

# Chapter 19

## Human Universals and Primate Sympleiomorphies: Establishing the Lemur Baseline

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*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.*

Alison Jolly (1966a: 165–166)

**Abstract** Social behavior, culture, and cognition are domains where presumably most human universals exist. Identification of these derived human traits depends and relies on comparisons with other primates, notably chimpanzees. This approach can also be used to reconstruct primate and human behavioral evolution. Accordingly, traits found in both *Homo* and *Pan* can be inferred to have existed in their last common ancestor as well. By analogy, traits shared between humans and other primates can be traced back even further down on our family tree. Here, we look at the other side of human universals, i.e., behavioral and cognitive traits of the most basal living primates, which ought to represent the common primate legacy upon which later taxon-specific specializations were built. Specifically, we review studies investigating cognitive abilities and social behavior of the lemuriform primates of Madagascar. The Malagasy lemurs are particularly important for this purpose because they alone, among strepsirrhine primates, have evolved group-living, which characterizes most living haplorrhines. Even though lemurs have relatively smaller brains than New and Old World monkeys and great apes, their ability to solve problems that require technical intelligence is qualitatively on par with that of haplorrhines. In the domain of social intelligence, however, lemurs deviate from the

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better-known haplorrhine models (i.e., cercopithecines) in several respects. Most importantly, their behavioral strategies reflect an emphasis on within-group competition, rather than cooperation, which may represent lemur-specific adaptations to an ecologically unpredictable environment, rather than fundamental deficits in social intelligence. In any event, a broad comparative perspective including the best living models of the earliest gregarious primates can enrich reconstructions and other evolutionary analyses of primate social behavior, including that of humans.

## 19.1 Introduction

Behavioral characteristics unique to *Homo sapiens* can only be identified as such by reference to a meaningful out-group. Because humans are members of the order Primates, this lineage provides the natural out-group for such comparisons. Primates, however, are a diverse group with hundreds of living species and 80 million years of evolutionary history, so that specific deviations from our basal evolutionary legacy may not be that evident. Specifically, our biological continuity with other animals is evident in those behavioral, morphological, and physiological traits that have a genetic basis and define our affiliation to vertebrates, mammals, primates, haplorrhines, catarrhines, and hominids. Our bodies and minds can therefore be seen as a complex puzzle made up of pieces we share with these various groups, interspersed with a few derived pieces. Traditionally, most comparative studies attempting to identify the derived human pieces of this puzzle have relied on the contrasts between humans and chimpanzees (*Pan troglodytes*). Sequencing of the chimpanzee genome revealed <1% difference with the human genome (Mikkelsen et al. 2005), and molecular clock studies pinpointed the last common ancestor of *Homo* and *Pan* at around 6 million years before the present (Bradley 2008). Chimpanzees (and bonobos) therefore provide the most immediate step back into our deep behavioral past and the most appropriate specific referents for comparative studies of human behavior (e.g., Boesch 2007; Whiten, this volume). This approach can also be used to reconstruct primate and human behavioral evolution. According to this logic, characteristics or traits found in both taxa today are assumed to have been already present in their most recent common ancestor, i.e., they represent plesiomorphies in the terminology of cladistics. In this terminology, human universals represent autapomorphies, i.e., derived traits that are unique to a terminal group.

Extending comparisons of behavioral traits beyond the obvious *Homo-Pan* contrasts has led to additional insights. For example, the demonstration of social and technical traditions in orangutans (*Pongo pygmaeus*) has led to the novel conclusion that such cultural abilities must have been shared by the last common ancestor of all great apes (van Schaik et al. 2003), which lived about 14 million years ago. Similarly, comparative studies of cognitive abilities of great apes and

other haplorrhine primates revealed that New and Old World monkeys share many common features, and that only the level of performance varied among species (Amici et al. 2008). These examples highlight the importance of considering behavioral plesiomorphies in the analysis of potential human (or hominid) universals. In other words, characteristics attributed to the last common ancestor of chimpanzees and humans (or of the hominids) may, in fact, have an even longer evolutionary history. Thus, comparative analyses of human behavior limited to chimpanzees or other great apes risk drawing inaccurate conclusions by failing to explicitly recognize primate symplesiomorphies, i.e., character states that originated in an earlier common ancestor.

Evidence for the existence of precursors of cognitive and social traits in the behavioral domains, where human universals are most pronounced, has been produced for various New and Old World primates, including great apes (reviewed in Tomasello and Call 1997). Capuchin monkeys (*Cebus* spp.) exhibit remarkable technical intelligence (Visalberghi 1993), all too familiar socio-emotional responses (Brosnan and de Waal 2003), and local variation in cultural traditions among wild populations (Perry and Manson 2003). These observations question the existence of a possible deep behavioral and cognitive gap between hominins or hominids and all other primates. On the other hand, there are pronounced grade shifts in relative brain size among primate lineages (Martin and Harvey 1985; Dunbar and Shultz 2007), which may underlie qualitative differences in their social behavior and cognitive abilities (Deaner et al. 2007; Shultz and Dunbar 2007, Dunbar this volume). The cognitive and cultural capabilities of haplorrhine primates have been reviewed elsewhere (e.g., Tomasello and Call 1997; Whiten and van Schaik 2007). Here, we extend these comparisons to the most basal living primates: the strepsirrhine suborder. While recent strepsirrhines (lemurs and lorises) have their own distinctive evolutionary history and adaptations, they have retained a number of primitive features that almost certainly characterized the earliest primates (Yoder 2007). These living species, therefore, represent the legacy upon which all living primates have built their specific derived adaptations.

Malagasy lemurs (Lemuriformes) are particularly interesting in this context, because they are the only strepsirrhines that have evolved multi-male multi-female groups, like those that are characteristic of most haplorrhines. Group-living lemurs therefore represent the most appropriate models to establish the baseline for primate social intelligence and complexity, whereas cognitive abilities related to technical intelligence should be found independent of a particular social system. The specific goal of this chapter is to summarize and evaluate studies of social and technical cognitive abilities among lemurs. Even though Alison Jolly (1966b) established the importance of comparative studies of lemur social intelligence in the early days of primatology, subsequent research on lemur cognition and social communication has not been conducted with the enthusiasm and rigor that has characterized similar research on haplorrhines, and great apes in particular, in recent decades. Nevertheless, by bringing together some old, often overlooked studies and some more recent

work, we can begin to sketch the outlines of lemur cognition and social behavior. This endeavor will help to put comparative work on human universals, and on hominid behavior more generally, into broader perspective, insofar as that a closer look at the basal living primates will provide baseline information about shared ancestral traits of all primates.

## 19.2 Lemurs

Based on genetic differences and several morphological features, primates can be divided into two suborders: strepsirrhines (lemurs and lorises) and haplorrhines (New and Old World monkeys including the great apes). The living lemurs represent the 100 or so endpoints of an adaptive radiation following a single successful colonization event of Madagascar during the Eocene (Karanth et al. 2005; Tattersall 2007). They can be grouped into five families and 15 genera, which, together with recently extinct taxa, exhibit almost the full range of diversity in social, ecological, and life-history adaptations found among all other primates (Richard and Dewar 1991). The majority of living lemurs are nocturnal and solitary or pair-living, but, according to recent genetic analyzes (Horvath et al. 2008), life in multi-male, multi-female groups has evolved independently in the Lemuridae (in the genera *Lemur*, *Eulemur*, *Hapalemur*, and *Varecia*) and Indridae (in the genus *Propithecus*). After controlling for body size and phylogenetic effects, lemur groups in both families are, on average, smaller than those of haplorrhines (Kappeler and Heymann 1996), and they are generally characterized by even adult sex ratios (Kappeler 2000). As in many haplorrhines, group-living lemurs are characterized by predominant female philopatry (Richard et al. 1993; Sussman 1992), diurnal activity (at least partially) (Kappeler and Erkert 2003; Erkert and Kappeler 2004), and their vocal repertoires sometimes include functionally referential calls (Fichtel and Kappeler 2002). Relative brain size of lemurs tends to be smaller than that of haplorrhines (Armstrong 1985; Dunbar 1998) and olfactory communication is used in a variety of behavioral contexts (Kappeler 1998; Pochron et al. 2005). Thus, the social systems (sensu Kappeler and van Schaik 2002) of lemurs exhibit a mixture of idiosyncrasies as well as convergences with those of other primates, but the basic pillars of sociality appear to be comparable.

Below, we summarize the results of a literature review of studies of lemur cognition and social behavior that bear relevance to the study of human behavioral universals. We divide this review into two sections that deal with technical and social intelligence, respectively. We do not attempt explicit and detailed comparisons with great apes or all other haplorrhines, and we refrain from extending comparisons to other mammalian orders. Instead, we aim to provide a concise summary of the socio-cognitive abilities of lemurs and other strepsirrhines that may contribute interesting baseline information about primate sociality for comparisons among other primates and mammals, including humans.

## 19.3 Technical Intelligence

### 19.3.1 *Space and Objects*

The most critical challenge to survival is the ability to deal effectively with (three-dimensional) space and objects, such as food, shelter, and predators. Physical cognition, i.e., the understanding of object features and their various spatial and causal interrelations, is presumably most adaptive in the contexts of foraging and locomotion. Independent of their social organization, most primates tend to remain within a particular home range. Cognitive abilities that enable animals to identify their position, to remember what is located where, and to travel efficiently between these sites, represent selective advantages (Anderson 1983; Gallistel 1989). Because successful foraging and efficient locomotion are general ecological problems, the relevant cognitive skills of lemurs are expected to be similar to those of other primates.

The cognitive abilities of lemurs in the context of spatial mapping and spatial memory have been the focus of experimental studies in captivity and, more recently, in observational and experimental studies in the wild. In Madagascar, gray mouse lemurs (*Microcebus murinus*) inhabit dry deciduous forests with pronounced seasonal fluctuations in food availability. During a long dry season, when food availability is low, mouse lemurs mainly rely on resources that are sparsely distributed but predictable in space, such as gum, secretions from colonial insects, and nectar (Dammhahn and Kappeler 2008). Field observations revealed that solitary mouse lemurs revisited stationary feeding sites more often than nonstationary feeding sites (Joly and Zimmermann 2007). Using an experimental approach, Lührs et al. (2009) set mouse lemurs a spatial memory task by confronting them with two different patterns of baited and non-baited artificial feeding stations. Mouse lemurs used spatial cues to relocate baited feeding stations and they were able to rapidly learn a new spatial arrangement. In a release experiment, they also exhibited high travel efficiency in directed movements, suggesting that their spatial memory is based on some kind of mental representation that is more detailed than a route-based network map (Lührs et al. 2009). The existence of a topological or route-based map has also been proposed for group movements of two group-living lemurs, Milne Edwards' sifakas (*Propithecus edwardsi*) and redfronted lemurs (*Eulemur fulvus rufus*, Erhart and Overdorff 2008). Because route-based mental representation of spatial relationships, straight-line travel, and efficient goal-directed movements between distant sites have been suggested for several haplorrhines (Boesch and Boesch 1984; Gallistel 1989; Garber 1988; Menzel 1991; Janson 1998; Noser and Byrne 2007), cognitive abilities in the context of spatial orientation do not appear to differ fundamentally between lemurs and other primates.

Another set of cognitive spatial skills is required to search for hidden food, as in object permanence experiments, or to trace invisible displacements of food hidden by an experimenter. When various lorises, ring-tailed (*Lemur catta*), and brown lemurs (*E. fulvus*) were tested for their ability to find hidden food, only one loris failed to master the task (Jolly 1964a). Object permanence was studied in

redfronted lemurs, mongoose lemurs (*E. mongoz*), ring-tailed lemurs, and bamboo lemurs (*Hapalemur griseus*) (Deppe et al. 2009). Lemurs performed well above chance levels in tracking food that had been in clear view before being hidden (visible displacements). However, when lemurs were not allowed to search for up to 25 s, performance declined with increasing time-delay. They did not outperform chance levels in tracking food in invisible displacement tasks. Many haplorrhine primates solve visible displacement tasks, whereas the ability to perform invisible displacement has been demonstrated in apes, rhesus macaques (*Macaca mulatta*), and cotton top tamarins (*Saguinus oedipus*) (de Blois et al. 1998; Call 2001; Hauser 2001; Neiworth et al. 2003; Mendes and Huber 2004).

Primates often face the problem of getting food that is out of reach, such as fruits at the periphery of a branch. Thus, spatial understanding of objects that allows them to determine to which branch a fruit is connected to pull it closer or to use another branch as a tool to bring fruits into reach should be advantageous. Detour problems test this kind of understanding. Lemurs quite successfully mastered detour problems, in which food was impaled on a bent wire and the subject had to move it to the left or right and had to push or pull the food (Davis and Leary 1968). Although Old World monkeys were best at performing these tasks, lemurs did not differ from some New World monkeys, and squirrel monkeys failed the task entirely.

Maze experiments represent another type of detour problems, in which the spatial memory of subjects is investigated. Picq (1993, 2007) conducted radial maze experiments with captive mouse lemurs. In this experimental setup, subjects learned to choose one out of eight possible arms to get access to a reward; in this case, a nest-box. Mouse lemurs mastered this task quickly, and their learning curves matched those of New and Old world primates, including chimpanzees.

Because of their fast life histories, mouse lemurs are also well suited to address questions of aging in memory. Picq (2007) applied different visual and spatial discrimination as well as generalization tasks in an eight-armed radial maze. Young mouse lemurs were able to learn all tasks quickly; older mouse lemurs performed as well as the young ones in some tasks, but showed impairment in several other tasks, indicating that the acquisition of skills is not affected, but the shifts in attention from visual to spatial cues and, thus, the flexible use of acquired memories in novel situations as well as the generation of novel solution strategies were impaired. Similar maze experiments with haplorrhines revealed that basic spatial memory skills are comparable across taxa (Tomasello and Call 1997). Other tasks, in which spatial understanding of objects is investigated, such as patterned-string problems, in which subjects have to disentangle strings differently to get a reward, or mental rotations skills, have not been conducted with lemurs so far.

### 19.3.2 Tools and Causality

Primate foods are either immediately ready to eat or require manipulation before ingestion. Manipulation tasks vary from simple to complex: from just picking

a fruit or leaf off the branch, through digging for roots, uncovering food items under leaves or tree barks, capturing mobile insects, using tools to open nuts, and modifying probes to fish for ants (van Schaik et al. 1999). Observations of wild lemurs revealed little evidence for object manipulation in a foraging context, except for the aye-aye (*Daubentonia madagascariensis*), which uses a thin, long, tap-scanning and probing middle finger to locate and extract insects embedded in trees or branches (Erickson 1995). Black (*E. macaco*) and brown lemurs sometimes manipulate millipedes vigorously, presumably in an effort to anoint their bodies with an insect repellent (Birkinshaw 1999; pers. observ.). No other manipulative interactions with food items by lemurs have been reported so far.

Studies of manipulative interactions with novel objects in captivity are more abundant. When various lorises were confronted with different complex novel objects, they either stared at them and struck them with their hand (Jolly 1964a, b) or pushed, pulled, or even grasped them (Ehrlich 1970; Renner et al. 1992). Parker (1973, 1974) compared manipulation behavior with hands and mouth towards novel objects in ring-tailed and black lemurs with that of several haplorrhines, including great apes. He found that manipulative behavior was most variable in great apes, slightly less variable in macaques, and least variable in langurs, spider monkeys, and gibbons. Both lemur species were intermediate between the great apes/macaques and the other cluster of species. Because differences between groups could not be explained by hand anatomy, but by habitat use, i.e., a distinction between feeding specialists and generalists, Parker (1973) suggested that broad-niched opportunists need to develop more explorative behavior than specialists to adapt to the wide variety of circumstances in their habitat. A similar pattern of object manipulation variability was found in another study comparing 74 species of primates. Lemurs, marmosets, and leaf-eating monkeys showed less variable behavior than frugivorous and insectivorous Old World monkeys, but not folivores. Capuchin monkeys, as well as great apes, showed the most variable behaviors (Torigoe 1985). Thus, lemur manipulatory skills are roughly comparable with those of at least some New and Old World monkeys.

In addition, more complex object manipulation skills appear to exist in gray mouse lemurs. In a series of experiments, individuals first had to open a plastic box in three different ways to get access to a reward (Schilling 2007). In the second task, the reward was hidden in a cylindrical box sliding inside an opaque second box. Subjects were required to manipulate a string to move the inner box closer in order to reach and pull out the reward. All mouse lemurs learned the tasks rapidly and improved over time. In the third task, mouse lemurs were tested with a vertical mirror box presenting a mealworm hanging behind an opaque wall in such a way that the reward could only be obtained by learning to use its reversed image. All but one individual mastered this rather complex task, which may require some form of mental rotation.

The aye-aye, which has the largest relative brain size among strepsirrhines (Stephan et al. 1988), uses a unique form of percussive tap-foraging, during which insect larvae are extracted from wood by a series of coordinated actions with the elongated third digit (Miliken et al. 1991; Lhota et al. 2008). They are also



able to open complex puzzle boxes and performed better than other lemurs on such a test (Digby et al. 2008). Opening of simple boxes has also been demonstrated in brown, black, and ring-tailed lemurs (Jolly 1964a, b; Kappeler 1987; Fornasieri et al. 1990; Anderson et al. 1992), though Fornasieri et al. (1990) stated that they showed “little comprehension” of the task.

Understanding of physical and causally relevant aspects of objects are prerequisites for using tools. Tool-use has been reported in several haplorrhine primates, with chimpanzees and orangutans exhibiting the most complex skills (Whiten et al. 1999; van Schaik et al. 2003; Moura and Lee 2004). In contrast, tool-use has not been reported from the wild for any strepsirrhine. However, there is one observation of aye-ayes manipulating an object that required some sort of sensorimotor intelligence that is also required for tool-use: they grasped and moved a liana over a branch under which they had been feeding to gain better access to a feeding site (Sterling 1994). These sensorimotor skills were examined in more detail in an experiment in which aye-ayes could use a simulated liana (rope) to get access to feeding cups fixed to the wall (Sterling and Povinelli 1999). However, they failed to move the rope horizontally close to the feeding cups, though they readily climbed up and down the simulated liana. The authors concluded that aye-ayes do not achieve comprehension to use tools, but rather may use trial-and-error learning to develop tool-use behavior.

Hence, the question arises whether strepsirrhines simply do not possess the underlying cognitive abilities to understand the functionality of objects for potential tool-use. In a recent study, Santos et al. (2005a) set up a series of experiments with brown and ring-tailed lemurs to address this question. They used and extended a design originally used with other haplorrhines (Hauser et al. 1999; Povinelli 2000; Fujita et al. 2003; Santos et al. 2006). In these experiments, lemurs were offered two cane-shaped tools to pull out-of-reach food items. In the first series of experiments, tools were identical and differed only in the orientation relative to the food reward, with one tool being more effective to reach the food. Lemurs had to choose the more effective tool and did so just as successfully as capuchins (Cummins-Sebree and Frigaszy 2001; Fujita et al. 2003). In the second experiment, lemurs were tested with novel tools differing from the originals in one dimension, to test whether they spontaneously attend to some of the features that are causally relevant for a successful pulling tool. Lemurs attended more to the sizes than to the colors of tools, but made no distinction between tools' shapes and textures. The next two experimental designs presented problems in which one of the tools had to be modified to access the food. In these tests, the authors used familiar, already successfully used tools, and unfamiliar tools. Lemurs did not prefer familiar over unfamiliar tools, indicating that they chose tools on the basis of features that were functionally relevant for the task. Thus, lemurs solved the can-pulling tasks like other tool-using haplorrhines, indicating that many primates share an ability to reason about basic functional properties of different objects, even if they do not use tools normally (see also Hauser et al. 2002; Spaulding and Hauser 2005). In contrast to this basic understanding of features of tools, regular tool users have a more



sophisticated understanding of causal relationships between features of the tool and the problems they can solve with it (Martin-Ordas et al. 2008; Seed et al. 2009). Orangutans, for example, even spat water spontaneously into a transparent tube to get access to an out-of-reach peanut floating inside the tube (Mendes et al. 2007).

### 19.3.3 *Features and Categories*

All primates locate and manipulate objects, which they identify on the basis of certain observable features. However, in some cases, primates also identify objects on the basis of conceptual categories that go beyond direct perception (Tomasello and Call 1997). Basic discrimination learning of objects that vary either in shape, color, pattern, brightness, location, or sound has been demonstrated in a variety of lemurs and other strepsirrhines (reviewed in Ehrlich et al. 1976; Meador et al. 1987; Tomasello and Call 1997).

Learning sets are tests in which individuals may become better at discrimination when they solve different sets of similar problems over time and have learned to deal with a particular type of problem in general. Numerous studies on learning set phenomena have led to the consensus that successful problem-solving indicates the use of some type of abstract rule (Harlow 1949, reviewed in Fobes and King 1982). Tests of object discrimination learning sets have been conducted with bushbabies, lorises, black and ring-tailed lemurs (Stevens 1965; Cooper 1974; Ohta 1983; Ohta et al. 1984, 1987). A comparison across the primate order revealed that there are no taxonomic differences with respect to success in object discrimination tasks: “*after 200 problems, approximately 80% correct performance is achieved by species as different from another as black lemurs, chimpanzees, rhesus macaques, and gorillas*” (Tomasello and Call 1997).

Reversal learning paradigms investigate the ability to reverse a previously learned discrimination. Subjects first learn an object discrimination to get a reward before a previously nonrewarded object becomes rewarded. This paradigm is thought to reflect a subject’s ability to form and use abstract rules or hypotheses (Rumbough 1970). When brown and ring-tailed, fork-marked (*Phaner* spp.), and mouse lemurs were subjected to this test paradigm, their performance was inferior to that of haplorrhines (Stevens 1965, reviewed in Rumbough 1997). However, more recent studies of mouse lemurs revealed that their reversal skills are comparable to those of haplorrhines (Picq 1993, 2007). Cross-modal transfer of objects from one perceptual domain to another also belongs to the kinds of tasks that go beyond stimulus-response associations. Only bushbabies (*Galago senegalensis*) among strepsirrhines were presented with this task, in which they were able to transfer learned responses from vision to audition (Ward et al. 1976).

The delayed response paradigm investigates a subject’s memory or ability to maintain a perception of an item when it is no longer available. Typically, the subject sees a reward hidden in one of two locations, and after a certain delay, it

may search for it. The few studies that applied this test paradigm to redfronted, mongoose, bamboo, ring-tailed, and ruffed lemurs (*Varecia variegata*), as well as to bushbabies, found that they were all inferior to haplorrhines in their performance (Harlow et al. 1932; Maslow and Harlow 1932; Jolly 1964a; Deppe et al. 2009).

Discrimination learning of relational categories involves a concept that can be learned only by comparing objects to one another and by inducing some relational difference (e.g., “larger than”). In oddity concept studies, subjects are presented three stimuli, two of which are the same. Subjects are rewarded for responding to the odd one; for example, in a “square–square–triangle” constellation. After that, some of the training subjects are confronted with three completely new objects (line–circle–line). In this paradigm, the inference is that subjects understand the concept of “odd.” This concept allows animals, for example, to categorize environmental features such as different food items. Davis et al. (1967) confronted several New World and Old World monkeys as well as ring-tailed lemurs with oddity problems, and found that the performance of ring-tailed lemurs was inferior to most haplorrhines, but better than guenons. In summary, there are no qualitative differences in performance across major primate radiations in object discrimination learning set formation tasks. However, a few studies on strepsirrhines suggest that they do not seem to be very skilled in reversal learning and delayed response, but they do seem to have an understanding of oddity problems.

The ability to form categories of objects belonging to same or different classes is another task that provides insights into cognitive abilities of animals. In such tests, subjects are presented with many objects simultaneously and asked to sort them into groups on the basis of their similarities and differences. This is a demanding task because subjects are required to coordinate both the similarities and differences of multiple objects simultaneously and then to manipulate the objects in line with that understanding. The only study of such capacities in strepsirrhine primates reported remarkable skills in serial ordering of objects in ring-tailed lemurs (Merritt et al. 2007).

Many animals are also able to organize sequences in memory and retrieve ordered sequences without language (Sands and Wright 1980; Straub and Terrace 1981). For example, capuchin monkeys and rhesus macaques were able to select a series of photographs according to a consistent arbitrary order (D’Amato and Colombo 1989; Terrace et al. 2003). In this simultaneous chaining paradigm, a series of arbitrary stimuli (such as photographs) are presented simultaneously in random spatial position on a touch-sensitive monitor. Subjects are rewarded when they respond in a prespecified arbitrary order without error. This paradigm is particularly useful for cognitive studies because it investigates the internal representation of the sequence. Merritt et al. (2007) tested ring-tailed lemurs with such a paradigm. Ring-tailed lemurs were capable of learning three-, four-, and five-items lists. Moreover, these lemurs showed a remarkable similarity in accuracy and reaction time with that of capuchin and rhesus monkeys (D’Amato and Colombo 1989; Terrace et al. 2003).

### 19.3.4 Quantities

Primates also need to have an understanding of quantities to estimate food availability at different feeding patches or the number of opponents in a potential fight. There have been many studies demonstrating that monkeys and apes are able to judge the absolute and relative numerosness of objects (Tomasello and Call 1997; Beran and Beran 2004; Hanus and Call 2007; Evans et al. 2009). For example, it has been shown that anthropoids possess numerical representation that is modulated by Weber's law, such that as the numerical magnitude increases, a larger disparity is needed to obtain the same level of discrimination. By applying a search task in which grapes were placed into a bucket, Lewis et al. (2005) studied mongoose lemurs' numerical ability. They were able to differentiate numerosities that differed by 1:2, but not those that differed by 2:3 or 3:4. Thus, lemurs' understanding of numerosity also seems to be modulated by Weber's law. Nevertheless, lemurs' numerical discrimination seems to be inferior to that of New World and Old World monkeys; tamarin monkeys (*Saguinus* spp.) were able to differentiate sequences of syllables that differed by 1:2 and 2:3 but not the 3:4 ratios (Hauser et al. 2003), and rhesus macaques even discriminated numerosities that differed by a 4:5 ratio (Brannon and Terrace 2000).

Expectation about numerical events has been studied in ring-tailed, brown, mongoose, and ruffed lemurs (Santos et al. 2005b). By using looking techniques, they explored how lemurs represent small numbers of objects spontaneously in the absence of explicit training (see Hauser 2000 for review). Santos and her colleagues conducted experiments that were modeled after Wynn's violation of expectancy paradigm for human infants (Wynn 1992), and tested whether lemurs look longer when the number of objects revealed behind a screen differs from the number that should be there. They presented lemurs with two lemons that disappeared sequentially behind an occluder; lemurs looked longer at an unexpected outcome of only one lemon than at an expected outcome of two lemons. Similarly, lemurs looked longer at an unexpected outcome of three lemons than towards an expected outcome of two lemons. In addition, lemurs attended to the size of objects; they looked longer at an object twice the size of the original object than at an expected outcome of two objects of the original size. Thus, these lemurs understand the outcome of simple arithmetic operations of  $1 + 1$  events. These findings are in line with those in human infants (Wynn 1992; Feigenson et al. 2002), rhesus macaques (Hauser et al. 1996), and cotton-top tamarins (Uller et al. 2001). However, capuchin monkeys (*Cebus apella*) have been shown to be able to judge the quantity of 1–5 items in a sequentially presented food choice experiment (Evans et al. 2009). Moreover, great apes were able to differentiate quantities of up to ten items when items were presented simultaneously. However, sequential presentation of food items resulted in a correct judgment of only up to six items (Hanus and Call 2007). Furthermore, some chimpanzees, which were trained in lexical language skills, could judge of up to ten sequentially presented items correctly (Beran and Beran 2004). Thus, without training, haplorrhine primates are able to perform arithmetic

operation of up to 6. Because newly hatched domestic chicks (*Gallus gallus*) are able to add and subtract up to five sequentially presented items, mental number representation might be present among many more vertebrates, however (Rugani et al. 2009).

## 19.4 Social Intelligence

There is a wealth of studies of social cognition in haplorrhine primates (Tomasello and Moll this volume, Cheney and Seyfarth this volume) from which the social brain hypothesis has been developed (Dunbar this volume). Strepsirrhines have not been well represented in this field of research – either because they are not interesting in this context due to their relatively small brain size (cf. Deaner et al. 2006) or because Jolly's (1966b) first impression of lemur intelligence has impeded subsequent research endeavors. However, there are some lemur studies that are relevant to assumptions and predictions of the social brain hypothesis, and show that group-living lemurs exhibit some interesting differences in their social lives from their haplorrhine cousins.

According to the social intelligence hypothesis, the challenges of living in social groups have favored the expansion and reorganization of the primate brain (Whiten and Byrne 1997; Dunbar and Shultz 2007; Silk 2007; Dunbar, this volume). Comparative studies of brain size among primates revealed that relative brain size correlates with several indices of social complexity, including group size (Dunbar 1995), number of females in the group (Lindenfors 2005), the frequency of coalitions (Dunbar and Shultz 2007), grooming clique size (Kudo and Dunbar 2001), the prevalence of social play (Lewis 2000), the frequency of tactical deception (Byrne and Corp 2004), and the frequency of social learning (Reader and Laland 2002). Below, we will summarize our current knowledge of lemur social complexity, focusing on group size and composition, the structure of social relationships (coalitions, cooperation, postconflict behavior, grooming networks), deception, social learning, and innovations, as well as communication. The aim of this review is not to be exhaustive, but rather to highlight the key differences and similarities.

### 19.4.1 *Social Complexity and the Structure of Social Relationships*

One way to test the social intelligence hypothesis experimentally is to examine whether species with complex social environments show unusual intelligence in nonsocial domains compared with closely related, less social species (Bond et al. 2003). Transitive inference (if  $A > B$  and  $B < C$ , then  $A > C$ ) is a form of

deductive reasoning that has been suggested as one cognitive mechanism with which animals could learn the many relationships within their group's dominance hierarchy. This process, thus, bears relevance to the social intelligence hypothesis, which posits evolutionary links between various forms of social and nonsocial cognition. The relationship between social complexity and transitive reasoning has been studied in ring-tailed and mongoose lemurs (MacLean et al. 2008). The group-living ring-tailed lemurs and the pair-living mongoose lemurs showed similar transitive inference, indicating that both species possess similar fundamental cognitive abilities in this respect, obscuring potential effects of group size and complexity.

Because females are philopatric in many haplorrhine primates and form long-term social networks, the average number of females per group has an evolutionary impact on the development of large brains (Lindenfors 2005), and, hence, social intelligence. Lemur groups usually contain only one to five reproductive females, which are also philopatric (Kappeler 2000). Social networks, such as matrilineal dominance hierarchies, in which maternal kin occupy adjacent ranks and females form close and stable relationships, have been described for many Old World monkeys (Silk 2007). Similar bonds have not been observed among lemurid females (reviewed in Kappeler 1999), even though transitive dominance relationships are established in most, but not all lemur species (Kappeler 1993b; Pereira et al. 1990). In species with dominance relationships, all females dominate all males (Jolly 1966a; Richard 1987; Pochron et al. 2003). Reproductive opportunities seem to be more limited for lemurid females than for cercopithecine females, because, on average, only one or two females give birth per year in groups of most lemurid species (Overdorff et al. 1999; Kappeler 2000; Pochron et al. 2004). Targeted aggression by female group members towards close relatives, often adolescent females, resulting in severe injury or eviction, has been observed in captive and field settings in representatives of both Lemuridae and Indriidae (Vick and Pereira 1989; Pereira 1993; Barthold et al. 2009; Kappeler unpubl. data). Furthermore, infanticide by females has been observed in several lemur species (Andrews 1998; Jolly et al. 2000). Coalitionary defense of home ranges against neighboring groups indicates that competition between groups is also pronounced (Nunn and Deaner 2004; Benadi et al. 2008). Because lemurs live in a relatively harsh and unpredictable environment with pronounced seasonality (Wright 1999; Dewar and Richard 2007), ecological factors may have favored competitive, rather than cooperative tendencies in group-living lemurid females.

Overt cooperative behavior, another hallmark of social complexity (Silk and Boyd this volume), has only rarely been observed in lemurs. Coalitions of related redfronted lemur males have been observed to take over other groups (Ostner and Kappeler 2004), and ring-tailed lemur males sometimes migrate in pairs or trios (Jones 1983; Sussman 1992). Only a tiny fraction of agonistic interactions among females involve coalitionary support (Pereira and Kappeler 1997) even though joint territorial defense is common (see above). Solitary species exhibit a spatio-genetic structure characterized by spatial clustering of related females (Kappeler et al. 2002; Wimmer et al. 2002), which may facilitate cooperative behavior among

relatives. For example, several gray mouse lemurs mobbed a snake that held a conspecific until it could escape (Eberle and Kappeler 2008), and communal breeding among closely related females with a high mortality risk may provide each of them with a form of family insurance (Eberle and Kappeler 2006).

Postconflict reconciliation is another important mechanism with which many haplorrhines deal with the disruptive social consequences of intragroup conflict on group cohesion (Aureli and de Waal 2000). Although reconciliation has also been described for other mammals (e.g., Cools et al. 2008), there is mixed evidence for lemurs. Reconciliation has been demonstrated in redfronted lemurs, albeit at relatively low levels, but it could not be demonstrated in ring-tailed lemurs, despite a clear dominance hierarchy and within-group kin structure (Kappeler 1993a). However, studies of other captive populations of ring-tailed lemurs found low levels or seasonal occurrence of reconciliatory behavior (Rolland and Roeder 2000; Palagi et al. 2005). Absence of reconciliatory behavior was reported for black lemurs (Roeder et al. 2002), whereas sifakas (*Propithecus verreauxi*) reconciled during the mating season (Palagi et al. 2008). Thus, in contrast to many haplorrhines, strategic use of affiliative interactions to foster social relationships is not pronounced among group-living lemurs.

Given their small group size, it is not surprising that lemur grooming networks are relatively small (Kudo and Dunbar 2001). Grooming cliques have been considered to be synonymous with coalition size, on the grounds that primates use grooming to reinforce the bonds on which coalitionary support is based (Seyfarth and Cheney 1984). This potential function of grooming has been studied in redfronted lemurs (Port et al. 2009). Here, the exchange of grooming bouts is highly reciprocal, but grooming is biased in favor of higher-ranking partners. In addition, aggression occurred at higher frequencies between classes of individuals that were characterized by nonreciprocal grooming, suggesting that grooming may serve as a means to reduce aggression in dyads with a high potential for conflicts. Thus, grooming might be exchanged for tolerance, suggesting that lemur grooming networks might form part of a biological market of the kind described for various Old World monkeys (Barrett et al. 1999; Henzi and Barrett 1999).

### ***19.4.2 Tactical Deception and Related Skills***

Neocortex size also predicts deception rate in primates (Byrne and Corp 2004). Deception of conspecifics is often thought to be evidence of considerable cognitive sophistication (Mitchell and Thompson 1986), and reflects very efficient learning ability and sensitivity to a wide range of social discriminations (Cheney and Seyfarth 1990; Byrne and Corp 2004; see also Trivers, this volume). Deception in lemurs seems to be rare. Deaner et al. (2006) tested ring-tailed lemurs with the classical deception paradigm of Menzel (1973), in which a subordinate was informed of the location of a hidden food item and was subsequently released into

an enclosure simultaneously with an uniformed dominant female. Male ring-tailed lemurs did not reliably deceive the dominant female, which is not too surprising given the natural response of a male towards a female in a feeding context in this species. However, recent field observations at artificial feeding platforms within the home ranges of wild red-fronted lemurs suggested that some males and females of two different groups behaved as if they deceived other group members. Several times when a group passed the platforms at distances of about 150 m, some individuals sneaked away silently (redfronted lemurs usually produce grunts while locomoting!), ran quickly towards the platforms, and depleted them before uttering their long distance contact calls to reestablish contact with their group (Lennart Pyritz pers. comm.). Experiments in captive settings also indicated that brown and black lemurs seem to learn to deceive a human competitor (Genty and Roeder 2006; Genty et al. 2008).

The same authors also report on self-control behavior in brown and black lemurs (Genty et al. 2004). Self-control has been operationally defined as the ability to inhibit a natural tendency to reach for the greater of two amounts of foods (Anderson 2001). Self-control behavior in preschool children, i.e., the ability to delay gratification, has been related to later cognitive competencies (Mischel et al. 1989). Brown and black lemurs initially chose the larger array of food, but learned after a correction procedure to choose the smaller array of food, indicating that they show some form of self-control (Genty et al. 2004). Similarly, several New World and Old World monkeys, chimpanzees, and even children over 4 years old initially showed the tendency to select the larger array of a reward (Boysen and Berntson 1995; Silberberg and Fujita 1996; Anderson et al. 2000; Kralik et al. 2002). Only orangutans showed the spontaneous ability to understand the task (Schumaker et al. 2001).

Studies in a wide range of species, including apes, dogs, and goats (Tomasello et al. 1998; Call et al. 2003; Kaminski et al. 2005) showed that individuals follow the gaze of others. Such shared attention is thought to underlie a theory of mind and language acquisition (Tomasello and Moll this volume). Earlier studies reported that ring-tailed lemurs do not follow human gaze (Itakura 1996; Anderson and Mitchell 1999). However, a recent study, in which ring-tailed lemurs were equipped with a novel telemetric gaze-tracking system, showed that they preferentially gaze towards others, and follow other lemurs' gaze while freely moving and interacting in naturalistic social and ecological environments (Shepherd and Platt 2008). Moreover, Ruiz et al. (2009) demonstrated that brown and black lemurs use coorientation to find hidden food in an object-choice experiment. Lemurs were more likely to choose correctly after having looked in the same direction as the model, in this case a photograph of a conspecific, indicating that the adaptive value of gaze following might be a way of reading the attentional focus of others. Interestingly, other primates have been shown to coorient with humans (Tomasello et al. 1998; Bräuer et al. 2005), but failed to reliably select the correct location of the hidden food by using human cues (Call et al. 2000; Hare and Tomasello 2004), which might be due to the fact that object-choice tasks and coorientation have been tested separately. The integration of both tasks revealed



that there is a connection between visual coorientation and foraging choice. These results, however, do not indicate that lemurs understand gaze as mental perspective taking of others. Objects or locations may simply become more salient for an observer, as a result of following another individual's attention to that object or location – a process that has been defined as “gaze-priming” (Ruiz et al. 2009). Thus, gaze-following or better gaze-priming ability is also present in strepsirrhines.

### ***19.4.3 Social Learning and Innovations***

The social intelligence hypothesis also invokes behavioral flexibility as a key advantage of enhanced brain size. Innovation and social learning allow animals to exploit the environment in new ways, and brain size seems to correlate with frequencies of innovation and social learning (Reader and Laland 2002). Feldman and Klopfer (1972) suggested that social learning, i.e., stimulus enhancement, may also play a role in object-choice performance in brown lemurs. Observations of predatory behavior on insects, small mammals, and birds in captive brown, black and ring-tailed lemurs also raised the question of whether such behavior may lead to the development of local traditions (Glander et al. 1985; Jolly and Oliver 1985). The first experimental study of the acquisition process of a novel behavior was conducted with ring-tailed lemurs (Kappeler 1987). Adult females, but not males, and juveniles acquired the novel behavior, and remembered it over several months. Similar experiments with brown, black, and ring-tailed lemurs also showed that novel behaviors, in this case opening a baited food-box, are learned socially (Fornasieri et al. 1990; Anderson et al. 1992). Social influences on feeding decisions involving familiar and novel food have been shown in black lemurs. In these experiments, the consumption of high-quality novel food was acquired individually, but the dominant female influenced the consumption rate of low-quality novel food (Gosset and Roeder 2001). Social influences have also been shown in the complex foraging behavior of aye-ayes. A comparison with ruffed lemurs revealed that aye-aye mothers co-fed and shared food with their infants and engaged in socially mediated learning more often than ruffed lemurs. As a consequence, ruffed lemurs showed less neophobia towards novel food and relied earlier on their own foraging decisions (Krakauer 2005).

Spontaneous innovation of a novel behavior has been reported for strepsirrhines only once so far. Semi-free-ranging ring-tailed lemurs developed a new behavior, that is, immersing the tail in water and then sucking on the wet tail. Almost all group members acquired “drinking-from-tail” behavior, and individuals who did not acquire it were allowed to drink from the wet tail of animals which did (Hosey et al. 1997).

In a similar vein, variation in antipredator behavior between populations has been documented in sifakas (Fichtel and van Schaik 2006, Fichtel and Kappeler unpubl. data). In primates, the usage and comprehension of alarm calls, i.e., their

association with predator-specific escape strategies, appear to be socially learned (Seyfarth and Cheney 1980; Fichtel 2008). Thus, alarm calls provide flexible behavioral mechanisms that allow animals to develop appropriate responses to local predators (Curio et al. 1978; Cook and Mineka 1989; Laland 2004). A comparison of three types of alarm calls and antipredator strategies in a semi-free-ranging and a wild population of Coquerels' sifakas (*Propithecus coquereli*) revealed that the captive and wild sifakas used their alarm calls in the same contexts, but exhibited similar behavioral responses in response to only two of the three calls. All members of the captive population, including a wild-caught individual, apparently associated the third alarm call with the presence of a raptor, whereas individuals of the wild population associated no specific threat with this particular call.

Similarly, a comparison of two wild populations of Verreaux's sifakas in habitats with a low and a high density of carnivores also revealed a different comprehension of the alarm calls given to these predators. Sifakas in the habitat with a high density of carnivores associated a predator-specific escape response with these alarm calls, whereas sifakas in the other habitat did not. This differential comprehension of alarm calls is likely to reflect the operation of social learning processes that caused changes in signal content due to changes in the set of predators to which these two populations have been exposed (Fichtel and van Schaik 2006). Thus, social learning appears to be present in lemurs, whereas innovations and tool-use seem to be extremely rare, indicating that the innovative and tool-using anthropoids show greater flexibility in developing new behavior to exploit the environment.

#### **19.4.4 Communication**

The evolution of language is clearly one hallmark of humans. Vocal communication of nonhuman primates is very different from human language (Cheney and Seyfarth, this volume). Nonhuman primates have a relatively small repertoire of vocalizations, whose production is predominantly innate (Winter et al. 1973; Hammerschmidt et al. 2001). Although their vocal repertoire is limited, it can provide listeners with an open-ended, highly modifiable, and cognitively rich set of meanings (Cheney and Seyfarth, this volume). In some cases, such as alarm calls, the context eliciting a vocalization is narrowed down to the eliciting stimulus, in this case the type of predator or danger. However, vocalizations given in other contexts, such as during social interactions, depend on both the immediate social context and the history of interactions between particular individuals.

Several haplorrhine primates have been reported to produce acoustically distinct alarm calls for different types of predators, the so-called functionally referential alarm calls (Seyfarth and Cheney 2003). Group-living lemurs have developed different kinds of alarm call systems, from functionally referential alarm calls in ring-tailed lemurs (Macedonia 1990; Pereira and Macedonia 1991),

to arousal-based alarm calls in ruffed lemurs (Macedonia 1990), and a mixed alarm call system in sifakas and redfronted lemurs (Fichtel and Kappeler 2002). The mixed alarm call system consists of functionally referential alarm calls for raptors and general alarm calls that are given in response to predators and other threats. Interestingly, the same sort of alarm call system has also been suggested to exist in some New World monkeys, i.e., saddleback tamarins (*Saguinus fuscicollis*), as well as white-faced and tufted capuchin monkeys (Fichtel et al. 2005; Kirchhof and Hammerschmidt 2006; Wheeler 2008). Nocturnal strepsirrhines do not seem to rely on early warning of predators, but produce general alarm calls that are primarily directed to predators or conspecifics (reviewed in Fichtel 2007). These calls may be the ancestral form of primate alarm calling.

As suggested by Cheney and Seyfarth (this volume), the vocalizations that baboons give during social interactions depend on both the immediate social context and the history of interactions between particular individuals. Although several lemurs are group-living, the usage and potential function of vocalizations during social interactions have not been studied yet. In the context of group coordination, some haplorrhine species produce a particular travel call to initiate group movements (reviewed in Boinski and Garber 2000). Sifakas converge in several fundamental proximate aspects of group coordination, but they do not use a particular call or other signals to initiate group movements (Trillmich et al. 2004).

Finally, several similarities seem to exist across primates, including humans, in acoustic features of the expression of the caller's arousal or emotional state. Specifically, primates use common principles, such as an energy shift towards higher frequencies, to encode basic emotions in vocalizations (Fichtel et al. 2001; Fichtel and Hammerschmidt 2002, 2003; Scheiner et al. 2002, 2006; Hammerschmidt and Jürgens 2007). Most of the basic emotions of humans appear to have deep phylogenetic roots, which extend back to the common ancestors of haplorrhine and strepsirrhine primates (Fessler and Gervais, this volume).

However, in the domain of visual communication, i.e., facial expressions and gestures, strepsirrhines clearly differ from haplorrhine primates. Only a few facial expressions have been reported in aggressive contexts in ring-tailed lemurs (Pereira and Kappeler 1997) and during play (play-face) in sifakas (pers. observ.). The use of manual gestures seems to be almost absent, though several nocturnal lemurs (red-tailed sportive lemurs (*Lepilemus ruficaudatus*), mouse lemurs) use a shaking fist to threaten conspecifics or predators (pers. observ.). Strepsirrhine primates also exhibit some body gestures constituting conspicuous displays. Just to list a few of them, lorises, for example, raise their arms around their head while moving their body in cobra-like fashion when threatened (Charles-Dominique 1977), male ring-tailed lemurs exhibit conspicuous displays during their famous "stink-fights": while standing bipedally, they move their tail through the legs, "parfume" it with their antibrachial glands, and wave it in a stereotyped fashion in front of opponents (Jolly 1966a). Redfronted lemurs exhibit a friendly reciprocal arm-over display in which they put the proximal arm over the partner's back (Pereira and Kappeler 1997), and sifakas move their heads abruptly into the neck and back when aroused (Jolly 1966a). Nevertheless, in haplorrhine primates, gestural signals seem to be

more flexible and subject to cultural transmission (Pollick and de Waal 2007; Fogassi and Ferrari 2007). For example, gestures in apes vary not only between social groups but also culturally between populations (Whiten et al. 1999; van Schaik et al. 2003; Pollick and de Waal 2007), leading to the hypothesis that the flexible use of gestures in combination with enhanced cognitive capacities played a crucial role in the evolution of human language (Arbib et al. 2008, Cheney and Seyfarth, this volume, Tomasello and Moll, this volume).

## 19.5 Discussion and Conclusions

This review indicates that primates are more heterogeneous with respect to aspects of social complexity and social intelligence than in the realm of physical intelligence. Even though only a few lemur species have been tested on various tasks, and the social structure of only a few species has been studied in detail in the wild, preliminary conclusions about the presence or absence of certain abilities and traits are beginning to emerge. More detailed comparisons of the level of cognitive performance have to await more tests with the same experimental paradigms in a larger number of lemur species, and more detailed comparisons of aspects of social structure related to social intelligence require additional studies of lemurs, New World monkeys, and colobines. On the basis of the available information, however, it is possible to begin characterizing the cognitive abilities of lemurs and to outline the cornerstones of their social complexity, but it remains difficult to separate traits that may have been present in the earliest primates and or haplorrhines from specific adaptations of lemurs that have evolved over the past 50 million years.

In most domains of technical cognition, in which experimental tests have been conducted, strepsirrhines seem to have the same sort of basic cognitive abilities as other primates, and the performance of lemurs was, in most cases, quantitatively not different from that of other primates (summarized in Table 19.1). In the domain of “space and objects,” lemurs have a route-based mental representation of spatial relationships, show straight-line traveling, and efficient goal-directed movements between distant sites. They also search for hidden food and are able to solve detour problems. Lemurs manipulate objects less than most haplorrhines, but that might be due to the dominance of their olfactory sense and the less dexterous use of their hands. In discrimination learning tasks, they appear to be a bit slower and more error-prone, but in learning-set tasks, they are as skilled as other primates. They also seem to have some cross-modal skills, and sorting tasks are mastered just as well by lemurs as by New World and Old World monkeys. Though their numerical discrimination skills seem to be inferior, they understand the outcome of simple arithmetic operations. Tool-use and the associated abilities are a striking exception from the lack of fundamental differences from haplorrhines in this cognitive domain. Thus, if we simply consider whether strepsirrhines are able to perform a certain task, their cognitive abilities in physical domains are, by and large, comparable to those of New and Old World monkeys.

**Table 19.1** Summary of studies of technical and social intelligence of lemurs and other strepsirrhines. The main categories in the left column are described in the text. The central columns summarize the names of species, in which the corresponding abilities or traits have been demonstrated

Categories	Examples	References
1. Technical intelligence		
<i>1.1 Space and objects</i>		
• Spatial memory	Mouse lemurs, redfronted lemurs, Milne Edwards Sifakas	Joly and Zimmermann (2007), Lührs et al. (2009), Erhart and Overdorff (2008)
• Hidden objects	Bushbabies, Bamboo lemurs, Brown lemurs, Mongoose lemurs, Redfronted lemurs, Ringtailed lemurs, Pottos	Jolly (1964a,b), Deppe et al. (2009)
• Invisible displacement	Bamboo lemurs, Mongoose lemurs, Redfronted lemurs, Ringtailed lemurs	Deppe et al. (2009)
• Detour problems, Bent wire, Maze experiments	Ringtailed lemurs, Mouse lemurs	Davis and Leary (1968), Picq (1993, 2007)
<i>1.2 Tools and causality</i>		
• Object manipulation	Bushbabies, Pottos, Mouse lemurs, Brown lemurs	Jolly (1964a,b), Parker (1973, 1974), Ehrlich et al. (1976), Torigoe (1985), Renner et al. (1992)
• Simple box	Ringtailed lemurs, Mouse lemurs, Black lemurs, Brown lemurs, Ringtailed lemurs	Kappeler (1987), Fornasieri et al. (1990), Anderson et al. (1992), Schilling (2007)
• Complex box	Mouse lemurs, Aye-Ayes	Schilling (2007), Digby et al. (2008)
Tool use		
• Wild, captivity	–	–
• Understanding of tools	Ringtailed lemurs	Santos et al. (2005a)
<i>1.3 Features and categories</i>		
• Learning sets	Bushbabies, Lorises, Black lemurs, Ringtailed lemurs	Stevens (1965), Cooper (1974), Ohta (1983), Ohta et al. (1984, 1987)
• Reversal learning	Brown lemurs, Ringtailed lemurs, Fork-marked lemurs, Mouse lemurs	Stevens (1965), Rumbough (1997), Picq (1993, 2007)
• Cross-modal transfer	Bushbabies	Ward et al. (1976)
• Delayed response	Bushbabies, Ringtailed lemurs, Ruffed lemurs	Harlow et al. (1932), Maslow and Harlow (1932), Jolly (1964a)
• Oddity	Ringtailed lemurs	Davis et al. (1967)
• Serial ordering	Ringtailed lemurs	Merritt et al. (2007)
• Quantities		
• Estimating numerosity	Mongoose lemurs	Lewis et al. (2005)
• Simple arithmetic operations of 1 + 1	Ringtailed lemurs, Brown lemurs, Mongoose lemurs, Ruffed lemurs	Santos et al. (2005b)

(continued)

**Table 19.1** (continued)

Categories	Examples	References
<b>2. Social intelligence</b>		
<i>2.1 Social complexity and structure of social relationships</i>		
• Coalitions	Redfronted lemurs, Ringtailed lemurs	Ostner and Kappeler (2004), Sussman (1992), Jones (1983)
• Cooperation	Mouse lemurs	Eberle and Kappeler (2006, 2008)
• Post-conflict behavior	Redfronted lemurs, Ringtailed lemurs, Black lemurs, Sifakas	Kappeler (1993b), Rolland and Roeder (2000), Palagi et al. (2005), Roeder et al. (2002), Palagi et al. (2008)
• Grooming networks	Redfronted lemurs	Port et al. (2009)
• Dominance relationships	Ringtailed lemurs, Sifakas	Kappeler (1993b), Pochron et al. (2003)
<i>2.2 Tactical deception and other related skills</i>		
• Tactical deception	Redfronted lemurs, Ringtailed lemurs, Brown lemurs	L. Pyritz pers. com., Deaner et al. (2006), Genty and Roeder (2006)
• Learning to deceive	Black lemurs	Genty et al. (2008)
• Self-control	Brown lemurs, Black lemurs	Genty et al. (2004)
• Gaze following	Ringtailed lemurs	Anderson and Mitchell (1999), Shepherd and Platt (2008), Ruiz et al. (2009)
<i>2.3 Social learning and innovations</i>		
• Social learning	Ringtailed lemurs, Brown lemurs, Black lemurs, Ruffed lemurs, Aye-aye	Feldman and Klopfer (1972), Glander et al. (1985), Jolly and Oliver (1985), Kappeler (1987), Fornasieri et al. (1990), Anderson et al. (1992), Gosset and Roeder (2001), Krakauer (2005)
• Innovations	Ringtailed lemurs	Hosey et al. (1997)
• Behavioral variation	Sifakas	Fichtel and van Schaik (2006)
<i>2.4 Vocal communication</i>		
• Functionally referential alarm calls	Ringtailed lemurs, Redfronted lemurs, Sifakas	Macedonia (1990), Pereira and Macedonia (1991), Fichtel and Kappeler (2002)
• Group coordination	Sifakas	Trillmich et al. (2004)
• Expressions of emotions	Redfronted lemurs	Fichtel and Hammerschmidt (2002)

On the basis of a meta-analysis of global cognition variables (detour, patterned string, invisible displacement, tool-use, reversal learning, oddity sorting, and delayed response), in which they ranked the performance of species, Deaner et al. (2006) concluded that strepsirrhines were inferior to most haplorrhines, but better than marmosets and talapoin monkeys (*Miopithecus talapopin*). This data set, however, included the performance of strepsirrhines in only four of the nine tasks

that were compared across species. Tomasello and Call (1997) identified 15 paradigms in the domain of physical cognition to which various primates were subjected. Our review revealed that strepsirrhines were able to perform successfully in 12 of these paradigms, but the level of performance in some tasks was not up to par with haplorrhines. Nothing is yet known about strepsirrhines' ability to understand natural categories and the conservation of quantities. Thus, the grade shifts in brain size are not reflected by fundamental gaps in performance in these spatial and physical abilities among primates; but great apes, in particular, are superior on several tasks.

In the realm of social intelligence, lemurs exhibit a number of traits that differ from those described for the better-known haplorrhines, despite basic similarities in several aspects of social organization, such as the multi-male, multi-female composition of groups, the existence of dominance relations, and female philopatry. However, within-group coalitions, even between mothers and daughters, are extremely rare or absent altogether, postconflict reconciliation is also rare, but some basic exchange between grooming and other social commodities may exist. Very limited preliminary evidence suggests that some basal aspects of tactical deception exist and that lemurs can follow the gaze of conspecifics. Social learning abilities are more widespread among lemurs, but true innovations of novel behaviors are apparently rare. As demonstrated by the study of behavioral variation in the meaning of alarm calls among sifaka populations, however, more discoveries of innovations and variation among populations are likely, once more than one population is considered as the representative of its species. Finally, lemurs also vocalize with functionally referential vocalizations, exhibit coordinated group movements, and express their emotional status in structural features of their vocalizations. However, in the domain of visual communication, i.e., the use of gestures and facial expressions, strepsirrhine primates clearly differ from haplorrhines and use less variable signals.

With this information, the outlines of a proto-typical primate social structure and social cognition begin to emerge. Many basic features of social complexity exist, albeit often in rudimentary form, in lemurs, so that the observed variation among major primate radiations is primarily one in quantity, rather than in quality. It is striking that lemur social relationships differ most from the better-known haplorrhine models. Lemurs exhibit more similarities in this respect with New World primates (e.g., small group size, female competition) (Wright 1997). More detailed studies of additional New World monkeys, but also colobines, are required to establish cercopithecine monkeys with maternal rank inheritance as the typical haplorrhine reference for comparison with other primates (see also Strier 1994). It is, therefore, difficult to evaluate the observed differences in social structure between lemurs and haplorrhines. Because the traits where lemurs deviate most obviously are functionally related to intense within-group competition, they may represent lemur autapomorphies, rather than primate symplesiomorphies. These lemur idiosyncrasies are thought to reflect either adaptations to unusually harsh ecological conditions (Wright 1999) or an intermediate stage in a transition from pair-living to group-living (van Schaik and Kappeler 1996).



In the quest to identify human behavioral universals, a broader comparative perspective is useful. By acknowledging the biological continuity of some traits and abilities across the primate lineage, more focused comparisons and reconstructions among the various species of *Homo*, *Pan*, and their common ancestors are possible (Chapais, this volume). Moreover, by mapping social and cognitive variation on the full range of primate brain sizes, major grade shifts during primate evolution will be easier to recognize; for this, a more fine-grained data set that includes more strepsirrhine species will be needed. Finally, lemurs should no longer be regarded as our embarrassing relatives, because their cognitive abilities and social complexity are not as utterly primitive as previously thought by some.

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