lessons. Minor regrets are that I didn't start doing yoga and running years ago.

What are the scariest things you have done? In practical terms — getting my Landrover across flooded rivers in Africa. In academic terms — taking the plunge to join a psychology department when I was originally trained as a zoologist. But fortunately both have turned out well.

What's next for you? We have quite an exciting new project on elephant matriarchs under way — comparing social knowledge in natural family groups in Kenya, where the matriarch is the oldest in a group of female relatives, with more artificial groups in South Africa formed by translocation in of elephants (often young individuals) from outside. In the longer term we will be examining how age and experience contribute to communication, cognitive abilities and behaviour in this large-brained long-lived species as it adjusts to different environments and stresses — and pinpointing how matriarchs signal to and control their groups. Our findings will have relevance for conservation as well as psychology and should enhance our understanding of the needs of poached and culled elephant populations throughout Africa. Alongside this, I am keen to expand work on domestic/companion animals — as these species can provide useful models both for getting at mammal cognitive abilities and, by virtue of their interactions with humans, exploring inter-specific communication. I also maintain a strong interest in the precursors of language and will continue collaborative work on the role of formants (the key acoustic parameters that define human vowel sounds) in the vocal communication systems of non-human mammals and on the evolution of mammal vocal repertoires.

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Quick guide

Lemurs

Anne D. Yoder

What is a lemur? Lemurs are non-human primates found on the island of Madagascar. They occur nowhere else on Earth. To put it succinctly: "To be a non-human primate from Madagascar is to be a lemur; to be a lemur is to be from Madagascar". All lemurs are classified within the primate suborder Lemuriformes. Some lemurs have latin binomials that actually contain the word 'lemur', for example the ring-tailed lemur *Lemur catta*, while others make no mention of the word, for example the aye-aye *Daubentonia madagascariensis* (Figure 1). Nonetheless, they are all lemurs, despite their remarkable levels of morphological, behavioral, ecological and physiological diversity. As two examples of the breadth of this diversity: the mouse lemur is the world's smallest living primate, weighing in at about 50–60 grams, is nocturnal, spends much of the dry season torporing, and eats primarily insects and small vertebrates; the indri, on the other hand, is the largest of the lemurs, weighing up to 10 kg, is diurnal, a spectacular leaper, and has a leaf-eating diet.

To use a single word as a descriptor for this vast array of non-human primates is entirely appropriate. Numerous independent molecular phylogenetic studies have shown that all lemurs evolved from a single common ancestor that arrived in Madagascar sometime early in the Cenozoic. Given that Madagascar was completely isolated from other landmasses at that time, and has been ever since, many biogeographers have concluded that lemurs must have dispersed to Madagascar by 'rafting'. Moreover, given the current best estimate of the timing of the initial lemur radiation, approximately 60 million years ago, one imagines that lemurs arrived in Madagascar relatively soon after the apparent faunal turnover at the Cretaceous/Tertiary (K/T) boundary. Thus, it is entirely possible that lemurs were the very first modern placental mammals to occupy Madagascar.

How many species of lemurs are there? Excellent question! And, depending upon whom you ask, you will likely receive a wide range of answers. Certainly, it seems safe to say that there are at least 50 species of living lemurs, though some estimates go as high as 80 species. For example, in 1994, when the first edition of Conservation International's field guide, *Lemurs of Madagascar*, was published, there were a mere 33 named species listed. Now, with the publication of the 2nd edition in 2006, there are more than 70 named species, with the promise of more to come. The question then becomes, why the discrepancy? Much of it comes down to the fact that defining and recognizing species is one of the most theoretically and operationally challenging tasks that biologists face. To some, species are "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (Ernst Mayr's Biological Species Concept, a mainstay of mammalogy's view of species). But, to an increasing number of biologists, the identification of a few geographically specific nucleotide substitutions in some mitochondrial gene or another is sufficient evidence for species designation.

In the case of lemurs, there are a number of mitigating factors with regard to the dizzying acceleration in species recognition. For one, there is extreme urgency with regard to conservation. By accurately recognizing the diversity and geographic specificity of lemur species, political pressures can be brought to bear on setting conservation priorities. Moreover, genetic tools are certainly playing a role by allowing biologists to quickly detect and describe biological diversity. But, perhaps the most interesting and meaningful factor is the biological phenomenon of 'cryptic' species

diversity. Cryptic species are those that cannot be readily distinguished by human eyes, but that, to the animals themselves, might exhibit any number of crucial differences in communication signals such as olfaction, or vocalization or behavior. In particular, the identification of cryptic species by genetic differences has radically affected the number of recognized mouse lemur species, as well as other nocturnal lemurs. In the case of mouse lemurs, there were two recognized species in 1994; now, there are as many as 16 described species. The real number lies somewhere in between (though certainly, towards the higher end), and the coming years, in which studies of behavior, morphology, and ecology can be added to the genetic evidence, will hopefully bring resolution to the complicated question of "how many lemur species are there?"

Are they 'ancestral' primates? The short answer is "no", they absolutely are not ancestral to other living primates. Lemurs are living members of the primate clade, with their own unique evolutionary history, and therefore cannot possibly be ancestral to their contemporaries. That being said, they do retain a number of 'primitive' features that almost certainly characterized the earliest primates. For example, they are far more reliant on olfaction than are anthropoid primates (monkeys, apes and humans). This is evidenced not only by behavior, but also by their long muzzles and wet noses, much as those seen in cats and dogs. Also, they tend to have smaller brains relative to body size, and less frontated orbits, than do anthropoid primates. In summary, certain lemurs may vaguely resemble the ancestral primate species, but they themselves are contemporary creatures, each with their unique evolutionary features.

What are the defining features of lemurs? There are no uniquely defining features of lemurs, beyond the fact that they all reside on Madagascar, and nowhere else. They, along with their closest relatives, the lorisiform primates

Figure 1. A glimpse of lemur diversity. The ring-tailed lemur (top), the aye-aye (bottom left), and the sifaka (bottom right). Photos by David Haring.

of Africa and Asia, do show a wonderfully strange conformation of the lower dentition called a 'toothcomb'. Virtually all lemurs, slow lorises and bushbabies (which together form the primate suborder, Strepsirrhini) have lower canines and incisors that are compressed and elongated to form a comb-like structure. This toothcomb is typically used for grooming, and indeed, the passage of hair over the teeth during grooming leaves diagnostic striations on the teeth that are readily identified by scanning electron microscope images. Amazingly, these very same striations have been revealed on the toothcomb teeth of the earliest known fossil strepsirrhines from Africa, estimated to be at least 40 million years old. As for the lemurs themselves, however, even though molecular phylogenetic studies have conclusively demonstrated that they are a unique clade, there are no discernable morphological synapomorphies. Instead, the lemuriform clade is typified more by extreme diversity than by any unifying form.

Why are lemurs important? Lemurs constitute more than 15% of living primate species diversity, though they occur on less than 0.4% of Earth's land surface area. Their remarkable diversity, single evolutionary origin, and restricted biogeographic distribution combine to make

them a remarkable illustration of the power of the evolutionary process to create varied biological types from a single ancestral form. Moreover, their close phylogenetic proximity to humans makes them invaluable subjects for comparative study. Presently, the power of this comparative framework is being realized in the study of primate genomics and cognition. Because the toothcombed primates are the sister clade to the Anthropoidea, comparisons between the two have the unique ability to reveal primate-specific traits that almost certainly originated with the ancestral primate species. The current project to sequence the genome of the gray mouse lemur, *Microcebus murinus* (http://www.genome.gov/10002154), is a preliminary but crucial step towards understanding the changes to the mammalian genome that characterize the primate genome. This comparison offers the singular opportunity for genomicists to recognize those traits that are diagnostic of primates, separate from all other mammals. It is an essential first step towards identifying those genomic traits that are unique to humans. In the same way, ground breaking studies of lemur cognition are showing that lemurs have abilities for list memorization and numerosity discrimination that are similar to those of monkeys. This latter finding, in particular, is revolutionary as it demonstrates that the higher cognitive functions thought to uniquely characterize anthropoid primates were almost certainly present in the earliest primates — mammals that first evolved some 80 million years ago. Without doubt, comparative studies of lemurs and humans will continue to refine and revolutionize our understanding of primate evolution and biology, from genotype to phenotype.

What does the future hold for lemurs? At first glance, the future does not look very good for lemurs in Madagascar, or for the habitats in which they reside. Forests are being destroyed at an alarming rate, and to be a lemur — any lemur — is to be an endangered species. There may be light at the end of the tunnel, however. Madagascar's current president, Marc Ravalomanana, is as committed to biodiversity preservation as any president in Madagascar's history. In September 2003, he announced to the world his commitment to triple the amount of Madagascar's protected areas within the following five years. Labeled as 'the Durban Vision', the plan is approaching its targeted year for realization. Big strides have been made towards achieving the stated goals. Moreover, in June 2007, the World Heritage Committee has named a significant proportion of Madagascar's eastern rainforests as one of three new UNESCO World Heritage List sites. Thus, we can hope that the global coordination of captive lemur breeding programs, and the protection of Madagascar's remaining natural habitats, will together provide a stable future for these fascinating primates.

Where can I find out more about lemurs and Madagascar?

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Primer

The amygdala

Joseph LeDoux

The amygdala is a complex structure involved in a wide range of normal behavioral functions and psychiatric conditions. Not so long ago it was an obscure region of the brain that attracted relatively little scientific interest. Today it is one of the most heavily studied brain areas, and practically a household word. Art critics are explaining the impact of a painting by its direct impact on the amygdala; essential oils are said to alter mood by affecting the amygdala; and there is a website where you can unleash your creativity by clicking your amygdala, and thereby popping your frontal cortex. In this Primer, I will focus on the scientific implications of the research, discussing the anatomical structure, connectivity, cellular properties and behavioral functions of the amygdala.

Anatomical organization

The amygdala was first recognized as a distinct brain region in the early 19th century. The name, derived from the Greek, was meant to denote an almond-like shape structure in the medial temporal lobe. Like most brain regions, the amygdala is not a single mass but is composed of distinct subareas or nuclei (Figure 1). The almond shaped area that gives the amygdala its name was really only one of these nuclei, the basal nucleus, rather than the whole structure.

Nuclei within brain areas like the amygdala are typically distinguished on the basis of histological criteria such as the density, configuration, shape and size of stained cells, the trajectory of fibers, and/or chemical signatures (Figure 1). Recently, more subtle measures, such as microscopic features of processes (axons and dendrites) have also been used. There has been much debate about how the amygdala should be partitioned on the basis of the various criteria, and how the