The authors found that not only could lemurs learn to order numerical values from 1 to 4 (with known stimuli presented during training and also with novel exemplars of the same numerical value) but also to transfer the numerical rules to novel values from 5 to 9. The same ability has been already found in squirrel monkeys, cebus monkeys, baboons, rhesus macaques and humans (Brannon and Terrace, 2000; Smith *et al.*, 2002; Judge *et al.,* 2005; Cantlon and Brennon, 2006). Therefore, Merritt *et al.* (2011) concluded that at a minimum, their results on lemurs suggested that within the primate lineage, the ability to form ordinal numerical rules is an evolutionary ability that emerged before the separation of strepsirrhine and haplorrhine primates (50–70 million years ago).

Box 9.1 by Evan L. MacLean and Brian Hare

Speaking of which: lemur cognition and sociality

Less than two decades ago – in a comprehensive review of research on primate cognition – Tomasello and Call noted that studies of lemurs were conspicuously lacking, leaving a void in our knowledge of primate cognitive diversity (Tomasello and Call, 1997). Recently however, studies of lemur cognition have proliferated shedding light on a wide range of important evolutionary questions. First, because lemurs are believed to resemble the earliest living primates more so than monkeys or apes, studies of lemur cognition allow powerful inferences about the cognitive characteristics of early primate species (Tattersall, 1982) For example, if lemurs, monkeys and apes share common mechanisms for solving a particular problem, then this aspect of cognition was likely present in the earliest primate species. If this ability is *not* found in other mammals closely related to primates (e.g. colugos or tree shrews) it is possible that these skills reflect a key cognitive adaptation that coincided with the emergence of the primate order. However, if monkeys and apes exhibit cognitive flexibility that is not found in lemurs, these traits may have evolved after the prosimian–anthropoid divergence. Thus lemurs play a special role both in identifying the aspects of cognition that are unique to primates, and also as a phylogenetic out-group for studies with monkeys and apes.

Second, comparative studies within lemurs present unique opportunities for testing hypotheses about the socioecological factors that favour cognitive evolution. Although lemurs are a closely related clade, lemur species have radiated into remarkably divergent ecological niches, and are characterised by a variety of activity patterns, diets and social systems. Therefore lemurs present a natural experiment in which close genetic relatives, with differing behavioural ecologies can be compared with one another. Against this backdrop, scientists have powerful opportunities to test hypotheses regarding how factors such as social living and dietary strategies relate to species differences in cognition (MacLean *et al.*, 2012). Indeed, early behavioural studies with lemurs provided the inspiration for important hypotheses about primate cognitive evolution, including Jolly's initial formulation of the Social Intelligence Hypothesis (Jolly, 1966). However, until recently few ecologically motivated studies of lemur cognition had been conducted.

Much of our work has attempted to test hypotheses about the adaptive value of cognition through comparisons of lemur species that differ in key aspects of their social organisation. The first of these studies was inspired by the hypothesis that transitive inference (if A > B and B > C, then A > C) is one cognitive mechanism through which individuals could rapidly infer dominance relationships between members of a social group (Cheney and Seyfarth, 1990). An earlier study with corvids had revealed an interesting species difference in which highly social pinyon jays learned to track and infer hierarchical information more readily than western scrub jays – a closely related but relatively non-social species (Bond *et al.*, 2003). Based on these findings we compared ring-tailed and mongoose lemurs – close relatives that differ markedly in their social organisation – in a similar paradigm. Consistent with the findings from corvids, highly social ring-tailed lemurs outperformed less social mongoose lemurs on tests of transitive reasoning (MacLean *et al.*, 2008). Interestingly, however, this species difference occurred only when the dyadic pairs in the hierarchy were presented in a randomly shuffled sequence prior to the test of transitive inference (e.g., C > D, A > B, F > G, B > C, D > E). In contrast, when the dyadic pairs comprising the hierarchy were retrained in a manner emphasising the underlying linearity of the sequence (e.g., A > B, B > C, C > D, etc.), both species performed similarly on subsequent tests of transitive inference. Therefore these findings suggested that the two species did not differ in their fundamental ability to make transitive inferences, but rather in their propensity to spontaneously extrapolate the hierarchy from a series of linked dyadic relationships. Interestingly, the condition in which ring-tailed lemurs outperformed mongoose lemurs is more likely to resemble the manner in which dyadic social interactions would be observed in nature. That is, an animal is likely to witness a variety of dyadic dominance interactions, occurring in a piecemeal fashion over time, and the ability to infer unobserved dominance relationships based on this information may be vital to success in large hierarchically organised societies.

Inspired by these findings we extended our focus to other lemur species, as well as additional measures of cognition. Because the Social Intelligence Hypothesis proposes that a key function of cognitive flexibility is to outwit conspecifics for access to food and mates, our next tests measured four lemur species' abilities to exploit social cues in a food competition paradigm. Similarly to previous studies with monkeys and apes, lemurs were first introduced to a human competitor who actively defended monopolisable food from the subject. After this introduction lemurs were tested in a series of trials in which they could attempt to pilfer one of two pieces of food nearby a human competitor. Critically, we varied which piece of food the human competitor could see creating the opportunity for lemurs to strategically target the unwatched item. Although all four lemur species learned to avoid the human competitor during the introductory trials, only the highly social ring-tailed lemurs systematically chose the unwatched item during test trials (Sandel *et al.*, 2011). Thus, these data suggested that in addition to living in social groups similar to those of Old World monkeys, some aspects of ring-tailed lemur social cognition may also be convergent with anthropoid primates.

Most recently, we implemented a modified version of this feeding competition task, as well as a non-social inhibitory control task with an expanded taxonomic sample including six lemur species. Based on the studies described above, we expected that lemur species characterised by large social groups would perform better in the food competition task than lemurs characterised by smaller societies. But would the pattern of species differences be similar for a non-social cognitive task? Are the evolutionary relationships between sociality and cognition domain specific, or does group living select for cognitive flexibility more broadly? The results of this study provided strong support for a domain-specific version of the Social Intelligence Hypothesis. Across the six lemur species, performance on the food competition task was significantly correlated with species-typical group size, suggesting a close relationship between social complexity and cognitive skills for outcompeting group mates. In contrast, although lemur species also varied significantly on the non-social inhibitory control test, there was no relationship between social group size and performance on this task.

In addition to the fascinating variance within these species, lemurs have also provided a foundation for developing cognitive tasks that can be employed in broader comparative studies. For example, the study of lemur inhibitory control described above was initiated through a collaborative working group tasked with coordinating advances in experimental and phylogenetic approaches to the study of cognitive evolution. Building on our initial success with lemurs, a collaborative network of researchers collected additional data from birds, rodents, carnivores and anthropoid primates, allowing a phylogenetic comparison of 32 species tested on this task (MacLean *et al.*, 2014). Given their remarkable behavioural and morphological variance, it is likely that lemurs will continue to play an important role in the development of cognitive tasks that can be used in future broad-scale studies of comparative cognition.

The studies described above illustrate the value of lemurs in testing hypotheses about the evolution of cognition. Although we have highlighted our research exploring the links between social systems and social cognition, variance in other aspects of lemur ecology provides similarly powerful opportunities for testing a wide range of evolutionary hypotheses. For example, a recent study with four lemur species revealed that highly frugivorous ruffed lemurs exhibited more robust spatial memory in a variety of contexts than less frugivorous species (Rosati *et al.*, 2014), including ring-tailed lemurs who outperform ruffed lemurs on some measures of social cognition. Thus variance in lemur cognition has likely evolved in response to diverse selective pressures, and the magnitude and direction of species differences in cognition are also likely to be domain specific. These findings underscore the need for additional studies that probe other domains of lemur cognition, and the relationships between these skills and species differences in socioecology.

A second exciting future direction in lemur research involves the direct comparison of lemur, monkey and ape cognition. Although lemur problem solving was once believed to differ qualitatively from that of monkeys and apes, recent research challenges this notion. For example, with regard to numerical discrimination, sequence learning and causal reasoning tasks, some lemur species perform quite similarly to monkeys (Santos *et al.*, 2005b; Merritt *et al.*, 2007; Jones *et al.*, 2014). In contrast, on other social-cognitive measures, the differences between lemurs and anthropoid primates appear to be more pronounced (Fichtel and Kappeler, 2010). Therefore an important aim for future research will be to identify the extent of similarity and difference between lemurs and anthropoid primates across a wide range of cognitive measures.

In sum, recent studies on lemur cognition have led to major insights about the processes through which cognition evolves, as well as the cognitive traits that are shared across primate species, or uniquely evolved in particular primate lineages. Ultimately however, we still have much to learn about the minds of lemurs, and many of the most exciting discoveries are surely yet to come.

9.3 Should I stay or should I go? Lemurs, patience and self-control

'The black-and-white ruffed lemur dangles by her hind legs at the top of the leafy canopy, plucking figs from the branch below. At some point she has consumed many of the figs from the branch, leaving a few small fruits hidden beneath the leaves. The lemur now faces a choice: should she continue to search for the remaining figs or move on to another branch full of fruit?'. This is how Stevens and Mühlhoff (2012) depict a case of intertemporal choice (a choice between options with different time delays to reward; Read, 2004) that a lemur may face in the wild. Over the last decade, lemurs' abilities have been tested under different