Miklosi to go into further detail on a particular point without interrupting the main text. The break out boxes are easy to locate and read as you are using this book as a reference guide on dog research. Overall, with the broad coverage of topics and the organization of the book, it will interest and be accessible to expert and dog lover alike.

To start, one of the book's highlights has to be the review of all of Miklosi and colleagues' work in one place. For example, we learn from their comparisons of wolves and dogs how the two species develop physically and behaviorally at very different rates; that dog puppies are more attracted and more comfortable around humans than wolves throughout their development; that, while dogs puppies are immediately able to use social information provided by humans, wolf puppies do not spontaneously use this same information; and that dogs actively look to humans for solutions to unsolvable problems while wolves look for solutions on their own. Together this work makes a convincing case that the process of domestication has had a profound effect on not just the morphology but also the psychology of dogs. Crucially, it seems that dog psychology has evolved such that dogs bond with humans in a way that wolves cannot. Miklosi stays appropriately close to the data and emphasizes the need for future research to tease apart various models of how selection during domestication may have shaped the dog, but in doing so points to future avenues of research.

There are many other surprising finds reviewed in this book. You will learn about work testing the ability of dogs to learn from humans and other dogs through various forms of social learning — including imitation. And studies examining whether the bark of the dog varies in its structure, such that both dogs and humans can discriminate different types of bark with different types of meaning. But there is more here than just behavioral work. You will also learn how researchers are harnessing the unmatched morphological variance in dogs to test hypotheses at the intersection of neurophysiology and cognition. For example, Miklosi explains how it was discovered that the width of the dog skull in relation to its length correlates with how the area in a dog's eye allowing for high acuity (where there is a high density population of ganglion cells in the retina) is shaped. Miklosi then outlines how he and colleagues used this neurophysiological finding to test whether Brachiocephalic (short-nosed) dogs were more skilled than Dolichocephalic (long-nosed) dogs at using gestural cues provided by humans. Consistent with the neurophysiological finding, short-nosed dogs such as pugs were more skilled at comprehending human gestures than long-nosed dogs such as collies. You will also learn how neuroendocrine techniques are helping to reveal individual differences in the stress reaction of dogs. When measuring the changes in cortisol when confronted with a strange human, neither bold nor shy dogs experience dramatic changes in cortisol levels when threatened by a strange human; instead, dogs that are not categorized in either extreme show the strongest physiological reaction to a stranger. This suggests that stress for dogs is caused by ambivalence in deciding how to react in the presence of a stranger.

This new book is a testament to the bright future of research on dogs. Miklosi has made the case for how important the dog is becoming in the study of animal psychology. The days of dogs being considered artificially created animals for use in conditioning studies have given way to the recognition of the dog's rich social life requiring it to adapt to the most complex primate of all. With the increasing costs and ethical dilemma often created by keeping nonhuman primates in laboratories, dogs may provide a particularly attractive option in the future for psychologists interested in studying the cognitive processes in nonhuman animals (pet dogs are recruited for non-invasive research as in studies of humans). Miklosi's new book will be a central fixture in all future work on dogs, as it will be the first place that students and experts alike will go to review unfamiliar topics or search for new research ideas. And it is not just researchers who will benefit. The book will be essential reading for all those using dogs as helpers for the handicapped, assistants to law enforcement, or just those who want to understand their best friend a little better.

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Elephant cognition

Lucy A. Bates, Joyce H. Poole and Richard W. Byrne

Why study elephant cognition?
Elephants have the largest absolute brain size of any land animal: 5.5 kg in Asian elephants and up to 6.5 kg in African savannah elephants. Larger brains should provide greater information processing power, but the high metabolic cost of brain tissue requires that animals only invest in large brains if they need to overcome some serious cognitive challenges. As a non-specialist browser, too large to be much threatened by predators, an elephant's biggest cognitive challenge is most likely to be social. All species of elephants form large social networks, with hierarchical, multi-level organisation, implying that elephants can deal with a degree of social complexity. Flexible problem solving would help, and elephants have the necessary brainpower. It is hardly surprising, then, that more and more researchers are becoming interested in the cognitive skills of these enigmatic animals.

For cognitive scientists, there is an additional reason to study elephants. Most research on animal minds has concentrated on species that are phylogenetically close to humans, such as the primates. Although this a natural starting point, such anthropocentrism has sometimes led to a bias in our understanding of animal cognition, with animals that are physically able to perform similar tasks to humans, such as tool making or keyboard use, being perceived as more 'intelligent'. Now, cognitive research on animals is increasingly conducted in ecologically valid ways on a wider range of domestic animals, birds, fish, and even invertebrates. Broadening the range of taxa examined and the types of question asked holds the promise of a truly comparative picture of animal mental skills. Elephants form part of the *Afrotheria*, more closely related to the small-brained aardvarks and manatees than to primates, so represent an obvious challenge for cognitive researchers.

What do we know about elephant society? Knowledge of elephant social lives, communication and ecology is largely based on long-term field studies of African elephants, though studies of captive Asian and African elephants have given additional insight into elephant reproductive physiology and chemosensory abilities.

Female elephant society is based around matrilineal relationships, whereas fluctuating sexual cycles influence the lives of males, who alternate between loose association with other males and moving between matrilineal groups in the constant search for sexually receptive females (Figure 1). Five social tiers have been distinguished within an elephant population, hierarchically arranged to form a fluid, fission–fusion society. The closest relationship is the mother–calf 'unit'. Females reach sexual maturity at 10–13 years old, giving birth to their first calf at around 14 years old after a 22-month gestation. Weaning occurs at 4 years, but daughters remain with their mother for life, resulting in a semi-permanent group of related females, the family. A matriarch, usually the oldest female, leads each family; however, in harsh conditions, a family may break up into sub-groups that travel independently for hours, days or weeks. Family relationships are important to females, and lead to cooperation between female kin. All female family members play a role in the successful rearing of offspring, frequently acting as allomothers who comfort, assist, play with and protect the offspring of their kin. Dominance within families is related to age, and the age of the matriarch directly influences the dominance of other females in between-family interactions. 'Bond groups' form between two or more families, usually ones that are matrilineally related. Bond groups show excited greeting displays at their reunion, as do sub-groups of a single family. Two further levels, clans and sub-populations, have been defined, based on residence areas and association patterns between bond groups.

Males leave their natal families and become independent at about 14 years old, joining up with other families or similar age males to form temporary groups until they reach physiological and behavioural sexual maturity. Potentially, males can father offspring at any age

Figure 1. Adult male with tusk broken in a recent fight over access to oestrus females (left); a young calf grows up with near-constant support of female relatives of all ages (right).

after independence, but because dominance is based on body size and males continue to grow until late in life, younger males have very little success. Furthermore, older musth males have the greatest paternity success because they are the preferred mates of females. Musth is an annual period of highly elevated testosterone, accompanied by an increased interest in females and heightened aggressiveness.

Males and females both range over large distances in their search for resources, so long-distance communication between family members and between sexually receptive males and females is critical. Communication is achieved over several kilometres by powerful low-frequency vocalisations that can be detected aurally and seismically, and via chemical signals released in the urine and other bodily secretions. At shorter ranges, vocal, chemical, visual and tactile displays are used; the exact communicative repertoire is unknown, but over 30 call types and 80 visual and tactile displays have been described for African elephants.

Clues to an advanced intelligence?
Elephants have long been revered, and stories of their superior intelligence abound in natural history literature. Elephants are said to dig wells to find hidden water sources, and then plug up the holes with chewed bark to prevent loss of the water to other animals. Working Asian elephants have been seen to stuff their bells with mud at night, apparently so that they can enter fields to raid crops undetected. These accounts have not been investigated systematically, but recently field experiments have been used to study what is perhaps the

elephant's most puzzling behaviour: their response to encountering the bones or carcasses of dead relatives. Elephants have regularly been seen to show intense concentration while they silently investigate elephant bones, sometimes for long periods. Experiments with artificially placed bones confirm that African elephants are more interested in the bones and tusks of dead elephants than similar-sized bones of other species. Although it is not known whether their reactions are specific to the bones of particular individuals, these results are consistent with the idea that elephants in some way understand and respond empathically to the death of a conspecific.

Tool use and mirror self-recognition are often taken to be indications of advanced mental capacity, both in animal cognition and developmental psychology. Both topics have been explored in elephants, with somewhat equivocal results. Of the two published accounts of mirror self-recognition tests in Asian elephants, one was negative and the other positive. Both can be criticised methodologically (in one, the accepted experimental protocols were not used, in the other the elephants were only given a few days exposure to the mirrors prior to testing). The jury is still out on whether elephants can recognise their reflections as themselves, and if so what sort of conception of self this implies.

Incontrovertibly, elephants use tools. Captive African elephants have been observed using at least 10 tool types, and tool use in wild elephants is not uncommon. But tool use is widespread among animals, even including invertebrates, and may not be cognitively demanding for an

animal with an appendage capable of holding a tool. Systematic tool manufacture or modification, however, has only been observed in a handful of species, principally chimpanzees, orangutans and New Caledonian crows. Asian elephants have been observed modifying large branches to use as fly switches: by breaking off smaller branches, a convenient tool for swatting flies results. However, for an animal that frequently breaks branches while eating, the cognitive challenge of discovering that these branches may also function as fly switches may not be great.

Tool using and self-recognition abilities, though important for humans, may not be the best place to begin a rigorous investigation of elephant cognition. Rather, it may be more useful first to understand the building blocks of an elephant's cognitive system: perception, memory, and comprehension.

How has elephant cognition been studied? Relatively few direct investigations of elephant cognitive skills have so far been carried out, for obvious practical reasons. In the 1950s, Rensch taught a five-year old captive Asian elephant 20 different visual discrimination pairs, where one pattern of each pair was rewarded. It took the female 330 trials to learn the first discrimination, but by the fourth pair, she needed only 10 trials to learn the discrimination, and she learnt the rest of the 20 pairs with little difficulty. Appreciating the gist of a task in this way ('learning set') is often taken as a sign of understanding, and certainly this elephant's performance was comparable to that of Old World monkeys and apes. But the relationship between this artificial task and the problems naturally encountered by elephants is unclear.

The long-running study of free-ranging African elephants in Amboseli National Park, Kenya, has enabled more ecologically valid tests of perception and memory to be conducted in recent years. Karen McComb and her colleagues have explored the apparently close-knit relationships of adult females, using experiments that rely on elephants' auditory abilities. Using playbacks of long-distance 'contact rumbles', the researchers showed that female elephants distinguish calls made by family and bond group members from

those made by unrelated individuals. In this way, they calculated that adult females must be familiar with the vocalizations of at least 100 other females, suggesting that elephants can use their excellent auditory discrimination, plus an extensive memory of other females' calls, to remain in contact with a wide social network even when apparently dispersed.

In the same population of elephants, we have subsequently used field experiments to ask other questions about elephant cognition. By experimentally presenting garments that gave either visual or olfactory cues to their wearers, we showed that elephants use subtle cues to discriminate between two different human ethnic groups that pose different levels of danger to them. This means that, in effect, elephants categorize a single species of potential predator into subclasses, suggesting a very human-like memory organization. In another experiment we investigated what elephants can learn from the scent of another's urine, beyond its oestrus or musth state. We moved urine deposits from known individuals to new locations where they were likely to be discovered. Elephants' reactions showed that they were able to recognise family members by scent, as they showed higher interest in the urine of absent family members than of strangers. Moreover, they were able to distinguish specific individuals within the family from urine scent alone, and reacted differently to scent from individuals in their current travel party according to how likely they were to have been at that place. It seems that elephants monitor and remember the locations of their kin by detecting cues in urine deposits, and use this information continually to update their knowledge of where these individuals are positioned in moving groups.

Researchers have made only a small start in investigating elephant cognition, but already impressive skills have been shown, intriguingly different to those of other taxa with advanced abilities, like corvids and apes. Developing our understanding of elephant perceptual and memory abilities should ultimately allow us to design appropriate and ecologically valid tests of more elusive cognitive skills such as social attribution, causal understanding and forward planning.

So, do elephants never forget? Well, Rensch re-tested the juvenile female on some of the visual discrimination pairs she had learnt after a one-year delay, and she achieved an accuracy rate of 73–100%. There is some suggestion that captive individuals can recognize the urine of their mothers, 2 to 27 years after separation. In field experiments, older matriarchs performed better than younger ones at discriminating between the contact calls of familiar and unfamiliar individuals. But permanence of memory may be over-valued: in dealing with a complex, fluid world it is equally important to forget out-of-date information, updating a mental model of reality that can allow efficient responses to changed circumstances. The recent findings that elephants hold in memory an expectation of where their family members are as they travel, and update this memory with new information from indirect cues, may hint at more important ways in which an elephant's cognition underpins its natural life.

Where can I find out more?
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