

Declaration of Karen McComb

I, Karen McComb, declare as follows:

Introduction and Qualifications

1. My name is Karen McComb. I was awarded my Bachelors of Science with 1st Class Honours in Zoology from the University of Edinburgh in 1984. I earned my PhD from the University of Cambridge from 1984-1988, under the supervision of Professor T.H. Clutton-Brock, for a thesis entitled “Roaring and reproduction in red deer (*Cervus elaphus*)”. I completed a Postdoctoral Research Fellowship from 1989-1990 at the University of Minnesota, and then was a Research Fellow at Newnham College, at the University of Cambridge, from 1990-1993. I have worked at the University of Sussex since 1993, where I have been a Lecturer/Senior Lecturer from 1993-2004, a Reader from 2004-2013, and a Professor (of Animal Behaviour and Cognition) since 2013. I work in the School of Psychology at University of Sussex in Brighton, United Kingdom and reside in East Sussex.

2. I submit this Declaration in support of the Nonhuman Rights Project, Inc.’s petition for a writ of habeas corpus regarding the captive elephants at the Pittsburgh Zoo & Aquarium. I am a nonparty to this proceeding.

3. My current research is directed towards the investigation of emotional awareness as a basis for social success in the domestic horse. Although the essential role that emotional intelligence plays in human social behaviour is well recognized, we collectively still know very little of how individual variation in the ability to identify and respond appropriately to emotional signals influences social integration and success in animal groups. My research team is designing a broad array of naturalistic tests to quantitatively assess individual differences in emotional abilities, which we will examine in relation to measures of social success. In addition to the scientific significance of my research, there are considerable implications for animal welfare, and my group’s findings will allow us to more accurately understand the emotional capacities and requirements of individual horses within the domestic environment.

4. My research career has centered on using naturalistic experiments to probe and understand vocal communication and cognitive abilities in a wide range of mammals, including African elephants, horses, lions, red deer, and domestic cats and dogs.

Through the design and implementation of novel experiments which provide a window into abilities that animals use to make every-day decisions in their native environments, I have made breakthroughs that have significantly advanced our fundamental understanding of animal minds and social behaviour. My research has contributed significantly towards advances in: (1) Understanding social cognition and conceptual knowledge. My work focusing on social cognition in domestic horses has led to fundamental insights about how individuals within a group recognize each other, and my research team provided the first systematic demonstration of cross-modal individual recognition of conspecifics in a nonhuman. This finding demonstrates how multi-sensory representations can underlie animals' knowledge of each other, and fundamentally advances our understanding of how conceptual knowledge may have arisen evolutionarily; (2) Understanding social intelligence in wild mammals. My original work evaluating social cognition in African lions laid the groundwork for understanding how the potential costs of fighting with larger groups over limited resources may have provided a selective evolutionary pressure for numerical assessment skills in social species. This potential biological basis for the evolution of mathematical abilities has led broadly to new research on other species based largely on my experimental paradigm. In my research with African elephants, I have demonstrated that the collective experiences and knowledge found in the oldest members of a group can influence the social knowledge of the group as a whole, which has provided fundamental insights into how cognitively advanced social mammals acquire and store information in the wild. Subsequent work provided the first empirical evidence that groups benefit from older leaders specifically due to the group's collectively enhanced ability to respond to predators based on the knowledge of the oldest individual, allowing for the development of intriguing hypotheses for the evolutionary benefits of longevity. More recent work demonstrated for the first time that elephants' knowledge of human predators is much more sophisticated than previously recognized, by showing that elephants can determine ethnicity, gender, and age of humans from acoustic cues in human voices; and (3) Understanding sexual signals and the origins of language. My original research on the function of roaring in red deer provided the foundation for a novel, systematic experimental approach to studying the role of vocal signaling in sexual selection in mammals. In a series of influential papers, my research group showed that formants, key parameters in human speech, play a critical role in the communication of non-human mammals. In addition,

I have used a comparative approach to demonstrate that increases in non-human primate group size and extent of social bonding are related to the development of larger vocal repertoires, providing new information for the scientific investigation of language evolution.

5. In addition to the scientific implications of my research, it has also had impacts for animal conservation and welfare. Specifically, by demonstrating the crucial role that the oldest individuals play in elephant social groups, we have shown how entire populations of cognitively advanced social mammals can be severely disrupted by the removal of even a few critical individuals. Our recent work has also shown that the effects of social disruption can have severe, long-term effects on the cognitive abilities of elephants. This research has significant implications for the conservation and welfare of both wild and captive animals, not just elephants but also other long-lived, large-brained social mammals such as whales and dolphins. Due to this work, I was invited to contribute to the recommendations of the recent Convention on the Conservation of Migratory Species of Wild Animals (CMS).

6. Along with my colleague David Reby, I developed a very successful research group in Mammal Vocal Communication and Cognition (<http://www.lifesci.sussex.ac.uk/cmvcv/Home.html>) at the University of Sussex. This research group has attracted and supported many talented postgraduates and independent research fellows. Currently, I have 3 PhD students and a postdoc, working with me on projects ranging from emotional awareness in domestic animals to investigating cultural differences between elephant populations.

7. I have been awarded significant extramural grants to fund my research throughout my career from a number of foundations and organizations, including: (1) Levehulme Trust Research Grants, in both 2009 and 2014; (2) a National Geographic grant in 2006; (3) a Waltham Foundation grant in 2002; (4) an EU Marie Curie grant in 2000; (5) a BBSRC research grant in 1996; (6) Tusk Trust grants, in 1994, 1995, and 1996; (7) a Nuffield Foundation grant in 1994; (8) a Royal Society Research grant in 1994; (9) and an NERC small project grant in 1993. Additionally, I have received a number of Royal Society Conference grants throughout my career, most recently in 2005 and 2009.

8. Over the course of my career, I have received several awards and honors related to my research, including; (1) the 2008 PNAS Cozzarelli Prize for outstanding originality

and scientific excellence for the article “Cross-modal individual recognition in domestic horses (*Equus caballus*)” with L. Proops and D. Reby; (2) the prize for best talk by a research student at the Association for the Study of Animal Behaviour Spring Conference in 1987 during my PhD at Cambridge; (3) The University of Edinburgh Class Medal & Ashworth Prize in Zoology in 1984; (4) the Class Medal and William Turner Award in Zoology in 1983; (5) the Moira Lyndsay Stewart Award in Zoology in 1982; and (6) the Jack Roberts Memorial Prize in Botany in 1982.

9. I have served with a number of professional organizations throughout my career, including: (1) as an appointed Reviewer for European Research Council grants in 2012; (2) as an academic Editor for *PLoS One* since 2007; (3) as part of the Editorial Board for *Bioacoustics* since 1997; (4) as a consulting Editor for *Animal Behaviour* from 1996-1998; (5) as a Council Member for the Association for the Study of Animal Behaviour (ASAB) from 1993-1997; (6) as a liaison representative for the ASAB with the Institute of Biology from 1995-1997; and (7) as a manuscript reviewer for a number of premier scientific publications, including *Science*, *Nature*, *Current Biology*, *Proceedings of the Royal Society B*, *Proceedings for the National Academy of Sciences*, *PLoS One*, and *Animal Behaviour*, as well as other journals.

10. I have organized a number of conferences during my career, including: (1) a symposium on “Mammal Vocal Communication: Insights into cognitive abilities and the origins of language” at the International Ethological Congress in Budapest, in August 2005 (with David Reby); and (2) the 1999 Association for the Study of Animal Behaviour Conference on “Evolution of Mind” in London, attended by more than 200 people.

11. I have given numerous professional academic lectures throughout my career. Some of these include: (1) an invited lecture to the Cetacean Culture Workshop in 2014, organized jointly by the Convention on the Conservation of Migratory Species of Wild Animals (CMS) and Whale and Dolphin Conservation (WDC); (2) a Plenary talk at the 2012 Association for the Study of Animal Behaviour meeting on “Cognition in the Wild”; (3) an invited lecture at the 2011 international workshop on communication and social cognition at the Institute of Evolutionary Biology and Environmental Studies at the University of Zurich; (4) an invited lecture at the 2010 International workshop on referential communication at the Wissenschaftskolleg zu Berlin, Institute for Advanced Study in Berlin; (5) a Plenary lecture at the 2010 Nordic meeting of the International

Society for Applied Ethology, in Kuopio, Finland; (6) an invited lecture at the 2009 International Ethological Congress in Rennes, France; (7) an invited lecture in 2009 at the Ecology and Evolutionary Biology Department at the University of Princeton; (8) an invited lecture at the Novartis day at the 2006 Royal Society Discussion meeting on Social Intelligence, in London; (9) an invited lecture (and conference organizer) at the 2005 International Ethological Congress Symposium on “Mammal Vocal Communication: insights into cognitive abilities and the origin of language” in Budapest; (10) a Keynote lecture at the 2003 British Association for the Advancement of Science Symposium on “Where do numbers come from?” at Salford, England; (11) a Plenary lecture at the 2002 Association for the Study of Animal Behaviour conference on “Information Gathering”; (12) an invited lecture at the 2001 symposium on Alternative Approaches to Studying Social Cognition at the International Ethological Congress in Tübingen, Germany; (13) an invited lecture at a 2000 International workshop on animal signaling, Talkbank, at the University of Philadelphia; and (14) a Plenary lecture at the 1999 Association for the Study of Animal Behaviour Conference on “Communication and Social Behaviour” in Lisbon.

12. In addition to academic lectures, I have given a number of public lectures over the course of my career, including: (1) as an invited panel member/speaker at the 2014 Festival of Sound, organized by Magdalene College at the University of Cambridge; (2) as an invited member/speaker at the 2012 Gulbenkian Foundation Supersonix Festival, organized on behalf of the Exhibition Road Cultural Group to focus on the art and science of sound and music-making; (3) a public lecture on “Animal Communication” in the “Learning about Animals” series in London in 2007; (4) a lecture to the 2006 Pet Care Trust Conference in Edinburgh; (5) a Press conference for the launch of my *Science* paper, organized by the American Academy for the Advancement of Science, at the London Zoo in 2001; (6) a lecture at the British Library National Sound Archive in 2000; and (7) a joint lecture with Cynthia Moss at a Royal Geographical Society lecture, attended by more than 600 members of the public, in 1996.

13. I have published over 50 peer-reviewed scientific articles over my career. These articles have been published in many of the world’s premier scientific journals, including: *Nature*, *Science*, *PNAS*, *Frontiers in Zoology*, *Animal Behaviour*, *Current Biology*, *Biology Letters*, *PLoS ONE*, *Proceedings of the Royal Society B*, *Ethology*,

Animal Cognition, *Journal of the Acoustical Society of America*, *Journal of Comparative Psychology*, *Advances in the Study of Behaviour*, *American Journal of Primatology*, *Behavioural Ecology*, and *Trends in Ecology & Evolution*. Six of these publications have been featured as cover articles in the journals *Science*, *Nature*, *PNAS*, *Proceedings of the Royal Society B*, and *Biology Letters*. Specific topics of these publications have included: Animals remember previous facial expressions that specific humans have exhibited; Elephants can determine ethnicity, gender, and age from acoustic cues in human voices; The Equine Facial Action Coding System; The eyes and ears are visual indicators of attention in domestic horses; Cross-modal discrimination of human gender by domestic dogs; Effects of social disruption in elephants persist decades after culling; The responses of young domestic horses (*Equus caballus*) to human-given cues; Leadership in elephants: the adaptive value of age; African wild dogs as a fugitive species: playback experiments investigate how wild dogs respond to their major competitors; Cross-modal perception of body size in domestic dogs; the use of human-given cues by domestic horses; Acoustic bases of motivational misattributions; Oestrus red deer hinds prefer male roars with higher fundamental frequencies; Size communication in domestic dog (*Canis familiaris*) growls; Manipulation by domestic cats: the cry embedded within the purr; Context-related variation in the vocal growling behaviour of the domestic dog; Cross-modal individual recognition in domestic horses; Human listeners attend to size information in domestic dog growls; Experimental investigation of referential looking in free-ranging barbary macaques; Female perception of size-related formant shifts in red deer (*Cervus elaphus*); African elephants show high levels of interest in the skulls and ivory of their own species; Co-evolution of vocal communication and sociality in primates; Long-distance communication of cues to social identity in African elephants; Vocal communication and reproduction in deer; Information content of female copulation calls in yellow baboons; Matriarchs act as repositories of social knowledge in African elephants; Elephant hunting and conservation; Roaring and social communication in African lions; Unusually extensive networks of vocal recognition in African elephants; Perception of female reproductive state from vocal cues; Female grouping as a defense against infanticide by males; Behavioural deception; Roaring and numerical assessment in contests between groups of female lions; Female lions can identify potentially infanticidal males from their roars; Roaring and oestrus; Roaring by red deer stags advances date of oestrus in hinds; and Are talkers the only thinkers?.

14. My scientific work has also been published as chapters in several books and edited volumes, including (1) *The Social Dog* (2014, editors J. Kaminski and S. Marshall-Pescini, Elsevier); (2) *The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal* (2011, University of Chicago Press); (3) *New Encyclopedia of Neuroscience* (2008, editor L.R. Squire, Academic Press); (4) *The Barbary macaque: biology, management, and conservation* (2006, editors J.K. Hodges and J. Cortes, Nottingham University Press); (5) *Animal Communication Networks* (2005, editor P.K. McGregor, Cambridge University Press); (6) *Studying Elephants* (1996, African Wildlife Foundation Technical Handbook series); and (7) *Playback and Studies of Animal Communication* (1992, editor P.K. McGregor, Plenum Publishing Corporation).

15. My work has garnered significant media coverage over the course of career. I have made appearances on British, American, Australian, Canadian, and German TV and radio stations (including BBC TV news, Discovery Channel, Radio 4 Today programme, and BBC Science in Action) and my work has been featured in articles in major British, European, and American newspapers (including The Guardian, Times, Liberation, National Geographic magazine, and New Scientist).

16. In April 2001, *Science* organized a press conference in London for the launch of my paper, which was featured as their cover story. Later cover stories in *Biology Letters* (2006), *PNAS* (2009), and *Proceedings of the Royal Society B* (2011) also generated significant media attention, as did my *Current Biology* paper in 2009 which featured as the most popular story on the BBC website, as well as the top Science and Entertainment story.

17. Several of my recent papers, including *Current Biology* (2018), *PNAS* (2014) and *Frontiers in Zoology* (2013) received unusually extensive world-wide media coverage. This included interviews on the Radio 4 Today Programme, ITV News at Ten, BBC World TV News, Newsround, BBC World Service, and Science in Action, as well as coverage in BBC Breakfast, BBC Radio 2, 3, and 4 news reports, Time magazine, The Economist, *Nature*, *Science*, National Geographic, and by more than 200 other news outlets in the UK and around the world.

18. My elephant research was covered in BBC's "Inside the Animal Mind" in February 2014, and my horse research was filmed for the BBC series "Talk to the Animals" which aired in July 2014. Both programmes were shown in prime-time slots and were

very well received by the public. My recent research on emotional awareness in horses also featured in the award-winning CBC documentary “Equus: story of the horse”.

19. I have done regular consultancies for the BBC and other companies making wildlife documentaries on animal communication. Most recently, I was a scientific consultant for the popular two-part BBC documentary “Talk to the Animals” (2014). I have also provided sound recordings for wildlife documentaries by the BBC and Windfall films, and have a sound recording credit (with Martyn Colbeck) on the BBC’s “Echo of the elephants: the next generation” (1995).

20. My work has been featured in a number of textbooks and popular books, including: (1) John Alcock’s and Lee Dugatkin’s major textbooks on Animal Behaviour; (2) new edition of the Krebs & Davies *An Introduction to Behavioural Ecology*; (3) new edition of Bradbury and Vehrencamp’s *Principles of Animal Communication*; (4) new edition of Shettleworth’s *Cognition, Evolution, and Behavior*; (5) Brian Butterworth’s *The Mathematical Brain*; (6) Tim Clutton-Brock’s *Mammal Societies*; and (7) as a chapter in the best-selling *Animal Wise* by Virginia Morell.

21. I provided photographic material to The Field Museum, in Chicago, for an exhibition on Mammoths and Mastodons, Titans of the Ice Age. This exhibit has been touring internationally.

22. My Curriculum Vitae fully sets forth my educational background and experience and is annexed hereto as “Exhibit A”.

Basis for opinions

23. The opinions I state in this Declaration are based on my professional knowledge, education, training, and years of experience observing and studying elephants and other social mammals, as well as my knowledge of peer-reviewed literature about elephant behaviour and intelligence published in the world’s most respected journals, periodicals and books that are generally accepted as authoritative in the field, and many of which were written by myself or colleagues whom I have known for several years and with whose research and field work I am personally familiar. A full reference list of peer-reviewed literature cited herein is annexed hereto as “Exhibit B”.

Opinions

Premise

24. Autonomy in humans is defined as self-determined behaviour that is based on freedom of choice. As a psychological concept it implies that the individual is directing their behaviour based on some non-observable, internal cognitive process, rather than simply responding reflexively. Although we cannot directly observe these internal processes in other people, we can explore and investigate them by observing, recording and analysing behaviour. For non-human animals, observing similar behaviour and recording evidence of shared cognitive capacities should, parsimoniously, lead to similar conclusions about autonomy.

25. I shall indicate which species, African (*Loxodonta Africana*) or Asian (*Elephas maximus*), specific observations relate to. If the general term “elephants” is used with no specific delineation, it can be assumed the comment relates to both species.

Brain And Development

26. Elephants are large-brained, with the biggest absolute brain size of any land animal (Cozzi et al 2001; Shoshani et al 2006). Even relative to their body sizes, elephant brains are large. Encephalization quotients (EQ) are a standardised measure of brain size relative to body size, and illustrate by how much a species’ brain size deviates from that expected for its body size. An EQ of one means the brain is exactly the size expected for that body, and values greater than one indicate a larger brain than expected (Jerison 1973). Elephants have an EQ of between 1.3 and 2.3 (varying between sex and African and Asian species). This means an elephant’s brain can be up to two and a half times larger than is expected for an animal of its size; this EQ is similar to that of the great apes, with whom elephants have not shared a common ancestor for almost 100 million years (Eisenberg 1981, Jerison 1973). Given how metabolically costly brain tissue is, the large brains of elephants would be expected to confer significant advantages; otherwise their size would be reduced. Presumably this advantage is allowing greater cognitive capacities and behavioural flexibility (Bates et al 2008a).

27. Generally, mammals are born with brains weighing up to 90% of the adult weight. This figure drops to about 50% for chimpanzees. Human baby brains weigh only about 27% of the adult brain weight (Dekaban & Sadowsky 1978). This long period of brain development over many years (termed ‘developmental delay’) is a key feature of human brain evolution and is thought to play a role in the emergence of our complex cognitive abilities, such as self-awareness, creativity, forward planning, decision making and

social interaction (Bjorkland 1997). Delayed development provides a longer period in which the brain may be shaped by experience and learning (Fuster 2002). Elephant brains at birth weigh only about 35% of their adult weight (Eltringham 1982), and elephants show a similarly protracted period of growth, development and learning (Lee 1986). This similar developmental delay in the elephant brain is therefore likely associated with the emergence of similarly complex cognitive abilities.

28. Despite nearly 100 million years of separate evolution (Hedges 2001), elephants share certain characteristics of our large brains, namely deep and complex folding of the cerebral cortex, large parietal and temporal lobes, and a large cerebellum (Cozzi et al 2001). The temporal and parietal lobes of the cerebral cortex manage communication, perception, and recognition and comprehension of physical actions, while the cerebellum is involved in planning, empathy, and predicting and understanding the actions of others (Barton 2012). Thus, the physical similarities between human and elephant brains occur in areas that are relevant to capacities necessary for autonomy and self-awareness.

29. Elephant brains hold three times more neurons than do human brains, with 97% of their found neurons in the cerebellum and 5.6 billion neurons in the cerebral cortex (Herculano-Houzel et al 2014); This figure for cortical neurons is lower than previous estimates, which suggested 11 billion cortical neurons for elephants and 11.5 billion for humans (Roth & Dicke 2005).

30. Elephant pyramidal neurons have a large dendritic tree, i.e. a large number of connections with other neurons for receiving and sending signals (Cozzi et al 2001; Jacobs et al 2011; Maseko et al 2012). The degree of complexity of pyramidal neurons is linked to cognitive ability, with more (and more complex) connections between pyramidal neurons being associated with increased cognitive capabilities (Elston 2003).

31. As described below, research demonstrates that along with these common brain and life-history characteristics, there is evidence that elephants may share many behavioural and intellectual capacities with humans, including: self-awareness, empathy, awareness of death, intentional communication, learning, memory, and categorisation abilities. Many of these capacities have previously been considered – erroneously – to be uniquely human, and each is fundamental to and characteristic of autonomy and self-determination.

Awareness Of Self And Others

32. An Asian elephant has been shown to exhibit Mirror Self Recognition (MSR) using Gallup's classic 'mark test' (Gallup 1970; Plotnik et al 2006). MSR is the ability to recognise a reflection in the mirror as oneself, and the mark test involves surreptitiously placing a coloured mark on an individual's forehead that it could not see or be aware of without the aid of a mirror. If the individual uses the mirror to investigate the mark, it is logical to assume that the individual recognises the reflection as itself. (See video [here](#)). Almost all animal species tested on this task fail: they do not recognise the image in the mirror as being a reflection of themselves. Indeed, the only other mammals beyond humans who have successfully passed the mark test and exhibit MSR are the great apes (chimpanzees, bonobos, gorillas, and orangutans) and bottlenose dolphins (Parker and Mitchell 1994, Reiss and Marino 2001). MSR is significant because it is considered by many to be a key identifier of self-awareness. Self-awareness is intimately related to autobiographical memory in humans (Prebble et al 2013), and is central to autonomy and being able to direct one's own behaviour to achieve personal goals and desires. By demonstrating that they can recognize themselves in a mirror, elephants appear to be holding a mental representation of themselves from another perspective, and thus be aware that they are a separate entity from others (Bates and Byrne 2014).

33. Related to possessing a sense of self is an understanding of death. Observing reactions to dead family or group members suggests such an awareness of death in only two animal genera beyond humans; chimpanzees and elephants (Anderson et al 2010, Douglas-Hamilton et al 2006). Having a mental representation of the self – a prerequisite for mirror-self recognition – probably also confers an ability to comprehend aspects of death. Wild African elephants have been shown experimentally to be more interested in the bones of dead elephants than the bones of other animals (McComb et al 2006) (See video [here](#)), and they have frequently been observed using their tusks, trunk or feet to attempt to lift sick, dying or dead individuals (Poole & Granli, 2011). Although they do not give up trying to lift or elicit movement from the body immediately, elephants appear to realise that once dead, the carcass cannot be helped anymore, and instead they engage in apparently "grief-stricken" behaviour, such as standing guard over the body, and protecting it from the approaches of predators (Poole & Granli, 2011). They also have been observed to cover the bodies of dead elephants

with dirt and vegetation (Moss 1992; Poole 1996). In the particular case of mothers who lose a calf, although they may remain with the calf's body for an extended period, they do not behave towards the body as they would a live calf. Indeed, the general demeanour of elephants who are attending to a dead elephant is one of grief, with slow movements and few vocalisations (Poole, pers. comm.). These behaviours are akin to human responses to the death of a close relative or friend, and illustrate that elephants appear to possess some understanding of life and the permanence of death (See photographs [here](#)).

34. The capacity for mentally representing the self as an individual entity has been linked to general empathic abilities (Gallup 1982), where empathy can be defined as identifying with and understanding another's experiences or feelings by relating personally to their situation. Empathy is an important component of human consciousness and autonomy, and is a cornerstone of normal social interaction. It goes beyond merely reading the emotional expressions of others. It requires modelling of the emotional states and desired goals that influence others' behaviour both in the past and future, and using this information to plan one's own actions; cognitive empathy is possible if one can adopt another's perspective, and attribute emotions to that other individual (Bates et al 2008b). Empathy is, therefore, a component of and reliant on 'Theory of Mind' - the ability to mentally represent and think about the knowledge, beliefs and emotional states of others, whilst recognising that these can be distinct from your own knowledge, beliefs and emotions (Premack and Woodruff 1978/ Frith and Frith 2005).

35. Elephants clearly and frequently display empathy in the form of protection, comfort, and consolation, as well as by actively helping those who are in difficulty, such as assisting injured individuals to stand and walk, or helping calves out of rivers or ditches with steep banks (Bates et al 2008b, Lee 1987) (See video [here](#)). Elephants have even been observed feeding those who are not able to use their own trunks to eat (see Poole and Granli, 2011).

36. In an analysis of behavioural data collected from wild African elephants over a 40-year continuous field study, Bates and colleagues concluded that as well as possessing their own intentions, elephants can diagnose animacy and goal directedness in others, understand the physical competence and emotional state of others, and attribute goals

and mental states (intentions) to others (Bates et al 2008b), as evidenced in the examples below:

'IB family is crossing river. Infant struggles to climb out of bank after its mother. An adult female [not the mother] is standing next to calf and moves closer as the infant struggles. Female does not push calf out with its trunk, but digs her tusks into the mud behind the calf's front right leg which acts to provide some anchorage for the calf, who then scrambles up and out and rejoins mother.' (See video [here](#))

'At 11.10ish Ella gives a 'lets go' rumble as she moves further down the swamp . . . At 11.19 Ella goes into the swamp. The entire group is in the swamp except Elspeth and her calf [<1 year] and Eudora [Elspeth's mother]. At 11.25 Eudora appears to 'lead' Elspeth and the calf to a good place to enter the swamp — the only place where there is no mud.'

Examples such as these demonstrate that the acting elephant (the adult female in the first example, and Eudora in the second) was able to understand the intentions of the other (the calf in the first case, and Elspeth in the second) – i.e. to either climb out of or into the water – and they could adjust their own behaviour in order to counteract the problem being faced by the other. Whilst humans may act in this helpful manner on a daily basis, such interactions have been recorded for very few non-human animals (Bates et al 2008b).

37. Experimental evidence from captive African elephants further demonstrates that elephants have the potential to attribute intentions to others, as they follow and understand human pointing gestures. The elephants understood that the human experimenter was pointing in order to communicate information to them about the location of a hidden object (Smet and Byrne 2013) (See video [here](#)). Attributing intentions and understanding another's reference point is central to empathy and theory of mind.

38. Evidence of 'natural pedagogy' is rare among non-human animals, with only a few potential examples of true teaching (whereby the teacher takes into account the knowledge states of the learner as they pass on relevant information) recorded anecdotally in chimpanzees (Boesch 1991) and killer whales (Guinet and Bouvier

1995)¹. Teaching is therefore still widely considered to be unique to humans (Csibra and Gergely 2009). Bates & Byrne's analysis of simulated oestrus behaviours in African elephants – whereby a non-cycling, sexually experienced older female will simulate the visual signals of being sexually receptive, even though she is not ready to mate or breed again – shows that these knowledgeable females can adopt false oestrus behaviours in order to demonstrate to naïve young females how to attract and respond appropriately to suitable males. The experienced females may be taking the youngster's lack of knowledge into account and actively showing them what to do; a possible example of true teaching as it is defined in humans. Whilst this possibility requires further investigation, this evidence, coupled with the data showing that they understand the ostensive cues in human pointing, suggests that elephants do share some executive skills with humans, namely understanding the intentions and knowledge states (minds) of others.

39. Further related to empathy, the occurrence of coalitions and cooperation have been documented in wild African elephants, particularly to defend family members or close allies from (potential) attacks by outsiders, such as when a family group tries to 'kidnap' a calf from an unrelated family (Lee 1987, Moss and Poole 1983). These behaviours are based on one elephant understanding the emotions and goals of the coalition partner (Bates et al 2008b).

40. Cooperation is also evident in experimental tests with captive Asian elephants, whereby elephants demonstrated they can work together in pairs to obtain a reward, and understood that it was pointless to attempt the task if their partner was not present or could not access the equipment (Plotnik et al. 2011) (See video [here](#)). Problem-solving and working together to achieve a collectively desired outcome involve mentally representing both a goal and the sequence of behaviours that is required to achieve that goal; it is based on (at the very least) short-term action planning.

41. Wild elephants have frequently been observed engaging in cooperative problem solving, for example when retrieving calves that have been kidnapped by other groups, or when helping calves out of steep, muddy river banks (Bates et al 2008b, Moss, 2011) These behaviours demonstrate the purposeful and well-coordinated social system of

¹ Functional teaching has been experimentally demonstrated in various animal species including ants, babblers, meerkats, cheetahs and some primates, but this is not the same as deliberate pedagogy, as it does not rely on representing the knowledge states of the learners.

elephants, and show that elephants can hold particular aims in mind and work together to achieve those goals. Such intentional, goal-directed action forms the foundation of independent agency, self-determination, and autonomy.

42. Elephants also show innovative problem solving in experimental tests of insight (Foerder et al 2011), where insight can be described as the ‘a-ha’ moment when a solution to a problem ‘suddenly’ becomes clear. (In cognitive psychology terms, insight is the ability to inspect and manipulate a mental representation of something, even when you can’t physically perceive or touch the something at the time. Or more simply, insight is thinking and using only thoughts to solve problems (*see* Richard Byrne, *Evolving Insight*, Oxford Online Press, 2016²). A juvenile male Asian elephant demonstrated just such a spontaneous action by moving a plastic cube and standing on it to obtain previously out-of-reach food. After solving this problem once, he showed flexibility and generalization of the technique to other, similar problems by using the same cube in different situations, or different objects in place of the cube when it was not available. (See video [here](#)). This experiment again demonstrates that elephants can choose the appropriate action and incorporate it into a sequence of behaviour in order to achieve a goal, which they kept in mind throughout the process.

43. Further experiments also demonstrate Asian elephants’ ability to understand goal-directed behaviour. When presented with food that was out of reach, but with some bits resting on a tray that could be pulled within reach, the elephants learned to pull only those trays that were baited with food (Irie-Sugimoto et al 2008). Success in this kind of ‘means-end’ task is a demonstration of causal knowledge, which requires understanding not just that two events are associated with each other but also that there is some mediating force that connects and affects the two which may be used to predict and control events. Moreover, understanding causation and inferring object relations may be related to understanding psychological causation, i.e., the appreciation that others are animate beings that generate their own behaviour and have mental states (e.g., intentions).

Communication and social learning

² Available at <https://global.oup.com/academic/product/evolving-insight-9780198757078?cc=us&lang=en&>.

44. Speech is a voluntary behaviour in humans, whereby a person can choose whether to utter words and thus communicate with another. Therefore speech and language are reflections of autonomous thinking and intentional behaviour. Elephants also use their vocalisations to share knowledge and information with others, apparently intentionally (Poole 2011). Male elephants primarily communicate about their sexual status, rank and identity, whereas females and dependents call to co-ordinate and reinforce their social units. Call types can generally be separated into calls produced primarily by the larynx (such as rumbles) or trunk calls (such as trumpets), with different calls in each category being used in different contexts (Poole 2011; Poole and Granli 2004; Soltis et al 2005; Wood et al 2005). Field experiments have shown that African elephants distinguish between different call types (for example, contact calls – rumbles that travel long distances to maintain associations between elephants that could be several kilometres apart, or oestrus rumbles – that occur after a female has copulated) and these different call types elicit different responses in the listeners. Elephant vocalisations are not simply reflexive, they have distinct meanings to listeners and they are truly communicative, similar to the volitional use of language in humans (Leighty et al 2008; Poole 1999; Poole 2011).

45. Furthermore, elephants have been shown to vocally imitate the sounds they hear around them, from the engines of passing trucks to the commands of human zookeepers (Poole et al 2005, Stoeger et al 2012). Imitating another's behaviour is demonstrative of a sense of self, as it is necessary to understand how one's own behaviour relates to the behaviour of others.

46. Elephants display a wide variety of gestures, signals and postures, used to communicate information to the audience (Poole and Granli gestures chapter 2011). Such signals are adopted in many different contexts, such as aggressive, sexual or socially integrative situations, and each signal is well defined and results in predictable responses from the audience. That is, each signal or gesture has a specific meaning both to the actor and recipient. Elephants' use of gestures demonstrates that they communicate intentionally and purposefully to share information with others and/or alter the others' behaviour to fit their own desires.

47. Experimental evidence demonstrates that African elephants recognize the importance of visual attentiveness of the intended recipient (in this case, human experimenters) of gestural communication (Smet & Byrne 2014), further supporting

the suggestion that elephants' gestural communication is intentional and purposeful. Furthermore, the ability to understand the visual attentiveness and perspective of others is crucial for empathy and mental-state understanding.

Memory And Categorisation

48. Elephants have both extensive and long-lasting memories, just as the folk stories and adages encourage us to believe. McComb et al. (2000), using experimental playback of long-distance contact calls in Amboseli National Park, Kenya, showed that African elephants remember and differentiate the voices of at least 100 other elephants. Each adult female elephant tested was familiar with the contact-call vocalizations of individuals from an average of 14 families in the population. When the calls were from the test elephants' own family, they contact-called in response and approached the location of the loudspeaker and when they were from another non-related but familiar family — that is, one that had previously been shown to have a high association index with the test group — they listened but remained relaxed. However, when a test group heard unfamiliar contact calls (from groups with a low association index with the test group), they bunched together and retreated from the area.

49. McComb et al. (2001) went on to show that this social knowledge accumulates with age, with older females having the best knowledge of the contact calls of other family groups. McComb et al. (2011) also showed that older females are better leaders, with more appropriate decision-making in response to potential threats (in this case, in the form of hearing lion roars). Younger matriarchs were less skilled at pinpointing roars from male lions, the most dangerous predators because they can subdue a young elephant even when hunting alone. Sensitivity to picking out the roars of male lions increased with increasing matriarch age, with the oldest, most experienced females showing the strongest response to this danger. These experimental studies show that elephants continue to learn and remember information about their environments throughout their lives, and this accrual of knowledge allows them to make better decisions and better lead their families as they grow older.

50. Further demonstration of elephants' long-term memory comes from data on their movement patterns. African elephants are known to move over very large distances in their search for food and water. Leggett (2006) used GPS collars to track the movements of elephants living in the Namib Desert. He recorded one group traveling

over 600 km in five months, and Viljoen (1989) showed that elephants in the same region visited water holes approximately every four days, even though some of them were more than 60km apart. Elephants inhabiting the deserts of both Namibia and Mali have been described traveling hundreds of kilometers to arrive at remote water sources shortly after the onset of a period of rainfall (Blake et al. 2003; Viljoen 1989), sometimes along routes that researchers believe have not been used for many years. These remarkable feats suggest exceptional cognitive mapping skills, reliant on the long-term memories of older individuals who traveled that path sometimes decades earlier. Indeed it has been confirmed that family groups with older matriarchs are better able to survive periods of drought. The older matriarchs lead their families over larger areas during droughts than those with younger matriarchs, again apparently drawing on their accrued knowledge (this time about the locations of permanent, drought-resistant sources of food and water) to better lead and protect their families (Foley, Pettorelli, and Foley 2008).

51. Very importantly, it has recently been shown that long-term memories, and the decision-making mechanisms that rely on this knowledge, are severely disrupted in elephants who have experienced trauma or extreme disruption due to ‘management’ practices initiated by humans. Shannon et al (2013) demonstrated that elephants in South Africa who had experienced trauma decades earlier showed significantly reduced social knowledge. During archaic culling practices, these elephants were forcibly separated from family members and subsequently translocated to new locations (practices which have also accompanied taking elephants into captivity). Two decades later, they still showed impoverished social knowledge and skills and impaired decision-making abilities, compared with an undisturbed population in Kenya. Disrupting elephants’ natural way of life can very negatively impact their knowledge and decision-making abilities.

52. Elephants demonstrate advanced “working memory” skills. Working memory is the ability to temporarily store, recall, manipulate and coordinate items from memory. Working memory directs attention to relevant information, and results in reasoning, planning, and coordination and execution of cognitive processes through use of a “central executive” (Baddeley 2000). Adult human working memory is generally thought to have a capacity of around seven items. In other words, we can keep about seven different items or pieces of information in mind at the same time (Miller 1956).

Bates and colleagues conducted experiments with wild elephants in Amboseli National Park, Kenya, manipulating the location of fresh urine samples from related or unrelated elephants. The elephants' responses to detecting urine from known individuals in surprising locations showed that they are able to continually track the locations of at least 17 family members in relation to themselves, as either absent, present in front of self, or present behind self (Bates et al. 2008a). This remarkable ability to hold in mind and regularly update information about the locations and movements of a large number of family members is best explained by predicting that elephants possess an unusually large working memory capacity, apparently much larger than that of humans.

53. Elephants show sophisticated categorisation of their environment, with skills on a par with those of humans. Bates and co-authors experimentally presented the elephants of Amboseli National Park, Kenya, with garments that gave olfactory or visual information about their human wearers — either Maasai moran (male warriors who traditionally attack and spear elephants on occasion as part of their rite of passage), or Kamba men (who are agriculturalists and traditionally pose little threat to elephants). In the first experiment, the only thing that differed between the cloths was the smell, derived from the ethnicity and/or lifestyle of the wearers. The elephants were significantly more likely to run away when they sniffed cloths worn by Maasai than those worn by Kamba men or no one at all (See video [here](#)). In a second experiment, the researchers presented the elephants with two cloths that had not been worn by anyone, but here one was white (a neutral stimulus) and the other was red — the color that is ritually worn by Maasai moran. With access only to these visual cues, the elephants showed significantly greater reaction to red garments than white, often including signs of aggression. Bates et al. concluded that elephants are able to categorize a single species (humans) into sub-classes (i.e. “dangerous” or “low risk”) based on either olfactory or visual cues alone (Bates et al. 2007). McComb et al. went on to show that the same elephants can also distinguish between human groups based on just their voices. The elephants reacted differently (and appropriately) depending on whether they heard Maasai or Kamba men speaking, and also whether they heard male or female Maasai (where female Maasai pose no threat as they are not involved in spearing events), and adult Maasai men or young Maasai boys (McComb et al. 2014). Scent, sounds, and visual signs associated specifically with Maasai men are categorized as “dangerous,” while neutral signals are attended to but categorized as “low risk.”

These sophisticated, multi-modal categorization skills may be exceptional among non-human animals. The above experiments also demonstrate the acute sensitivity that elephants have to the human world, monitoring our behavior and learning to recognize situations where humans might cause them harm.

Summary

54. As will be evident from this Declaration, both African and Asian elephants have been shown to demonstrate highly advanced cognitive abilities and levels of emotional awareness, sharing many key traits with humans. Based on the evidence presented, it seems clear that they should be treated as autonomous beings who direct their behaviour based on complex internal cognitive processes, rather than simply responding reflexively.

55. Scientific knowledge about elephant intelligence has been increasing rapidly in recent decades: what we currently know is only a tiny fraction of what elephant brains are likely to be capable of, with recent advances underlining just how sophisticated elephant behavior and cognition is likely to be.

I declare under penalty of perjury under the law of the Commonwealth of Pennsylvania that the foregoing is true and correct.

Signed on the 12th day of May,
at POLEGATE BN26 5RD, EAST SUSSEX
(date) 12th (month) 5 (year) 2025
(county or other location, and state) SUSSEX.

.....
(country) U.K.
(printed name) PROF. KAREN MCCOMB
(signature) [Handwritten Signature]

Prof. Karen McComb: Curriculum Vitae

School of Psychology
University of Sussex
Falmer, Brighton BN1 9QH

karenm@sussex.ac.uk
+ 44 (0)1273 678610

***Job title: Professor of
Animal Behaviour & Cognition***



SCIENTIFIC CAREER & QUALIFICATIONS

B.Sc., University of Edinburgh (1980-1984)

- 1st Class Honours in Zoology

Ph.D., University of Cambridge (1984-1988)

- Thesis title: Roaring and reproduction in red deer (*Cervus elaphus*).
Supervised by Prof. T.H. Clutton-Brock

Research Fellow, University of Minnesota (1989 - 90)

Research Fellow, Newnham College, University of Cambridge (1990 - 93)

Lecturer / Senior Lecturer, University of Sussex (1993 - 2004)

Reader, University of Sussex (2004 - 2013)

Professor, University of Sussex (2013 - present)

PRIZES & AWARDS

University & early career

- University of Edinburgh Class Medal & Ashworth Prize in Zoology (1984), Class Medal & William Turner Award in Zoology (1983), Moira Lyndsay Stewart Award in Zoology & Jack Roberts Memorial Prize in Botany (1982).
- Prize for best talk by a research student at the Association for the Study of Animal Behaviour Spring Conference (1987) during PhD at Cambridge.

Recent career

- *PNAS* Cozzarelli Prize (2008) for outstanding originality and scientific excellence for article "Cross-modal individual recognition in domestic horses (*Equus caballus*)" with L. Proops and D. Reby. I led this study, taking a major role in conceiving and designing the experiment and writing the paper.
<http://www.pnas.org/site/misc/cozzarelliprize.shtml>

CURRENT RESEARCH FOCUS

My current research is focused on investigating emotional awareness as a basis for social success in a non-human - the domestic horse. Despite the key role that emotional intelligence is believed to play in human social behaviour - we still know little of how individual differences in abilities to identify and respond appropriately to the emotional signals of others determine social integration and success in animal groups. With the strong research team that I have built in this area, I am developing a novel battery of naturalistic tests to quantitatively assess individual differences in emotional abilities and directly relating performance to measures of social success. As well as its scientific importance, our work has considerable significance for animal welfare and will allow us to better understand the emotional capacities and requirements of individual horses within the domestic environment.

SUMMARY OF RESEARCH CAREER

My research career has focused on using naturalistic experiments to provide important new insights into vocal communication and cognitive abilities in a wide range of mammals including African elephants, horses, lions, red deer and domestic cats and dogs. By devising novel experimental designs that tap into abilities animals use in decision-making in their natural environments, I have made significant breakthroughs in a number of key areas including:

Advances in our understanding of social cognition and conceptual knowledge

I previously led major new work on social cognition in domestic horses, including developing novel paradigms to examine cross-modal individual recognition in this species. Our study in *PNAS* (Proops et al., 2009), which was awarded the Cozzarelli Prize, provided the first systematic demonstration of cross-modal individual recognition of conspecifics in a nonhuman. This constituted a major advance, suggesting that rich multi-sensory representations could underlie animals' knowledge of each other. I am now initiating experimental studies on horses that will extend our understanding of animal social cognition to encompass decision-making about one of the most pertinent available indices of another's response - their emotional state (see current research above).

Advances in our understanding of social intelligence in wild mammals

My original work on social cognition in African lions (McComb et al., 2004) was important in showing that the costs of fighting with larger groups could have selected for numerical assessment skills in social species - suggesting a possible biological basis for the evolution of mathematical abilities and stimulating new research on other species based on my experimental paradigm. In a highly cited cover article in *Science* (McComb et al., 2001), I subsequently used playback experiments on African elephants to demonstrate that the possession of enhanced discriminatory abilities by the oldest individual in a group could influence the social knowledge of the group as a whole, providing the first insights into how cognitively advanced social mammals acquire and store information in the wild. I also provided the first empirical evidence that groups benefit from older leaders because of their enhanced ability to make crucial decisions about predatory threat, throwing new light on selection for longevity (McComb et al., 2011). Our most recent *PNAS* paper

(McComb et al., 2014) demonstrated that elephants' knowledge of human predators was extremely precise - revealing unusual abilities to determine ethnicity, gender and age from acoustic cues in human voices.

Advances in our understanding of sexual signals and the origins of language

My original papers on the functions of roaring in red deer provided the basis for a new systematic experimental approach to studying the role of vocal signals in sexual selection in mammals (e.g. McComb, 1987, which was a cover story in *Nature*). I realised early on the importance of applying source-filter theory to the study of mammal vocal communication and subsequently developed this approach with David Reby (originally my postdoc) and Ben Charlton (our PhD student) in a series of influential papers showing that formants, key parameters in human speech, also play a crucial role in the communication of non-human mammals (e.g. Reby & McComb, 2003; Reby et al., 2005). This work is given detailed coverage in the new edition of the flagship behavioural ecology text (Davies, Krebs & West, 2012 *An Introduction to Behavioural Ecology*). I have also used a comparative approach to show that evolutionary increases in the size of non-human primate vocal repertoires have been associated with increases in group size and extent of social bonding, results that have added new perspectives to ongoing debates about language evolution (McComb & Semple, 2005).

As well as its scientific significance, my work has also had important practical consequences for animal conservation and welfare. In particular, by revealing the key role that the oldest individuals play in elephant social groups, we demonstrated how whole populations of cognitively advanced social mammals could be dramatically affected by the removal of just a few key individuals (McComb et al. 2001 & 2011). In addition, our recent work illustrating that social disruption can have very significant long-term effects on elephant cognitive abilities had implications for the conservation and welfare of both wild and captive animals. As a result of the above findings, which are relevant to the conservation and welfare not just of elephants but also of other long lived, large-brained social mammals such as whales and dolphins, I was invited to contribute to the recommendations of the recent Convention on the Conservation of Migratory Species of Wild Animals (CMS).

SUMMARY OF TEACHING

I have always aimed to deliver excellence in Teaching and Learning at both undergraduate and postgraduate (MSc & PhD) levels. At undergraduate level, I currently organise and teach a successful final year module in Animal Vocal Communication and contribute to modules on Psychobiology and Contemporary Issues in Psychology. I also teach on post-graduate modules on Social Neuroscience and Voice Analysis and Re-synthesis.

Student feedback comments on Animal Vocal Communication illustrate the key elements that the students appreciate: "Most interesting course I have taken while at Sussex doing Psychology, very up to date research, great teaching, got to go into lab and discover how real research is conducted", "This was the best course of my degree", "The practical sessions reinforced what was learnt in the lectures, but in a fun way. Karen is very enthusiastic about this course and about the subject area

which makes it a much more interesting and enjoyable class”, “The workshops encourage critical thinking about experimental design and enable us to apply what we have learned in lectures”, “Karen is clearly passionate about her subject and is very willing to discuss topic areas further when asked. It’s also really nice to have someone lecturing who contributes so much to the scientific literature covered in the course”.

Undergraduates and MSc students have benefitted from conducting their research projects as part of my lab, where they become integrated members of the research group. Several of these projects have contributed to significant publications on which students have been co-authors) and inspired students to go on to further MSc and PhD degrees themselves. My PhD students and postdocs have also performed outstandingly and many have gone on to very successful academic careers.

ADDITIONAL SCHOOL & UNIVERSITY CONTRIBUTION

I have held a number of significant administrative responsibilities within the university, notably:

- Chair of Postgraduate Exam Board 2014 - present
- Deputy Chair of Postgraduate Exam Board 2013
- Co-ordinator of undergraduate research projects for School of Psychology (2005 onwards) and previously for Experimental Psychology (1998/99 onwards)
- Exam Board secretary (2001-2003)
- Member of Academic Appeals Board (2002)
- Internal assessor for Periodic Review of Teaching in Biology (1997)

Mammal Vocal Communication and Cognition Research Group

In addition to fulfilling the specific internal roles above, I have served the university through developing, alongside my colleague David Reby, a highly successful research group in Mammal Vocal Communication and Cognition <http://www.lifesci.sussex.ac.uk/cmvcvcr/Home.html>

This has attracted and supported talented postgraduates and independent research fellows. At present, I have 3 PhD students, a postdoc and a full-time research assistant, working on projects ranging from social communication in African lions to emotional awareness in horses; an additional postdoc on culture in elephants is expected next year. Along with David Reby’s students and collaborators, this makes for a vibrant research community.

I have also significantly enhanced the University’s profile through the success of my external academic and public activities as documented below.

MEMBERSHIPS & NETWORKS

(i) Journals & academic affiliations

- UFAW link representative for University of Sussex 2014 onwards.

- Academic editor for *PLoS ONE* 2007 onwards.
- Editorial board of *Bioacoustics* 1997 onwards.
- Consulting editor for *Animal Behaviour* 1996-1998
- Council member for the Association for the Study of Animal Behaviour 1993-1996. ASAB liaison representative for the Institute of Biology 1995-1997
- Reviewer for *Science*, *Nature*, *Current Biology*, *Proceedings of the Royal Society B*, *Proceedings for the National Academy of Sciences*, *PLoS ONE*, *Animal Behaviour* and other journals
- Appointed reviewer for European Research Council grants 2012

(ii) Conference organisation

- Organised symposium on “Mammal vocal communication: insights into cognitive abilities and the origins of language” at the International Ethological Congress in Budapest, August 2005 (with David Reby)
- Organiser of the Association for the Study of Animal Behaviour Conference on “Evolution of Mind” held in London in December 1999 (with Stuart Semple), attended by more than 200 people

(iii) Recent invited academic lectures

- Invited speaker, Cetacean Culture Workshop, organised jointly by the Convention on the Conservation of Migratory Species of Wild Animals (CMS), and Whale and Dolphin Conservation (WDC) (April 2014)
- Plenary talk at the Association for the Study of Animal Behaviour meeting on “Cognition in the Wild” (December 2012)
- Invited speaker, International workshop on communication and social cognition, Institute of Evolutionary Biology and Environmental Studies, University of Zurich (March 2011)
- Invited speaker, International workshop on referential communication, Wissenschaftskolleg zu Berlin, Institute for Advanced Study, Berlin, (June 2010)
- Plenary speaker, International Society for Applied Ethology, Nordic meeting, Kuopio, Finland (January 2010)
- Invited speaker, International Ethological Congress, Rennes (August 2009)
- Invited speaker, Ecology and Evolutionary Biology, University of Princeton (April 2009)
- Invited speaker, Novartis day at the Royal Society Discussion meeting on Social Intelligence in London (May 2006)
- Invited speaker (and organiser), International Ethological Congress Symposium on “Mammal vocal communication: insights into cognitive abilities and the origins of language”, Budapest (August, 2005)
- Keynote speaker, British Association for the Advancement of Science, Symposium on “Where do numbers come from”, Salford (September 2003)
- Plenary speaker, Association for the Study of Animal Behaviour conference on Information Gathering (December 2002)
- Invited speaker, symposium on Alternative Approaches to Studying Social Cognition, International Ethological Congress, Tübingen (August 2001)

- Invited participant, International workshop on animal signalling, TalkBank, University of Philadelphia (May 2000)
- Plenary speaker, Association for the Study of Animal Behaviour Conference on Communication and Social Behaviour, Lisbon (July 1999)

BUSINESS, ENTERPRISE & THE COMMUNITY

(i) Lectures to the general public / industry

- Invited panel member/speaker Festival of Sound, organised by Magdalene College, University of Cambridge (December 2014)
- Invited panel member/speaker in Gulbenkian Foundation Supersonix Festival, organised on behalf of the Exhibition Road Cultural Group to focus on the art and science of sound & music-making (June 2012)
- Public lecture on 'Animal Communication' in Learning About Animals series in London (May 2007)
- Lecture to the Pet Care Trust Conference in Edinburgh (November 2006)
- Press conference at London Zoo in April 2001 for launch of my *Science* paper, organised by the American Academy for the Advancement of Science
- Lecture at the British Library National Sound Archive (December 2000)
- Royal Geographical Society lecture (jointly with Cynthia Moss) attended by more than 600 members of the public (November 1996)

(ii) Media involvement & TV documentaries

- There has been considerable media coverage of my work over the years, with appearances on British, American, Australian, Canadian and German TV and radio stations (including BBC TV news, Discovery Channel, Radio 4 Today programme and BBC Science in Action) and articles in major British, European and American newspapers (eg, The Guardian, Times, Liberation, National Geographic magazine, New Scientist). *Science* organised a press conference in London in April 2001 for the launch of my paper, which was their cover story - and later cover stories in *Biology Letters* (2006), *PNAS* (2009) and *Proceedings of the Royal Society B* (2011) also generated widespread media attention, as did my *Current Biology* paper in 2009 which featured as the most popular story on the BBC web site, as well as the top science and environment story. Two of my most recent papers - in *PNAS* (2014) and *Frontiers in Zoology* (2013) - received unusually extensive world-wide coverage, as did a recent *Current Biology* (2014) paper with my PhD student. This included interviews on the Radio 4 Today Programme, ITV News at Ten, BBC World TV News, Newsround, BBC World Service, and Science in Action, as well as being covered in BBC Breakfast, BBC Radio 2, 3 & 4 news reports, Time Magazine, The Economist, *Nature*, *Science*, National Geographic and by more than 200 other news outlets here and abroad.
- I have done regular consultancies for the BBC and other companies making wildlife documentaries on animal communication. Most recently, I was scientific consultant for the popular two-part BBC documentary "Talk to the Animals" (2014). I have also provided sound recordings for wildlife documentaries by the BBC and Windfall films and have a sound recording

credit (with Martyn Colbeck) on the BBC's "Echo of the elephants: the next generation" (1995).

- My elephant research was covered in BBC's "Inside the Animal Mind" in February 2014 and my horse research was filmed for the BBC series "Talk to the Animals" which aired in July 2014. Both programmes were given prime-time slots and were very well received by the public.

(iii) Educational Displays for Museums

- I provided photographic material to The Field Museum, Chicago for an exhibition on Mammoths and Mastodons, Titans of the Ice Age. This exhibition is currently on tour round the world.

(iv) Contribution to Primary Education

- I was invited to write an autobiographical outline for "STEM stories" an NSF project designed to encourage girls in the U.S.A. to pursue careers in Science by introducing them to the senior scientists in particular fields (<http://www.stemstories.org/>).

(v) Contribution to major textbooks and popular books

- My work has featured in John Alcock's and Lee Dugatkin's major textbooks on Animal Behaviour and currently receives detailed coverage in the new editions of the Krebs & Davies *An Introduction to Behavioural Ecology*, Bradbury & Vehrencamp's *Principles of Animal Communication* and Shettleworth's *Cognition, Evolution and Behavior*. It has also been reported in popular books including Brian Butterworth's *The Mathematical Brain* and there is a chapter on my research in the best-selling book: *Animal Wise* by Virginia Morell.

RESEARCH GRANTS

I have received consistent funding for my research over the years, most notably from The Leverhulme Trust and BBSRC:

Leverhulme Trust Research Grant (PI): £285,389 (Jan 2014) *Emotional awareness as a basis for social success in a non-human: the domestic horse*. This project is currently in progress and employs 2 full-time research staff – Dr Leanne Proops (PDRF) and Ms Kate Grounds (RA).

Leverhulme Trust Research Grant (PI): £174,892 (Mar 2009) *Age and experience as determinants of acquired knowledge in a non-human mammal*.

National Geographic grant (PI): \$27,000 plus PDRA salaried by Durban (Jan 2006) *Elephant matriarchs and conservation*.

Waltham Foundation grant (PI): £9,632 (July 2002) *The Function of Purring in Cats: Seismic and Airborne Communication*.

EU Marie Curie grant (Co-PI/Supervisor of PDRF): 114,072 Euro (Oct 2000) *Origin, Structure & Function of Sender-related Acoustical Features in Sexually Selected Mammal Vocalisations*.

BBSRC research grant (PI): £166,092 (Mar 1996)
Communication Networks, Social Organisation and Reproductive Success.

Tusk Trust grants (PI): 3 x £1,500 (awarded 1994, 1995 & 1998)
Acoustic Communications in Elephants.

Nuffield Foundation grant (PI): £3,960 (Nov 1994)
Acoustic Communication in Social Mammals.

Royal Society Research grant (PI): £9,253 (Mar 1994)
Infrasonic Signalling in Elephants.

NERC small project grant (PI): £14, 832 (Oct 1993)
Acoustic Communication & the Evolution of Mammal Social Systems.

In addition I have had a number of Royal Society Conference grants, most recently in 2005 & 2009.

SCIENTIFIC PUBLICATIONS

JOURNAL ARTICLES

* McComb, K. Shannon, G., Sayialel, K. & Moss, C. (2014) Elephants can determine ethnicity, gender, and age from acoustic cues in human voices *PNAS* 111(14), 5433-5438.

* cover article and subject of a *PNAS* commentary

Wathan, J. & McComb, K. (2014) The eyes and ears are visual indicators of attention in domestic horses. *Current Biology* 24, R1-R2.

Ratcliffe, V.F., McComb, K. & Reby, D. (2014) Cross-modal discrimination of human gender by domestic dogs. *Animal Behaviour* 91, 127-135.

* Shannon, G., Slotow, R., Durant, S.M., Sayialel, K.N., Poole, J., Moss, C. & McComb, K. (2013) Effects of social disruption in elephants persist decades after culling. *Frontiers in Zoology* 2013, 10: 62.

* shared first authorship

Proops, L., Rayner, J., Taylor, A. M. and McComb, K. (2013) The responses of young domestic horses (*Equus caballus*) to human-given cues. *PloS ONE*, 8 (6). e67000.

Proops, L. & McComb, K. (2012) Cross-modal individual recognition in domestic horses (*Equus caballus*) extends to familiar humans. *Proceedings of the Royal Society B, London* 279, 3131-3138.

* McComb K., Shannon G., Durant S.M., Sayialel K., Slotow R., Poole J., and Moss C. (2011) Leadership in elephants: the adaptive value of age. *Proceedings of the Royal Society B, London* 278, 3270-3276; doi:10.1098/rspb.2011.0168.

* cover article

Webster, H., McNutt, J. W. & McComb, K. (2011) African wild dogs as a fugitive species: playback experiments investigate how wild dogs respond to their major competitors. *Ethology* 117, 1-10.

Taylor A. M., Reby D. & McComb K. (2011) Cross modal perception of body size in domestic dogs (*Canis familiaris*). *PLoS ONE* 6, e17069.

Webster, H. McNutt, J.W & McComb, K. (2010) Eavesdropping and risk assessment between lions, spotted hyenas and African wild dogs. *Ethology* 116, 233-239.

Proops, L. & McComb, K. (2010) Attributing attention: the use of human-given cues by domestic horses (*Equus caballus*). *Animal Cognition* 13, 197-205.

Proops, L., Walton, M. & McComb, K. (2010) The use of human-given cues by domestic horses (*Equus caballus*) during an object choice task *Animal Behaviour* 79, 1205-1209.

Taylor A. M., Reby D. & McComb K. (2010) Why Do Large Dogs Sound More Aggressive to Human Listeners: Acoustic Bases of Motivational Misattributions. *Ethology* 116, 1155-1162.

Reby D., Charlton B., Locatelli Y. & McComb K. (2010) Oestrous red deer hinds prefer male roars with higher fundamental frequencies. *Proceedings of the Royal Society B, London* 277, 2747-2753.

Taylor, A. M., Reby, D. & McComb, K. (2010) Size Communication in domestic dog (*Canis familiaris*) growls. *Animal Behaviour* 79, 205-210.

McComb, K., Taylor, A.M., Wilson, C. & Charlton, B., (2009) Manipulation by domestic cats: the cry embedded within the purr. *Current Biology* 19, R507-508.

Taylor, A., Reby, D. & McComb, K. (2009) Context-related variation in the vocal growling behaviour of the domestic dog (*Canis familiaris*). *Ethology* 115, 905-915.

* Proops, L., McComb, K. & Reby, D. (2009) Cross-modal individual recognition in domestic horses. *Proceedings of the National Academy of Sciences* 106, 947-951.

* cover article and subject of a PNAS commentary

Charlton, B., McComb, K. & Reby, D. (2008) Red deer hinds use formant frequencies in the male roar as acoustic cues to body size and maturity. *Ethology* 114, 1023-1031.

Charlton, B., Reby, D. & McComb, K. (2008) Effect of combined source (F0) and filter (formant) variation on red deer hind responses to male roars. *Journal of the Acoustical Society of America* 123, 2936-2943.

Taylor, A. M., Reby, D. & McComb, K. (2008) Human listeners attend to size information in domestic dog growls. *Journal of the Acoustical Society of America* 123, 2903-2909.

Roberts, S.G.B., McComb, K. & Ruffman, T. (2008) An experimental investigation of referential looking in free-ranging barbary macaques (*Macaca Sylvanus*). *Journal of Comparative Psychology* 122, 94-99.

Charlton B., Reby, D. & McComb, K. (2007) Female red deer prefer the roars of larger males. *Biology Letters (The Royal Society)* 3, 382-385.

Charlton, B., Reby, D. & McComb, K. (2007) Female perception of size-related formant shifts in red deer (*Cervus elaphus*). *Animal Behaviour* 74, 707-714.

* McComb, K., Baker, L. & Moss, C. (2006) African elephants show high levels of interest in the skulls and ivory of their own species. *Biology Letters (The Royal Society)* 2, 26-28.

* cover article

McComb, K. & Semple, S. (2005) Co-evolution of vocal communication and sociality in primates. *Biology Letters (The Royal Society)* 1, 381-385.

* Reby, D., McComb, K., Cargnelutti, B., Darwin, C. J, Fitch, W. T. & Clutton-Brock, T.H. (2005) Red deer stags use formants as assessment cues during intra-sexual agonistic interactions. *Proc. Roy. Soc. Lond. B.* 272, 941-947.

* shared first authorship

McComb, K., Reby, D., Baker, L., Moss, C. & Sayialel, S. (2003) Long-distance communication of cues to social identity in African elephants. *Animal Behaviour* 65, 317-329.

Reby, D. & McComb, K. (2003) Vocal communication and reproduction in deer. *Advances in the Study of Behaviour* 33, 231-264.

Reby, D. & McComb, K. (2003) Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Animal Behaviour* 65, 519-530.

Semple, S, McComb, K., Alberts, S. & Altmann, J. (2002) Information content of female copulation calls in yellow baboons. *American Journal of Primatology* 56, 43-56.

* McComb, K., Moss, C., Durant, S., Baker, L. & Sayialel, S. (2001) Matriarchs act as repositories of social knowledge in African elephants. *Science* 292, 491-494.

* cover article

McComb, K., Moss, C. & Durant, S. (2001) Elephant hunting and conservation. *Science* 293, 2203-2204.

Grinnell, J. & McComb, K. (2001) Roaring and social communication in African lions: the limitations imposed by listeners. *Animal Behaviour* 62, 93-98.

McComb, K, Moss, C., Sayialel, S. & Baker, L. (2000) Unusually extensive networks of vocal recognition in African elephants. *Animal Behaviour* 59, 1103-1109.

Semple, S. & McComb, K. (2000) Perception of female reproductive state from vocal cues in a mammal species. *Proc. Roy. Soc. Lond. B.* 267, 707-712.

Grinnell, J. & McComb, K. (1996) Female grouping as a defense against infanticide by males: evidence from field playback experiments on African lions. *Behavioural Ecology* 7, 55-59.

Semple, S & McComb, K. (1996a) Behavioural deception. *Trends in Ecology & Evolution* 11, 434-437.

Semple, S & McComb, K. (1996b) Deception: the correct path to enlightenment? Reply to Getty & Christy. *Trends in Ecology & Evolution* 12, 160.

Clutton-Brock, T.H., McComb, K.E. & Deutsch, J.C. (1996) Multiple factors affect the distribution of females in lek-breeding ungulates: a rejoinder to Carbone and Taborsky. *Behavioural Ecology* 7, 373-378.

McComb, K., Packer, C. & Pusey, A. (1994) Roaring and numerical assessment in contests between groups of female lions *Panthera leo*. *Animal Behaviour* 47, 379-387.

McComb, K. & Clutton-Brock, T. (1994) Is mate choice copying or aggregation responsible for skewed distributions of females on leks?. *Proc. Roy. Soc. Lond. B.* 225, 13-19.

McComb, K., Pusey, A., Packer, C. & Grinnell, J. (1993) Female lions can identify potentially infanticidal males from their roars. *Proc. Roy. Soc. Lond. B.* 252, 59-64.

Clutton-Brock, T. & McComb, K. (1993) Experimental tests of copying and mate choice in fallow deer. *Behavioural Ecology* 4, 191-193.

McComb, K.E. (1991) Female choice for high roaring rates in red deer (*Cervus elaphus*). *Animal Behaviour* 41, 79-88.

McComb, K. (1988) Roaring and oestrus. *Nature* 332, 24.

McComb, K.E. (1988) Roaring and reproduction in red deer (*Cervus elaphus*) *Ph.D. Thesis*, University of Cambridge.

* McComb, K. (1987) Roaring by red deer stags advances date of oestrus in hinds. *Nature* 330, 648-649.

* cover article

CONTRIBUTIONS TO EDITED VOLUMES & BOOK CHAPTERS

Taylor, A.M., Ratcliffe, V., McComb, K & Reby, D. (2014) Auditory communication in domestic dogs: vocal signalling in the extended social environment of a companion animal. In: ***The Social Dog*** (eds J. Kaminski and S. Marshall-Pescini) Elsevier.

McComb K., Reby D. & Moss C. (2011) Vocal communication and social knowledge in African Elephants. In: ***The Amboseli Elephants: a long-term perspective on a long-lived mammal*** (ed. C.J.Moss & H.J. Croze). Chicago: Chicago University Press.

McComb, K. & Reby, D. (2008) Communication in terrestrial animals. In ***New Encyclopedia of Neuroscience*** (ed. L.R. Squire).

Semple, S. & McComb, K. (2006) The function of female copulation calls in the genus *Macaca*: insights from the Barbary macaque. In ***The Barbary macaque: biology, management and conservation*** (J.K. Hodges and J. Cortes, eds). Nottingham: Nottingham University Press, pages 81-93.

McComb, K. & Reby, D. (2005) Vocal Communication Networks in Large Terrestrial Mammals In: ***Animal Communication Networks*** (ed. P.K. McGregor). Cambridge: Cambridge University Press pp. 372-389.

McComb, K. (1996) Studying vocal communication in elephants. In: ***Studying Elephants*** African Wildlife Foundation Technical Handbook series, Nairobi, pages 112-119.

McComb, K. (1992) Playback as a tool for studying contests between social groups. In: ***Playback and Studies of Animal Communication***. ed. by P.K. McGregor. Plenum Publishing Corporation, London, pages 111-119.

McGregor, P.K., Catchpole, C.K., Dabelsteen, T., Falls, J.B., Fusani, L., Gerhardt, H.C., Gilbert, F., Horn, A.G., Klump, G.M., Kroodsma, D.E., Lambrechts, M.M., McComb, K., Nelson, D.A., Pepperberg, I.M., Ratcliffe, L., Searcy, W.A. & Weary, D.M. (1992) Design of playback experiments. In: ***Playback and Studies of Animal Communication***. ed. by P.K. McGregor. Plenum Publishing Corporation, London, pages 1-9.

OTHER SIGNIFICANT PUBLICATIONS

McComb, K. (2007) Q&A ***Current Biology*** 17, R864-866.

McComb, K & Semple, S. (1998) Are talkers the only thinkers? ***Nature*** 395, 656 -657.

Exhibit B

References cited

- Anderson, J.R., A. Gillies & L.C. Lock (2010) *Pan* thanatology. *Current Biology*, **20** (8): R349-351.
- Baddeley, A. D. (2000) The episodic buffer: A new component of working memory? *Trends in Cognitive Sciences*, **4** (11): 417-423.
- Barton, R.A. (2012) Embodied cognitive evolution and the cerebellum. *Philosophical Transactions of the Royal Society, Series B*, **367**: 2097-2107.
- Bates L.A., K. Sayialel, N.W. Njiraini, J.H. Poole, C.J. Moss & R.W. Byrne (2007) Elephants classify human ethnic groups by odour and garment colour. *Current Biology* **17** (22): 1938-1942.
- Bates L.A., J.H. Poole & R.W. Byrne (2008a) Elephant cognition. *Current Biology* **18** (13): R544-R546.
- Bates L.A., P.C. Lee, N. Njiraini, J.H. Poole, K. Sayialel, S. Sayialel, C.J. Moss & R.W. Byrne (2008b) Do elephants show empathy? *Journal of Consciousness Studies* **15** (10-11): 204-225.
- Bates L.A. & R.W. Byrne (2014) Primate Social Cognition: What we have learned from nonhuman primates and other animals. In: *APA Handbook of Personality and Social Psychology Vol. 1. Attitudes and Social Cognition*. Eds. M.Mikulincer & P.R. Shaver. APA, Washington, DC.
- Bjorkland, D.F. (1997) The Role of Immaturity in Human Development. *Psychological Bulletin*, **122** (2): 153-169.
- Blake, S., P. Bouche, L.E.L. Rasmussen, A. Orlando, & I. Douglas-Hamilton (2003) The last Sahelian Elephants: Ranging behaviour, population status and recent history of the desert elephants of Mali. *Save the Elephants*.
- Boesch, C. (1991) Teaching among wild chimpanzees. *Animal Behaviour*, **41**:530-532.
- Byrne, R.W. (2016) *Evolving Insight*. Oxford University Press.
- Cozzi, B., S. Spagnoli, & L. Bruno (2001) An overview of the central nervous system of the elephant through a critical appraisal of the literature published in the XIX and XX centuries. *Brain Research Bulletin*, **54**:219-227.
- Csibra, G. & Gergely, G. (2009) Natural pedagogy. *Trends in Cognitive Science*, **13**: 148-153.

- Dekaban, A.S. & Sadowsky, D. (1978) Changes in brain weights during the span of human life: relation of brain weights to body heights and body weights. *Annals of Neurology*, **4**:345-356.
- Douglas-Hamilton, I., S. Bhalla, G. Wittemyer, & F. Vollrath, (2006) Behavioural reactions of elephants towards a dying and deceased matriarch? *Applied Animal Behaviour Science*, **100**: 87-102.
- Eisenberg, J.E. (1981) *The mammalian radiations: an analysis of trends in evolution, adaptation, and behavior*. Chicago: University of Chicago Press.
- Elston, G.N. (2003) Cortex, Cognition and the Cell: New Insights into the Pyramidal Neuron and Prefrontal Function. *Cerebral Cortex*, **13** (11):1124–1138.
- Eltringham, S.K. (1982) *Elephants*. Poole, Dorset: Blandford Press.
- Foley, C.A.H., N. Pettorelli, & L. Foley. (2008) Severe drought and calf survival in elephants. *Biology Letters*, **4**:541–544.
- Foerder, P., M. Galloway, T. Barthel, D.E. Moore III & D. Reiss (2011) Insightful Problem Solving in an Asian Elephant. *PLoS One*, **6** (8): e23251.
- Frith, C. & U. Frith (2005) Theory of Mind. *Current Biology*, **15** (17): R644- R645:
- Fuster, J.M. (2002) Frontal lobe and cognitive development. *Journal of Neurocytology*, **31**: 373–385.
- Gallup, G.G., Jr (1970) Chimpanzees: self-recognition. *Science*, **167**: 86-87.
- Gallup, G.G., Jr (1982) Self-awareness and the emergence of mind in primates. *American Journal of Primatology*, **2**(3): 237-248.
- Guinet, C., & J. Bouvier, (1995) Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. *Canadian Journal of Zoology*, **73**: 27-33.
- Herculano-Houzel S, Avelino-de-Souza K, Neves K, Porfírio J, Messeder D, Mattos Feijó L, Maldonado J, Manger PR. (2014) The elephant brain in numbers. *Front Neuroanat*. Jun 12;8:46.
- Hedges, S. B. (2001) Afrotheria: Plate tectonics meets genomics. *Proceedings of the National Academy of Sciences USA*, **98**: 1-2.
- Irie-Sugimoto, N., T. Kobayashi, T. Sato, & T. Hasegawa. (2008) Evidence of means-end behavior in Asian elephants (*Elephas maximus*). *Animal Cognition*, **11**: 359–65.
- Jerison, H.J. (1973) *Evolution of the brain and intelligence*. New York: Academic Press.

- Jacobs, B. et al (2011) Neuronal morphology in the African elephant (*Loxodonta africana*) neocortex. *Brain Structure and Function*, **215**: 273-298.
- Lee, P.C. (1986) Early social development among African elephant calves. *National Geographic Research*, **2**: 388–401.
- Lee, P.C. (1987) Allomothering among African elephants. *Animal Behaviour*, **35**: 278-291.
- Leggett, K.E.A. (2006) Home range and seasonal movement of elephants in the Kunene Region, northwestern Namibia. *African Zoology*, **41** (1): 17–36.
- Leighty, K.A., J. Soltis, K. Leong, & A. Savage (2008) Antiphonal exchanges in African elephants (*Loxodonta africana*): Collective response to a shared stimulus, social facilitation, or true communicative event? *Behaviour*, **145**: 297–312.
- McComb, K., C. Moss, S. Sayialel, & L. Baker. 2000. Unusually extensive networks of vocal recognition in African elephants. *Animal Behaviour*, **59**: 1103–1109.
- McComb, K., C.J. Moss, S.M. Durant, L. Baker & S. Sayialel (2001) Matriarchs as repositories of social knowledge in African elephants. *Science*, **292**: 491–494.
- McComb, K., L. Baker, & C. Moss (2006) African elephants show high levels of interest in the skulls and ivory of their own species. *Biology Letters*, **2**: 26–28.
- McComb, K., G. Shannon, S.M. Durant, K. Sayialel, R. Slotow, J.H. Poole, & C. Moss (2011) Leadership in elephants: the adaptive value of age. *Proceedings of the Royal Society, Series B*, **278** (1722): 3270-3276.
- McComb, K., G. Shannon, K.N. Sayialel, & C. Moss (2014) Elephants can determine ethnicity, gender, and age from acoustic cues in human voices. *Proceedings of the National Academy of Sciences*, **111** (14): 5433-5438.
- Miller, G.A. (1956) The magical number seven, plus-or-minus two: Some limits on our capacity for processing information. *Psychological Review*, **63**: 81-97.
- Moss, C.J. (1992) *Echo of the elephants: The story of an elephant family*. London: BCA.
- Moss, C.J. & J.H. Poole (1983) Relationships and social structure of African elephants. In *Primate social relationships: An integrated approach*, ed. R. A. Hinde, 314–25. Oxford: Blackwells.
- Parker, S.T., R.W. Mitchell & M.L. Boccia (1994) *Self-awareness in animals and humans: Developmental Perspectives*. New York: Cambridge University Press.
- Plotnik, J.M., F.B.M. de Waal & D. Reiss (2006) Self-recognition in an Asian elephant. *Proceedings of the National Academy of Sciences USA*, **103**: 17053–7.

- Plotnik, J.M. R. Lair, W. Suphachoksahakun & F.B.M. de Waal (2011) Elephants know when they need a helping trunk in a cooperative task. *Proceedings of the National Academy of Sciences*, **108** (12): 5116–5121.
- Poole, J.H. (1996) *Coming of age with elephants*. New York: Hyperion
- Poole, J.H. (1999) Signals and assessment in African elephants: Evidence from playback experiments. *Animal Behaviour*, **58**: 185–193.
- Poole, J.H. (2011) The behavioral contexts of African elephant acoustic communication. In: *The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal*. Moss, C.J. & Croze, H.J. (Eds.) Chicago: *University of Chicago Press*.
- Poole, J. H. & Granli, P. K. 2004. The visual, tactile and acoustic signals of play in African savannah elephants. In (ed.) Jayewardene, Jayantha. *Endangered Elephants, past present & future*. Proceedings of the Symposium on Human Elephant Relationships and Conflicts, Sri Lanka, September 2003. Biodiversity & Elephant Conservation Trust, Colombo. Pages 44-50.
- Poole, J.H. & P.K. Granli (2011) Signals, Gestures, and Behavior of African Elephants. In: *The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal*. Moss, C.J. & Croze, H.J. (Eds.) Chicago: *University of Chicago Press*.
- Poole, J.H., P.L. Tyack, A.S. Stoeger-Horwath & S. Watwood (2005) Elephants are capable of vocal learning. *Nature*, **434**: 455–456.
- Prebble, S.C., D.R. Addis & L.J. Tippet (2013) Autobiographical memory and sense of self. *Psychological Bulletin*, **139** (4): 815-840.
- Premack, D. & G. Woodruff (1978) Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences*, **1**: 515–526.
- Reiss, D., & L. Marino (2001) Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. *Proceedings of the National Academy of Sciences, USA*, **98**: 5937–42.
- Roth, G. & U. Dicke (2005) Evolution of the brain and intelligence. *Trends in Cognitive Sciences*, **9**: 250–257.
- Shannon, G., R. Slotow, S.M. Durant, K.N. Sayialel, J.H. Poole, C. Moss & K. McComb (2013) Effects of social disruption in elephants persist decades after culling. *Frontiers in Zoology*, **10** (62): 1-10.
- Shoshani, J., W.J. Kupsky & G.H. Marchant (2006) Elephant brains. Part I: Gross morphology, functions, comparative anatomy, and evolution. *Brain Research Bulletin*, **70**: 124–157.

- Smet, A.F. & R.W. Byrne (2013) African elephants can use human pointing cues to find hidden food. *Current Biology*, **23** (20): 2033-2037.
- Smet, A.F. & R.W. Byrne (2014) African elephants recognize visual attention from face and body orientation. *Biology Letters*, **10**: 20140428.
- Soltis J., K. Leong & A. Savage (2005) African elephant vocal communication I: Antiphonal calling behavior among affiliated females. *Animal Behaviour*, **70**: 579-587.
- Stoeger, A.S., D. Mietchen, S. Oh, S. de Silva, C.T. Herbst, S. Kwon & W.T. Fitch (2012) An Asian Elephant Imitates Human Speech. *Current Biology*, **22**(22): 2144-8
- Viljoen, P. J. (1989) Spatial distribution and movements of elephants (*Loxodonta africana*) in the northern Namib desert region of Kaokoveld, South West Africa–Namibia. *Journal of Zoology*, **219**: 1–19.
- Wood, J.D., B. McCowan, W.R. Langbauer, J.J. Viloen & L.A. Hart (2005) Classification of African elephant *Loxodonta africana* rumbles using acoustic parameters and cluster analysis. *Bioacoustics*, **15**: 143–161.