1 Introduction

1.1 Aims and Scope

Though now greatly diminished in diversity, living elephants represent the sole survivors of what was once a much more speciose clade, dispersed throughout North and South America, Eurasia, and Africa. One of the primary motivations for this book is to explore possible generalities in the evolution of behavior in social species. The book offers an updated synthesis of research on elephant behavior that has taken off since previous compilations. Often, when searching for the evolutionary underpinnings of human social behavior, language, cognition, and so on, the tendency among anthropologists and biologists has been to look to our primate relatives. Research is therefore often dominated by the quest for *homologous* features, that is, those that might have been derived from our shared common ancestors. This seems often motivated by a desire to identify which features are uniquely human, as opposed to those maintaining continuity with related lineages. To take a morphological example – our bipedalism is unique, involving a realignment of the pelvis and thigh bones as well as our toes, but built upon a skeletal structure that is homologous with other primates. However, limiting the inquiry to any single clade presents the difficulty that there may be evolutionary constraints or predispositions for the entire clade that are difficult to rule out. Occasionally, there have been attempts at identifying attributes that might have arisen independently across lineages owing to similar social or ecological pressures. Such has been the case in studies of communication and cognition. For instance, many different primate and nonprimate species have evolved alarm calls that categorically pick out predators of a particular type. This is often termed convergent evolution, giving rise to *analogous* features. Analogous structures are relatively easy to spot when they involve physical forms (e.g. the wings of bats and birds, which have evolved independently) but more difficult when they concern invisible structures such as dominance hierarchies. But, in principle, it is conceivable that there are environmental pressures, social or ecological, that shape behavior as much as they shape morphology – indeed, this provides much of the motivation behind the field of behavioral ecology. Just as wings are shaped by the laws of aerodynamics, so too must behavior be shaped by the (messier) forces of ecology. The most interesting opportunity presented by collecting the scattered findings of many independent studies into the long format of a book is the chance to compare across different systems. For the same reason, I take extra care to explicitly identify the particular populations

 https://doi.org/10.1017/9781316534380.002

and locations being discussed and try not to overextend conclusions. At the same time, I do try to piece different studies together into a cohesive whole and, in closing certain chapters or sections, take the liberty (and pleasure!) of speculating in some imaginative directions.

Elephants are large-brained, long-lived mammals that exhibit a diverse and intriguing array of social and cognitive abilities. There is a tendency to think, among scientists as much as the general public, that an elephant is an elephant is an elephant. By virtue of large ears and long noses they all appear rather similar to one another and distinct from everything else. Indeed, much of the popular perception of elephants has rested for a great many years on research on a single species – African savanna elephants. It is not difficult to see why: They are charismatic, highly visible, and perpetually (unfortunately) the targets of hunting and trafficking. However, this is now changing, as both the research and policy realms catch on to the fact that elephants are far more varied than was initially suspected. Elephants are fascinating subjects of study because they exploit a range of ecosystems and represent social intelligence that is independently evolved from other social mammals such as that of primates, marine mammals, or even other ungulates, offering opportunities to explore what general principles may be applicable across very different systems. The ancestors of elephants also coevolved with our own, locked in the perpetual dance between prey and predator.

A second, urgent, motivation for this book is that elephant populations are under intense pressure globally, all of them being classified as either "Endangered" or "Critically Endangered." Until recently, only two species of elephant were formally recognized. There are now three. The African continent is inhabited by the African savanna elephant (*Loxodonta africana*) and African forest elephant (*Loxodonta cyclotis*). Separated from this genus by an evolutionary time span of approximately six million years (roughly the same amount of time separating lions, tigers, and leopards from their last common ancestor), the Asian elephant (*Elephas maximus*) dwells in a variety of habitats ranging from grasslands to dense forests in Asia. Though classified as a single species, Asian elephants also come in different varieties, the mainland elephant (*E. m. maximus*) – found in India, Sri Lanka, and Southeast Asia – the Bornean elephant (*E. m. borneensis*), and the Sumatran elephant (*E. m. sumatranus*). For brevity, African savanna elephants will be referred to as savanna elephants throughout this book, while African forest elephants will be referred to as forest elephants. Mainland Asian elephants will be referred to as Asian elephants, and the island populations will be referred to as Bornean or Sumatran elephants respectively, recognizing the diversity of habitat types in which Asian elephants are found.

Elephants have never been more threatened than they are now, in the face of our unprecedented population growth and consumption habits. The largest surviving land vertebrate forces us to confront a critical issue – the need to share space with wildlife and wilderness on a finite and crowded planet. The horde of threats elephants face vary across species and populations: Whereas ivory poaching is the most serious threat for *L. africana* and *L. cyclotis*, habitat loss and conflict are of grave concern for *E. maximus*. Though overshadowed by the ivory crisis, another issue African elephants face is increasing and intensifying conflict with burgeoning human populations. Elephant populations in the central African forests have experienced a precipitous decline of 60% in the late 2000s (Maisels et al., 2013). All forest-dwelling elephants on both continents are threatened by the expansion of logging and plantation activities driven by international trade, even as fresh research is uncovering fascinating secrets of their hidden societies. The loss of not just individuals, but populations, impoverishes not only biodiversity, but also our ability to understand the evolution of a unique and already depauperate clade within the animal kingdom (Caro & Sherman, 2011).

Generally, elephants' ability to persist in the face of modern threats depends largely on their capacity to adapt to landscapes increasingly altered by humans. Behavioral flexibility has conferred considerable historic success on elephants, and ensuring their future requires that we understand and conserve that flexibility. Determining where and how elephants might fare outside captivity or small, isolated protected areas is a key conservation priority for elephants and their habitats. In an age of landscape-scale conservation planning, understanding how elephants perceive their world is key for creating appropriate linkages in mosaics of land use and mitigating the potential for conflict. Some areas in the southern African region are already encountering problems following successful conservation efforts, as increasing elephant populations interface more frequently with human populations. Numbers alone cannot ensure future persistence: What matters is not only how many animals are left, but also the relationships and experiences of those survivors.

Elephants have also long held cultural value and fascination for people – the very ones who may at times be involved in conflict with these mammals, as much as the distant consumers of products produced at the expense of native habitats. The future of successful conservation solutions lies in overcoming not only physical but also psychological barriers; the capacity of elephants to evoke human empathy may be the key to protecting people, elephants, and the ecosystems that support both. Thus, elephant conservation depends greatly on human behavior as well. This volume will examine the implications of certain human activities and decisions for elephant behavior, and vice versa, to better understand what has worked so far and what has not. I hope it will facilitate and encourage collaboration between behavioral biologists and conservation practitioners of all stripes, within or outside academia.

I must first place boundaries identifying what will not be found in this volume, which is necessarily limited in scope. I do not address elephant evolution or physiological adaptations in depth, as these topics are discussed elsewhere (Shoshani & Tassy, 1996; Sukumar, 2003), except as a launching point for understanding elephant behavior as it manifests today. I provide only light coverage of a body of earlier research pertaining to the interaction of elephants and their habitats in savanna environments, which has been reviewed in Sukumar (2003), focusing instead on more recent work that provides a comparative perspective. I use primary peer-reviewed literature and limit the inclusion of material found in other books (e.g. *The Amboseli Elephants* by Moss et al. (2011a)) only to observations that are not reported in primary literature and which, again, are necessary for making comparisons among populations or species. I avoid discussing unpublished data with the exception of published theses and some of my own lab group's work in progress, as I cannot otherwise attest to their quality. It is also not my aim to discuss the welfare and ethics of elephants in captivity; those interested in these topics are directed to Wemmer and Christen (2008). Lastly, some elephant species and populations have been studied far more extensively than others. To cover each in proportion to the number of studies would result in a fairly lopsided discussion with heavy bias toward particular geographies. In trying to balance the content across taxa and locations, I therefore necessarily trade off being comprehensive.

1.2 Behavior in Conservation: Frameworks for Integration

Animals interact with the conspecifics, other species, and the environment. This truism constitutes the sum total of behavior, and understanding this multifaceted complex is the aim of those who study animal behavior. Such studies, however, are unfortunately viewed by some as a luxury of little consequence to the practical challenges of conservation – especially for species or populations that do not lend themselves easily to observation. That wildlife management has historically relegated behavior to a black box, focusing instead on more tangible numerical quantities such as population abundance, growth rates, habitat extent, and so on, is therefore perhaps not so surprising. On the academic side, the role that behavioral research can and does contribute significantly to solving actual conservation challenges has been viewed with a mix of tempered skepticism (Angeloni et al., 2008; Caro, 2007; Caro & Sherman, 2011, 2013) or hopeful optimism (Blumstein & Fernández-Juricic, 2010; Caro & Sherman, 2013; Greggor et al., 2016); substantial overlap among the two sets notwithstanding (full disclosure: I include myself in the ranks of skeptical hopefuls). The divide may have been reinforced over time by differing priorities, not only among the practitioners but also scientific publishers (Angeloni et al., 2008).

And yet there has been a gradual increase in the recognition that behavioral variables are pivotal to the success or failure of conservation efforts over preceding decades, even if the rate of increase in scientific publications that jointly mention behavior as well as conservation seems an imperfect reflection of this (Angeloni et al., 2008; Nelson, 2014). It is my hope that by consolidating the recent behavioral research for elephants specifically, this volume makes this research more accessible to those who would wish to use it while highlighting areas in which more work is needed. Here, I briefly provide some background to the study of behavior for those who are unfamiliar with this. I then outline frameworks that have been developed in recent years that link behavioral research with applied conservation and management, to put this book in context and clarify terminology.

1.2.1 Levels of Causality and the Comparative Method

Readers unfamiliar with the study of animal behavior may find it helpful to bear in mind one of the first sets of organizing principles outlined in the field by Niko

Tinbergen, one of its founders. They are often referred to as *levels of causation*, paralleling the schema of causalities laid out by Aristotle (Hladký & Havlíček, 2013). Tinbergen (1963) explicitly identified four possible categories of explanation for any and all behavior:

- *Mechanistic*: The physical processes that go on within an organism that directly control its behavior (sensory stimuli, hormonal pathways, neuronal processes, etc.).
- *Ontogenetic*: Processes that occur over the development (ontogeny) and lifetime of an individual.
- *Functional*: The consequence a behavior has on an individual's (or population's) propensity to leave offspring, that is, its effect on fitness or its adaptive value.
- *Phylogenetic*: The context of an organism's evolutionary history, which can both constrain and enable evolution in a certain direction.

A well-studied example that is often used is that of birdsong. The question "What makes a bird sing?" can be answered in four different ways. A mechanistic explanation may discuss how changes in daylight or day length stimulate certain hormones or neurotransmitters in the brain, which then fires off signals to the syrinx, resulting in song production. An ontogenetic explanation may discuss the process by which a bird learns to sing through observation of other older individuals, imitating and developing its own species-specific repertoire. A functional explanation may outline the ways in which songs are necessary in order to attract mates and display one's own health and vigor. A phylogenetic explanation situates a songbird's ability to sing in the fact that it is a member of a closely related group of species, all of which have the ability to learn vocal production. Likewise, the last level of explanation offers some insight as to why other bird species, which are *not* songbirds, do not also sing. The glory of song, even if adaptive, is not really an option for an ostrich (at least, in the near future).

From this, it should be evident that the four levels of explanation are complementary rather than competing, although in specific instances it might be difficult to avoid muddling them together. In particular, the first two are typically subsumed under the heading of *proximate* causes (with the term "proximate" sometimes becoming synonymous with "mechanistic"), whereas the second two are often described as *ultimate* (with the term "ultimate" sometimes being used interchangeably with "functional"; see Bateson & Laland, 2013; Mayr, 1961). The distinctions are not merely semantic, however, because confusing one type of explanation for another can hinder understanding of the interplay between levels and lead to unnecessary disputes (Laland et al., 2011; MacDougall-Shackleton, 2011). Behavioral ecology concerns itself largely with questions pertaining to the ultimate causes. So too, in this book, I will be focused more heavily on the functional and phylogenetic explanations than on the mechanistic or ontogenetic (though with some exceptions, such as in thinking about learning, cognition, and communication). I mention these qualifications here as I will not continuously flag the terms explicitly.

Just as with physical structures, the current utility of a behavior need not necessarily reflect the historic pressures that drove its evolution (Bateson & Laland, 2013). To paraphrase the population geneticist Theodosius Dobzhansky (1973), nothing in behavior makes sense except in the light of comparison.[1] The *comparative method* is therefore an invaluable means of trying to understand the function or adaptive utility of a behavior through comparisons of species or populations. Different populations or closely related sister taxa that share a phylogenetic history but occupy different environments may exhibit corresponding behavioral differences. Conversely, distantly related taxa may show convergent patterns in response to similar selective pressures. Comparisons offer a way to extract general principles that would be impossible to infer through the study of single populations or species. A frequent error is to forget phylogenetic explanations or constraints entirely and view all behavior as shaped by its immediate utility (Bateson & Laland, 2013). On the other hand, some behaviors may not make sense without understanding the broader historic context. Unfortunately, these confusions are likely to increase as species and populations become extinct, eroding the capacity for comparative study and thus threatening the some of the very means by which the discipline of animal behavior progresses (Caro & Sherman, 2011, 2012).

1.2.2 Conservation and Behavior

Those interested in a thorough treatment of conservation behavior as an emerging discipline may refer to Berger-Tal and Salz (2016). Blumstein and Fernandez-Juricic (2010) provide an accessible starting point for integrating the study of behavior with conservation, defining the subject of "conservation behavior" as "the application of knowledge of animal behavior to solve wildlife conservation problems." They lay out a detailed rationale, characterization, and tools for this enterprise, taking the very applied perspective that because behavior is "at the root" of many conservation problems, behavioral knowledge at the level of single species should be centrally integrated into conservation plans, while recognizing that large-scale conservation measures of course involve many species. What are the types of conservation problems that have behavior at their root?

Captive breeding to rescue small populations is a paradigm example of an applied problem in which behavioral understanding seems invaluable. One has to ensure that the ordinary behaviors that enable an individual to successfully rear young are successfully duplicated by humans, while being careful not to introduce further disruptions to the animals while they are in human care, especially if the aim is to eventually release these individuals back into the wild. The mechanistic and ontogenetic levels may be of greatest concern. For instance, the abilities to recognize other members of their own species and, in the case of gregarious species, to actually prefer their company to that of humans, are critical. Once released, individuals must know how to forage, recognize and avoid predators (including humans), and eventually find a mate (and compete for one, if required). If they are successful, they may need to rear offspring. Any individual of a species can only acquire those skills and abilities that

[1] "Nothing in Biology Makes Sense Except in the Light of Evolution" is the title of a 1973 essay by Dobzhansky.

are possible within the constraints of its evolutionary history, a consideration that may not be at the forefront of breeding efforts but which may latently affect the results; thus, breeding efforts would benefit from a comparative perspective. For instance, might the behavior of a more common species be instructive in designing the breeding program? If surrogates from a different species are used, might their behavior be appropriate models for the species being reared? One might ask whether sister species require similar or different social environments early in life, given their natural histories? When a young animal is brought into the highly artificial environment that captive breeding represents, fulfilling each of these requirements may be a tall order, yet nevertheless essential.

More broadly, reproduction is a domain of behavior that is accompanied by a host of complex behaviors in many species, ranging from competition during courtship to the act of mating itself. For some species, these might involve relatively hardwired displays. But for elephants and many mammals in the wild, learned tactics allow individuals to successfully compete for mates or establish dominance, such as the experience young males might obtain by sparring. Likewise, for females it is important to learn to assess high-quality males and behave appropriately during reproductive periods so as to avoid injury to themselves. In social species, especially those which live and breed communally, the "Allee effect" (Allee et al., 1949) represents a well-known phenomenon whereby populations exhibit nonlinear declines as a function of decreasing group size, which are often underpinned by the accompanying social interactions. For example, the need for assistance when rearing offspring or simply the opportunity to learn how to be a good parent through the example set by others.

For elephants, it is seldom the case that captive breeding programs are designed with the intention of eventual release; more often, the aim is to maintain a captive population. However, programs for rehabilitating individuals brought in from the wild face similar challenges. For those programs that aim to replenish the population of elephants in captivity, it is worth asking whether there is a behavioral rather than purely physiological basis for why elephants reproduce so poorly in many captive settings yet appear to do well in others. Some may also raise ethical and moral issues regarding elephants in captivity, on the grounds of whether their behavior is suitably "normal" in the sense that they do not experience undue suffering. Here the question of what elephants in captivity truly contribute to conservation is one worth deeply considering. If their role is to serve as ambassadors for their species, then it is imperative to understand how best to meet their needs relative to what they would experience in the wild.

Another set of conservation challenges centers on land-use planning. At a basic level, one would want to know what the habitat requirements of an individual are before designing reserves and corridors. In doing so, it would be well to recognize that wildlife cannot be expected to simply stay in the areas allocated to them – they will need move to meet their feeding and reproduction requirements. Often landscapes are modified with economic or development goals in mind, with reserves and corridors occupying compromised spaces. "Conflicts," or more generally, negative interactions, may therefore arise at the boundaries – such as over agriculture or livestock or through collisions between wildlife and human transportation devices. As climate changes and landscapes continue to be modified through human activity, we will be faced with the enormous challenge of making our spaces conducive to such movement while minimizing disturbance to both humans and wildlife. Movement is therefore among the most problematic and yet essential behaviors with which conservationists and wildlife managers must contend. Perhaps for this reason, it has the distinction of being a behavioral domain with entire subdisciplines devoted to it (movement ecology and spatial ecology).

Preserving long-distance migration and preventing human–wildlife conflict are related concerns that preoccupy many practitioners and policymakers. Initially assumed to be an innate ability, there is increasing evidence that at least for some species, migration also depends heavily on learning and cultural transmission of knowledge (Festa-Bianchet, 2018; Jesmer et al., 2018). Although individuals of a species may have exhibited such behavior over millennia constituting hundreds of generations, these are clearly fragile processes that are incredibly vulnerable to disturbance, especially if components of the behavior have to be learned anew with each generation. This involves recognizing specific timing cues such as changes in temperature or day length, or in food quality or availability. It then requires coordinating with conspecifics during the actual migration event, learning the routes and resources along the way along with vigilance against the potential dangers one may encounter. Lack of appropriate experience, the absence of knowledgeable leaders to guide movements, even over shorter distances, and the disappearance of critical resources along movement paths can all potentially disrupt such behavior. The ability to successfully participate in migration events will again have consequences for an individual's fitness and phylogenetic effects insofar as the behavior persists in future generations. On the flip side, when animals are forcibly moved as part of a management initiative, not only spatial but social factors (such as acceptance by local conspecifics) may influence their ability to successfully establish themselves at new locations. Problematic behaviors may also be spread from one population to another via social transmission.

As managers and policymakers, it is important to anticipate any unintended adverse consequences that a management action might have. Reproduction and movement are just two domains of behavior in which the relevance to conservation and management are so obvious that they have benefited from early recognition; the list is much longer (those interested may begin with Greggor et al., 2016). Yet other aspects of behavior, notably areas such as personality, cognition, and culture, have been more neglected until recently. If, for example, if one continuously removes (by lethal or nonlethal means) problem animals without letting them reproduce, one may be removing precisely those individuals that are bold and curious. If such attributes have a genetic component, we may effectively be removing these attributes from the gene pool, leaving behind a population that is on the whole less exploratory and less able to cope if conditions change, such as the preferred food items go into decline. In the long term, this threatens the evolutionary potential of the population in the face of environmental changes.

1.2.3 Behavioral Variation and Flexibility

Behavior is a phenotype, broadly defined as the outward result of interactions between genotype and environment. Because the phenotype is what natural selection can directly act on, and because selection requires standing variation, it follows that in order for organisms to evolutionarily adapt their behavior, they must have preexisting behavioral variation (see also Bateson & Laland, 2013, and references therein). As alluded to in preceding sections, it is crucial to recognize that behavior is itself something that might need protecting (Caro & Sherman, 2012). If we view organisms as complex biological machines, it is evident that disruptions at any level of behavior can have consequences not only for individual members of a species but also programs aiming to protect or restore populations. Long-distance migration is again a perfect example of this, in which the loss of skilled and knowledgeable individuals can extinguish the behavior itself within a population. The upshot of knowing this is that one can appreciate the importance of social contact in the reintroduction of a species and can facilitate it if necessary. Berger-Tal et al. (2011) provide a framework for thinking about behavioral variation in relation to conservation aims. The central issue is the need to recognize that, along with genetic variation, individuals within or among populations of the same species exhibit behavioral variation.

For instance, individuals may exhibit regional differences in food preferences, and correspondingly manifest behavioral adaptations suitable to tackling those food preferences. Given time, those preferences may lead to morphological changes such as changes in the physical structures involved in feeding (Odling-Smee et al., 2003). Of course, it is also possible that behavioral shifts follow physical changes – the more traditional view. Projecting toward the future, the ability of populations to continue adapting in the face of changing environments will require that there is not only sufficient genetic diversity (where the term "diversity" refers to not just any neutral variation, but variation that is *structured by natural selection*) but also behavioral diversity – the willingness to explore and exploit new food sources.

These inclinations may be tied to certain types of personalities, which again represent standing variation. Some individuals may be more inclined to be exploratory than others and thus more readily try novel food sources, potentially enjoying less competition from others. Novel food sources might include recently introduced non-native species, or simply changes in the demographics of existing species such that once-common food sources are scarce and once-rare food sources are more common. The flip side of this is that novel food sources might be toxic. Human refuse (i.e. garbage) is a particularly problematic novel food source that may be readily exploited by some individuals, bringing them into contact with both harmful substances such as heavy metals and plastics as well as pathogens. It is clear from this example that what is adaptive under some circumstances may not be in others.

Behavioral variation is different from flexibility (also termed "plasticity"), where a single individual might employ a host of different strategies (which may or may not be learned) or modify strategies through learning, a process that occurs at the ontogenetic level, as already mentioned. Although behavioral flexibility may sometimes be confusingly referred to as "adaptability," it does not necessarily refer to *evolutionary* adaptability. In common parlance, the term "adaptability" might refer to an individual's ability to modify his or her own behavior in an advantageous manner. Nevertheless, behavioral flexibility refers to an individual-level characteristic, whereas true adaptability refers to a population-level characteristic. To go back to the example of feeding, it might mean being able to exploit different food sources at different times of year. This could itself be a genetic trait. Over the long term, if individuals that are more behaviorally flexible are also more successful at leaving offspring, and this trait is itself heritable, one could say that behavioral flexibility is adaptive.

In summary, individuals may demonstrate flexibility or plasticity in their own behavior; there may be variation among individuals in the different types of strategies they employ and the degree of flexibility they demonstrate; and finally there may be variation among different populations of the same species as a result of selection or culture. These ideas are exceedingly relevant for protecting and managing elephants. The cognitive and behavioral complexity of elephants – male and female – presents both challenges and opportunities for conservation. The challenges are that populations can be sensitive to disturbances and management strategies (e.g. culling) in unforeseen ways; individuals may find ways around methods designed to reduce conflict by learning from one another. The opportunities include novel solutions to conservation challenges based on our expanding understanding of elephant sociality, communication, and motivation. Likewise, as habitats diminish it becomes crucially important to recognize that the depletion of distinct subpopulations represents not just loss of genetic diversity but also behavioral diversity, which might hold the key to maintaining resilience in this long-lived species, which is destined to witness a generation of rapid change. The recognition that conserving species requires more than simply managing numbers is finally gaining traction, particularly in arenas such as reintroduction programs, conserving migratory species, and addressing human–wildlife conflict. One indicator of this shift is the movement toward considering cultural units as being significant for conservation, in addition to the standard focus on species and genotypes (Brakes et al., 2019).

1.3 How This Book Is Organized

This volume takes behavior as the central organizing principle, with different domains of behavior contextualized with the relevant theoretical background. Rather than take up specific conservation or management issues and examine which behaviors are relevant to them, which would result in a very disjointed discussion of behavior or artificially separate the academic study of "behavior" from applied "conservation" via distinct sections or chapters, I discuss the conservation implications of particular behaviors as they naturally arise. The result should be that the two are naturally interwoven in readers' minds, just as they are in reality. The themes and stances sketched out in the preceding sections will therefore appear throughout, but not be invoked explicitly. Those coming from a more applied perspective are advised to start with a concrete problem first and then refer to the relevant behaviors (Blumstein & Fernández-Juricic, 2010; Caro, 2007), whereas students looking for research ideas in particular domains might first notice the gaps that are identified as needing exploration and then, given what is learned, consider how they might inform practical conservation or management activities. I also found that there is no single format that works equally well for all chapters. Therefore, instead of organizing each individual chapter the same way, they are somewhat idiosyncratically carved up into sections that make sense for the topic at hand.

Chapter 2 sets the stage by discussing the likely origins of the living elephants and their relationships to one another, together with the ecological conditions that may have prevailed upon their lineages. Predation and resource availability, the forces of selection that operate on all life forms, are no less important for the largest land mammals ever to have graced the earth than they are for the smallest. And yet the living elephants have somehow managed to avoid the wave of extinctions that overcame other large-bodied vertebrates throughout the globe. I examine why this may be, and what it tells us about the prospects for elephants' continued persistence in the face of rapid change.

Chapter 3 builds on this background to describe what is known so far about the structure of female societies. Because elephants exhibit sexual segregation upon reaching adolescence, the social contexts of males and females have to be treated distinctly. Females, having to invest heavily in the production and care of offspring, are sensitive to three pressures: resource availability, predation, and competition from other individuals. In this chapter I examine how why these factors may interact to shape female social relationships in the three species. Hand in hand with this, I consider how social and ecological disturbances have been shown to impact elephant societies and explore the responses of various elephant populations.

Chapter 4 explores male social life, which is to some extent inseparable from discussion of reproduction and mating. Freed from the duties of parental care, male elephants are primarily concerned with gaining access to sufficient nutrition for themselves and improving their prospects of reproducing successfully. I discuss how male social life begins to diverge from that of females upon reaching sexual maturity and how relationships among males manifest. I then examine reproductive strategies in both sexes, highlighting some of the similarities shared by all elephant species by virtue of their basic physiology, irrespective of their ecologies. This in turn shapes reproductive tactics uniquely employed by male elephants that distinguish them from other species. I conclude by examining some consequential differences between the Asian and African species both in terms of evolution and conservation, arising from one conspicuous dissimilarity: the absence of tusks in many Asian elephants.

Chapter 5 considers the role that elephants play in ecosystems. Elephants are variously referred to as flagship species, keystone species, ecosystem engineers, and even "mega-gardeners" (Blake & Hedges, 2004; Campos-Arceiz & Blake, 2011). These monikers all allude to elephants' ability to modify habitats and participate in a variety of ecological interactions, for the most part thanks to their sheer size. I examine their interactions, both with the species they exploit and those that exploit them. Aside from this, I consider their dependence and impact on natural resources, as well as the effect of artificial resources. I then introduce the concept of the "landscape of fear," which provides an intriguing lens through which to view behavior insofar as it is a response to perceived threats in the environment. The consequent use or avoidance of certain areas may thus depend not only on what is present in those areas, but also on what is absent.

Chapter 6 explores elephant movements and space use in greater detail. This chapter is grouped by habitat and landscape type, subdivided further by geographic regions. I use this structure to try and present a somewhat cohesive picture of the factors driving space use, where different species might share commonalities but also underscore conservation challenges relevant to their particular context. The examples often demonstrate why it is important to consider departures from assumptions made by classical theories, such as optimal foraging theory and the ideal free distribution, when contending with materially embodied species facing real problems physically embedded in space and time, as opposed to theoretical constructs or simulations.

Chapter 7 considers communication and cognition as flipsides of the same coin, recognizing the close relationship between dominant modes of communication and dominant modes of perception. I begin with different sensory modalities, which include the chemosensory apparatus, tactile perceptions, use of vibrations in air and ground, and visual domain. I discuss sensory signals and cues in terms of how they may be actively or passively employed. Among specialists of these topics, the term "signal" generally refers to something that the animal actively produces in order to broadcast itself to other conspecifics (such as a vocalization or controlled chemical secretion), whereas the term "cue" can refer to something produced either inadvertently or signals for which the subject was not the intended target (e.g. vocalizations of other species, seismic vibrations due to footfalls), as well as environmental stimuli (e.g. the scent of ripening fruit). I then move deeper into what we know of the elephant mind, considering various kinds of awareness, knowledge, and emotion. Lastly, I circle back around to elephant societies and the prospect of culture, which represent a sum total greater than the constituent individuals.

In the final chapter, I consider the long history and inherent challenges of human–elephant interactions on shared landscapes. In particular, I reflect on the question of whether we have an adequate understanding of the types of landscapes on which elephants have long lived and the processes that maintained them. Humans may have had a crucial role to play. Despite our role as predators in many ecosystems, we have also served as ecosystems' stewards and guardians. These relationships were in many cases disrupted throughout the world during a multicentury process triggered by the radical transformation of landscapes and societies that took place around the globe during colonialism. The reverberations of this era persist and continue to be felt. But as our own population keeps rising to dizzying heights, accompanied by the unpredictability of a changing climate, the ability of the past to guide the future seems limited. Yet, in looking forward, I think it is imperative to learn from our past in order to ensure a just and sustainable future for both our species and the many others that live alongside us.