The Missing Lemur Link

An Ancestral Step in the Evolution of Human Behaviour

Lemurs share a common distant ancestor with humans. Following their own evolutionary pathway, lemurs provide the ideal model to shed light on the behavioural traits of primates, including conflict management, communication strategies and society building, and how these aspects of social living relate to those found in the anthropoid primates.

Adopting a comparative approach throughout, lemur behaviour is cross-examined with that of monkeys, apes and humans. This book reviews and expands upon the newest fields of research in lemur behavioural biology, including recent analytical approaches that have so far been limited to studies of haplorrhine primates. Different methodological approaches are harmonised in this volume to break conceptual walls between both primate taxa and different disciplines.

Through a focus on the methodologies behind lemur behaviour and social interactions, future primate researchers will be encouraged to produce directly comparable results.

Ivan Norscia carries out research at the Natural History Museum, University of Pisa, Italy. He started investigating the behavioural ecology of lemurs in dry and wet forests of Madagascar and through his research has contributed to the redefinition of a lemur species (*Avahi meridionalis*). His research later expanded to the behaviour of monkeys, apes and humans.

Elisabetta Palagi is a department member of the Natural History Museum, University of Pisa, Italy. Her research centres upon lemur individual recognition and multimodal signalling, which has expanded to other primate and non-primate animals. Most recently, in conjunction with Ivan Norscia, she has adopted a cross-species comparison approach to shed light on the biological foundation of human behaviour.

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In memory of primatologist and mentor Alison Jolly,
and beloved friend Letizia Pantani

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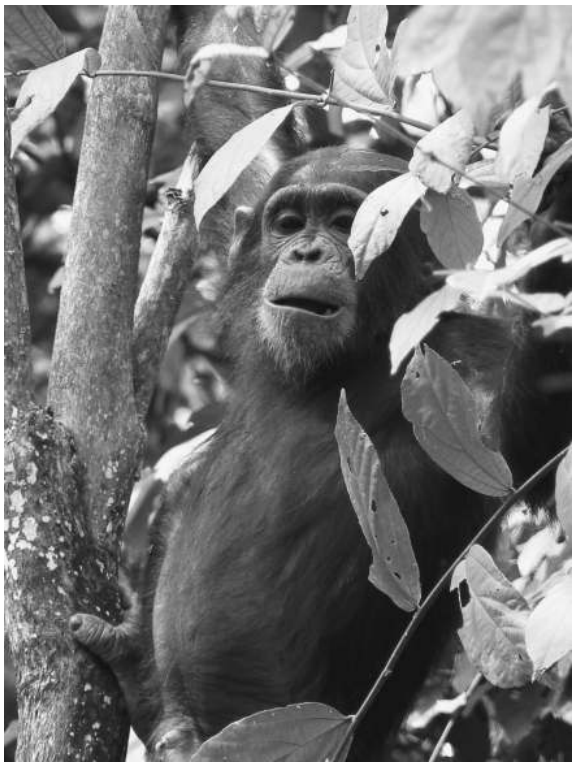
A message from Jane Goodall

In 1960 Dr Louis Leakey, palaeontologist and anthropologist, suggested that I should travel to the Gombe National Park, in what is now Tanzania, to study the behaviour of the chimpanzees there. He believed that apes and humans shared a common ancestor some 6 or 7 million years ago and that an understanding of chimpanzee behaviour in the wild might help him better understand how our prehistoric ancestors may have behaved. Subsequently, when I had been in the field for some 18 months, he arranged for me to go to Cambridge University to work for a PhD (although I had never been to college). In the early sixties ethologists tended to be reductionists, searching for simple explanations for very complex behaviours. When I talked about the Gombe chimpanzees having different personalities, complex cognitive abilities, minds, and emotions such as pleasure and sadness, anger, frustration and so on, I was accused of anthropomorphism as those attributes, I was told, were unique to the human animal. Some scientists were even shocked that I referred to the chimpanzees by names rather than numbers. Fortunately, I had learned from my dog, as a child, that none of that was true.

Since those days the science of animal behaviour has come a long way and there have been many studies of animal cognition, animal emotions and even personality. In other words the sharp line once believed to separate humans from the rest of the animal kingdom was blurred. There was a difference of degree between the behaviour of humans and chimpanzees, but not of kind. Since then other studies have shown that many of the complex behaviours shared by the great apes and humans are present also in monkeys. And during the last decade the barrier between monkeys and lemurs has also been found to be increasingly fragile. Lemurs – the spirits of our ancestors according to some Malagasy traditions – exchange services, suffer and manage anxiety, reconcile, and use play to increase tolerance towards unfamiliar individuals.

*Many species of lemurs are extremely endangered, and an understanding of their behaviour, in addition to helping us to understand the origins of some of our own behaviour, is also crucial for determining the best conservation strategies. We need to understand how the lemurs interact with each other and with their forest environment. We need to understand the complexity of the natural world in order to save biodiversity. And we need to inform and educate people so that they understand how the different species of animals and plants in a given ecosystem are interdependent on each other and why it is important to save this complex environment not only to protect wildlife but also for their own future well-being. This vision is in line with the core values of the Jane Goodall Institute that I founded in 1977 (*www.janegoodall.org*).*

Respect, nourish and protect all living things; people, animals and the environment are all interconnected. Knowledge leads to understanding, and understanding



Chimpanzee juvenile at Gombe Stream National Park, Tanzania. Photo: Ivan Norscia.

will encourage us to take action. Every individual has the ability to make a positive difference. Flexibility and open-mindedness are essential to enable us to respond to a changing world. Integrity and compassion are required in all that we do and say.

The primates of Madagascar, as well as the primates of the rest of the world, are our closest relatives and deserve our attention and care. This book helps us to better understand lemurs and their place in the evolutionary path that our own species has followed.

Foreword

We human beings are distinctly unusual in the way we behave, and most particularly in the way in which we process information about the world around us. The final finishing touches to the distinctive manner in which we think and interact seem to have been acquired rather recently. But they were based upon, and made possible by, a complex biological edifice that had been under construction for a very long time indeed. If anything that happened along the winding road of primate and human evolution had failed to happen, for whatever reason, we would not be the creatures we are today. As a result, we are not only who we are, but we are also who we were. Arguably, that long history stretches back to the very beginnings of life on planet Earth; but probably the most useful place to start any rational account of it is with the origin and early evolution of our own unique mammalian order, Primates.

The primate – and ultimately human – edifice has been built, incrementally, over the past sixty million years or so. The foundations and lower floors of that edifice were furnished by the early primates, whose fossils we know from North American, Eurasian and African rocks dating between about sixty and forty million years ago. But these forms are long vanished; and the closest thing we have to living, observable, analogies for those ancient relatives are the strepsirrhine primates of the tropical Old World. Also including a handful of nocturnal species from tropical Africa and Asia, the strepsirrhines are incomparably well represented by the lemurs of the mini-continent of Madagascar. Isolated in their island domain for upward of fifty million years, the lemurs have radiated into an astonishing array of adaptive types: large and small, nocturnal and diurnal, suspensory and cursorial, leaf-eating and fruit-eating, highly arboreal and at least partly terrestrial, eurytopes and stenotopes, gregarious and solitary. Sadly, the larger-bodied representatives of this amazingly diverse and apparently monophyletic primate group are recently extinct, at least partly due to the depredations of humankind. But the surviving species, reckoned to number between fifty and a hundred, depending on the criteria you use to recognise them, still present us with a mind-boggling adaptive diversity.

Nonetheless, despite their undeniable diversity in phylogeny and form, in certain fundamental – and particularly cognitive – respects, all of the Malagasy primates represent variations on a single basic theme: a theme apparently close to what was also exemplified by those early primates from which we, too, ultimately sprang. Accordingly, if we can contrive to fathom the ways in which lemurs interact with each other and with the world around them, we will have made a major stride towards understanding the biological underpinnings on which the yet more complex cognitive modes of human beings and other 'higher' primates are based.

Strepsirrhine primates have wet muzzles, the better to smell with, and possess functional Jacobson's organs that amplify the sense of smell. Their cousins the

haplorrhines, namely monkeys, apes and humans, have dry noses and upper lips. Correlated with their olfactory prowess, many strepsirrhines have specialised scent glands, which they use to mark branches, their own tails, or even each other. Most groom themselves and each other with a tooth-comb composed of the lower canines and incisors, and not with their hands like monkeys and apes. Their upper canines, however, are fiercely sharp, honing against a lower premolar. The specialised organs of both aggression and of mutual trust or affection are right there at the front of the face. Lemurs use their hands mostly for locomotion, or for handling food. The only highly manipulative strepsirrhine is the weird and wonderful aye-aye, with its specialised finger for tapping to test hollow objects and probing into the hollow, once interesting contents are found. For many years, other strepsirrhines were thought stupid because they did not pass hand-oriented psychological tests, and this book deals with newer research that gives them problems to solve according to their own inclinations.

One of the biggest outstanding questions is to what extent the social relations of strepsirrhines resemble the complex relations of monkeys and apes, and in this domain one major problem that has so far resisted complete solution is why, in most species of Malagasy lemurs, females are clearly dominant over the males. Female dominance sets the lemurs apart from the huge majority of other mammals, including almost all monkeys and apes. Meanwhile, for those species that lead 'solitary' lives, sociality turns out to be largely a question of keeping track of neighbours, male and female, in a widespread community. This book offers new insights about the relationship of this complex of strepsirrhine abilities to their social behaviours. In some cases these insights challenge previous thinking: for instance, about reconciliation after aggression, and about the social roles of play and grooming. There are also some unnoticed parallels, such as why both sifakas and human beings carry sexual signals on their (and our) chests.

The Missing Lemur Link results from a unique collaboration between a laboratory scientist who has spent many years closely observing lemur behaviours in controlled situations, and an inveterate field worker who deeply understands the complex and unpredictable natural world in which his subjects live. Both authors are widely versed in studies of other primates as well as of the lemurs, and this enables them to make considerable progress in these pages towards a synthesis of the vast amount of information on communication and other forms of primate interaction that has by now accumulated. This aspect of their work makes this book a truly a path-breaking contribution because, largely as a result of the lemurs' apparently rather elementary forms of face-to-face social interaction and of their high dependence on olfaction, researchers have tended to compartmentalise them away from the other primates. Yet there are clearly cognitive continuities between the strepsirrhine and haplorrhine primate suborders, and characterising these commonalities will provide an essential key to understanding how modern anthropoids emerged from an ultimately quite strepsirrhine-like ancestral condition. In these pages Elisabetta Palagi and Ivan Norscia have performed an enormous service to primatology by

focusing on methodology in a way that will encourage future researchers on primates of all groups to produce directly comparable results.

Most gratifyingly of all, this excellent new book shows us just how much has been achieved in the study of the lemurs in recent years, and firmly points the way ahead.

Alison Jolly & Ian Tattersall