ELEPHANTS AND ETHICS

[FIGURE] FIG 0.0



Edited by CHRISTEN WEMMER AND CATHERINE A. CHRISTEN

ELEPHANTS AND ETHICS

TOWARD A MORALITY OF COEXISTENCE Foreword by John Seidensticker

THE JOHNS HOPKINS UNIVERSITY PRESS BALTIMORE © 2008 The Johns Hopkins University Press All rights reserved. Published 2008 Printed in the United States of America on acid-free paper 1 2 3 4 5 6 7 8 9

> The Johns Hopkins University Press 2715 North Charles Street Baltimore, Maryland 21218-4363 www.press.jhu.edu

Library of Congress Cataloging-in-Publication Data Elephants and ethics: toward a morality of coexistence / Christen Wemmer and Catherine A. Christen, edited by ; foreword by John Seidensticker. page cm. Includes bibliographical references and index. ISBN-13: 978-0-8018-8818-2 (hardcover : alk. paper) ISBN-10: 0-8018-8818-2 (hardcover : alk. paper) 1. Elephants-Effect of human beings on-Moral and ethical aspects. 2. Animal welfare-Moral and ethical aspects. I. Wemmer, Christen M. II. Christen, Catherine A. (Catherine Ann) нv4747.n48 2008

179'.3-dc22 2007036045

A catalog record for this book is available from the British Library.

Frontispiece: Prithiviraj Fernando Figure on page 00: Christen Wemmer

Special discounts are available for bulk purchases of this book. For more information, please contact Special Sales at 410-516-6936 or specialsales@press .jhu.edu.

The Johns Hopkins University Press uses environmentally friendly book materials, including recycled text paper that is composed of at least 30 percent post-consumer waste, whenever possible. All of our book papers are acid-free, and our jackets and covers are printed on paper with recycled content.

Chapter Opening Art Credits 1: Jordana Meyer 2: Smithsonian Institution Archives, SIA2008-0924 3: Donna Nissani 4: Petter Granli / elephantvoices.org 5: Courtesy John Edwards, London 6: Jessie Cohen, Smithsonian's National Zoo 7: Janine L. Brown 8: Disney's Animal Kingdom 9: Mehgan Murphy, Smithsonian's National Zoo 10: Smithsonian Institution Archives, SIA2008-0922 11: Feld Entertainment, Inc. 12: Smithsonian Institution Archives, SIA2008-0926 13: Disney's Animal Kingdom 14: Jessie Cohen, Smithsonian's National Zoo 15: Disney's Animal Kingdom

16: Prithiviraj Fernando

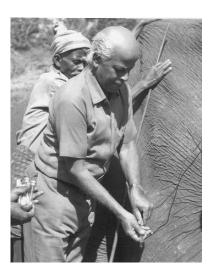
17: Petter Granli / elephantvoices.org

18: Hank Hammatt

19: Petter Granli / elephantvoices.org

20: Jordana Meyer

- 21: Stephen Blake, Wildlife Conservation Society
- 22: Joyce Poole / elephantvoices.org



V. Krishnamurthy (1927–2002)

This volume is dedicated to the memory of Dr. V. Krishnamurthy, a remarkable Forest Veterinary Surgeon of India's Tamil Nadu Forest Department. Doc devoted his humble life to the care and welfare of Asian elephants. He enriched his colleagues by sharing his peaceful wisdom and his penetrating understanding of elephants. His unwavering ethical convictions are a legacy of hope for those who carry the torch.

CONTENTS

Foreword, by John Seidensticker / xi

Preface / xv

1. INTRODUCTION / 1 NEVER FORGETTING THE IMPORTANCE OF ETHICAL TREATMENT OF ELEPHANTS Christen Wemmer and Catherine A. Christen

PART I. OVERVIEW OF ELEPHANT PHILOSOPHY AND SCIENCE

- 2. ELEPHANTS IN TIME AND SPACE / 00 EVOLUTION AND ECOLOGY Raman Sukumar
- 3. PERSONHOOD, MEMORY, AND ELEPHANT MANAGEMENT / 00 Gary Varner
- 4. ELEPHANT SOCIALITY AND COMPLEXITY / 00 THE SCIENTIFIC EVIDENCE Joyce H. Poole and Cynthia J. Moss
- 5. ELEPHANTS, ETHICS, AND HISTORY / 00 Nigel Rothfels
- 6. PAIN, STRESS, AND SUFFERING IN ELEPHANTS / 00 WHAT IS THE EVIDENCE AND HOW CAN WE MEASURE IT? Janine L. Brown, Nadja Wielebnowski, and Jacob V. Cheeran

PART II. ELEPHANTS IN THE SERVICE OF PEOPLE: CULTURAL DIFFERENCES AND ETHICAL RELATIVITY

- 7. ELEPHANTS AND PEOPLE IN INDIA / 00 HISTORICAL PATTERNS OF CAPTURE AND MANAGEMENT Dhriti K. Lahiri Choudhury
- 8. CARROTS AND STICKS, PEOPLE AND ELEPHANTS / 00 RANK, DOMINATION, AND TRAINING John Lehnhardt and Marie Galloway

viii CONTENTS

- 9. CANVAS TO CONCRETE / 00 ELEPHANTS AND THE CIRCUS-ZOO RELATIONSHIP Michael D. Kreger
- 10. WHY CIRCUSES ARE UNSUITED TO ELEPHANTS / 00 Lori Alward
- 11. VIEW FROM THE BIG TOP / 00 WHY ELEPHANTS BELONG IN NORTH AMERICAN CIRCUSES Dennis Schmitt
- 12. THE CHALLENGES OF MEETING THE NEEDS OF CAPTIVE ELEPHANTS / 00 Jane Garrison
- 13. MOST ZOOS DO NOT DESERVE ELEPHANTS / 00 David Hancocks
- 14. ZOOS AS RESPONSIBLE STEWARDS OF ELEPHANTS / 00 Michael Hutchins, Brandie Smith, and Mike Keele
- 15. CAN WE ASSESS THE NEEDS OF ELEPHANTS IN ZOOS? CAN WE MEET THE NEEDS OF ELEPHANTS IN ZOOS? / 00 Jill D. Mellen, Joseph C. E. Barber, and Gary W. Miller
- **16. GIANTS IN CHAINS** / 00 HISTORY, BIOLOGY, AND PRESERVATION OF ASIAN ELEPHANTS IN CAPTIVITY Fred Kurt, Khyne U Mar, and Marion E. Garaï

PART III. ELEPHANTS AND PEOPLE IN NATURE: THE ETHICS OF CONFLICTS AND ACCOMMODATIONS

- 17. RESTORING INTERDEPENDENCE BETWEEN PEOPLE AND ELEPHANTS / 00 A SRI LANKAN CASE STUDY Lalith Seneviratne and Greg D. Rossel
- SUMATRAN ELEPHANTS IN CRISIS / 00 TIME FOR CHANGE Susan K. Mikota, Hank Hammatt, and Yudha Fahrimal
- 19. HUMAN-ELEPHANT CONFLICTS IN AFRICA / 00 WHO HAS THE RIGHT OF WAY? Winnie Kiiru
- 20. PLAYING ELEPHANT GOD / 00 ETHICS OF MANAGING WILD AFRICAN ELEPHANT POPULATIONS Ian Whyte and Richard Fayrer-Hosken

ix CONTENTS

- 21. TOWARD AN ETHIC OF INTIMACY / 00 TOURING AND TROPHY HUNTING FOR ELEPHANTS IN AFRICA Rebecca Hardin
- 22. THE ETHICS OF GLOBAL ENFORCEMENT / 00 ZIMBABWE AND THE POLITICS OF THE IVORY TRADE Rosaleen Duffy

Contributors

Index

[FIGURE] Figure 4.0 Here

4 ELEPHANT SOCIALITY AND COMPLEXITY THE SCIENTIFIC EVIDENCE

JOYCE H. POOLE AND CYNTHIA J. MOSS

Conventional wisdom places elephants among the more intelligent, socially intricate, and emotionally complex nonhuman species. Hancocks (Chapter 13 in this volume), citing Morris and Morris (1966) and Kellert (1989), notes that people rank elephants among the "most-liked" animals and consider the intelligence of elephants to be one of the most preferential factors. This popular conception reflects a long-term legacy of both legend and research about elephants. Scientists and philosophers, going back to Aristotle, have claimed elephants to be highly intelligent, and some have even viewed them as quasi-moral agents (Meredith 2001). This chapter examines what is currently known about the intelligence and complexity of elephants and attempts to answer whether they are deserving of special moral consideration.

Although the social complexity of elephants has been studied in depth, little systematic research on their cognitive abilities has been carried out until very recently (see Rensch 1956, 1957; Hart et al. 2001; McComb et al. 2001; Nissani 2004; Douglas-Hamilton et al. 2006; McComb, Bates, and Moss 2006; Plotnik, de Waal, and Reiss 2006). Though this body of research is growing rapidly, much of what is currently claimed regarding the superior intelligence of elephants is based on anecdotal evidence. Anecdotal evidence falls into several categories, and as long as the nature of this evidence is understood, some of it may be used to substantiate certain claims. For example, much critical data related to elephant cognition are based on rare behavior, which scientists have observed on an *ad libitum* (discretionary) basis. The observations of these scientists, who are trained in the interpretation of behavior, are an important data set (Byrne 1997a).

In this chapter, we provide empirical verification of elephant intelligence and social complexity. We examine such factors as social structure and flexibility, social network size, social learning, behavioral innovation, relative brain size and complexity, memory, and communication. We discuss Machiavellian intelligence, insight, and theory of mind, mirror self-recognition, and reaction to death. We argue that current and emerging evidence indicates we should err on the side of caution and treat elephants with special consideration. Evidence for these arguments comes in the form of scientific publications, previously unpublished data, and scientific records of

rare behaviors. To reduce speculation as to the validity of the accounts of rare behavior, we rely on our own observations or those of our colleagues. The previously unpublished data presented in this essay come primarily from the Amboseli Elephant Research Project (AERP), a thirty-four-year study of known individuals in Amboseli National Park, Kenya.

Three recognized species of elephants exist: Asian elephants, *Elephas maximus*, African savannah elephants, *Loxodonta africana*, and African forest elephants, *L. cyclotis*. This chapter applies generally to all elephants. Although conclusions regarding the behavior of wild elephants come primarily from observations of African savannah elephants in Amboseli, and conclusions from experimental studies of captive elephants are primarily based on Asian elephants, it is generally acknowledged that there is broad similarity among the three species (Payne 2003; Sukumar 2003). Except where particularly relevant we have not attempted to compare elephants with other species.

The point of this chapter is not to argue that elephants deserve unprecedented rights that other species do not. Perhaps other animals also deserve such consideration, but we are not qualified to judge that. Many mammals may equal or even surpass elephants in their individual abilities, but we argue that it is the totality of elephant characteristics that makes them deserving of special consideration.

This chapter relies on a common understanding of certain basic concepts of elephant social structure. We define these here.

Family unit or *family:* One or more adult females and calves with a high frequency of association over time, who act in a coordinated manner and exhibit affiliative behavior toward one another (Moss and Poole 1983). This term does not exclude two or more adult females without offspring, or a single adult female and one or more juveniles who are not her immediate offspring, making up a family. The term family and family unit may be used interchangeably. In Amboseli, each family is referred to by a two-letter code, such as AA, AB, and so on.

Bond group: Two or more family units who associate with one another at high frequency relative to their associations with other family units in the population and whose members display affiliative behavior toward one another (Moss and Poole 1983).

Group: Any number of elephants of any age or sex moving together in a coordinated manner with no single member or subgroup at a distance from its nearest neighbor greater than the diameter of the main body of the group at its widest point.

Aggregation: A group specifically made up of more than one family unit with or without associating independent adult males.

Fission-fusion society: In relation to elephants the term fission-fusion society refers both to the slow changes in the structure of families or bond

groups that occur over the course of years or decades and the very rapid changes that occur in social group composition over the course of hours.

In Amboseli, we have collected records on family group associations in two basic ways: as *sightings* records and as *census* records. *Sightings* record the presence of families, or portions of families, in any group that is encountered in the course of a day. Presence requires at least one member of a family to be sighted. We maintain the records in a Microsoft Access database (henceforth cited in this chapter as "AERP database") that contained more than 34,000 records as of the end of 2005. *Censuses* record the presence or absence of each family member at a sighting.

Social Complexity and Flexibility

Elephants live in a fluid, multitiered, fission-fusion society where group membership changes frequently, forming and dividing along lines that may be predicated on close social bonds, home range, and season (Douglas-Hamilton 1972; Moss and Poole 1983; Sukumar 2003; Wittemyer, Douglas-Hamilton, and Getz 2005; Archie, Moss, and Alberts 2005; Moss and Lee, forthcoming). Families are composed of a discrete, predictable composition of individuals, but over the course of hours or days, these groups may temporarily separate and reunite or they may mingle with other social groups to form larger social units. The close and lasting social relationships formed by elephants are remarkable in the context of their fluid social system (Archie et al. 2005; Moss and Lee, forthcoming). In fact, this combination of social qualities—close and enduring cooperative social relationships, and fission-fusion sociality—exists in only a small number of cooperatively hunting carnivores (e.g., hyenas, lions, and sperm whales) and also a few primates (e.g., chimpanzees and humans; Archie et al. 2005; Moss and Lee, forthcoming).

Relationships radiate out from the mother-offspring bond through members of the family, bond group, clan, subpopulation, to independent adult males and even beyond the population to strangers. Although special relationships between individual elephants may last a lifetime, the quality of relationships and the structure and degree of cohesion in an individual's social network may also change through time. With a maximum lifespan in the wild of sixty-five years (Moss 2001; AERP database), elephants are unusually long-lived mammals (Eisenberg 1981) and thus their relationships are extremely long term.

Like many sexually dimorphic mammals, adult male and female elephants live in very different social worlds (Moss 1988; Poole 1994). A complex network of bonds between individuals and families characterizes the lives of females and their offspring, while fluctuating sexual cycles distinguish the dynamic activities, associations, and relationships of males (Moss and Poole 1983). Elephants show strong individual personalities that affect —forthcoming. [FIGURE] Figure 4.1 about here



Figure 4.1 Families may temporarily separate and reunite or they may mingle with other social groups to form larger social units. The close and lasting social relationships formed by elephants are remarkable in the context of their fluid social system.

Photograph courtesy of Petter Granli / ElephantVoices.org

how they interact with other elephants and how well they are able to influence members of their group (Moss and Lee, forthcoming).

Elephant Social Structure

Members of an elephant family exhibit a high frequency of association over time, display strongly affiliative behavior, including a pattern of greeting ceremonies (Moss 1981) and are highly cooperative in group defense, resource acquisition, offspring care, and decision making (Douglas-Hamilton 1972; Dublin 1983; Moss and Poole 1983; Lee 1987; Moss 1988; Poole 1998; Payne 2003). A matriarch, usually the oldest female, leads each family, and most, though not all family members, are genetically related. Archie et al. have found complete uniformity of mitochondrial DNA (mtDNA) haplotypes in approximately 90% of Amboseli families. Average pair-wise relatedness between adults in families is 0.14, similar to the value expected in first cousins (r = 0.125) (Archie et al. 2005). Over thirty-four years of study in Amboseli, through 2004, there have been sixty-one families, seven of which no longer exist because of the deaths of their members. In the same period of time, new family units have been formed by five fissions and two fusions. Family membership has ranged from two to fifty-two individuals and, in 2002, averaged 18.7 individuals (Moss and Lee, forthcoming).

—forthcoming. [FIGURE] Figures 4.2 and 4.3 about here



Figure 4.2 An African (*top*) and Asian (*bottom*) elephant family group walks in close proximity, providing care and reassurance to infants and calves. *Photograph of African elephants courtesy of Petter Granli / ElephantVoices.org; photograph of Asian elephants courtesy of Joyce Poole / ElephantVoices.org*

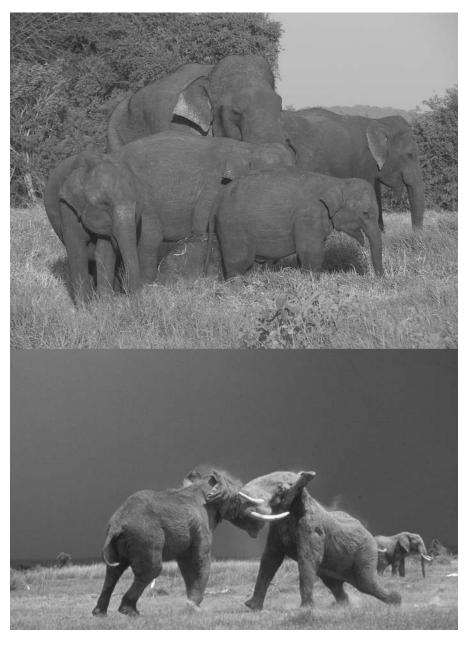


Figure 4.3 An Asian male elephant in musth tests females for receptivity (*top*); two African elephant males in musth duel for supremacy and access to an estrous female (*bottom*).

Photograph of Asian elephants courtesy of Petter Granli / ElephantVoices.org; photograph of African elephants courtesy of Joyce Poole / ElephantVoices.org

Above the level of the family unit a second tier of relationships exists within bond groups (Douglas-Hamilton 1972; Moss and Poole 1983; Wittemyer et al. 2005). A bond group may include as many as five families (Moss 1988). Although the ties between individuals at this level are weaker than those within a family, bond group members also exhibit greeting ceremonies, form alliances against aggressors, assist in the care of one another's offspring, and defend one another in times of danger. Since the majority of bond groups are probably fission products of former families (Moss 1988) most carry the same mtDNA haplotype (Archie et al. 2005). Yet, rarely, there do exist bond groups (closely cooperating individuals) composed of unrelated families. Archie et al. (2005) have pointed out that even within families there are individuals who, through chance demographic events, have no close relatives. Yet, these individuals still benefit from the same cooperative behavior. Cohesion within families and bond groups varies significantly and depends upon a combination of factors, including individual personalities, the formation and dissolution of individual social bonds, the strength of the matriarch's leadership, historical events such as deaths of influential individuals, the type of habitat, and the season (Moss and Lee, forthcoming).

Clans are the next social level and have been defined as families who share the same dry-season home range (Laws and Parker 1968; Douglas-Hamilton 1972; Moss and Poole 1983). A clan is usually composed of several bond groups and numerous families, such that several hundred elephants may make up a clan. Playback experiments using individual vocalizations (McComb, Moss, Sayialel, and Baker 2000) indicate that elephants, too, distinguish between more familiar associates (typically clan members) and less familiar ones (typically nonclan).

Many of Amboseli's elephants are still in the same family, occupying the same home range that they were thirty-four years ago, while some families have shifted clan, or exchanged bond group. A few individuals whose families have gone extinct have been adopted by unrelated families, and in one case, individuals abandoned their natal family to create a new family with members of a previously unrelated family (Moss 1988; AERP database). Long-term records demonstrate both the extraordinary fidelity and unusual flexibility of elephant social relationships (Moss and Lee, forthcoming).

During dry conditions, families tend to move in relatively small groups in their clan area, but when resources are abundant, families may gather in large aggregations in an expanded range (Poole and Moss 1989). In these aggregations, several clans may intermingle. Far from being random, the fission and fusion of elephant groups follow predictable patterns, tending toward association according to hierarchical clustering into families, bond groups and clans, and breaking down in the reverse order. Elephants ag-

gregate for different purposes (Western and Lindsay 1984), including antipredation (Laws, Parker, and Johnstone 1975), social benefits (Moss 1981), and improved mating opportunities (Poole and Moss 1989).

Although many mammals may follow some of the patterns exhibited by elephants, the combination of enormous social fluidity and durability of elephant associations and relationships is remarkable and rivals that of chimpanzees and humans in its complexity (McComb et al. 2000; Archie et al. 2005; Moss and Lee, forthcoming). Also notable is that kinship is not the only determinant of social bonds. Female elephants with few kin are not excluded from the benefits of sociality.

Young male elephants grow up in the tightly bonded society of females, maintaining close relationships with their relatives and participating in the many social events that affect their family, albeit at a lower intensity than their female agemates (Lee and Moss 1999; Poole, forthcoming). Males depart from their natal families between 9 and 18 years of age (Lee and Moss 1999). A newly independent male must acquire a fresh set of behaviors to adapt to the society of males, where body size and fluctuating sexual state determine interactions and relationships (Poole 1989a). His transition from one society to the other occurs gradually, but dramatically, over a period of several years (Lee, Poole, and Moss, forthcoming). During this time, a young male spends much of his time getting to know his agemates, and sparring and playing with novel partners from outside his natal family (Lee 1986). Thus he gathers information crucial to his longevity and reproductive success (Poole 1989a, 1989b; Lee et al., forthcoming; Poole, Lee, and Moss, forthcoming). Once fully independent, he forms relatively few close and long-lasting bonds with other elephants. Though males are often seen in small, all-male groups and may form lasting associations with certain individuals, these are rather loose arrangements (Croze 1972; Lee et al., forthcoming). During sexually active periods males rove from one family group to the next, using olfactory and acoustic cues to search for receptive females (Poole and Moss 1989).

Elephants Have an Unusually Large Social Network The social complexity hypothesis proposes that high intelligence has evolved to help individuals anticipate the plastic and often unpredictable behavior of group members (Jolly 1966). Social complexity has been cited as one indicator of intelligence (Byrne and Whiten 1988), and group size has been used as a measure of social complexity (Dunbar 1992). *Group* in this sense refers to long-term associates whose characteristics and histories are likely known to one another, rather than a temporary aggregation of strangers. This concept works well for species that live in stable, impermeable groups, but less well for species like humans, chimpanzees, whales, and elephants, that do not. For fission-fusion societies the term "social net-

work" encompasses such long-term associates. Just how large is an elephant's social network?

The Amboseli population is relatively small (1,417 at December 2005) compared with other elephant populations; yet, it is, nonetheless, a large society (McComb et al. 2000). In Amboseli, a female elephant may encounter literally hundreds of other individuals in the course of her daily range, and 34 years of records show that each family has been found with every other family in the population at least once (Moss and Lee, forthcoming).

Taking Amboseli's GB family as an example, we may estimate the size of one female's social network. Between 1974 and 2002, the GB family has grown from fourteen to thirty-seven members. Over this time, any given member of Amboseli's GB family found herself in a median group size of thirty-nine individuals, although at any particular moment she might (rarely) have been alone, with a small portion of her family, or in a group of 550 individuals (interquartile range 25–95; N = 1,294; AERP database). Members of the GB family have been sighted without other families on 428 occasions and with other families (in aggregations) 866 times. Of these 866 sightings, 59% of the aggregations included the IB family. The GB family was seen in aggregations with fifty other families, too, of which fourteen particular families were present in 15–30% of the sightings. Taking the population's current average family size, these close associates account for an estimated 261 elephants of which 125 (48%) are adult females at least ten years of age.

The question remains, however, do these animals know one another as individuals? To show that these are not just temporary aggregations of strangers, we must prove that elephants are able to distinguish between individuals, and to retain this knowledge over time. Work by biochemist Rasmussen and veterinarian Krishnamurthy (2000) found that offspring flehmen (a "chemical analysis" accomplished by touching the tip of the trunk on a liquid substance and placing it against the vomeronasal organ on the roof of the mouth) twice as often when presented with their mother's urine than with any other individual's urine, suggesting that they are able to distinguish their mother's urine. Even after a twenty-seven-year separation an offspring showed a flehmen response to its mother's urine (Rasmussen and Krishnamurthy 2000). Elephants answer the contact calls of close relatives, and, working in Amboseli, ethologist McComb et al. (2000) found that playing back the contact call of an elephant who had died elicited contact calling by her family unit almost a year after her death. Mc-Comb et al. (2000) also found that elephants recognized and usually answered the individual voices of their own family and bond group (ca. 40– 60 individuals), and they also distinguished between familiar and less familiar elephants on the basis of how often they were encountered. Mc-Comb et al. (2000) predicted that the females would have to be familiar

with the voices of at least 100 *adult* females to make the observed discriminations, indicating that elephants have one of the largest known social networks of any nonhuman species.

Males, too, make use of social knowledge in a large network. Complementary male postures in long-distance dyadic interactions (i.e., those between a paired group of individuals) indicate that males recognize one another visually, and that they are aware of one another's relative size, strength, and condition (Poole 1982, 1989a). An instance of such interaction would be a higher-ranking male posturing with Head-High; Ear-Spreading; Ear-Folding; Advance-Toward, while the corresponding *lower-ranking male is* posturing with Head-Low, Ear-Flattening; Turn-Away; Retreat-From; (Poole 1987, 1999a; Kahl and Armstrong 2000; Poole and Granli 2003). Males also use sound (Poole et al. 1988; Poole and Moss 1989; Langbauer et al. 1991) and scent (Rasmussen et al. 1982; Rasmussen and Schulte 1998), to remotely monitor the location of receptive females. Approximately, three weeks before true estrus and ovulation, female elephants exhibit a period of estrouslike behavior, referred to as "pre-estrus" (Poole and Moss 1989), that is associated with an anovulatory LH (lutenizing hormone) surge (Kapustin et al. 1996) and increasing pheromone secretions (Rasmussen, Krishnamurthy, and Sukumar 2005). Males accompanying a female during the pre-estrus are likely to be the same individuals who associate with her later during her true estrus (AERP database). During the intervening days, these same males may be many kilometers apart from that female, searching for, or consorting with, other females (AERP database). The median number of males in association with an estrous female in Amboseli is 5 (interquartile range 3–8; range 1–40; N = 728; AERP database). Because upward of 100 adult males may associate with female groups in the population at any given time, there is strong suggestion that individual males may relocate a female during true estrus using acoustic and olfactory cues as well as memory of her individual identity and clan area, and therefore of her likely location.

Although other mammals are also able to recognize the voices and scents of conspecifics (members of their own species), the sheer number and longterm retention of social information makes elephants unusual. McComb et al. (2001) showed that such vocal discriminations are learned through years of experience and older individuals are more discerning than younger ones. McComb et al. (2000) argue that an unusually large and fluid social network may be a phenomenon unique to long-lived mammals like elephants, equipped with long-range signaling capability and the mental capacity for extensive social recognition.

Rate of Change in Social Setting

Given a large and fluid social network in which group composition changes rapidly, elephants may encounter literally hundreds of individuals each day.

For example, of the 1,294 sightings of the GB family, 311 (24.0%) were of groups of 100 individuals or more; 190 (14.7%) were of groups of 150 elephants or more, and 122 (4%) were of groups of 200 elephants or greater. The number of elephants encountered by each female each day, and the rate of change, prove unusually large, especially when one considers that these data represent instantaneous sightings and that groups change in size and composition many times per day (Mutinda 2003).

Sexually active males, searching from group to group for receptive females, may also meet and interact with hundreds of different individuals, male, and female, in the course of a day (Poole and Moss 1989). The nature of a male's interactions with those he meets is strongly influenced by his age, body condition, and sexual state (Poole 1982, 1989a).

Elephants are able to recognize the voices, scent, and appearance of many individuals, some of whom they encounter only relatively rarely. Although the social setting of many other species may also change during the course of a day, the sheer number of individuals involved and the hierarchical nature of the formation and dissolution of aggregations make elephants unusual. Under these circumstances, the importance of being able to distinguish genuine strangers from a wide range of more regular associates is not insignificant (McComb et al. 2001).

Social Learning

There is empirical evidence that social learning and behavioral innovation are positively correlated with brain size in mammals (Reader and Laland 2002). Both behavioral innovation and social learning are essential elements in the development and maintenance of elephant social complexity.

Learning What to Eat

Infant elephants must learn and practice complex coordination of the trunk and apply this gradually acquired skill to the procurement of appropriate foods (Lee and Moss 1999). Calves begin to sample potential food items when they are 1 to 2 months old. Sampling consists of grasping objects with their trunk, rolling food items in their trunk, and placing food matter in their mouths. At times young calves may chew, but sampling starts well before actual ingestion. Calves gradually acquire foraging knowledge by sampling what adults are eating. They attain this information by placing their trunks in the mouths of adults and pulling out food items, stealing food from their mothers and allomothers, as well as by eating the fresh dung of other elephants (Eisenberg 1981). Throughout their first five years, calves spend 15.8% of their social contact time exploring the food intake of others (Lee and Moss 1999). Elephants have many food sources, and social learning allows calves to exploit a wide range of these seasonally and geographically varying species (Lee and Moss 1999).

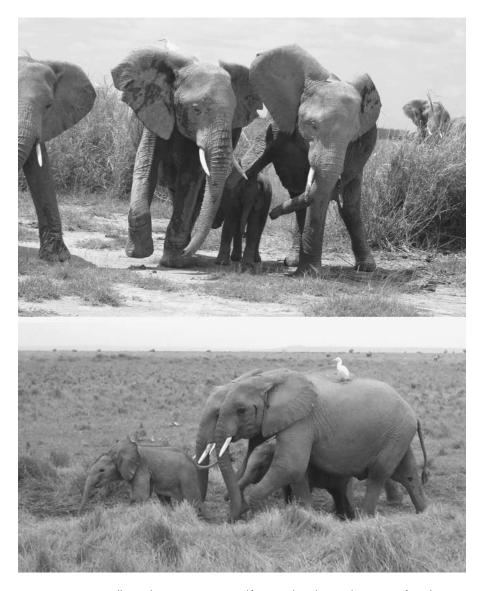


Figure 4.4 Allomothering increases calf survival and provides young females with an array of caretaking experiences that persist until they give birth to their own first calf. A juvenile female rescues her younger sibling from an attempted kidnapping by a nonfamily juvenile female and calls for the assistance of her mother (*top*); juvenile females shepherd infant Emily Kate back to her mother (*bottom*).

Photograph courtesy of Petter Granli / ElephantVoices.org

Learning to Care for Calves

Juvenile females play a vital role in the care of young calves (Lee 1987). Allomothering both increases calf survival (Lee and Moss 1986) and provides young females with an array of caretaking experiences that persist until they give birth to their own first calf). Despite this practical social experience,

first-born infants still have higher mortality rates than infants born to experienced mothers (Moss 1994), indicating that even by the age of first parturition (14–15 years) female elephants still have much to learn about mothering. The calves of inexperienced mothers show higher levels of distress than do calves born to experienced mothers, who appear to be more responsive to calf demands for food and protection, with obvious consequences for calf growth and survival (Lee and Moss 1999). In addition, first-time, or primiparous, mothers are given more assistance from family members than are older mothers. Knowledge gained from experiences over a succession of births plays an important role in calf survival.

—survival. [FIGURE] Figure 4.4 about here

Social Learning as an Aspect of Female Reproductive Behavior Some behaviors essential to mate choice, such as consort behavior, appear to require a social context for learning. Young estrous females do not demonstrate the estrous behavior typical of older females and are frequently chased and mounted by a succession of young and nonmusth males (Moss 1983). As a female gains individual experience through successive estrous periods her responses to males change; she learns to avoid young males and to select and go into consort only with large musth males (Moss 1983; Poole 1989b). Both the acquisition of estrous behaviors and the choice of mates appear to be facilitated by the presence and behavior of the mothers of these young females (AERP database). Mothers of young estrous females are often observed exhibiting estrous postures and behaviors when not in estrus themselves (AERP database; J. Poole, personal observation). Mothers (and occasionally nonmother matriarchs) may be observed to approach and avoid males, run with their young estrous daughters (or young estrous members of their family) during long chases and occasionally make postcopulatory calls after the young female is mated (BBC) Natural History Unit 1995). The behavior of mothers and daughters during a daughter's first estrous period not only indicates the importance of a social context for learning, but also suggests that mother elephants may be engaged in a rudimentary form of true teaching.

The birth of a female's first calf is another documented event where the presence and behavior of experienced females aids inexperienced mothers. Experienced family members assist young females to cope with the physical demands of birth, including helping a newborn to its feet, and with the immediate protection and socialization of the newborn calf (Moss 1988; Lee and Moss 1999).

Social Learning as an Element in Male Independence

In exploratory and play behavior, young males seek same-sex play partners outside the family, thereby socializing and bonding with their future peer group while simultaneously assessing the strength of their future rivals (Lee

1986). This male behavior can be linked to male emigration from the natal family, an event that occurs at an average age of 14 years (Lee and Moss 1999). The process of a male's departure from his family averages 16 months, but ranges anywhere from 5 to 35 months (Lee et al., forthcoming). The wide range in duration indicates that the process of male independence is probably a highly individualized event. Male mortality in the 10–20-year age bracket is also significantly higher than in females (Moss 2001). To survive on their own newly independent males require sufficient social experience with other males along with knowledge of male areas of residence and surrounding habitat (Lee and Moss 1999).

Social Learning and Role Models in Male Reproductive Behavior Young males appear to learn to distinguish between reproductive odors. For example, young males, though not older males, often mistake the smell of a pre-estrous female or one who has just given birth, for that of a receptive female (J. Poole, personal observation). Successful mounting and intromission, too, appears to require considerable skill and experience. This learning process may, in part, be gained by watching the behavior of older, more experienced males. Young male elephants are often observed to follow older must males, testing the same urine spots and females that they do. Musth males are extremely tolerant of these youngsters, allowing them to stand less than a meter from an estrous female while older males are kept at long distances (Poole 1982). Experience from southern Africa also highlights the importance of social learning in the acquisition of appropriate male reproductive behavior (Slotow et al. 2000). Juvenile male elephants that experienced their families killed in a culling operation and were then introduced to areas without adult role models exhibited abnormal reproductive behavior as young adults, including the mounting, tusking and killing of black rhinos. While trauma is likely to have been a causal factor in the development of this abnormal behavior (Bradshaw et al. 2005), it is also likely that the absence of adult males contributed to the inappropriate sexual reaction of these young males.

The Role of Social Learning in Tool Manufacture and Use

Elephants are unusual among nonprimates in that they use and even manufacture simple tools. The sensorimotor specializations of the trunk are extensive (Rasmussen and Munger 1996), allowing delicate manipulations of both large and small objects. Elephants pick up objects (logs, rocks) and throw them at opponents, use sticks to remove parasites, branches as fly switches, and logs to neutralize electric fences (Poole 1998). A study of Asian elephants by ethologist and sociologist Lynette Hart and colleagues (2001) indicates that elephants modify the length of long branches to make a suitable fly switch. That study also describes the role of social learning in

the acquisition of tool use. Adult Asian elephants modify branches by pulling off leaves and shortening sticks to create fly switches of ideal length. Two young elephants, ages 18 and 9 months, imitated the fly switching behavior of adults. The 18–month-old calf was able to remove a side branch successfully and was coordinated in switching with the modified shorter branch. The 9–month-old showed only uncoordinated attempts to switch, but her movements appeared to imitate the fly switching behavior of older elephants.

Vocal Learning

Very few mammals are capable of producing or modifying sounds in response to auditory experience (McCowen and Reiss 1997; Tyack and Sayigh 1997; Janik and Slater 2000). Those that can include humans, some marine mammals (e.g., bottlenose dolphins, Tursiops truncates; harbor seals, *Phoca vitulina*; humpback whales, *Megaptera novaeangliae*) and bats. Despite the obvious significance of vocal imitation for human-language acquisition, there is scant evidence for vocal production learning in other primates. Recently, Poole et al. 2005 provided two examples of vocal imitation in African elephants: A young female elephant who imitated the sounds of trucks, and an African male zoo elephant who imitated the chirping sounds of the Asian elephants with whom he was raised. Earlier reports have described Asian elephants who have learned to produce whistling sounds by blowing air through their trunks, and still other elephants who have imitated this innovative whistling technique (Wemmer and Mishra 1982; Wemmer, Mishra, and Dinerstein 1985; I. Douglas-Hamilton, personal communication). Vocal production learning enables a flexible and open communication system, involving both behavioral innovation and social learning, in which animals may learn to imitate sounds not typical of their species. Poole et al. 2005 suggest that vocal learning should likely occur in other species in which long-lived social bonds are based on individual-specific relationships and involve fluid group membership, and where vocal communication functions in maintaining contact, in individual or group recognition and in mediating social interactions.

One of the hypotheses of the origin of human language is that it arose to encode increasingly complex information about social relationships (Worden 1998; Dunbar 2003; Pinker 2003). The association between species that show vocal production learning abilities and those with fission-fusion societies supports this hypothesis (e.g., cetaceans, elephants, chimpanzees, humans). In describing the social origin of language hypothesis, Pinker (2003), has suggested that sociality, knowledge gathering, and language co-evolved in humans, in that language reinforces social relationships and provides a mechanism for distributing knowledge to associates. These three characteristics of human societies appear to be evident, to a lesser extent, in elephants.



Figure 4.5 Members of an elephant family exhibit a high frequency of association over time and display strongly affiliative behavior, including a pattern of greeting ceremonies. Here mother and daughter greet one another. *Photograph courtesy of Petter Granli / ElephantVoices.org*

Communication as a Measure of Social and Cognitive Flexibility Species that make use of both *contextual* learning (behavioral context and sequential positioning) and *production* learning (modification based on experience) are theoretically capable of developing a more complex acoustic communication system than species utilizing only the former. Each additional form of vocal learning can increase the complexity of a communication system; the more forms present the greater the system's potential for openness and plasticity (Janik and Slater 2000).

Elephants make use of both contextual and production learning and, as predicted, their acoustic communication system includes an extensive vocal repertoire with a high degree of variability both within and between individuals (Poole et al. 1988; Langbauer 2000; McComb et al. 2000; Leong et al. 2003; Soltis, Leong, and Savage 2005a, 2005b; Poole, forthcoming). Elephants also have a wide range of visual and tactile gestures and displays (Kahl and Armstrong 2000; Poole and Granli 2003) and intricate chemical communication (Rasmussen and Krishnamurthy 2000). Together this complex suite of vocal, chemical, visual, and tactile signals mediates the intricate teamwork displayed by members of an elephant family (Poole,

forthcoming; Poole and Granli 2003). Day to day decision making (e.g., deciding when and where to go; antipredator responses) involves broad vocal participation and often includes the building of consensus through vocal exchanges that may take up to an hour (J. Poole, personal observation; C. Moss, personal observation).

—observation. [FIGURE] Figure 4.5 about here

Indicators of Elephant Intelligence

Brain Size and Complexity

Until recently, only scant information was available on the brains of elephants, with the majority of the literature based on only a few specimens (Cozzi, Spagnoli, and Bruno 2001). Recent work has added to our knowledge (Hakeem et al. 2005; Shoshani, Kupsky, and Marchant 2006). The brains of Asian and African elephants rank among the highest of all animals for absolute and relative mass and cortical expansion and complexity, features comparable only to those of some of the cetaceans, the great apes, and humans. Weighing 4.5–6.5 kilograms, the elephant's brain is the largest in absolute mass among land mammals (Cozzi et al. 2001), with the brain of *E. maximus* weighing up to 5.5 kilograms, and that of *L. africana* being slightly heavier and larger. The temporal lobes of the elephant's brain, which are thought to function in recognition, storage and retrieval of information related to sight, touch, smell, and hearing, are especially large and extremely complex (Shoshani 1998; Shoshani et al. 2006).

The encephalization quotient (EQ), the ratio between the observed and expected brain weight for a defined body weight (Jerison 1973), implicitly holds that body size is taken as a "given" and selection operates only on brain size. An EQ equal to 1.0 is an "average" mammalian brain. Primates all have relatively high EQs, with *Homo sapiens* at 7.0+ demonstrating a quotient far above that of all other mammals. Elephant values, at between 1.7 (Shoshani 1998; Eisenberg 1981) and 2.3 (Cutler 1979) are comparable to those of larger primates (e.g., chimpanzee: 2.2–2.4; gorilla: 1.4–1.7; orangutan: 1.6–1.9; Eisenberg 1981). Where sexual dimorphism is pronounced, as in elephants, males have lower EQ values than females (EQ L. africana: male: ca. 1.0; female: 2.0; Eisenberg 1981). Clearly age and sex are important criteria in determining the importance of EQ, and for a variety of reasons many have argued that EQ may not be a particularly useful guide to relative intelligence (e.g., Byrne 1996; Roth 1999). Neurobiologist Roth (1999) and cognitive ethologist Byrne (1996) argue that what should be important for intelligence is the absolute number of nerve cells in the brain, as more nerve cells mean the potential for more complicated networks. Elephants have a very thick cerebral cortex, and although its cell density is lower than that of humans, elephants are estimated to have as many neurons as humans, namely between 10¹¹ and 10¹². Shoshani et al. (2006) pos-

tulate that convergent evolution as seen in complex learned skills and behavior may be responsible for the many similarities observed between the human and elephant brain.

Long-Term Memory

As a general rule vertebrate species with absolutely large brains have developed the neocortex (the complicated parts of the cerebral cortex) to a greater degree, have greater capacity for learning, and seem to be able to learn more complicated tasks than vertebrates with absolutely smaller brains (Rensch 1956, 1957). In addition, it seems that larger animals with large brains also have the ability to retain information for longer than smaller animals with smaller brains. In other words they have better memory (Rensch 1956, 1957). Exceptionally large and long-lived, elephants accumulate and retain social and ecological knowledge, remembering other individuals (McComb et al. 2000; Rasmussen and Krishnamurthy 2000; McComb et al. 2001) and places (Viljoen 1990; Shoshani and Eisenberg 1992) for years.

In experimental trials, elephants show an excellent ability to learn and remember a large set of visual symbols and acoustic tones or commands over long periods (Rensch 1957). Playback experiments in Amboseli also provide good evidence for an elephant's exceptional memory. Companions use powerful calls to stay in contact when visually separated (Poole et al. 1988). As mentioned previously, elephants remember the contact calls of family and bond group members and distinguish them from those of females outside these categories; moreover they can also discriminate between the calls of family units farther removed than bond group members on the basis of how frequently they have encountered them (McComb et al. 2000). In fact, McComb et al. (2000) predicted that females would have to be familiar with (i.e., remember) the contact calls from at least 100 adult females in order to perform these discriminations. McComb et al. 2001 also found that older matriarchs possessed enhanced socially relevant, discriminatory abilities, which are learned and remembered over many years of experience. These older females acted as a repository of social knowledge that contributed to increased fitness for the entire family.

In addition, playback to her family unit of the contact call of a 15–yearold female that had died elicited contact calling three months after her death, and contact calling and approach to the loudspeaker twenty-three months after her death (McComb et al. 2000). Also, playback of the contact call of a female who had departed from her family to join another one, twelve years previously, also elicited contact calling (McComb et al. 2000).

Accounts of rare events by qualified observers also indicate that elephants are able to remember the voice and perhaps scent of individual people for over twelve years (R. Moore, personal communication; J. Poole,

personal observation) and individual elephants for over 23 years (C. Buckley, personal communication). In the latter case, the specific protective behavior of elephant Shirley (ca. 53 years) toward Jenny (ca. 30 years), when reunited, suggested that they not only remembered one another, but also remembered the adult-juvenile relationship they had once shared. In the mid 1980s, one of us (J. Poole) established a relationship with Vladimir, a wild male elephant, who sometimes came to her car window allowing her to touch him (Poole 1996). In 2003, after a twelve-year separation, Poole met Vladimir, then aged 34 years, and called to him. He walked up to her window and allowed her to touch him. To the best of our knowledge, he has not interacted with any other person in this manner (AERP colleagues, personal communication).

Machiavellian Intelligence In Elephants

The term Machiavellian intelligence was coined to refer to the hypothesis that increased intelligence was linked to the evolution, through competitive tactics, of socially complex behavior predicated upon a good memory for socially relevant information (Byrne and Whiten 1988; Byrne 1996). The principles of Machiavellian intelligence were originally used to explain the socially complex behavior of monkeys and apes, but more recently, nonprimate species have been shown to exhibit similar traits (see Byrne 1996). Typical social traits include the formation of long-term social relationships, use of third party or triadic intervention to decide the outcome of competitive encounters, dependence on a network of allies, grooming used to build up a network of support, active reconciliation used to repair strained relationships, use of tactical deception, and the classification of others by dominance rank, affiliation or group membership. Successful use of these social tactics demands good perception and discrimination, attention to social attributes and good memory, all of which are displayed by elephants. The abilities ascribed to Machiavellian intelligence require neocortical enlargement and exceptional memory to retain and process socially relevant information (Byrne 1997b), qualities that are, again, characteristic of elephants.

Elephants are contenders for rank among those species possessing Machiavellian intelligence, in every respect. The formation of long-term relationships is the very essence of elephant society and a network of allies, who are usually though not always genetically related, defines the elephant family and bond group. These supportive relationships are maintained not by social grooming as in primates (Dunbar 1988), but through an elaborate system of vocal, visual, chemical and tactile signals and ceremonies between relatives and friends (Moss 1988; Poole et al. 1988; see also Poole and Granli 2003, 2004). The most well known of these is the greeting ceremony (Moss 1988), but reunions are by no means the only situation under which such a display of "bonding" occurs. Similar exuberant demonstrations of

the importance of a social bond occur in a multitude of different contexts, including, among others: after a family member's infant or calf has been lost, frightened, or denied access to the breast; if a member of the family has been chased or harassed by another elephant; when a baby is born; or following a disturbing or exciting event (Poole, forthcoming).

When key relationships are put at risk by conflict, some primates make efforts to reconcile, and dyads that reconcile are more likely to continue to support one another (Cords 1997; de Waal and van Roosmalen 1979). Similarly, conflict between two individuals in an elephant family typically results in vocal reconciliation that—even more sociably—usually involves the intervention of a third party (J. Poole, personal observation). Third parties play an important role in deciding the outcome of conflicts among elephants, including support given to genetically unrelated individuals (Moss 1988; Payne 2003 Archie et al. 2005). These "friendships" are maintained by reciprocal altruism (Payne 2003). Work by McComb et al. (2000) shows clearly that elephants are able to recognize and respond appropriately to the voices of others and that they are able to classify others by group membership at the very least. Finally, there are many accounts of tactical deception by elephants, though these are mostly anecdotal reports by elephant keepers rather than data based on experimental trials or observations in the wild (e.g., see Rensch 1957; Chadwick 1992; Poole 1998). Many of these extraordinary accounts are of elephants deceiving their keepers to obtain food or freedom. Detailed documentation of such tactical deception is now needed.

Anticipatory Planning, Insight, and Theory of Mind

The combination of longevity, long-term memory, social learning, and behavioral innovation might lead us to expect elephants to display other cognitive abilities, such as insight and theory of mind. Insight refers to behavior that shows the understanding of relations between stimuli and events, while theory of mind is defined as an ability to understand that others see, feel, and know (see also Varner, Chapter 3 in this volume).

In the wild, anecdotal evidence certainly suggests the use of insight by elephants in response to electric fences. Elephants frequently disable electric fences by dropping logs onto them, or by uprooting and pushing trees onto them, causing live wires to sag onto ground wires, thus shorting the fence (Laikipia Ranch, Kenya, fence maintenance crew, personal communication; Seneviratne and Rossel, Chapter 17 in this volume). Reports exist of elephants lifting their infants over fences (Chadwick 1992; Ngulia Sanctuary, Tsavo National Park, Kenya, fence maintenance crew, personal communication). In captivity, elephants have been known touse sticks to pull out-of-reach food closer; open faucets, and, once these were bolted shut, use rocks to break the nuts loose from the bolt; throw tires onto nearby branches to weight them down to a level within reach; make a pile

of tires to stand on so as to reach branches otherwise out of grasp (Chadwick 1992). Shoshani and Eisenberg (1992) recount an extraordinary tale of an elephant that ingeniously placed vegetation under his feet to prevent himself from sinking into muddy ground where he was tied, as he could not reach dry ground. Evolutionary biologist Bernhard Rensch's (1957) observations of the ability of domesticated elephants to work with minimal instruction and their talent to function as a team with extraordinary balance and coordination, pushing and dragging heavy logs up inclined bars onto a truck, caused him to credit elephants with true insight or "ideation"—the ability to anticipate what will come of certain actions.

Behavior that qualifies as insight cannot be genetically wired or acquired by trial and error. The problem must be new, or the animal must come up with a new solution. The correct behavioral sequence must be arrived at suddenly and completely and carried out relatively smoothly, with all its constituent elements purposefully aimed at a single goal (Nissani 2004).

In Amboseli one of us (J. Poole) also witnessed behavior that meets these criteria. In 1999 Poole witnessed Ella giving birth, an event accompanied by thirty minutes of excited vocalizations by her family and other females (Poole 1999b). The commotion attracted other elephants, including young and inexperienced Ramon, who upon sniffing Ella, mounted her, his body and feet suspended above the newborn. Matriarch Echo, and her adult daughter, Erin, rushed immediately to Ella's side, backing, in parallel, purposefully toward her and placing themselves resolutely on either side of her. In what appeared to be a very deliberate attempt to prevent the male from crushing the infant when he dismounted, their behavior appeared to be a case of true insight. Both authors also witnessed Victoria and Virginia (the two oldest females in a large family) rush to stand on either side of Vega, who had been darted with an immobilizing drug, and push into her, thus holding her up and preventing her from falling down. Only after forceful driving at them with vehicles would they give up.

Theory of mind accounts exist, too, with an often-related tale being that of Chandrasekhan, the elephant that would not lower a pillar of wood into a hole containing a sleeping dog until the dog was chased away (Shoshani and Eisenberg 1992). Many accounts are available from the wild, too. For example, the respected naturalist Tony Archer (personal communication) witnessed a young male repeatedly tusk a crippled female who had fallen behind her family. A large, older female (possibly a relative) suddenly ran from 40 meters away to chase the male and, having seen him off, returned to touch the other female gently on her withered leg. The specific behavior of the older female also indicated that she might have understood the particular feelings of the crippled female, possibly demonstrating her possession of theory of mind.

While it may be possible to explain some of these accounts as examples

of genetically wired behavior or trial-and-error learning, without invoking insight or an ability of elephants to understand that others see, feel, and know (i.e., theory of mind) recent work by geneticist Moti Nissani (2004) indicates we should be cautious in drawing such conclusions. In three experiments using captive individuals, Wanda and Winky, Nissani explored the question of whether elephants are capable of theory of mind and insight, by focusing on whether elephants know that people use the sense of sight (see Varner, Chapter 3, for more details). Although Nissani's research is not conclusive, it adds to growing evidence supporting the view that elephants may be capable of both insight and theory of mind.

In the human brain, there exist multiple mirror neuron systems. Mirror neurons are cells in the brain that specialize in carrying out and understanding not only the actions of others but their intentions as well as the social meaning of complex behavior and secondary emotions such as disgust, shame, and guilt. By simulating a "mirror image" of another's actions in our brain we are able to empathize, imitate, and acquire language. Mirror neurons are, in effect, the source of our theory of mind. In a sense, mirror neurons absorb culture directly, with each generation teaching the next through sharing, imitation, and observation (cited in Blakeslee 2006).

Research by neuroscientist Giacomo Rizzolatti, on mirror neurons in the brains of monkeys have found that these cells, too, are active *in situa*tions that would inspire empathetic feelings (described in Blakeslee 2006). Some elephants have been observed attempting to raise an immobilized or dying elephant to its feet (J. Poole and C. Moss, personal observation; Douglas-Hamilton et al. 2006) or returning to the corpse of a dead companion many times over the course of days and weeks (Douglas-Hamilton et al. 2006). Taken together, these mirror neuron studies and elephant observations suggest that monkeys and probably other highly social species like apes, elephants, dolphins, and even dogs experience empathetic feelings and that the basis for theory of mind exists in a network of cells with the same origin as our own more complex capability.

Some years ago one of us (J. Poole) watched elephant Eliot flinch violently as Eudora, 10 meters away, reached out her trunk to test if an electric fence was connected. We suggest that Eliot's mirror neurons were actively firing as she experienced a moment of fear in anticipation of Eudora's potential shock. Vocal production learning and other imitative abilities in elephants may be yet another piece of evidence in the jigsaw puzzle pointing to elephant theory of mind.

Self-Recognition in Elephants

Self-directed behaviors in front of a mirror have been interpreted as indicative of self-recognition (Gallup 1970). Furthermore, researchers maintain that if an animal recognizes itself, then it must have, however rudimentary,

a sense of self. Mirror self-recognition (MSR) has, thus, been expected to correlate with higher forms of both altruistic behavior and empathy. Dozens of primate species have been exhaustively tested for self-recognition using the mirror-mark test, and only the great apes have conclusively passed the test (Gallup, Anderson, and Shillito 2002). In 2001, mirror self-recognition was demonstrated in bottlenose dolphins, a species also noted for complex social behavior and empathetic traits (Reiss and Marino 2001). Recently, Plotnik et al. (2006) demonstrated that elephants, too, are capable of mirror self-recognition (see also Varner, Chapter 3). Plotnik et al. postulate that MSR in apes, dolphins and elephants offers persuasive evidence for convergent evolution in the self-other distinction that underlies the social complexity, cooperation and altruistic tendencies noted among these large-brained mammals.

Reaction to Trauma and Death

Recent work by trauma researchers Bradshaw et al. (2005) suggests that early disruption of attachment can result in social trauma that may affect the physiology, behavior, and culture of elephants over generations. Such disruption occurs during culls where adults are killed and infants are spared during capture and abusive training of infants for captive use; and during high-level poaching. An intact social order may buffer trauma, but as human populations increase more elephants are living in environments influenced by relentless human disturbances. The consequences of these experiences can be seen in abnormal levels of aggression in the wild (Slotow et al. 2000) and in captivity (see also Hancocks, Chapter 13 in this volume).

A discussion of elephant cognitive capacities would be incomplete without the mention of elephants' reaction to death. Elephants exhibit a variety of responses to dying or dead elephants and their bones, including touching with the trunk and feet, attempted lifting and carrying of the body or bones, mounting, feeding, body guarding, covering, and burying (Douglas-Hamilton and Douglas-Hamilton 1975; Moss 1975, 1988, 1992; BBC Natural History Unit 1992, 2005; Poole 1996; Payne 2003; Douglas-Hamilton et al. 2006; McComb et al. 2006). Although elephants exhibit this behavior primarily toward other elephants, they may also stand over or cover the bodies of humans or other animals that they kill (Poole 1996) or of those that they find killed by predators (N. Njiraini, S. Sayialel, and N. Sayialel, personal communication). People have known about the reaction of elephants to death for thousands of years (Meredith 2001) and as far as we are aware no one has yet come up with a plausible alternative to the explanation that elephants have, however basic, a concept of death.

In summary, relative to other mammals, including humans, elephants are unusually long-lived and exhibit a high degree of social complexity. Their —volume). [FIGURE] Figure 4.6 about here



Figure 4.6 Early disruption of attachment such as occurred during culls where adults were killed and infants were spared can result in social trauma that may affect the physiology, behavior, and culture of elephants over generations. *Photograph courtesy of Oria Douglas-Hamilton*

development includes social learning and behavioral innovation, both of which are manifested in the use and modification of rudimentary tools and in vocal learning. Elephants have extensive neocortical development, very good memory and are evidently adept users of Machiavellian intelligence. Mirror self-recognition by elephants indicates self-awareness (Plotnik et al. 2006), and numerous observations suggest elephants have a rudimentary theory of mind and anticipatory planning capabilities that may include imagining future events, such as pain inflicted on themselves and others and possibly their own deaths. Although many other species may rival elephants in one capability or another, there are few that equal or surpass elephants in the totality of their social and behavioral complexity.

The evidence presented in this chapter, including the recently published Bradshaw et al. 2005 report on the long-term effects of trauma, indicates that we must err on the side of caution when welfare issues are being weighed, and that individual elephant well-being, not commercial gain, must be the priority. This conclusion has broad implications for the management of elephants in the wild and in captivity. It is not within the scope of this essay to set guidelines for the treatment and care of elephants, but certain guiding principles, most of which are discussed in Clubb and Mason's report about European zoo elephants (2002) and in Kane, Forthman, and Hancocks (2005a, 2005b), should be put into practice.

As large, highly social, and intelligent animals, elephants require ample, environmentally complex space and a sufficient number of conspecifics for social contact and learning. We should be moving toward a situation in which institutions are permitted to keep elephants only if the captive situations provide sufficient space for adequate exercise and stimulation and allow the elephants to choose among social partners.

In seasonally cold climates, elephants are usually restricted to indoor barns when the outside temperature goes below about 4.4 degrees centigrade. In zoos that experience long, severe winters elephants may be indoors, with inadequate space, exercise, and social stimulation for months at a stretch. Because of the many negative consequences of restricted space on elephant physical and emotional well-being, zoos located in areas with prolonged cold winters should be precluded from keeping elephants.

Elephants (including males) should be allowed access to a social group, not kept in isolation. Males should be allowed to remain with their family until the age of natural dispersal; females should remain together for life. During parturition females should remain unchained and in the company of family members, particularly if experienced females are present. Infants and calves should not be removed from the care of their mothers and family members. Most elephant mothers in zoos were not themselves exposed to allomothering experiences, and their very poor success as mothers is a clear consequence. The tradition of removing an elephant from its social group for the purpose of exchange with other zoos or circuses should cease. All forms of physical discipline and punishment must be discontinued and chaining should stop unless absolutely necessary for veterinary care. Thus, on the basis of all these criteria, circuses are not an appropriate environment for elephants and most zoos will have to make substantial changes to meet the most basic needs of elephants.

In the wild the practice of abducting young elephants from their families should end. The culling of elephants should be avoided except where all other options have been exhausted. When culling is deemed essential it should include whole families; infants and calves should not be spared for export to zoos, circuses, safari parks, or private reserves. The parallel practice of introducing traumatized youngsters to new areas without adult role models should stop. Alternative practices to culling such as translocation and birth control also have welfare implications, and these must be carefully evaluated. Human-elephant conflict is the cause for increasing ethical dilemmas, and in cases where it is deemed that an elephant must be euthanized, it should be done efficiently and humanely.

What is the right way to treat beings such as elephants? As writer Douglas Chadwick (1992, 475) states, "If a continuum exists between us and such beings in terms of anatomy, physiology, social behavior, and intelligence, it follows that there should be some continuum of moral stan-

dards." Based on available evidence, the time has come for us to move beyond old patterns in the treatment of elephants. We must acknowledge and accept new standards for the future.

References

- AERP Database. Data extracted from the long-term sightings, censuses, or field notes of the Amboseli Elephant Research Project.
- Archie, E. A., Moss, C. J., and Alberts, S. C. 2005. The ties that bind: Genetic relatedness predicts the fission and fusion of social groups in wild African elephants. *Proceedings of the Royal Society B* 273: 513–522.
- BBC Natural History Unit. 1992. Echo of the Elephants. Cinematography by Martyn Colbeck.
- BBC Natural History Unit. 1995. *Echo of the Elephants: the Next Generation*. Cinematography by Martyn Colbeck.
- BBC Natural History Unit. 2005 *Echo of the Elephants: the Last Chapter*? Cinematography by Martyn Colbeck.
- Blakeslee, S. 2006. Cells that read minds. *New York Times*, January 10. http://query.nytimes .com/gst/fullpage.html?res=9900E3D81F30F9
- Bradshaw, G. A., Schore, A. N., Brown, J. L., Poole, J. H., and Moss, C. J. 2005. Elephant breakdown. Social trauma: Early trauma and social disruption can affect the physiology, behaviour, and culture of animals and humans over generations. *Nature* 433: 807.
- Byrne, R. W. 1996. Relating brain size to intelligence in primates. In P. A. Mellars and K. R. Gibson (eds.), *Modelling the early human mind* (pp. 49–56). Cambridge: Macdonald Institute for Archaeological Research.
- Byrne, R. W. 1997a. What's the use of anecdotes? Distinguishing psychological mechanisms in primate tactical deception. In R. W. Mitchell, N. S. Thompson, and H. L. Miles (eds.), Anthropomorphism, Anecdotes, and Animals (pp. 134–150). Albany: State University of New York Press.
- Byrne, R. W. 1997b. Machiavellian intelligence. Evolutionary Anthropology 5: 172–180.
- Byrne, R., and Whiten, A. (eds.). 1988. *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans*. New York: Oxford University Press.
- Chadwick, D. H. 1992. The fate of the elephant. San Francisco: Sierra Club Books.
- Clubb, R., and Mason, G. 2002. A review of the welfare of zoo elephants in Europe. Horsham, UK: Royal Society for the Prevention of Cruelty to Animals (RSPCA).
- Cords, M. 1997. Friendships, alliances, reciprocity, and repair. In A. Whiten and R. W. Byrne (eds.), *Machiavellian intelligence II: Extensions and evaluations* (pp. 24–49). Cambridge: Cambridge University Press.
- Cozzi, B., Spagnoli, S., and Bruno, L. 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.
- Croze, H. 1972. The Seronera bull problem: Part I. The elephants. *East African Wildlife Journal* 12: 1–27.
- Cutler, R. G. 1979. Evolution of longevity in ungulates and carnivores. *Gerontology* 25: 69–86.
- de Waal, F., and van Roosmalen, A. 1979. Reconciliation and consolation among chimpanzees. *Behavioral Ecology and Sociobiology* 5: 55–56.
- Douglas-Hamilton, I. 1972. On the ecology and behaviour of the African elephant. DPhil diss., Oxford University.
- Douglas-Hamilton, I., and Douglas-Hamilton, O. 1975. *Among the elephants*. New York: Viking Press.
- Douglas-Hamilton, I., Bhalla, S., Wittemyer, G., and Vollrath, F. 2006. Behavioural reactions of elephants towards a dying and deceased matriarch. *Applied Animal Behaviour Science*. 100: 87–102.
- Dublin, H. T. 1983. Cooperation and reproductive competition among female African ele-

phants. In S. Wasser (ed.), *Social behavior of female vertebrates* (pp. 291–313). New York: Academic Press.

- Dunbar, R. I. M. 1988. Primate Social Systems. London: Croom Helm.
- Dunbar, R. I. M. 1992. Neocortex size as a constraint on group size in primates. *Journal of Human Evolution* 20: 469–493.
- Dunbar, R. I. M. 2003. The social brain: Mind, language, and society in evolutionary perspective. Annual Review of Anthropology 32: 163–181.
- Eisenberg, J. F. 1981. The mammalian radiations: An analysis of trends in evolution, adaptation and behavior. Chicago: University of Chicago Press.
- Gallup, G. G., Jr. 1970. Chimpanzees: Self-recognition. Science 167: 86-87.
- Gallup, G. G., Jr., Anderson, J. R., and Shillito, D. J. 2002. The mirror test. In M. Bekoff, C. Allen, and G. M. Burghardt (eds.), *The cognitive animal: Empirical and theoretical perspectives on animal cognition* (pp. 325–334). Cambridge, MA: MIT Press.
- Hakeem, A. Y., Hof, P. R., Sherwood, C. C., Switzer, R. C., III, Rasmussen, L. E. L., and Allman, J. M. 2005. Brain of the African elephant (*Loxodonta africana*): Neuroanatomy from magnetic resonance images. *Anatomical Record Part A* 287A:1117–1127.
- Hart, B. L., Hart, L. A., McCoy, M., and Sarath, C. R. 2001. Cognitive behaviour in Asian elephants: Use and modification of branches for fly switching. *Animal Behaviour* 62: 839–847.
- Janik, V. M., and Slater, P. J. B. 2000. The different roles of social learning in vocal communication. *Animal Behaviour* 60: 1–11.
- Jerison, H. J. 1973. Evolution of the brain and intelligence. New York: Academic Press.
- Jolly, A. 1966. Lemur social behavior and primate intelligence. Science 153: 501–506.
- Kahl, M. P., and Armstrong, B. D. 2000. Visual and tactile displays in African elephants, Loxodonta africana: A progress report (1991–1997). Elephant 2 (4): 19–21.
- Kane, L., Forthman, D. L., and Hancocks, D. (eds.). 2005a. Best Practices by the Coalition for Captive Elephant Well-Being. Madison, WI: Coalition for Captive Elephant Well-Being. Accessed online at http://www.elephantcare.org/protoman.htm.
- Kane, L., Forthman, D. L., and Hancocks, D. (eds.). 2005b. Optimal Conditions for Captive Elephants: A Report by the Coalition for Captive Elephant Well-Being. Madison, WI: Coalition for Captive Elephant Well-Being. Accessed online at http://www.elephantcare.org/protoman.htm.
- Kapustin, N., Critser, J. K., Olsen, D., and Malven, P. V. 1996. Nonluteal estrous cycles of 3–week duration are initiated by anovulatory luteinizing hormone peaks in African elephants. *Biology of Reproduction* 55: 1147–1154.
- Kellert, S. R. 1989. Perceptions of animals in America. In R. J. Hoage (ed.), Perceptions of animals in American culture (pp. 5–24). Washington, D.C.: Smithsonian Institution Press.
- Langbauer, W. R., Jr. 2000. Elephant communication. Zoo Biology 19: 425-445.
- Langbauer, W. R., Jr., Payne, K. B., Charif, R., Rapaport, L., and Osborn, F. 1991. African elephants respond to distant playback of low-frequency conspecific calls. *Journal of Experimental Biology* 157: 35–46.
- Laws, R. M., and Parker, I. S. C. 1968. Recent studies on elephant populations in East Africa. Symposia of the Zoological Society of London 21: 319–359.
- Laws, R. M., Parker, I. S. C., and Johnstone, R. C. B. 1975. *Elephants and their habitats*. Oxford: Clarendon Press.
- 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.
- Lee, P. C., and Moss, C. J. 1986. Early maternal investment in male and female African elephant calves. *Behavioural Ecology and Sociobiology* 18: 353–361.
- Lee, P. C., and Moss, C. J. 1999. The social context for learning and behavioural development among wild African elephants. In H. O. Box and K. R. Gibson (eds.). *Mammalian social learning: Comparative and ecological perspectives* (pp. 102–125). Cambridge: Cambridge University Press.

- Lee, P. C., Poole, J. H., and Moss, C. J. Forthcoming. Male elephant social dynamics: Independence and beyond. In C. J. Moss, and H. J. Croze (eds.), *The Amboseli elephants:* A long-term perspective on a long-lived mammal. Chicago: University of Chicago Press.
- Leong, K. M., Ortolani, A., Burks, K. D., Mellen, J. D., and Savage, A. 2003. Quantifying acoustic and temporal characteristics of vocalisations for a group of captive African elephants *Loxodonta africana*. *Bioacoutics* 13: 213–232.
- McComb, K., Bates, L., and Moss, C. 2006. African elephants show high levels of interest in the skulls and ivory of their own species. *Biology Letters* 2: 26–28.
- McComb, K., Moss, C., Durant, S., Sayialel, S., and Baker, L. 2001. Matriarchs as repositories of social knowledge. *Science* 292: 491–494.
- McComb, K., Moss, C., Sayialel, S., and Baker, L. 2000. Unusually extensive networks of vocal recognition in African elephants. *Animal Behaviour* 59: 1103–1109.
- McCowan, B., and Reiss, D. 1997. Vocal learning in captive bottlenose dolphins: A comparison with humans and nonhuman animals. In C. T. Snowdon and M. Hausberger (eds.), Social influences on vocal development (pp. 178–207). Cambridge: Cambridge University Press.

Meredith, M. 2001. Africa's elephants: A biography. London: Hodder and Staughton.

- Morris, R., and Morris, D. 1966. Men and pandas. New York: McGraw-Hill.
- Moss, C. 1975. Portraits in the wild: Behavior studies of East African mammals. Boston: Houghton Mifflin.
- Moss, C. 1981. Social circles. Wildlife News 16: 2-7.
- Moss C. 1983. Oestrous behaviour and female choice in the African elephant. *Behaviour* 86: 167–96.
- Moss C. 1988. *Elephant memories: Thirteen years in the life of an elephant family.* New York: William Morrow and Company.
- Moss C. 1992. Echo of the elephants: The story of an elephant family. London: BBC Books.
- Moss, C. 1994. Some reproductive parameters in a population of African elephants, Loxodonta africana. In C. S. Bambra (ed.), Proceedings of the 2nd international NCRR (National Centre for Research in Reproduction) conference on advances in reproductive research in man and animals, held in Nairobi, Kenya, 3–9 May 1992 (pp. 284– 292). Nairobi: Institute of Primate Research.
- Moss, C. 2001. The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *Journal of the Zoological Society of London*. 255: 145–156.
- Moss, C., and Lee, P. C. Forthcoming. Female elephant social dynamics: Fidelity and flexibility. In C. J. Moss, and H. J. Croze (eds.), *Amboseli elephants: A long-term per*spective on a long-lived mammal. Chicago: University of Chicago Press.
- Moss, C. J., and Poole, J. 1983. Relationships and social structure in African elephants. In R. A. Hinde (ed.), *Primate social relationships: An integrated approach* (pp. 315– 325). Oxford: Blackwell Scientific.
- Mutinda, H. S. 2003. Social determinants of movements and aggregation among free ranging elephants (*Loxodonta africana*, Blumenbach) in Amboseli, Kenya. PhD diss., University of Nairobi.
- Nissani, M. 2004. Theory of mind and insight in chimpanzees, elephants and other animals? In L. J. Rogers and G. Kaplan (eds.), *Comparative vertebrate cognition: Are primates superior to non-primates*? (pp. 227–261). New York: Kluwer Academic/ Plenum Publishers.
- Payne, K. 2003. Sources of social complexity in the three elephant species. In F. B. M. de Waal and P. L. Tyack (eds.), *Animal social complexity: Intelligence, culture, and individualized societies* (pp. 57–85). Cambridge, MA: Harvard University Press.
- Pinker, S. 2003. Language as an adaptation to the cognitive niche. In M. H. Christiansen and S. Kirby (eds.), *Language evolution* (pp. 16–37). Oxford: Oxford University Press.
- Plotnik, J. M., de Waal, F. B. M., and Reiss, D. 2006. Self-recognition in an Asian elephant. Proceedings of the National Academy of Sciences 103: 17053–17057.

- Poole, J. H. 1982. Musth and male-male competition in the African elephant. DPhil diss, University of Cambridge.
- Poole, J. H. 1987. Rutting behaviour in African elephants: The phenomenon of musth. *Behaviour* 102: 283–316.
- Poole, J. H. 1989a. Announcing intent: The aggressive state of musth in African elephants. *Animal Behaviour* 37: 140–152.
- Poole, J. H. 1989b. Mate guarding, reproductive success and female choice in African elephants. Animal Behaviour 37: 842–849.
- Poole, J. H. 1994. Sex differences in the behavior of African elephants. In R. Short and E. Balaban (eds.), *The differences between the sexes* (pp. 331–346). Cambridge: Cambridge University Press.
- Poole, J. H. 1996. Coming of age with elephants: A memoir. New York: Hyperion Press.
- Poole, J. H. 1998. An exploration of a commonality between ourselves and elephants. *Etica & Animali* 9: 85–110.
- Poole, J. H. 1999a. Signals and assessment in African elephants: Evidence from playback experiments. *Animal Behaviour* 58: 185–193.
- Poole, J. H. 1999b. Ella's Easter baby. Care for the Wild News 15: 24-25.
- Poole, J. H. Forthcoming. The social contexts of elephant vocal communication. In C. J. Moss, and H. J. Croze (eds.), *The Amboseli elephants: A long-term perspective on a long-lived mammal*. Chicago: University of Chicago Press.
- Poole, J. H., Payne, K. B., Langbauer, W., Jr., and Moss, C. J. 1988. The social contexts of some very low frequency calls of African elephants. *Behavioral Ecology and Sociobiology* 22: 385–392.
- Poole, J. H., and Moss, C. J. 1989. Elephant mate searching: Group dynamics and vocal and olfactory communication. In P. A. Jewell and G. M. O. Maloiy (eds.), *The biology* of large African mammals in their environment: the proceedings of a symposium held at the Zoological Society of London on 19th and 20th May, 1988 (pp. 111–125). Oxford: Clarendon Press.
- Poole, J., and Granli, P. 2003. Elephant visual and tactile signals database. www.Elephant Voices.org.
- Poole, J. H., and Granli, P. K. 2004. The visual, tactile and acoustic signals of play in African savannah elephants. In J. Jayewardene (ed.), *Endangered elephants, past, present and future: Proceedings of the symposium on human elephant relationships and conflicts, Sri Lanka, September 2003* (pp. 44–50). Colombo: Biodiversity and Elephant Conservation Trust.
- Poole, J. H., Lee, P. C., and Moss, C. J. Forthcoming. Long-term reproductive patterns and musth. In C. J. Moss, and H. J. Croze (eds.), *The Amboseli elephants: A long-term perspective on a long-lived mammal.* Chicago: University of Chicago Press.
- Poole, J. H., Tyack, P. L., Stoeger-Horwath, A. S., and Watwood, S. 2005. Elephants are capable of vocal learning. *Nature* 434: 455–456.
- Povinelli, D. J. 1989. Failure to find self-recognition in Asian elephants (*Elephas maximus*) in contrast to their use of mirror cues to discover hidden food. *Journal of Comparative Psychology* 103: 122–131.
- Rasmussen, L. E. L., and Schulte, B. A. 1998. Chemical signals in the reproduction of Asian (*Elephas maximus*) and African (*Loxodonta africana*) elephants. *Animal Reproduction Science* 53: 19–34.
- Rasmussen, L. E., Schmidt, M. J., Henneous, R., Groves, D., and Daves, G. D., Jr. 1982. Asian bull elephants: Flehmen-like responses to extractable components in female elephant estrous urine. *Science* 217: 159–162.
- Rasmussen, L. E. L., and Munger, B. 1996. The sensorimotor specializations of the trunk tip of the Asian elephant, *Elephas maximus*. *Anatomical Record* 246: 127–134.
- Rasmussen, L. E. L., and Krishnamurthy, V. 2000. How chemical signals integrate Asian elephant society: The known and the unknown. *Zoo Biology* 19: 405–423.

Rasmussen, L. E. L., Krishnamurthy, V., and Sukumar, R. 2005. Behavioral and chemical

confirmation of the preovulatory pheromone, (*Z*)-7–dodecenyl acetate, in wild Asian elephants: Its relationship to musth. *Behaviour* 142: 351–396.

- Reader, S. M., and Laland, K. N. 2002. Social intelligence, innovation, and enhanced brain size in primates. *Evolution* 99: 4436–4441.
- Reiss, D., and Marino, L. 2001. Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. *Proceedings of the National Academy of Sciences* 98: 5937–5942.
- Rensch, B. 1956. Increase of learning capability with increase of brain-size. American Naturalist 90: 81–95.
- Rensch, B. 1957. The intelligence of elephants. Scientific American 196: 44-49.
- Roth, G. 1999. Kleine Gehirne—grosse Gehirn. Evolutionare Aspekte und funktionelle Konsequnzen. *Naturwissenschaftliche Rundschau* 52: 213–219.
- Shoshani, J. 1998. Understanding proboscidean evolution: A formidable task. Trends in Ecology and Evolution 13: 480–487.
- Shoshani, J., and Eisenberg, J. 1992. Intelligence and survival. In H. Shoshani (ed.), *Elephants: Majestic creatures of the wild*. Singapore: Weldon Owen.
- Shoshani, J., Kupsky, W. J., and Marchant, G. H., 2006. Elephant brain: Part I. Gross morphology, functions, comparative anatomy, and evolution. *Brain Research Bulletin* 70:124–157.
- Slotow, R., van Dyke, G., Poole, J., Page, B., and Klocke, A. 2000. Older bull elephants control young males: Orphaned male adolescents go on killing sprees if mature males aren't around. *Nature* 408: 425–426.
- Smolker, R. A., and Pepper, J. W. 1999. Whistle convergence among allied male bottlenose dolphins (Delphinidae, *Tursiops* sp.). *Ethology* 105: 595–617.
- Soltis, J., Leong, K., and Savage, A. 2005a. African elephant vocal communication: I. Antiphonal calling behavior among affiliated females. *Animal Behaviour* 70: 579–587.
- Soltis, J., Leong, K., and Savage, A. 2005b. African elephant vocal communication: II. Rumble variation reflects the individual identity and emotional state of callers. *Animal Behaviour* 70: 589–599.
- Sukumar, R. 2003. *The living elephants: Evolutionary ecology, behavior, and conservation.* New York: Oxford University Press.
- Tyack, P., and Sayigh, L. S. 1997. Vocal learning in cetaceans. In C. T. Snowdon and M. Hausberger (eds.), *Social influences on vocal development* (pp. 208–233). Cambridge: Cambridge University Press.
- Viljoen, P. J. 1990. Daily movements of desert dwelling elephants in the northern Namib Desert. *South African Wildlife Research* 20 (2): 69–72.
- Wemmer, C., and Mishra, H. R. 1982. Observational learning by an Asian elephant of an unusual sound production method. *Mammalia* 46: 557.
- Wemmer, C., Mishra, H., and Dinerstein, E. 1985. Unusual use of the trunk for sound production in a captive Asian elephant: A second case. *Journal of the Bombay Natural History Society* 82: 187.
- Western, D., and Lindsay, W. K. 1984. Seasonal herd dynamics of a savanna elephant population. *African Journal of Ecology* 22: 229–244.
- Wittemyer, G., Douglas-Hamilton, I., and Getz, W. M. 2005. The socioecology of elephants: Analysis of the processes creating multitiered social structures. *Animal Behaviour.* 69: 1357–1371.
- Worden, R. 1998. The evolution of language from social intelligence. In J. R. Hurford, M. Studdert-Kennedy, and C. Knight (eds.), *Approaches to the evolution of language: Social and cognitive bases* (pp. 148–168). Cambridge: Cambridge University Press.

CONTRIBUTORS

Lori Alward, PhD Tacoma Community House Tacoma, Washington, USA

Joseph C. E. Barber, PhD Disney's Animal Kingdom Orlando, Florida, USA

Janine L. Brown, PhD Smithsonian's National Zoological Park Conservation and Research Center Front Royal, Virginia, USA

Jacob V. Cheeran, DVM Project Elephant Government of India Thrissur, India

Catherine A. Christen, PhD Smithsonian's National Zoological Park Conservation and Research Center Front Royal, Virginia, USA

Smithsonian Institution Archives Washington, DC, USA

Rosaleen Duffy, PhD Professor of International Politics University of Manchester Manchester, United Kingdom Yudha Fahrimal, DVM Universitas Syiah Kuala Darussalam, Banda Aceh Sumatra, Indonesia

Richard Fayrer-Hosken, BVSc, PhD Department of Large Animal Medicine College of Veterinary Medicine University of Georgia Athens, Georgia, USA

Marie Galloway Smithsonian's National Zoological Park Washington, DC, USA

Marion E. Garaï, PhD Space for Elephants Foundation KwaZulu Natal, South Africa

Jane Garrison Los Angeles, California, USA

Hank Hammatt Elephant Care International Hohenwald, Tennessee, USA

David Hancocks Melbourne, Australia

Rebecca Hardin, PhD Department of Anthropology and School of Natural Resources and Environment University of Michigan Ann Arbor, Michigan, USA Harvard Academy for International and Area Studies Cambridge, Massachusetts, USA

Michael Hutchins, PhD The Wildlife Society Bethesda, MD, USA

Graduate Program in Conservation Biology and Sustainable Development University of Maryland College Park Maryland, USA

Center for Conservation and Behavior Georgia Institute of Technology Atlanta, Georgia, USA

Mike Keele Oregon Zoo Portland, Oregon, USA

Winnie Kiiru, MSc Born Free Foundation Nairobi, Kenya

Michael D. Kreger, PhD U.S. Fish and Wildlife Service Arlington, Virginia, USA

Fred Kurt, PhD Research Institute of Wildlife Ecology University of Veterinary Medicine Vienna, Austria

470 CONTRIBUTORS

Dhriti K. Lahiri Choudhury, PhD Department of English Rabindra Bharati University Calcutta, India

John Lehnhardt Disney's Animal Kingdom Orlando, Florida, USA

Khyne U Mar, PhD, FRCVS Elephant Family-UK London, United Kingdom

Jill D. Mellen, PhD Disney's Animal Kingdom Orlando, Florida, USA

Susan K. Mikota, DVM Elephant Care International Hohenwald, Tennessee, USA

Gary W. Miller Disney's Animal Kingdom Orlando, Florida, USA

Cynthia J. Moss, ScD Amboseli Elephant Research Project Amboseli Trust for Elephants Nairobi, Kenya

Joyce H. Poole, PhD Amboseli Elephant Research Project Amboseli Trust for Elephants Nairobi, Kenya Greg D. Rossel Motorola Corporation Fort Worth, Texas, USA

Nigel Rothfels, PhD College of Letters and Science University of Wisconsin– Milwaukee Milwaukee, Wisconsin, USA

Dennis Schmitt, DVM, PhD Ringling Bros. and Barnum & Bailey Department of Veterinary Services Polk City, Florida, USA Department of Agriculture Missouri State University Springfield, Missouri, USA

John Seidensticker, PhD Smithsonian's National Zoological Park Washington, DC, USA

Lalith Seneviratne Colombo, Sri Lanka

Brandie Smith, MS Department of Conservation and Science Association of Zoos and Aquariums Silver Spring, Maryland, USA Raman Sukumar, PhD Center for Ecological Sciences Indian Institute of Science Bangalore, India

Gary Varner, PhD Philosophy Department Texas A&M University College Station, Texas, USA

Christen Wemmer, PhD Smithsonian's National Zoological Park Conservation and Research Center Front Royal, Virginia, USA California Academy of Sciences San Francisco, California, USA

Ian Whyte, PhD South African National Parks Kruger National Park, South Africa

Nadja Wielebnowski, PhD Chicago Zoological Society Brookfield Zoo Brookfield, Illinois, USA Wemmer and Christen/ Elephants and Ethics