only for ruffed lemurs and ring-tailed lemurs). Comparison to chance level (dotted line at 50%): all three species: human and photo of a conspecific: ***p<0.001, ring-tailed lemurs: photo human: *p=0.041 (all other conditions: p=ns, see Table 3). Represented are medians (black bars), interquartile ranges (boxes), upper and lower hinges (whiskers), outliers (circles), averages (squares), and chance level (dashed line).

Table 4 The influence of species, category, location, sex and age on the performance in the object-choice experiments (binomial GLMM, comparison to null model: χ^2=35.7, df=7, P<0.001; p-values are adjusted for multiple testing).

Fixed effects	Estimate	SE	P-value
Intercept (Ring-tailed, Photo Conspecific)	0.70	0.12	
Ruffed lemurs - Ring-tailed lemurs	-0.01	0.14	1.00
Mouse lemurs - Ring-tailed lemurs	-0.06	0.16	0.91
Ruffed lemurs - Mouse lemurs	0.05	0.17	0.95
Human - Photo Conspecific	0.17	0.12	0.34
Photo Human - Photo Conspecific	-0.53	0.12	**<0.001 *****
Photo Human - Human	-0.70	0.12	**<0.001 *****
Location (DPZ)	-0.03	0.13	0.80
Sex (m)	0.04	0.10	0.71
Age	0.00	0.02	0.91

***<0.001 - significance levels

Ring-tailed and ruffed lemurs exposed to higher levels of contact with humans performed better when a human experimenter provided the cues than lemurs that were exposed to lower levels of human contact (Table 5 & Fig. 4). There were no significant differences in performance between locations after the presentation of a human or conspecific photo demonstrator (Table 5).

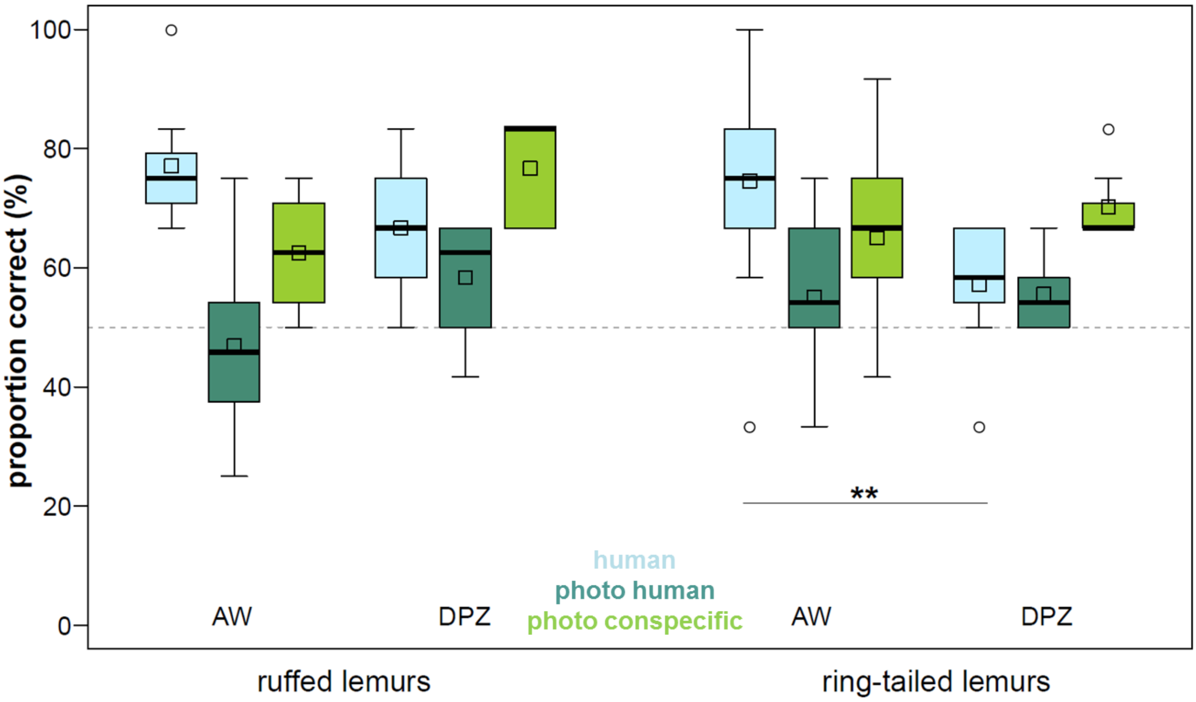

Figure 4 Percentage of correct choices in response to human and conspecific demonstrators in the population with higher (AW) and lower (DPZ) levels of human socialisation (**p=0.003, see Table 5). Represented are medians (black bars), interquartile ranges (boxes), upper and lower hinges (whiskers), outliers (circles), averages (squares), and the chance level (50%; dashed line).

Table 5 Influence of location on performance with the human and conspecific demonstrators of the object-choice experiments (binomial GLMMs, comparison to null models: ring-tailed lemurs (human): χ^2=7.79, df=1, P=0.005; ruffed lemurs (human): χ^2=2.01, df=1, P=0.16).

Fixed effects	**Estimate**	**SE**	**P-value**
Ruffed lemurs			
Human - location	-0.52	0.37	0.16
Photo Human - location	0.46	0.36	0.20
Photo Conspecific - location	0.68	0.37	0.07
Ring-tailed lemurs			
Human - location	-0.79	0.27	**0.003** **
Photo Human - location	-0.03	0.28	0.90
Photo Conspecific - location	0.24	0.27	0.38

**<0.01 - significance levels

Discussion

In this study, we showed that ring-tailed and ruffed lemurs followed the gaze of conspecifics depicted in videos, but not of conspecifics presented on photos and humans depicted in videos or photos. Ring-tailed lemurs also followed the gaze of a human demonstrator, whereas ruffed and mouse lemurs did not. All three species 308 made use of social-visual cues in form of gazing or pointing gestures presented by a human or a conspecific photo to solve an object-choice task. In addition, the level of contact with humans influenced ring-tailed and ruffed lemurs' performance, which is important to consider in future studies of other species.

Ring-tailed and ruffed lemurs followed the gaze of a conspecific depicted in videos, supporting the notion that lemurs do follow the gaze of conspecifics (Shepherd & Platt, 2008). However, only ring-tailed lemurs followed the gaze of a human demonstrator, which is line with a previous study on human gaze-following in ring-tailed lemurs, suggesting that the ability to follow human gaze indicates an example of convergent socio-cognitive evolution with haplorhine primates (Sandel et al., 2011). Interestingly, in the conspecific demonstrator conditions still photos were not as effective as videos in eliciting gaze following responses, indicating that not only species identity of the demonstrator, but also active motions contain salient information. Because many species make use of socio-visual cues presented by conspecifics, including reptiles (Wilkinson et al., 2010), birds (Kehmeier et al., 2011) and other primates (Kano & Call, 2014; Tomasello et al., 1998), social coorientation appears to be a basic cognitive skill of terrestrial vertebrates.

In the object-choice experiment, all lemur species made use of socio-visual cues given by humans and conspecifics on photos to infer the correct location of the hidden reward. Because in this, but also in the gaze following experiment, mouse lemurs performed with similar success as the two other species, living in groups or activity pattern *per se* do not appear to promote this ability. Moreover, because many species of birds and mammals are able to use socio-visual cues in object-choice experiments (Miklósi et al., 1998; Kaminski et al., 2005; Ruiz et al., 2009; Schmidt et al., 2011; Malassis & Delfour, 2015; Nawroth et al., 2016), this might also be a basic cognitive ability.

In both experiments, cues provided by conspecifics were more salient than cues provided by a human demonstrator for these lemurs. Interestingly, in the gaze-following experiment lemurs were more attentive to videos than to photos presenting conspecifics, whereas it was the other way around in the object choice experiment. In the gaze following experiment, where individuals had to follow the movement of the eyes or the head of a demonstrator, moving actions might be explicit, whereas in the object-choice experiment still photos may have provided less unequivocal cues compared to a video. Thus, these results only partly support other studies questioning the ecological validity of photos in socio-cognitive experiments (Bovet & Vauclair, 2000; Morton et al., 2016; Waitt & Buchanan-Smith, 2006), indicating a need for additional experiments with real-life conspecifics to assess the ecological validity of photos or videos in socio-cognitive experiments (Loretto et al., 2010; Schloegl et al., 2008; Wilkinson et al., 2010).

Finally, ring-tailed and ruffed lemur populations with more intense and regular contact with humans performed better in these tasks. Either lemurs performed better because they had more experience with humans gesturing, or they were less fearful of humans and hence more likely to focus on any given cue in the presence of a human. Since all individuals were well habituated to the presence of a human experimenter before the beginning of the experiment, we think that differences in performance between the two populations are rather due to their general experience with humans. The level of human socialisation also influenced performance in tasks involving socio-visual cues in several other species (Itakura, 2004; Maros et al., 2008; Miklósi et al., 2003; Lyn et al., 2010). For example, bonobos and chimpanzees reared in a socially complex human environment performed better in response to human gestures than standard-reared 355 individuals (Lyn et al., 2010). Moreover, the level of socialisation influenced performance in wolves, but not in dog puppies (Hare et al., 2002; Miklósi et al., 2003). Hence, the nature and frequency of human contact can influence the animals' performance in socio-cognitive experiments involving a human; a potential bias that should be considered in future studies.

Acknowledgements

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Supplementary Materials

General Information

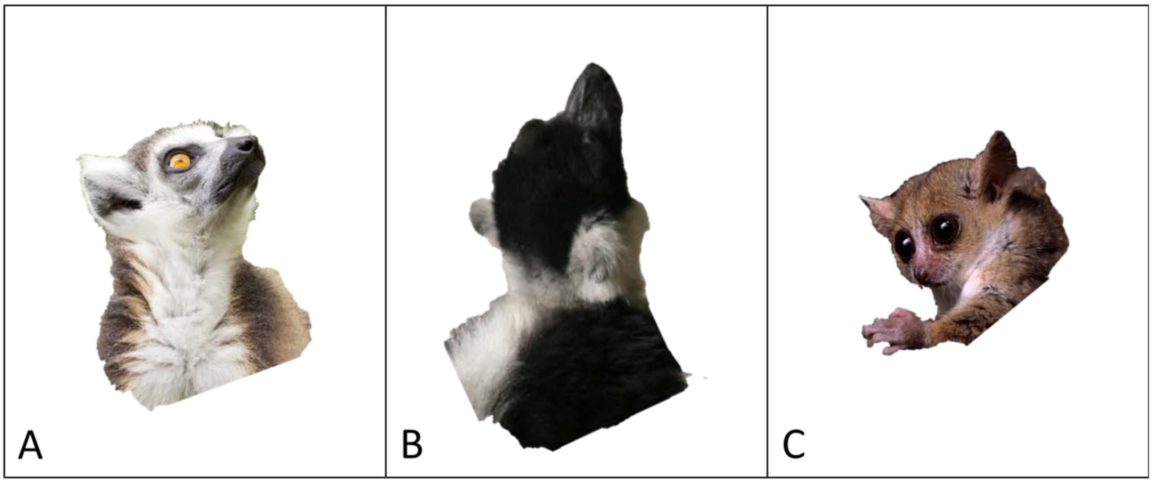

Figure S1 Examples for the presented conspecific photo cues. **A:** Ring-tailed lemur gazing upwards with its *head & eyes* (exp. 1b) **B:** Ruffed lemur gazing upwards showing its *back* (exp. 1c) **C:** Mouse lemur *pointing & looking* towards to the left side (exp. 2b).

Table S1 Number of study subjects in both locations.

species	location	males	females	age range (years)
ring-tailed lemurs	DPZ	1-2	4-5	3-10
	Affenwald	10-11	5-9	3-17
ruffed lemurs	DPZ	3	1-2	3-12
	Affenwald	4	3-4	3-20
mouse lemurs	DPZ	4-7	7-9	4-7

Experiments 1 & 2: Gaze Following & Pointing Cues

Table S2 Influence of task on performance within the different categories of the gaze following experiment; Tukey's multiple comparison analyses for all three species.

Fixed effects	**Estimate**	**SE**	**P-value**
Human			
Head - Eyes	0.93	0.29	**0.0082 ****
Head - Back	0.18	0.30	0.93
Eyes - Back	0.74	0.28	**0.0442 ***
Photo Conspecific			
Head - Eyes	0.20	0.28	0.90
Head - Back	-0.24	0.28	0.83
Eyes - Back	-0.04	0.29	1.00
Photo Human			
Head - Eyes	-0.27	0.33	0.85
Head - Back	0.10	0.31	0.99
Eyes - Back	-0.37	0.32	0.67
Video Conspecific			
Head - Eyes	-0.11	0.30	0.98
Head - Back	0.35	0.30	0.65
Eyes - Back	0.25	0.30	0.85
Video Human			
Head - Eyes	0.06	0.34	1.00
Head - Back	0.39	0.33	0.65
Eyes - Back	-0.33	0.34	0.76

**<0.01; *<0.05 - significance levels

Table S3 The influence of task on performance within the different categories of the pointing cues experiment (Tukey's multiple comparison analyses).

Fixed effects	**Estimate**	**SE**	**P-value**
Look - Look & Point			
Human	0.12	0.18	0.48
Photo Human	-0.09	0.17	0.60
Video Human	-0.17	0.19	0.39
Photo Conspecific	0.13	0.17	0.45
Video Conspecific	-0.32	0.20	0.11

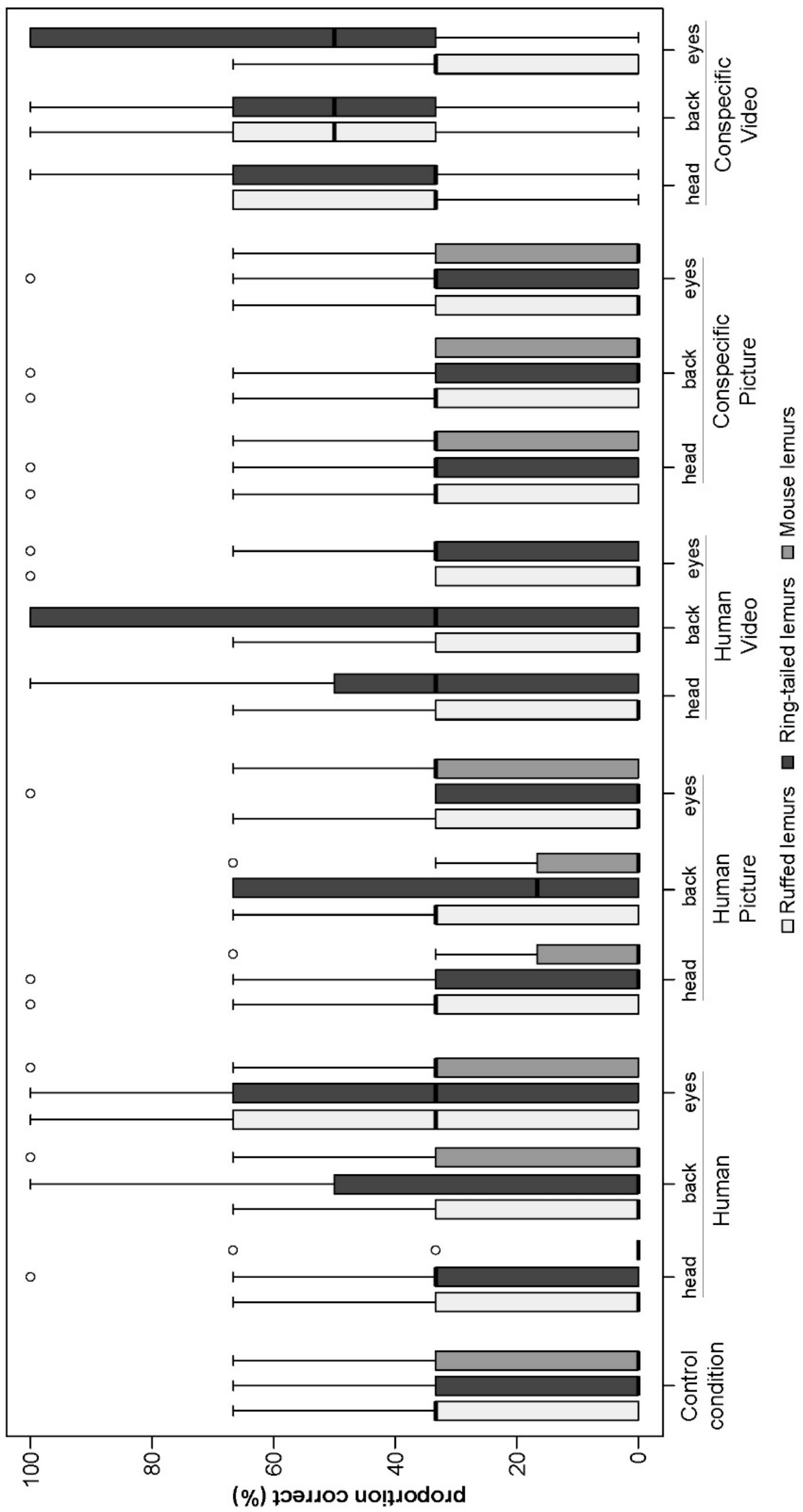

Figure S2 Comparison of the lemurs’ performance in the different treatments of the gaze following experiment: The control condition and the five categories (human, photo conspecific/human, video conspecific/human), split up into the separate tasks (head, back and eyes). Represented are medians (black bars), interquartile ranges (boxes), upper and lower hinges (whiskers), and outliers (circles).

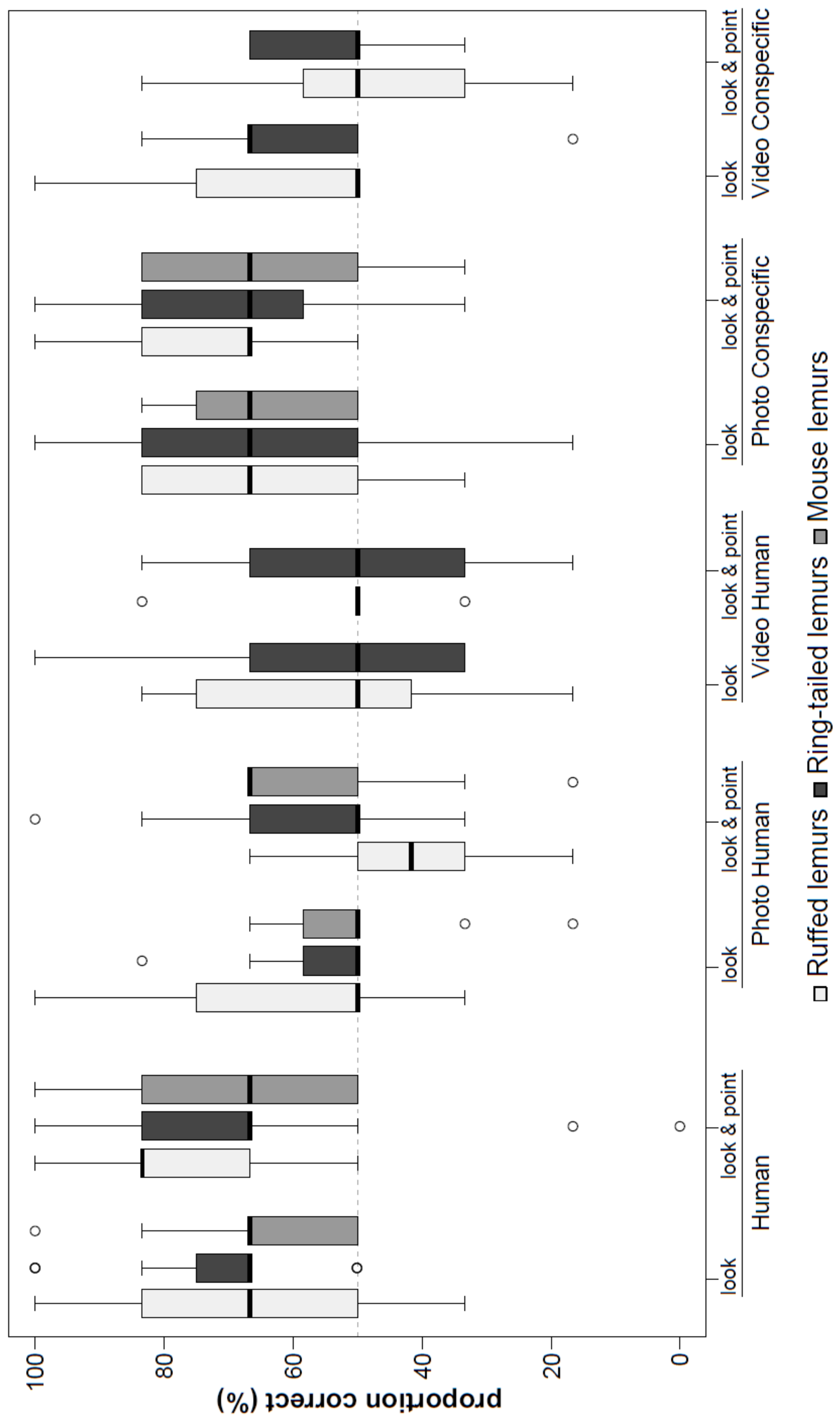

Figure S3 Performance of lemurs' in the pointing cues experiment. Shown are the five different categories (human, photo conspecific/human and video conspecific/human) split up into the separate tasks (look and look & point). Represented are medians (black bars), interquartile ranges (boxes), upper and lower hinges (whiskers), and outliers (circles).

General Discussion

In this thesis, I systematically investigated the cognitive skills of lemurs. My results indicate that overall, they have slightly more pronounced physical than social cognitive abilities. Furthermore, their performance compares to that of Old World monkeys and great apes in many aspects of both domains. Still, comparing the overall results revealed that apes outperformed lemurs in the physical domain, while all species performed equally in the social domain. In this last section of my dissertation, I will review and discuss my main results concerning the cognitive skills of lemurs and address questions and theories on the evolution of primate cognition. An important point in my discussion will be the applicability of studies in comparative cognition to different species and I will reflect on the balance between replication and adaptation of methodologies. Furthermore, I will discuss what this study adds to the overall picture of cognitive skills in animals and in the end, I will draw conclusions in view of future studies and directions in the field of comparative cognition.

6.1 Interpreting the results of the PCTB – Lemurs vs. Apes & Monkeys

The overall results of my study emphasise that interspecific differences in cognitive skills can vary considerably among different cognitive tasks. Lemurs performed at the same level as apes and monkeys in the scales on quantity and communication and, when excluding the tool use task, also in the scale causality. In the scale space, lemurs performed worse than haplorhines and they performed worse than chimpanzees for social learning, but outperformed both great ape species concerning theory of mind. However, even though all seven species differed less than expected in their performance in the tasks of the PCTB, I do not claim that the cognitive skills of lemurs equal that of monkeys or great apes in general, but only in some of the tasks as they are designed in the PCTB. Thus, I want to discuss three possible explanations for these partly unexpected results of the overall comparison:

First, as discussed in detail in Chapter 3, one reason for these results might be the tasks themselves, in that the cognitive abilities they test are simply too basal to reveal interspecific differences (Schmitt et al., 2012). A variety of studies already showed that even insects or fish can accomplish basal cognitive tasks (e.g. Chittka & Geiger, 1995; Chittka & Niven, 2009; Fuss et al., 2014; Schluessel et al., 2015; Loukola et al., 2017). Therefore, expanding the test battery by including more complex tests might reveal stronger interspecific differences. A good addition in the physical domain would be a task on reversal learning as suggested by Vanessa Schmitt (2012). Reversal learning is more demanding than basic numerical tasks, as individuals have to choose the smaller amount of food or tokens to give a correct response (Schmitt, 2012). Especially in the social domain additional experiments, which exclude possible non-social influences, appear advisable, since several of the tests of the PCTB might be influenced by non-social cues, such as local enhancement (discussed in *Chapters 3* & *5* and see below). Two examples for possible additions that might yield new insights in the social domain would be experiments on cooperation between individuals or on their prosocial behaviour towards conspecifics. In most cooperative setups, two individuals need to organise and work together to obtain an out-of-reach food reward (e.g. Melis et al., 2006 a, b). During prosocial choice tests, on the other hand, an individual commonly has to choose whether to provide a reward only to itself or in addition also to a conspecific individual (e.g. Cronin et al., 2012; Burkart et al., 2007).

Secondly, in most of the experiments only a few individuals of each species performed above chance on the individual level (see *Chapter 3*, Table 1). Thus, another possible explanation for the unexpectedly similar results of all seven species is that differences between the species cannot be found in their performances but are reflected in their learning curves (see *Chapter 3*). Commonly, for most cognitive tasks and species, continuing to retest the same setup leads to an improvement over time in the performance of the individuals, which is called learning effect. Within the tasks of the PCTB, I could not find an effect of learning for lemurs between first and last trials, however, the number of trials administered per task was limited on purpose (mostly only 6 trials). Still, the continued testing in the tool use task in Chapter 4 indicated that species differ in the amount of trials (or time) they need as practice until they can successfully conduct a task (MacLean et al., 2014). Ring-tailed lemurs which could solve the tool use task needed fewer trials than solving individuals of both other species, which however, might be based on their slightly higher level of dexterity (see *Chapter 4*; Peckre et al., 2016). Thus, interspecific differences might be more readily detectable in the time different species need to reach a certain criterion of correct choices in each task (e.g. 80 % correct; see *Chapter 3*), rather than in overall performance. Hence, if testing of individuals in the tasks of the PCTB could be continued, the species-specific learning curves could be explored and compared between species (see *Chapter 4*). However, it should be noted that testing all individuals until they reach criterion in all tasks of the PCTB would surely be a time consuming and costly work.

Finally, some of the tasks of the PCTB can be solved by simply using associative learning or even local enhancement and do not necessarily require actual mental representation (Terkel, 1995; Elgier et al., 2012; Schmitt, 2012); i.e. inferring the rewards' location through true understanding of the indicating pointing gesture or other presented cues. Local enhancement in this context means that the movement of the demonstrator towards one cup (intentions task) or the spatial closeness of her finger to it (comprehension task), leads to an enhanced attention of the individual to this location, which will increase the chances that it will choose this cup (e.g. Terkel, 1995; Mikolasch et al., 2012). Thus, a choice based on local enhancement might not reflect the cognitive skills the test aimed for, but simply reveal the individuals' focus of attention.

6.2 A brief Comparison to Gibbons

As mentioned in the introduction, white-handed gibbons have also been tested using a subset of the tasks of the PCTB (Yocom, 2010), and their performance fits well into the overall picture of unexpected results. This subset included the noise, shape and tool properties tasks from the physical domain, and the comprehension, pointing cups, attentional state and intentions tasks from the social domain. When I summarised these seven tasks on domain-level and compared them to the results of the lemurs in the corresponding experiments, ring-tailed and mouse lemurs performed slightly worse compared to gibbons in the physical domain, while ruffed lemurs matched their performance (see *Appendix*, Fig. A1). In the social domain, however, gibbons were marginally outperformed by all three lemur species. A closer look at the average performances in the different tasks revealed that gibbons performed at the same level as the lemurs in the noise task of the physical domain, but slightly better in the shape and tool properties tasks (see *Appendix*, Table A1). Similarly, they outperformed lemurs in the social domain only in the pointing cups task, but performed inferior in the other three social tasks. However, as mentioned before, the pointing cups task, in which gibbons excelled, is not completely convincing for a test of social skills, since it could simply be testing spatial memory. As a reason for the gibbons' poor performance in most of the tasks of the social domain, Yocom (2010) argued with their rather unique social structure of living in pair-bonded social groups (Bartlett, 2007). However, this argument does not match the results of my study, since mouse lemurs live mainly solitarily and still performed better than gibbons in the social domain. Similarly, comparing the overall performance of lemurs and gibbons rules out brain size as a simple reason for a higher level of cognitive skills, as gibbons have much bigger brains than lemurs (Isler et al., 2008), and should hence have outperformed them. Still, a comparison of the performance of gibbons with all seven non-human primate species in the entire setup of the PCTB would be desirable and might facilitate more distinct assumptions.

6.3 How did (Primate) Cognition evolve?

The overall results of my study allow a critical evaluation and discussion of the hypotheses on the evolution of primate cognition, particularly in the light of the different socioecological traits the three lemur species of my study represent.

To evaluate the *General intelligence hypothesis* (Spearman, 1904), it is important to know about the brain measurements of the seven non-human primate species. Concerning absolute brain size, the great ape species lead the way with the largest brains, followed by baboons and macaques, and within the three lemur species ruffed lemurs have the largest and mouse lemurs the smallest brains (see *Appendix*, Fig. A2; Isler et al., 2008). In contrast, relative brain sizes show a reversed picture, as mouse lemurs have by far the biggest brains in relation to their body mass. Macaques have the second biggest relative brain size and all other species show a roughly equal relation between brain and body mass (see *Appendix*, Fig. A2; Isler et al., 2008). However, even with both brain measurements showing very distinct differences between species, my overall results reveal no clear evidence in favour of the *General intelligence hypothesis*, since neither absolute nor relative brain size can offer a sensible explanation for the distribution of cognitive skills. For the physical domain, absolute brain size appears to predict cognitive skills better than relative brain size (MacLean et al., 2014), but my results offer no support for a domain-general one-to-one relationship between brain size and cognitive performance. Thus, my results seem to confirm findings of studies on primates and other taxa such as dogs or insects, which also could not find a clear-cut relationship (e.g. Hare et al., 2002; Chittka & Niven, 2009; Schmitt et al., 2012; MacLean et al., 2013; DeCasien et al., 2017).

However, in recent years, the number of experimental studies and comparative meta-analyses investigating the presence of a single “general intelligence” factor (*g* factor) in animals has increased, particularly in primates (reviewed in Burkart et al., 2016). While some studies could not find evidence for *g* (e.g. Herrmann et al., 2010), others, including some comprehensive meta-analyses, reported *g* on intra- as well as interspecific level (e.g. Deaner et al., 2006; Banerjee et al., 2009; Reader et al., 2011; Hopkins et al., 2014). In a literature-based meta-analysis involving 62 non-human primate species, Reader et al. (2011) included measures of innovation, social learning, tool use, extractive foraging and tactical deception. Their results show evidence for *g* on the interspecific level, which was also correlated with brain size. Thus, *g* as a factor of general intelligence in species is still debated and future studies will be needed to unveil further evidence concerning a domain-general distribution of cognitive skills.

Another aspect worthwhile mentioning is that focussing solely on brain size has been increasingly criticised due to the high degree of modularity in the brain (Barton, 2000; Barton & Harvey, 2000; Healy & Rowe, 2007, 2013). This modularity implies that not necessarily the entire brain responds to specific evolutionary selection pressures, but that only certain brain regions change in size, while others remain unaltered (Harvey & Krebs, 1990; Barton, 2000; Barton & Harvey, 2000; Venditti, 2017). Still, since for many species data on particular brain regions (e.g. the neocortex) is not available yet, such detailed comparisons are currently not possible (Venditti, 2017).

Connecting the evolution of intelligence to the diet of a species and its foraging effort (Clutton-Brock & Harvey, 1980; Milton, 1981; Byrne, 1996), the *Ecological intelligence hypothesis* is still one of the most popular evolutionary theories. Nevertheless, despite very recent additional support for this hypothesis (DeCasien et al., 2017), my results do not reflect a distinct correlation between diet (% of fruit; see Table

S1, *Chapter 3*, p. 51) and cognitive performance of the species. Particularly within the three lemur species, the highly frugivorous ruffed lemurs should have outperformed both omnivorous species, but overall performances showed no significant differences. Furthermore, all three species scored equally in every task of the physical domain and ruffed lemurs were even slightly outperformed by the omnivorous mouse lemurs the scale space (see Fig. 3, *Chapter 3*). In contrast, when comparing the spatial memory skills of four lemur species, Rosati and colleagues (2014) found that frugivorous ruffed lemurs showed better spatial understanding and memory than the omnivorous and folivorous species tested. This reduced spatial memory has also been found comparing frugivorous spider monkeys (*Ateles geoffroyi*) to folivorous howler monkeys (*Alouatta palliata*; Milton, 1981).

In the social domain, all seven species performed roughly equal, except from a slightly superior performance by the baboons (see *Chapter 3*). These overall results seem to oppose the *Social intelligence hypothesis*, as the tested species have different social systems and different average group sizes (see Table S1, *Chapter 3*, p. 51), which should have been reflected in their performance in the social-cognitive tasks. My results thus offer further support for those studies, which could not find a correlation between various social measures and brain size and hence question the generality of the *Social brain hypothesis* (e.g. Shultz & Dunbar, 2007; Finarelli & Flynn, 2009; Byrne & Bates, 2010; Schmitt et al., 2012; Benson-Amram et al., 2016; DeCasien et al., 2017). Still, many studies on the *Social brain hypothesis* have used average group size as a proxy for social complexity (e.g. Shultz & Dunbar, 2007; MacLean et al., 2013; DeCasien et al., 2017), which is questionable since group sizes also vary greatly within species (Venditti, 2017). To give an example, group size in ring-tailed lemurs can range from 4 up to 31 individuals per group (Sussman, 1991; Hood & Jolly, 1995) and these differences can be even more pronounced in other species and taxa (e.g. for primates: DeCasien et al., 2017, supplementary table). Additionally, living in large groups does not automatically imply a higher rate of social interactions or social partners than living in smaller groups. Therefore, the number of differentiated relationships that individuals have within a group was recently suggested to be a more representative reflection of the social complexity of a species (Bergman & Beehner, 2015; Venditti, 2017). Average measures of this proxy across species are still incomplete, but it would be interesting to include it in future comprehensive meta-analyses.

My results also do not offer support for the *Cooperative breeding hypothesis*, since the ruffed lemurs, which exhibit the highest levels of allomaternal care of all seven species (see Table S1, *Chapter 3*, p. 51), should have outperformed the others in the social domain, which they did not (Hrdy, 1999, 2009; Burkart et al., 2009; van Schaik & Burkart, 2011). An important next step in exploring the influence of cooperative breeding on cognitive skills would be to apply the PCTB to New World monkey species, since they have not been tested so far. This might offer important insight as allomaternal care is relatively common in New World monkeys compared to Old World monkeys and strepsirrhines (Chism, 2000; Ross & MacLarnon, 2000).

Concerning the *Cultural intelligence hypothesis* children were predicted to socially outperform all non-human primates which they did in both previous studies (Herrmann et al., 2007, 2010; Schmitt et al., 2012). The fact that lemurs' performance was equal to that of haplorhines in the social domain supports this hypothesis. However, whether it is generally possible to test this hypothesis using the PCTB is debatable, as the PCTB might not be optimal for comparing primates and children, which is the essential comparison for this hypothesis though (Yocom, 2010; Schmitt et al., 2012). As mentioned in the introduction, testing of the social domain is likely biased in favour of children since they conduct all tests with a conspecific as demonstrator (see *Chapter 5*). Therefore, a comparison between children and non-human primates in the social domain seems unreasonable, as it might lead to an underestimation of the distribution of social cognitive abilities. After all, a human demonstrator might not be able to cross the cognitive boundary required for an understanding of signals from a member of another species (Boesch, 2007; Ruiz et al. 2009; Botting et al. 2011; see *Chapter 5*).

In summary, the overall picture of the performances of the seven non-human primate species in the PCTB is not clearly explicable by any of the main hypotheses concerning the evolution of cognition. Still, there are some overall conclusions to be drawn from these results, which are 1.) they do not support the direct correlation between brain size and cognitive skills, 2.) cognitive abilities (in primates) are not distributed in a domain-general but rather in a domain-specific pattern, and thus, 3.) studying the cognitive skills of an animal species requires a set of tasks covering both cognitive domains to avoid biased results.

6.4 Comparative Cognition – Problems and Pitfalls

In the quest to understand the cognitive evolution in animals and the distribution of cognitive skills between species, systematic, comparative studies across a wide range of species are mandatory (MacLean, 2012). Therefore, the original PCTB appears to be the most suitable approach to the field of comparative cognition, as it allows a comparison between various primate species (Herrmann et al., 2007). However, it has certain limitations, such as the problem of using a human demonstrator for all species in the social cognitive tasks mentioned above. In theory, when excluding children, the conditions concerning the demonstrator in the social domain should be identical for all non-human primate species, which should permit an interspecific comparison. Still, my results confirmed that the level of socialisation with humans has to be considered when conducting socio-cognitive experiments with several species or even just several populations of the same species (see *Chapter 5*; Hare et al., 2002; Miklósi et al., 2003; Maros et al., 2008). In both, ring-tailed and ruffed lemurs, the level of socialisation to humans had a positive effect on the performance in the task on understanding human pointing cues (see *Chapter 5*, experiment 2).

Additionally, a human demonstrator might more generally not have the same influence on different species (Kano & Call, 2014; Schmitt et al., 2014). In the gaze following task (see *Chapter 5*, experiment 1) the results of the lemurs suggest that differences between species might exist at least in the social domain. Ring-tailed lemurs were the only species that looked up more often after the gaze cue presented by the human demonstrator than in the control condition, although all three species performed equally well with the photo of a conspecific. Similar differences were found between several hominid species when tested for gaze following using interspecific gaze cues (Kano & Call, 2014). Chimpanzees and children did only follow the gaze of their own species, whereas orangutans, bonobos and adult humans also followed the gaze of all other tested hominid species. Kano and Call (2014) argued that attention levels towards the presented videos varied between species, which however, would be supported by my own findings that lemurs could focus on the videos for only a short time before being distracted or losing interest (see *Chapter 5*, discussion). This inattentiveness was reflected in the poor performance in the pointing cues task when presenting the video demonstrator.

These results indicate that, at least for the social domain, an individuals' performance can be influenced by the species of the demonstrator, even if only by a lowered level of attention. Thus, in the last years, researchers have increasingly started working with touchscreens in cognitive experiments on various species, to avoid any involvement or distraction by a human experimenter during trials (e.g. Taylor et al., 2002; Leighty & Fragaszy, 2003; Joly et al., 2014; Martin et al., 2014; O'Hara et al., 2016). This approach additionally excludes a Clever Hans effect, as the tested animals cannot use inadvertent cues from human experimenters, such as gaze direction or body position, to increase their performance in cognitive tasks (e.g. Umiker-Sebeok & Sebeok, 1981; Miklósi et al., 1998; Lit et al., 2011).

However, the inattentiveness towards the video demonstrator also points out other possible influences during testing, which are the test subjects' attentional and motivational state towards the experimental setup (Ehrlich et al., 1976). Although these are not easy to measure or evaluate, they can potentially have a strong impact on the performance of individuals during cognitive experiments (Botting et al., 2011; Auersperg et al., 2011, 2012; Teschke et al., 2013). During testing of the lemurs for this thesis, I did not incorporate direct measures of attention or motivation, but instead always tried to ensure both by carefully observing the test subjects and stopping trials or sessions when an individual was obviously inattentive towards the setup (see *Chapter 3*, Methods). Individuals had to enter the testing facilities voluntarily each day and could take "days-off-work" if they wanted to, which should ensure their general motivation during the tests in addition to the food rewards. To avoid a lack of motivation, rather recent studies worked with automated experimental systems via touch screens, which are offered to the test subjects all-day. With these systems, subjects can choose to work whenever they are motivated to do so or can even freely select the task they want to work on in each session (Fagot et al., 2015; Calapai et al., 2017).

To investigate some of the inter-individual differences in performance in the tasks of the PCTB, I conducted additional tests on each individual's level of inhibitory control and some of their personality traits (Herrmann et al., 2007; Schmitt et al., 2012). As mentioned previously (see *Chapter 3*), performances of ring-tailed and ruffed lemurs in the physical domain did not correlate with any of the observed measurements of personality (latency, proximity and duration). In the social domain, no such correlation was found for ring-tailed lemurs, whereas ruffed lemurs that approached new stimuli more slowly (latency) and less closely (proximity) performed significantly better. One explanation for this correlation might be that this more careful approach allows individuals to better assess a situation before acting on a stimulus or in a cognitive task, although this ability should have been reflected in the performance of the physical domain as well.

Concerning the individuals' level of inhibitory control, studies by Amici and colleagues (2008, 2010) tested several haplorhine primate species in tasks of the physical domain as well as their level of inhibitory control. They found that increased cognitive skills were best explained by socioecological factors of a species and in particular high levels of fission-fusion dynamics. Lemurs' performances in the physical domain and the inhibitory control task in the current thesis, however, did not confirm any of these assumptions. Although ruffed lemurs exhibit a dynamic fission-fusion system (Baden et al., 2015; Holmes et al., 2016), they did not outperform the ring-tailed lemurs living in stable groups or the mainly solitary mouse lemurs. Performance in the inhibitory control task revealed no differences between species and level of inhibitory control also did not correlate with performance in the two domains of the PCTB (see *Chapter 3*). Another study using a setup possibly more suited for testing inhibitory control involved a detour reaching task, but could also find no significant differences between ring-tailed and ruffed lemurs (MacLean et al., 2013, 2014).

The fact that the PCTB is increasingly applied to new species, also from other taxa than primates (currently ongoing work: parrots, Krasheninnikova; ravens (*Corvus corax*), Sima & Pika; personal communication) offers the unique chance of an extremely broad and comprehensive comparison that may generate answers to important questions on the evolution of cognition. However, it also bears problems that always arise in comparative studies covering socioecologically very different species, since these differences might influence their performance when tested with identical methods (Yocom, 2010; Schmitt et al., 2012; Teschke et al., 2013). For example, the seven non-human primate species tested so far, show huge variation in their manipulative skills and dexterity (Torigoe, 1985; Holtkötter, 1997). Thus, a comparison of results of behavioural or cognitive experiments across species is usually not that simple and either fails due to major variation in the experimental set-up or due to the incapability of species to perform certain tests (Teschke et al., 2013). To continue the example of the tested primate species, a comparison between species of which some have physical limitations that influence their general ability to solve a task, such as lemurs in the tool use task (see *Chapter 4*), appears rather inappropriate and does not offer a reasonable comparison of their cognitive skills. Thus, for comparative research on cognitive abilities of animals the most difficult, but also essential task is to develop experimental setups with high ecological and social significance, that are manageable for a great number of species or adaptable in a way which does not change the task and its difficulty (e.g. Auersperg et al., 2011, 2013; MacLean et al., 2012; Schmitt et al., 2012).

6.5 What to do next? – An Outlook

Despite the new insight on lemur cognition my study offers, there is still a long road ahead to unravel all pieces to the puzzle of cognitive evolution. Earlier in this discussion I mentioned some possible future steps concerning the PCTB, but in general the importance of such comparative research for cognitive studies cannot be stressed enough (MacLean et al., 2012). The only way to gain reasonable information about interspecific cognitive differences is to test multiple species with the same task and evaluate their performances. Moreover, the variability of species differences in performance between tasks in my study supports the notion that comparing several species in their performances within only a single task or scale can lead to very biased results which could then cause misleading assumptions (Amici et al., 2010; MacLean et al., 2012; Schmitt et al., 2012). To give an example of a flawed interpretation: if I took the scale theory of mind as the sole measure of social cognitive skills, a comparison of the non-human primate results would lead me to conclude that monkeys and lemurs had a higher level of social cognitive skills than great apes (see Fig. 3, *Chapter 3*).

Thus, comprehensive approaches that cover a wide range of different cognitive tasks are vital to drawing valid conclusions (Amici et al., 2010).

In her thesis on long-tailed macaques and olive baboons, Vanessa Schmitt (2012) already suggested various reasonable changes and additions to the PCTB for future studies. An example would be the use of tokens or pebbles instead of actual food pieces in both experiments on numerical understanding, since she could show that the sight of the food while choosing between different quantities negatively influences the performance of individuals (Schmitt & Fischer, 2011). In the following I want to discuss further desirable future steps concerning the PCTB and comparative cognitive research in general.

6.5.1 Including more Species

Despite those shortcomings mentioned previously, the PCTB is currently still one of the most comprehensive setups in comparative cognition. Hence, in order to gain more insight into the distribution of cognitive skills, it would be desirable to apply these methods to a wide range of species, also from outside the primate order. As mentioned above, an inclusion of New World monkeys could improve the picture of primate cognition, as assembled by the results of the PCTB. Results on cognitive skills in the PCTB from all branches of the primate tree and beyond would additionally allow valid phylogenetic linearized least-square regressions (PGLS) to control for phylogenetic distances (Pagel, 1997; Nunn, 2011). To give an example, a PGLS could be used to determine whether general performance in both domains is influenced by brain size (relative and absolute), group size, home range size (absolute and in relation to body size) or feeding ecology (e.g. frugivorous, omnivorous, folivorous), as recently underpinned by DeCasien and colleagues (2017). Additionally, a PGLS would allow inferring whether the performance in the social domain is influenced by the level of allomaternal care that the tested species exhibit (high, medium, low; Isler & van Schaik, 2012), as suggested by the *Cooperative breeding hypothesis* (Hrdy, 1999, 2009). Such large-scale comparisons, ideally including several species from each branch of the primate tree, could yield more distinct answers concerning the complicated correlations among the different variables, such as cognitive skills, brain size, social skills or the diet of a species.

6.5.2 The Adapted PCTB

To apply the PCTB to a much broader range of species and taxa, and thereby enable a meaningful comparison, certain tasks would need to be adapted to make them solvable from a physical point of view (Schmitt et al., 2012). As previously mentioned, particularly the tool use and the social learning task are affected, since fine motor control is required in both, for example to insert a stick into a tube. Lemurs do not possess such manipulative skills (Torigoe, 1985; Holtkötter, 1997), let alone species from totally different genera, such as goats or rats. All species are in general able to conduct object-choice tasks by pointing with their paw or head towards the chosen item or just by walking towards it (e.g. Maros et al., 2008; Plotnik et al., 2013). These object-choice tasks constitute the basis for many experiments of the PCTB, but the necessary level of dexterity for the two tasks mentioned above limits the large-scale multispecies comparability of the test battery.

To give an example, an alternative setup of the social learning task could be an artificial feeding box, which offers several methods (e.g. pushing, pulling or sliding) to open a trap door to obtain a food reward (Schnoell & Fichtel, 2012). To test for social learning in the sense of the PCTB, it would then be possible to train an individual for one of the possible methods and use it as a conspecific demonstrator. Adapted in the right way, a similar setup would not need a high level of fine motor control and species without precision grip or even without hands or paws should be able to solve it by manipulating the door with their heads, mouths or beaks. However, an adaptation of the PCTB would also imply that those revised tasks needed retesting of those species that have already completed the test battery to assure an unbiased comparison.

6.5.3 Going Wild – the Value of Field Studies

It is of vital importance for the overall picture of cognitive evolution to include the species' socioecology and their naturally occurring cognitive capabilities. Hence, in addition to behavioural observations from the wild already conducted in many species, it would be essential to also increase the number of cognitive field experiments (e.g. Lührs et al., 2009; Thornton & Samson, 2012; Pyritz et al., 2013). However, cognitive studies are generally more difficult to conduct in the field, since many experimental setups require previous training sessions for the subjects. This is also the case for most experiments of the PCTB, in which individuals first have to be trained to actually be able to participate at all (Herrmann et al., 2007; Schmitt et al., 2012; see *Chapter 3*). Furthermore, in captivity it is possible to conduct experiments under controlled conditions which are identical for each individual, which is usually not feasible in the field.

Nevertheless, future cognitive research should try to find setups which are applicable to captive as well as wild individuals of the same species, as this would yield a more comprehensive picture of the cognitive skills of that species. Such an approach could also help to further investigate the influence of socialisation to humans. Further, additional information on naturally occurring cognitive traits of a species could also support conservation efforts (Greggor et al., 2014). In a recent study, Auersperg et al. (2011, 2013) designed a complex problem solving test box which has the advantage of being generally applicable in the wild as well, since no previous training sessions are necessary. This transparent box contains a visible food reward in its centre which can be accessed through four different ways of manipulation. Each of these accesses can also be blocked separately to encourage further exploration of the box, which offers various options for interspecific comparisons. Hence, this promising approach takes the adaptability as well as comparability between species into account and similar studies will be part of the future of comparative cognitive research.

6.6 General Conclusions

As the first systematic test battery of this magnitude that has been applied to strepsirrhine primates and in particular a nocturnal species, the results of my study offer substantial new insights and implications for general testing methods in comparative cognitive research and for understanding the evolution of primate cognition. I could show that lemurs' physical and social cognitive abilities are not that different from haplorhine primates', at least in the tests of the PCTB. Lemurs showed a good understanding for quantities and spatial-causal relations between objects, such as the properties of a functional pulling tool. They could use human communicative gestures and intentional actions as cues to locate hidden rewards, but did not follow human gaze or try to attract the experimenters' attention. The overall results of my study neither support a direct correlation between brain size and general cognitive skills of a species, nor reinforce the idea that cognitive abilities in primates are distributed in a domain-general pattern. In fact, I could show that a diverse set of different cognitive experiments from both the physical and the social domain is essential when studying the cognitive abilities of a species or even attempting to compare the performance of several species. The future of cognitive research belongs to these systematic and comparative studies, which will help to solve the puzzle of cognitive evolution.

General Appendix

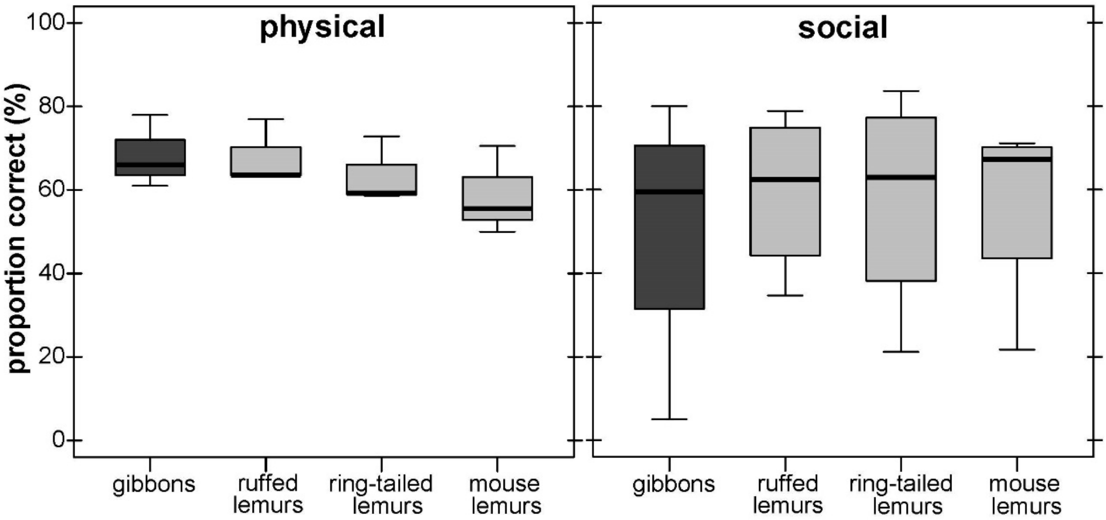

Figure A1 Performance of the lemur species compared to gibbons in both domains. Represented are medians (black bars), interquartile ranges (boxes) and upper and lower hinges (whiskers).

Table A1 Results of the seven experiments conducted with gibbons and lemurs. Average performances in % and summarised for each domain (grey; PHYS=physical, SOC=social). Tool props=tool properties, comp= comprehension, point cups=pointing cups, attent state=attentional state, intent=intentions.

species	noise	shape	tool props	PHYS	comp	point cups	attent state	intent	SOC
gibbons	61.0	78.0	66.0	68.3	58.0	80.0	5.0	61.0	51.0
ruffed lemurs	63.5	76.9	63.6	68.0	70.9	53.9	34.6	78.9	59.6
ring-tailed lemurs	59.3	72.8	58.6	63.6	70.8	55.1	21.2	83.6	57.7
mouse lemurs	50.0	70.6	55.6	58.7	65.4	69.2	21.7	71.1	56.8

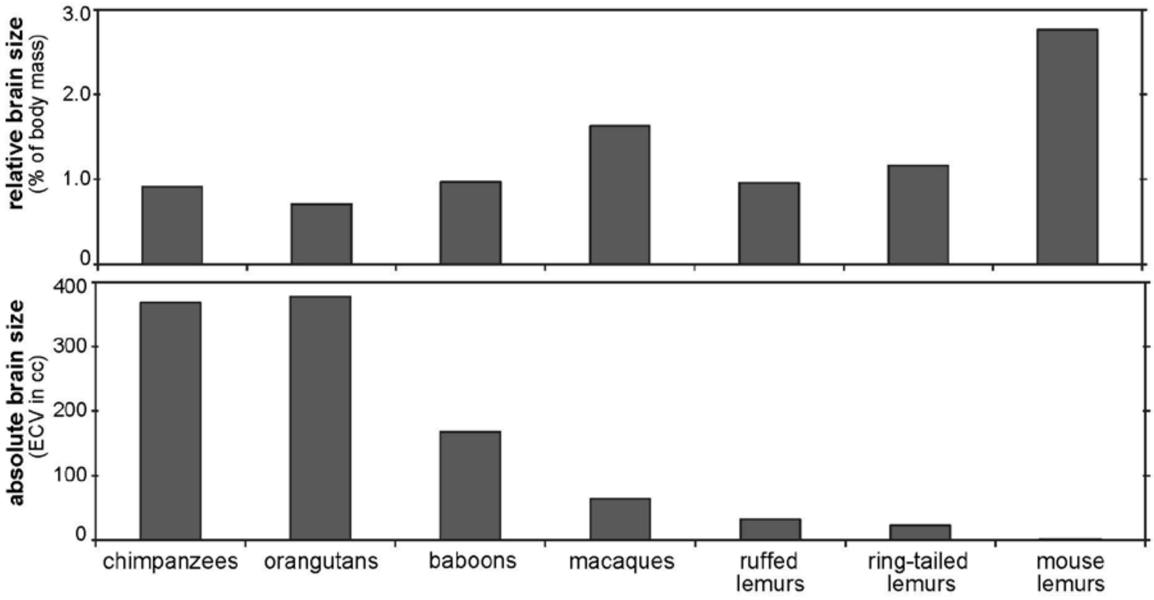

Figure A2 Absolute and relative brain sizes of all seven species of the PCTB. Relative brain size calculated with (100/body mass (g))*brain mass (g); measures for ECV, brain- and body mass from Isler et al., 2008.

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Publications

Kittler K, Dietzel S (2016). Female infanticide and female-directed lethal targeted aggression in a group of ring-tailed lemurs (*Lemur catta*). *Primate Biology*, 3, 41–46.

Kittler K, Schnoell AV, Fichtel C (2015). Cognition in ring-tailed lemurs. *Folia Primatologica*, 86, 106–116.

Kittler K, Kappeler P, Fichtel C (2018). Instrumental Problem-Solving Abilities in Three Lemur Species. *Journal of Comparative Psychology*, in press.

Submitted:

Kittler K, Kappeler P, Fichtel C (2018). Comparing lemurs’ understanding of social gaze and pointing cues using a human demonstrator and modelled conspecifics. *Animal Cognition*

Kittler K, Kappeler P, Fichtel C (2018). The lemur baseline: How lemurs compare to monkeys and apes in the Primate Cognition Test Battery. *Animal Cognition*

Kittler K, Heistermann M, Kappeler P, Fichtel C (2018). Closer to the edge? Behavioural and physiological responses of Verreaux’s sifakas (*Propithecus verreauxi*) to forest edges. *Animal Conservation*

Conference contributions

Kittler K, Kappeler PM, Fichtel C. Understanding of pointing cues in lemurs. (Oral presentation, Leibniz-ScienceCampus Graduate meeting on "Primate Cognition", Reinhausen 2016)

Kittler K, Kappeler PM, Fichtel C. Human vs. conspecific demonstrator - Understanding of pointing cues in three captive lemur species. (Poster, European Conference on Behavioural Biology, Vienna, Austria 2016)

Kittler K, Kappeler PM, Fichtel C. Tool time - The use and understanding of tools in three lemur species. (Oral presentation, Meeting of the Ethological Society, Göttingen 2016)

Kittler K, Kappeler PM, Fichtel C. Tool use in three species of lemurs? (Poster, Meeting of the Ethological Society, Hamburg 2015)

Kittler K, Kappeler PM, Fichtel C. Pointing cues - human vs. conspecific demonstrator. (Poster, Symposium: CRC Evolution of Social Behaviour, Göttingen 2014)

Kittler K, Fichtel C, Kappeler PM. Roots of Primate Cognition - The Primate Cognition Test Battery (*PCTB*) applied to three species of lemurs. (Oral presentation, Graduate meeting of the Zoological Society, Bremen 2014)

Kittler K, Fichtel C, Kappeler PM. Roots of Primate Cognition - The Primate Cognition Test Battery (*PCTB*) applied to three species of lemurs. (Methodologies Poster, Meeting of the Ethological Society, Tutzing 2014)

Research experience

2013-2016	Data collection for the PhD-thesis at the DPZ and the Affenwald Straußberg
2014	Seminar on „*Animal Research Training*", Fjord&Bælt Kerteminde (Denmark)
2013	Research assistant in the „*Behavioural Ecology and Sociobiology Unit*", German Primate Center (DPZ)
2012	Data collection for the Master thesis, DPZ field site Kirindy (Madagascar, 3.5 months)
2010	Reasearch-internship, DPZ field site Kirindy (Madagascar, 3 months)
2010-2012	Student research assistant in the CRC Junior Research Group „*Evolution of Cooperation and Prosocial Behaviour"*
2011	Zoological excursion, field station „*Khonin Nuga*" (Northern-Mongolia)
2009	Marine ecology excursion, Giglio (Italy)

Declaration

I hereby confirm that this thesis entitled “*Roots of primate cognition*” describes my own work. It was conducted and composed independently, without the use of any utilities other than those indicated in the text.

Göttingen, May 19th, 2017 ___________________________________

Klara Kittler