Chapter 11
The Ecology of Large Herbivores of South and Southeast Asia: Synthesis and Future Directions

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Abstract The countries of South and Southeast Asia (SSEA) are home to a diverse array of large native herbivores, but the majority of these species are currently threatened with extinction. Ensuring the future survival of these species and the integrity of the ecological services they provide will require concerted management efforts, but these need to be built on a strong scientific foundation, which is currently lacking. In particular, there is an urgent need for research efforts to: (i) generate baseline data on the current status and distribution of large herbivores species in South and Southeast Asia, (ii) quantify vital rates of species and identify factors that regulate the population dynamics of different species across their ranges, (iii) understand the role of large herbivores in regulating community and ecosystem processes, and how their losses are likely to affect ecosystems, and (iv) characterize the ecological and socioeconomic drivers of human–herbivore conflicts to identify the most effective ways of reducing conflict and thereby sustain large herbivore populations across the landscape. The large herbivores of South and Southeast Asia also offer unlimited opportunities for addressing a diverse array of other basic, as well as applied, scientific questions ranging from evolution and behavior to disease dynamics and the responses of herbivore populations to changing climates. Besides establishing and sustaining research initiatives that will generate much-needed long-term scientific data on large herbivores, there is also an urgent need for greater cooperation between ecologists, sociologists, economists, politicians, land managers, and the public if we are to ensure the long-term survival of large herbivores in the region.

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Large herbivores in SSEA currently face unprecedented threats from habitat loss, land-use change, and direct persecution through hunting as a result of growing human populations in the region (Schipper et al. 2008; Hoffmann et al. 2011; Ripple et al. 2015). Of the 83 species found here, nearly 37 % (31 species) are under imminent threat of extinction, with 8 species (10 %) listed as critically endangered and another 23 species (28 %) classified as endangered by the IUCN (Table 1.1 in Chap. 1, also see Fig. 2.21). An additional 35 % of the species are listed as either vulnerable (21 species) or near threatened (8 species, Table 1.1), and there is insufficient data for 9 species (11 %, classified as data deficient by the IUCN, Table 1.1 in Chap. 1, also see Fig. 2.21). Furthermore, nearly a quarter of the large herbivores in SSEA (~22 species) are potentially 'political endemics' (i.e., restricted to one country), which considerably increases their extinction risk depending on the cultural and political willingness and ability of nations to protect them (Ceballos et al. 2005). The mammal fauna of Southeast Asia, including large herbivores, also show some of the greatest range reductions since the nineteenth century, and thus local population extinctions, of all mammals globally (Ceballos and Ehrlich 2002; Morrison et al. 2007; Ripple et al. 2015). Clearly, the need for immediate conservation efforts to secure the long-term future of large herbivores in SSEA cannot be overstressed.

Ultimately, for conservation efforts in the region to be successful, they must be built on a strong foundation of in-depth scientific knowledge of the natural history and ecology of the species or guild in question, and the ecological roles they play in ecosystems. In putting this book together, we have tried to highlight and showcase some of the ongoing and past work on large herbivore ecology in SSEA. While this synthesis is by no means exhaustive, what is abundantly clear from this effort is that research on large herbivore ecology in SSEA remains largely inadequate (see Chap. 1). Neither the quantum of research being carried out in the region, nor its focus in terms of patterns and underlying processes, and spatial and temporal scales of enquiry, is sufficient to make scientifically informed management decisions for the conservation of large herbivores in SSEA (see Fig. 1.2). In this scenario, any rigorous piece of research on large herbivore ecology, irrespective of the specific question being addressed, is likely to be of significant value. However, in the following sections, we highlight some minimum data requirements and broad synthetic research themes which we believe are particularly critical and urgent, and which we hope will benefit management by filling in existing knowledge gaps and also serve to stimulate future scientific research.

11.1 Filling in the Blanks: Status and Distribution of Large Herbivores

Despite a long tradition of natural history in the region dating back to colonial times and even earlier (Jerdon 1874; Brander 1923; Peacock 1933), much remains unknown about the basic ecology of many herbivores in SSEA. This is particularly true of small-bodied forest dwelling ungulates such as muntjacs and chevrotains that inhabit the Southeast Asian countries of Myanmar, Thailand, Laos, Vietnam and Philippines, most of which are classified as data deficient by the IUCN (Table 1.2). While it is understandable that detailed information about these forest dwelling species, which are typically rare and occur at low densities, is lacking, what is more concerning is that our knowledge of even the larger, more widespread herbivore species in SSEA is fairly limited. For example, a search on Web of Science with the topic 'sambar deer'—possibly the most widespread large herbivore in SSEA—yielded 127 citations, in contrast to 'white tailed deer', which produced 5875 hits. Importantly, only a very small fraction of these papers directly addressed the ecology of the sambar, or provided insights for their conservation; a situation that is likely to hold true for most large herbivores in SSEA.

As a starting point, we need more detailed information about the current distribution and status of most of the large herbivores of SSEA; a minimum requirement for both managers and scientists alike. At present, coarse-scale distribution maps are available for many large herbivore species in the region, and these have proved extremely valuable for global and regional status assessments (Ceballos and Ehrlich 2002, 2006; Ceballos et al. 2005; Schipper et al. 2008; Morrison et al. 2007). However, their utility for conservation programs, as well as for understanding factors that regulate herbivore distribution patterns at smaller scales, is limited. Generating fine-scale distribution and status maps for the diverse array of herbivores in SSEA is not a trivial exercise, and the efforts required to establish rigorous local-scale monitoring efforts will undoubtedly be substantial. However, relatively rapid approaches such as key informant surveys within an occupancy-modeling framework have proven effective as a first cut, not only for generating finer-scale maps of the current distribution of animals, but also for uncovering spatiotemporal patterns of change in their distribution and abundance (Karanth et al. 2010; Pillay et al. 2011, 2014). While such 'rapid' assessments can be particularly useful in assessing trends over large geographic areas, they are not a substitute for more detailed and sustained monitoring of 'priority' populations of herbivores in the long-term, both inside and outside protected areas.

Long-term monitoring of herbivore populations and habitats is critical for assessing the efficacy of existing management programs, or alternately the need for new management initiatives, as they provide information about population trends and can serve as early-warning indicators of population declines (Beever and Woodward 2011). Given the logistical, financial, and manpower constraints involved with setting up and sustaining such initiatives over the long term, it is amply clear that they must ultimately be implemented and coordinated by land

managers and forest department officials. Annual monitoring of wildlife populations by land managers is already in place in many protected areas in SSEA, but these efforts have often been criticized for a lack of scientific rigor (Karanth et al. 2003). A monitoring program that is poorly designed or poorly executed, or both, neither answers the question it was designed to answer, nor provides data that is scientifically useful, and is essentially a waste of valuable resources (financial, manpower, time, etc.) that could have been more effectively utilized elsewhere (Reynolds et al. 2011; Beever and Woodhouse 2011).

Given the economic, political, social, and time constraints that land managers in SSEA constantly face, it is becoming increasingly clear that collaborations between the scientific community and managers can benefit the design, execution, and evaluation of scientifically rigorous monitoring programs. Thoughtfully conceived, well-designed monitoring efforts, when replicated and coordinated across larger scales, can uncover broad-scale patterns and identify drivers of herbivore population dynamics across environmental gradients, help detect phenomena such as thresholds and nonlinear dynamics, while also allowing for more robust inferences by increasing sample size and statistical power (Beever and Woodward 2011).

Besides serving as a basic template for conservation planning, distribution maps and long-term data on population trends of species across their geographic ranges will also serve as a critical resource for scientists, both from the region and elsewhere. At present, even the little data that is available is not easily accessible to the scientific community at large. The unfortunate consequence is that neither the scientists benefit from access to the data, nor do the managers benefit from the insights that the scientific community can bring to management and conservation planning from the analysis of such data. The need for greater data transparency and public sharing of data cannot be overstated at the current time, especially given the critical status of many large herbivore species in the region. In particular, we envision an increasing role in the future for open-science initiatives and data-sharing portals (e.g., India Biodiversity Portal; http://indiabiodiversity.org) in providing open and free access to biodiversity information from the region.

11.2 Regulators of Large Herbivore Population Dynamics

Besides providing information about population trends, long-term data on herbivore populations are also critical for understanding the factors that regulate and limit herbivore population numbers; a prerequisite to their effective management (Gordon et al. 2004). Our knowledge of what limits herbivore numbers, as well as the factors that cause them to fluctuate over time, has increased substantially in recent decades, thanks largely to a few long-term ecological studies of population and community dynamics in North America and Europe (see Gaillard et al. 1998, 2000; Gordon et al. 2004 and references therein). Seminal analyses of long-term population data from multiple herbivore species (see Gaillard et al. 1998, 2000) have provided us with critical insights into the relative importance of density-dependent and

density-independent factors that influence population dynamics, and how these in turn are influenced by factors such as the age-structure (Coulson et al. 2001), breeding system (Milner-Gulland et al. 2003), age- and sex-specific survival and emigration rates (Clutton-Brock et al. 2002), and harvesting (Clutton-Brock et al. 2002) of the population. The contribution of these studies to both our understanding of herbivore population dynamics, as well as their management cannot be overstated. However, the fact still remains that the majority of these studies come from temperate ecosystems, while most ungulates are tropical (Gaillard et al. 1998, 2000).

Because of differences between tropical and temperate ecosystems in terms of their seasonality, temperature versus water limitation during the lean season, disease prevalence and predation, drawing inferences about the population dynamics of tropical herbivores based on studies largely conducted in temperate ecosystems may not be straightforward (Gaillard et al. 1998, 2000). Furthermore, long-term term studies of large herbivore population dynamics from systems that still retain their complete complement of native predators, as is still the case in many areas in SSEA, is limited (Gaillard et al. 2000). Classic work from North America has highlighted the extent to which apex predators such as wolves and cougars are capable of limiting herbivore populations (Beschta and Ripple 2009; Ripple and Beschta 2012), and how extirpation or recolonization of predators can have effects that cascade through the ecosystem, influencing not only herbivore and plant trophic levels, but also other taxa such as beavers, song birds, and fish (Hebblewhite et al. 2005; Ripple and Beschta 2006), as well as ecosystem processes such as nutrient cycling (Frank 2008), river morphology, and hydrological flows (Beschta and Ripple 2012). In tropical ecosystems too, predation has, likewise, been argued to be an important regulator of population dynamics for some herbivore species and populations, but not for others (Sinclair 1985; Gasaway et al. 1996; Grange et al. 2004; Grange and Duncan 2006; Mduma et al. 1999).

At present, there is an almost complete lack of information about the long-term population dynamics and vital rates for most species of large herbivores in SSEA (see Chap. 10; Gaillard et al. 2000), and about the relative importance of 'bottom-up' versus 'top-down' forces in regulating herbivore population dynamics in the region. To our knowledge, the ongoing study of blackbuck at Velavadar National Park (See Chap. 6; Jhala and Isvaran) represents one of the only long-term studies of a species from SSEA, one that has provided us with critical insights into the factors regulating blackbuck population dynamics, vital rates, and behavior in this semi-arid system. To similarly generate accurate vital rates of other species, we require studies involving marked individuals that are monitored over time (Gaillard et al. 1998). Where it is not possible to mark individuals for one reason or another, long-term data on the abundance of the sexes, different age-classes, or even just total population size, can nevertheless provide us with insights into factors regulating herbivore populations. In this regard, ongoing long-term efforts to monitor prey populations as part of tiger conservation efforts across SSEA (see Chap. 9; Karanth and Nichols 1998; Karanth et al. 2004) are a potential source of valuable data that can contribute to a better understanding of herbivore population dynamics in the region.

The diverse array of large herbivores found in SSEA, spanning a range of body sizes and feeding strategies, provides unlimited opportunities to address basic and applied questions of both scientific and management relevance. Further, the range of habitats and environments occupied by large herbivores in SSEA, from high-altitude cold deserts to tropical rainforests, as well as the range in predator diversity and biomass, from sites with full to progressively depauperate complements of predators, allows us to address fundamental questions about the relative importance of predation versus resource-limitation in regulating herbivore populations, and how they vary as a function of herbivore body size and along resource gradients (Hopcraft et al. 2010; Fritz et al. 2011). Understanding predator-control of herbivore populations is particularly important for management in light of current poaching-driven declines and local extinctions of predators in SSEA (e.g., the local extinction of tigers in Sariska National Park, India). From a conservation perspective, there is also an urgent need for studies that investigate how hunting of large herbivores, which is both prevalent and widespread in SSEA (Madhusudhan and Karanth 2002; Velho et al. 2012), impacts vital rates and population trends of different large herbivore species.

11.3 Community and Ecosystem Consequences of Herbivory

Large herbivores are well recognized as important regulators of community and ecosystem processes. They can induce significant shifts in plant community composition and diversity, with effects that diverge widely between different ecosystems depending on site productivity and precipitation, evolutionary history of herbivory, herbivore body size, feeding selectivity of herbivores, temporal patterns of herbivory, and differences between plant species in their ability to tolerate or recover from herbivory (Milchunas et al. 1988; Augustine and McNaughton 1998; Olff and Ritchie 1998; Proulx and Mazumder 1998; Bakker et al. 2006; Diaz et al. 2007). Large herbivores also play critical roles in regulating tree community composition and the balance between trees and grasses in ecosystems by acting as agents of seed dispersal (see Chap. 5; Miller 1996), and through their effects on the growth, reproduction, recruitment and mortality of trees (Prins and van der Jeugd 1993; Augustine and McNaughton 2004; Sankaran et al. 2004, 2008, 2013; Goheen et al. 2007; Guldemond and van Aarde 2008), with such effects further modulated through interactions with fire regimes (Dublin et al. 1990; Holdo 2007; Staver et al. 2009). Large herbivore effects can also extend beyond the primary producer level, percolating through to influence the abundance of multiple other taxa including arthropods, reptiles, birds, and rodents (Pringle et al. 2007; Greenwald et al. 2008; Banks et al. 2010; Goheen et al. 2010; Foster et al. 2014). Finally, large herbivores also play critical roles in regulating the carbon and nutrient economy of ecosystems, both directly through consumption of plant material, and indirectly by redistributing nutrients across the landscape and by returning them to soils in more readily

available forms via dung and urine (McNaughton 1985; Augustine and McNaughton 1998; Ritchie et al. 1998). Herbivores stimulate primary production and enhance nutrient cycling rates in fertile ecosystems when herbivory is nonselective and occurs early in the growing season, while depressing them in nutrient-poor ecosystems, and under conditions of chronic and selective herbivory (Augustine and McNaughton 1998; Ritchie et al. 1998).

Our understanding of the ecology of large herbivores in SSEA is perhaps nowhere as lacking as when it comes to understanding their roles in influencing community and ecosystem processes (also see Fig. 1.2). There have only been a handful of studies in SSEA that have used exclosures to experimentally assess herbivore effects on plant community composition and richness (see Chaps. 7 and 8; Sankaran and McNaughton 1999; Sankaran 2005; Bagchi et al. 2012), and on ecosystem processes such as carbon and nutrient cycling (see Chaps. 7 and 8; Bagchi and Ritchie 2010a, b, 2012; also see Pandey and Singh 1992; Moe and Wegge 2008). These studies have largely been restricted to herbaceous communities in grassland and savanna ecosystems, and we are unaware of any studies that have looked at herbivore effects on tree dynamics, or ecosystem processes in mixed tree-grass ecosystems and forests of SSEA. Thus, while we have some information about the roles that large herbivores play as seed dispersers (Chap. 5), we know very little about how large herbivores influence tree community composition and patterns of tree recruitment, growth, and mortality. Given the widespread declines in herbivore numbers across large parts of SSEA, there is an urgent need for research programs that focus on understanding herbivore effects at the community and ecosystem level across different ecosystem types in the region. This is critical if we are to predict how the effects of such herbivore losses are likely to cascade through ecosystems influencing not only plant communities but also other taxa and ecosystem processes, and how these are likely to vary across ecosystem types, with implications for their effective management.

11.4 Conflict and Coexistence

As human populations expand and rates of land-use conversion intensify, wildlife populations will undoubtedly come into increasing contact with humans and livestock in the future. Nowhere is this problem likely to be more acute than in SSEA. In the majority of cases, such increased contact will almost certainly translate to increased levels of conflict, either actual or perceived, in the form of increased crop depredation by wildlife, heightened competition between livestock and native herbivores, increased hunting and persecution of wildlife by humans, and greater loss of property and potentially, human life. Such conflict is doubly problematic; it can seriously undermine conservation prospects by eroding the willingness of local communities to conserve wildlife, while simultaneously having negative consequences for large herbivores through loss of habitat, increased disease risk, reduce forage availability as a result of competition with livestock, and increased persecution

by humans (Madhusudhan 2003, 2004; Mishra et al. 2004). The resolution of such conflict to ensure the long-term persistence of large herbivores in the region will ultimately hinge on successful cooperation between ecologists, sociologists, economists, politicians, managers and the public (Gordon et al. 2004). Ecologists, nevertheless, have much to contribute to conflict resolution by (i) identifying the extent to which native and domestic herbivores compete with or facilitate one another, the conditions under which each occurs, and the implications of such interactions for native herbivore populations (Bagchi et al. 2004; Madhusudhan 2004; Mishra et al. 2004; Bhatnagar et al. 2006; Odadi et al. 2011), (ii) identifying the ecological determinants of conflict such as crop raiding, including its spatial and temporal patterns of occurrence (Owen 2013), (iii) understanding the impacts in terms of disease prevalence and transmission of increasing contact between wild and domestic herbivores (Kilpatrick et al. 2009), (iv) understanding the population and genetic consequences of retaliatory killing of large herbivores by humans (Ginsberg and Milner-Gulland 1994; Mysterud 2011), and (v) helping local communities and land managers by determining the most effective ways of reducing conflict and managing large herbivore populations in the landscape (Mishra et al. 2003; Gordon et al. 2004). Such efforts are particularly critical given that significant wildlife populations currently persist outside protected areas, and conservation efforts must, by necessity, also extend to these human-dominated landscapes (Chazdon et al. 2009; Hoffmann et al. 2015).

11.5 Concluding Statements

The research themes and data requirements that we have highlighted in the previous sections represent but the bare minimum in terms of understanding the factors that limit herbivore populations in SSEA, and the roles that large herbivores play in influencing community and ecosystem processes in the region. The large herbivore guild of SSEA also provides a wealth of opportunity for addressing a diverse array of other basic, as well as applied, scientific questions relating to their evolutionary history and genetics (Chap. 2; Guha et al. 2007; James et al. 2008; Khaledi et al. 2009; Vidya et al. 2009), behavior (See Chap. 6; Isvaran 2005, 2007), body size and foraging ecology (Chap. 4; Ahrestani et al. 2012; English et al. 2014), habitat use and distribution patterns (see Chap. 3; Odden et al. 2005; Sridhara et al. 2013; Sharma et al. 2014), and their effects on plants (Chap. 7; Bagchi and Ritchie 2011), to name a few. In addition, a key area of research that has been largely neglected in SSEA, but one that is likely to become increasingly important for management in the future, is the role of disease in regulating wildlife populations. Most previous studies of disease have been carried out on captive populations of large herbivores (Fig. 1.2), and its role in regulating herbivore population numbers and community structure, as well as the factors that regulate the spatial dynamics of disease transmission in the wild including disease prevalence, persistence, and spread remain largely unknown.

The bulk of ecological research in SSEA has, thus far, been disproportionately centered on tropical forests and global biodiversity hotspots. However, hotspots of mammalian diversity are not necessarily congruent with 'general purpose' biodiversity hotspots, with less than 2 % of the prime area of large herbivore diversity estimated to overlap with 'global' biodiversity hotspots (Olff et al. 2002). Future efforts must, therefore, extend beyond the boundaries of global biodiversity hotspots to also encompass areas that are critical for large mammalian herbivores in the region (Olff et al. 2002; Ahrestani et al. 2011). There is also a need for sustained research efforts in 'priority' herbivore areas in order to generate much needed long-term time series data on herbivore population dynamics and ecology. The majority of research on large herbivores in SSEA thus far represent but a 'one-off' effort, addressing a specific question on a particular species in a particular location, with little to no follow-up research. As a result, for most species and sites, we lack even the most basic of foundations, built on a core body of past research, upon which to build and address questions of scientific and management relevance. Long-term studies of the blackbuck in Velavadar National Park (Chap. 6), mountain ungulates in the trans-Himalaya (Chap. 3) and monitoring of prey populations as part of tiger conservation efforts across SSEA (Chap. 9; Karanth and Nichols 1998; Karanth et al. 2004) represent welcome exceptions, but many more such efforts are currently needed. Finally, future research on large herbivores in SSEA must be set within the overarching context of climate change, as it is becoming increasingly evident that climatic variability and extreme events can exert significant, and often nonlinear, controls on herbivore populations (Coulson et al. 2001; Mysterud et al. 2001; Post and Forchhammer 2008; Post et al. 2009).

In closing, we hope that the understanding and the ongoing research on large herbivores in SSEA that this volume showcases serves to stimulate future research on this prominent but neglected guild. If we are to successfully manage and ensure the continued persistence of the diverse large herbivores of South and Southeast Asia, there is then an urgent need to immediately initiate research efforts that are ultimately sustained in the long term. At present, much remains unknown about the ecology of these species and the ecological roles they play in ecosystems, and the opportunities for future research are immense.

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