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Conserving Wildlife in African Landscapes

Kenya's Ewaso Ecosystem

Edited by
Nicholas J. Georgiadis

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ABSTRACT
Georgiadis, Nicholas J., editor. Conserving Wildlife in African Landscapes: Kenya's Ewaso Ecosystem. *Smithsonian Contributions to Zoology*, number 632, vi + 123 pages, 37 figures, 10 tables, 2011.—During the last two decades, conservation strategies in Africa have changed from an almost exclusive focus on large mammals in protected areas to an emphasis on conserving ecological processes at the level of entire landscapes and on the role of human communities. The papers assembled in this volume address diverse aspects of conserving the Ewaso landscape in northern Kenya, where concerted and prodigious efforts to conserve wildlife and natural resources have achieved substantial progress. Topics range from interpreting evidence for continuity and change in patterns of human settlement in the region to describing ecological interactions between wildlife, people, and livestock that are harmful or helpful; from the challenges of adapting livestock management in the presence of predators to legal mechanisms for conserving wildlife habitat on private land. In the final chapter, results of a strategic planning exercise are described for conserving essential elements in the entire landscape—the first of its kind in Kenya. Today, national policy and political will are still insufficiently aligned with this landscape conservation imperative to effect the changes that are necessary to conserve Kenya's biodiversity. We hope this volume will help propagate awareness about the importance and threatened status of Kenya's ecosystems and promote confidence that a policy can be crafted that will reverse their decline.

Cover image: Giraffes in the Ewaso landscape of Kenya. Photo by Nicholas J. Georgiadis.

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Nicholas J. Georgiadis

FRONTISPIECE. Typical assemblage of herbivores (giraffes and zebras) in the Ewaso landscape of Kenya. Mount Kenya is in the background. Photo by Nicholas J. Georgiadis.

Introduction: Conserving Wildlife in Kenya's Ewaso Landscape

Nicholas J. Georgiadis

The papers assembled in this volume are disparate in subject, discipline, treatment, and outlook, but they have two unifying threads. The first is that directly or indirectly, they all address aspects of what in recent decades has become a global environmental imperative, generally referred to as "landscape conservation." The second is that all chapters focus geographically on the Ewaso landscape in northern Kenya (defined in Box 1; outlined by a rectangle in the inset of Figure 1), where concerted and prodigious efforts to conserve wildlife and natural resources over the last 20 years have achieved substantial progress. This work is not a "how-to" handbook, nor does it aim to cover all aspects of this increasingly complex and multifaceted endeavor. Rather, it provides an opportunity to document progress in ways intended to facilitate further advancement toward landscape conservation in this and other regions like it.

In this introduction, a brief history recounts how conservation strategies at global, national, and local levels have changed from an almost exclusive focus on charismatic species and protected areas to emphasizing landscape-level processes, human communities, and economic incentives. The structure of the book is described, with sketches of the rationale and content of each paper. The final section sketches the outlook for wildlife in Kenya's landscapes.

CHANGING PARADIGMS IN CONSERVATION

The late 1980s marked a turning point for conservation in a district of northern Kenya, across much of Africa, and throughout the world in distinct but related ways. In the Laikipia rangelands of northern Kenya, ranchers who had once regarded wildlife as a liability began to collaborate with each other in the conservation and management of wildlife on their land. At the time, the

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BOX 1. Defining the Ewaso ecosystem.

For the purposes of this book, the Ewaso ecosystem is arbitrarily defined by the geographical extents of two large-scale processes that have been selected as long-term targets for conservation: dry-season river flow and elephant migration. Two "water towers" that collect much of the region's rainfall, the Aberdare Range (3,999 m) in the southwest and Mount Kenya (5,199 m) in the southeast, are drained to the north by many streams that ultimately combine to form two perennial rivers (Figure 1). These are the Ewaso Nyiro and Ewaso Narok, which are confluent in the central "Laikipia Plateau," continuing to flow northward and then eastward through the Samburu, Buffalo Springs, and Shaba National Reserves and ultimately to the Lorian Swamp. This drainage system is not exceptional in that water abstraction for irrigation and household use has escalated in recent decades, particularly in the upper reaches of the catchment, leaving progressively less water available for people, livestock, and wildlife in the drylands below. Accordingly, the functional ecosystem "boundary" encompasses the upper drainage basin of the Ewaso Nyiro and Ewaso Narok rivers as far as the eastern boundary of Samburu District.

Elephants have been shown to migrate immense distances up and down elevation and rainfall gradients in this region, seeking food and water on a seasonal basis. Reasoning that the viability of elephants in the region depends on their seasonal migrations, and that if elephant migration can be conserved, then many other species and ecosystem processes will also benefit, elephants have assumed strategic prominence in conservation planning for this landscape. Accordingly, the known extents of their migrations beyond the Ewaso Basin are also encompassed within the rectangle that delineates the Ewaso ecosystem.

These criteria define a vast (~40,000 km^2) and geographically diverse region, including the entirety of Laikipia District (9,666 km^2) and parts of adjacent Samburu, Meru, Isiolo, and Marsabit Districts to the north and east (Figure 2). A wide diversity of habitats, land cover types, and land uses (Figure 2) are associated with the elevation and climatic gradients that characterize this region, from cool, wet highlands in the south to hot, dry lowlands in the north. Most of the wildlife occur in the wetter, southwestern sector of the region, on private ranches in Laikipia District (Figure 3). These range from alpine moorlands above 3,000 m on Mount Kenya and the Aberdare Range, through protected montane rain forests and an intensively cultivated moist zone to dry savanna grasslands and bushlands at lower elevations. Mean annual rainfall varies from around 300 mm in the northeast to more than 1000 mm in the south, increasing with elevation to around 1300 mm in the forested zones on Mount Kenya. Rainfall is highly variable but trimodal, falling mainly in April–May, November, and August, with a pronounced dry season in January–March.

dominant conservation paradigm in Africa, which had fixated on large mammals in protected areas for over 60 years, began to be replaced by a more inclusive approach, which recognized humans as an integral component of biodiverse landscapes and the need for conservation to account human needs and effects. The persistence of biodiversity was seen to depend on active conservation not only in parks and reserves but also in areas that lacked formal protection, and were occupied by humans and livestock (see discussion in Hutton et al., 2005). At the same time, a conceptual revolution among public and private agencies in the United States sparked what is today a global conservation agenda, originally known as "ecosystem management" (Grumbine, 1994, 1997; Keough and Blahna, 2006), that aims to sustain the integrity of ecological processes across vast landscapes. Twenty years on, the papers in this volume document some of the approaches and progress toward landscape conservation that have been achieved in the Ewaso landscape of northern Kenya.

Ranchers in Laikipia District, the southwestern sector of the Ewaso region, were motivated to promote wildlife as a source of income by a weakening beef market (Heath, 2000) and by growing recognition of the potential value of wildlife on their land. After a 14-year hiatus, Kenya was once again experimenting with sanctioned harvesting of wildlife on private land (Kock, 1995). Those wishing to participate were required by the national conservation authority, Kenya Wildlife Service (KWS), to create and join management associations. To meet this need, the Laikipia Wildlife Forum (LWF) was launched in 1991 as a company of private and communal landholders with a shared interest in wildlife management and conservation. With investors foreseeing greater returns from nonconsumptive uses of wildlife, ecotourism enterprises proliferated on private and communal properties in the region. Cooperation among landholders favoring wildlife was spurred by growing awareness of the need to maintain sufficient space for species like elephants, lions, and wild dogs, whose survival depended on continuing freedom to range across far greater areas than even the largest individual property.

That most of Africa's protected areas were never designed to maintain, on their own, ecologically viable populations of these wide-ranging mammals has long been recognized and often repeated, at least in the conservation

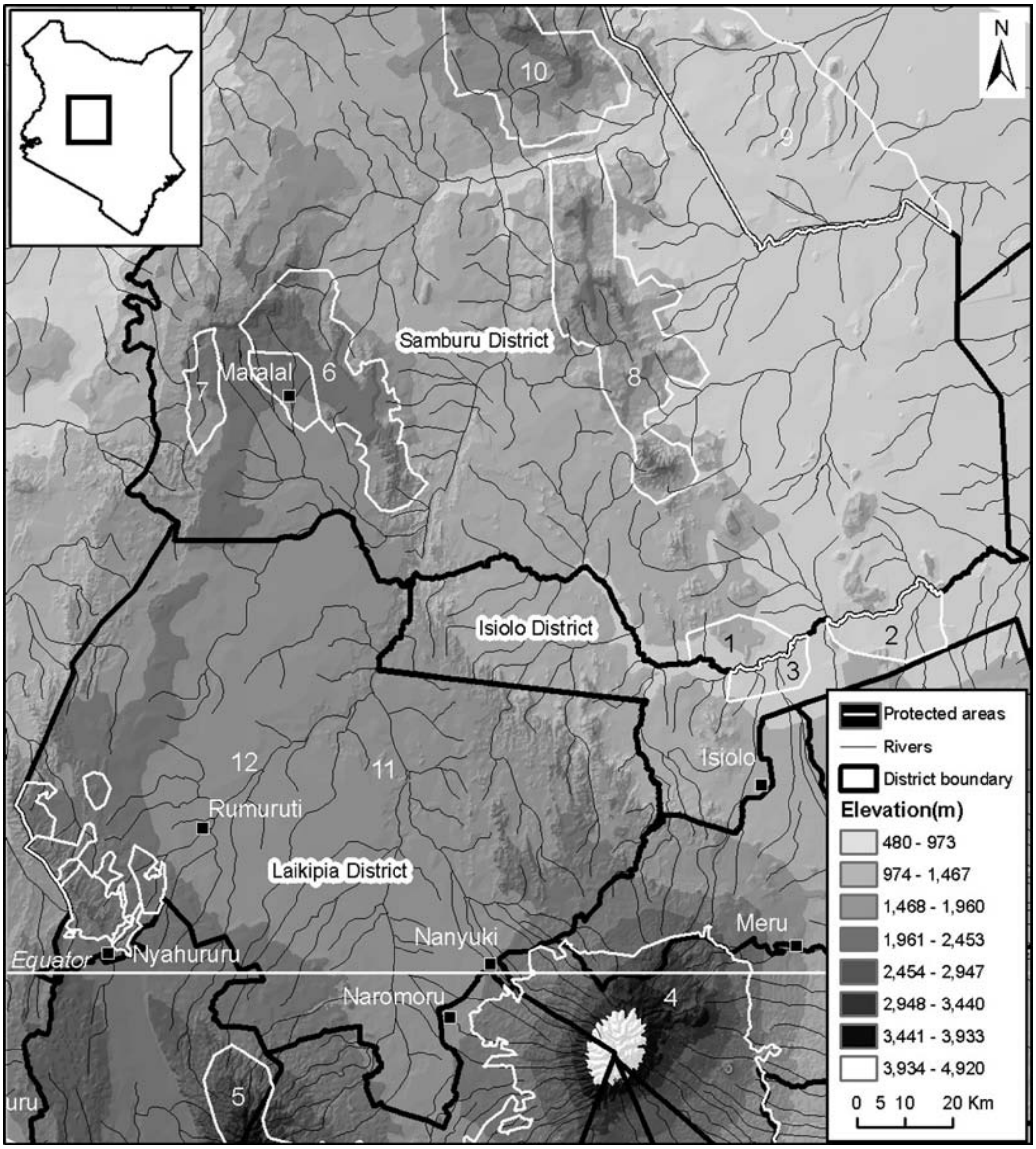

FIGURE 1. Relief and drainage in the Ewaso ecosystem. The region is bounded in the west by the Rift Valley and in the south by Mount Kenya and the Aberdare Highlands. Protected areas are outlined in white as follows: 1, Samburu National Reserve (NR); 2, Shaba NR; 3, Buffalo Springs NR; 4, Mount Kenya National Park (NP); 5, Aberdare NP; 6, Karisia Hills Forest Reserve (FR); 7, Maralal FR; 8, Matthews Range FR; 9, Loisai NR; 10, Ndoto Mountains FR. Major rivers are as follows: 11, Ewaso Nyiro; 12. Ewaso Narok.

literature (Soulé et al., 1979; Western and Ssemakula, 1981; Western, 1982, 1989; Western and Gichohi, 1993; Newmark, 1996, 2008). In most cases, the wild animals that generate tourism revenue for national or local governments within unfenced parks and reserves would soon perish if denied access to surrounding lands that are privately or communally held. But to most who own or use this land, wildlife is a liability. They may incur losses from crop raiding or be threatened or even killed by elephants, and their livestock are vulnerable to predators and disease (Woodroffe et al., 2005). Almost invariably, wildlife ultimately lose these conflicts with humans, becoming displaced by development and incompatible land use changes. As a result, wildlife is increasingly confined to protected

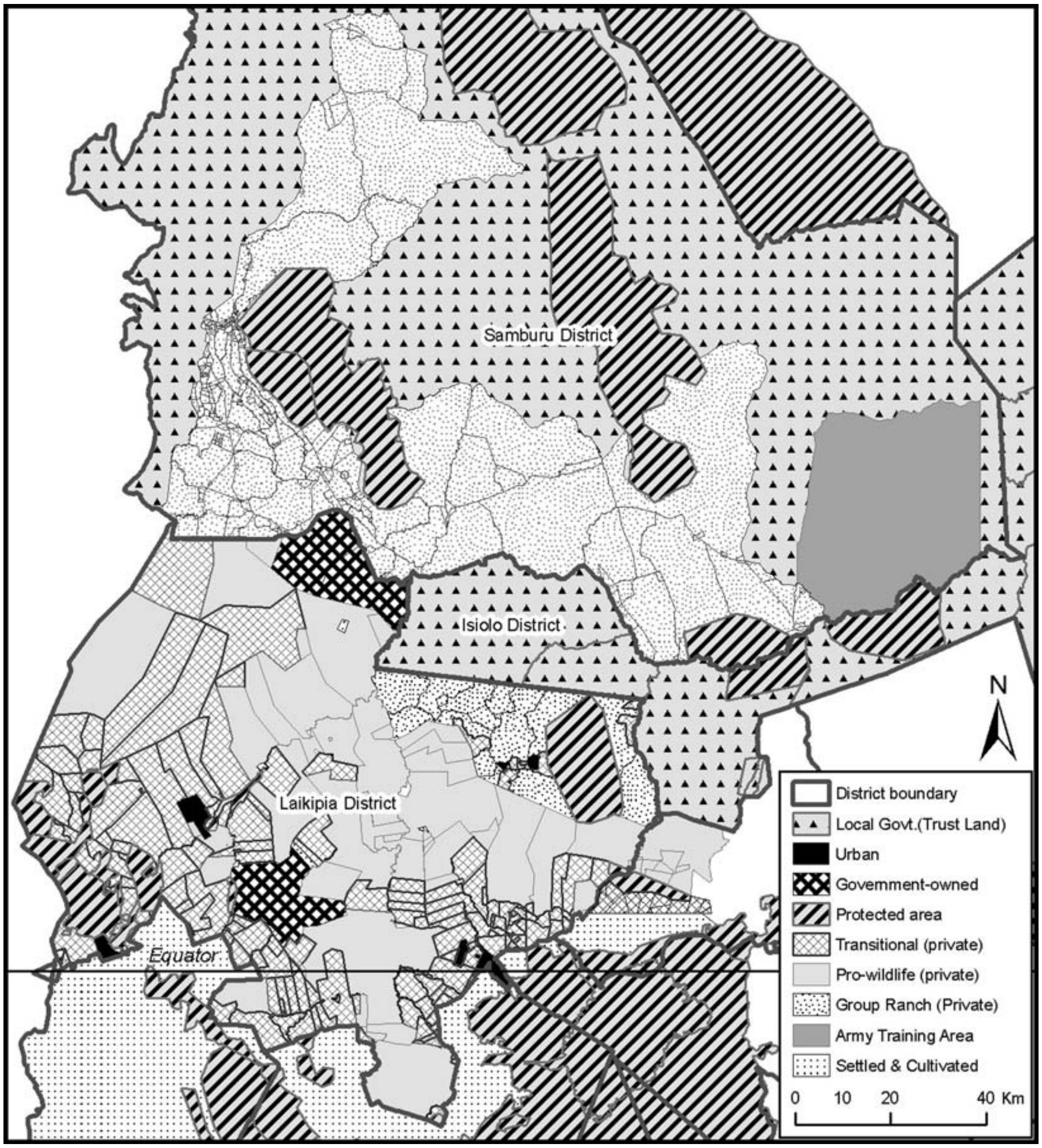

FIGURE 2. Land use in the Ewaso ecosystem.

islands that are too small to ensure their long-term viability. With diminishing options to expand existing parks and reserves, attention turned toward habitat and biodiversity conservation in areas that were not formally protected, most of them communally owned or used. A variety of conservation initiatives, labeled integrated conservation and development projects, community-based conservation projects, and numerous variations on this theme spread across the continent from southern Africa, aiming to create incentives for landholders and land users to conserve wildlife and natural resources (e.g., Western and Wright, 1994; Barrow and Murphree, 2001; Fabricius et al., 2004; Child, 2004).

Similar concerns in North America about the inadequacy of national parks to sustain viable populations of large mammals like grizzly bears and progressive habitat fragmentation in natural areas adjacent to parks prompted a search for ways to conserve large-scale ecological processes across diverse landscapes, only parts of which were formally protected. Today, an ecosystem or landscape approach dominates most conservation strategies, aspiring to integrate the use and management of natural resources

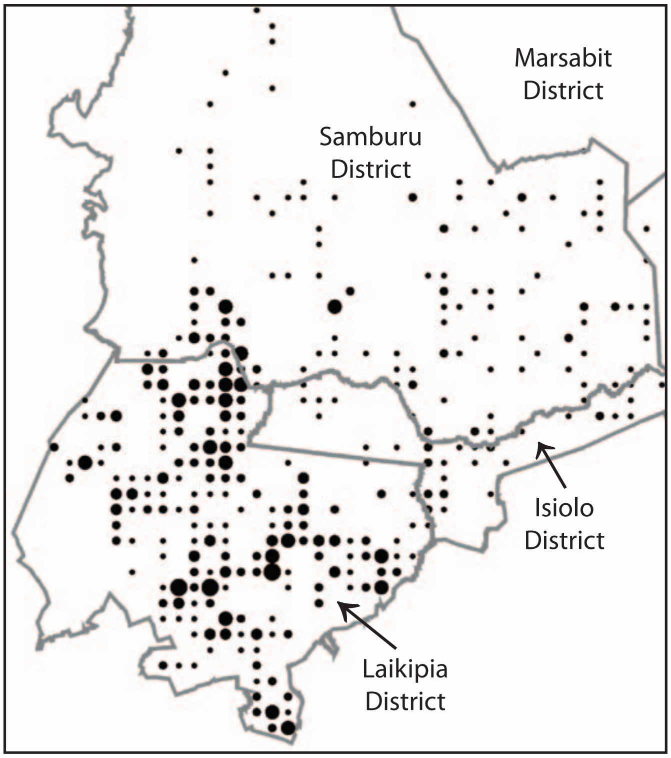

FIGURE 3. Relative abundance and distribution of wildlife (black dots) in the Ewaso ecosystem, with the majority on pro-wildlife ranches in Laikipia District (source: Department of Resource Surveys and Remote Sensing survey, February 2001).

in sustainable ways across spatial scales that better match the historical extents of natural ecosystem processes (e.g., Pirot et al., 2000).

Economic rationale provided the impetus for these changing conservation strategies. In many African cases, landholders and land users were not expected to conserve biodiversity unless they benefited, largely by realizing market values of wildlife via ecotourism, trophy hunting, or sale of live animals (e.g. Child et al., 1997). The ecosystem management approach went still further, ultimately calling for the full value of "ecosystem services" to be assessed and captured (e.g., Daily, 1997), for the full costs of economic development to be accounted, and for development and exploitation of natural resources to be appropriately priced and thus truly sustainable.

About to come of age, these community- and market-based approaches to landscape conservation have had mixed results. Some community-based projects in Africa have made remarkable progress (e.g., Weaver and Skyer, 2003), but most have struggled to alleviate poverty, conserve biodiversity, or both, for several reasons (Newmark and Hough, 2000). The conception and operation of community-owned enterprises have inherent uncertainties as to individual rights and communal benefits, hampering solutions that are both workable and equitable (Logan and Moseley, 2000; Mburu and Birner, 2002; Walpole and Thouless, 2005). National or local governments have been reluctant to devolve to local communities the responsibility for and ownership of—or at least rights to—land and wildlife (Child and Jones, 2006). The management and governance capacity of communities often fall short of the minimum needed to sustain small businesses (Spiteri and Nepal, 2006). Wildlife and natural habitats continue to lose ground wherever competing land uses provide greater benefits to landholders (Norton-Griffiths and Southey, 1995). Conserving ecosystem services will not necessarily conserve biodiversity (Ghazoul, 2007). Basing a strategy on biodiversity does not necessarily conserve large-bodied wildlife. And it seems unlikely that the inclusive costs of development, or the full value of ecosystem services, will be captured by markets soon enough to make a substantial difference (Egoh et al., 2007; Kroeger and Casey, 2007). For many large African mammals, their habitats, and the large-scale ecological processes that they define, overall trends continue downward.

These discouraging trends have led some to reconsider the validity and potential of incentive-based approaches to conservation in human-occupied landscapes and to recommend a return to providing sanctuary for wildlife in additional protected areas (see discussion in Hutton et al., 2005), or Transfrontier Conservation Areas (Hanks, 2003; Wolmer, 2003; Munthali, 2007). Although this will help, opportunities to create or expand protected areas continue to diminish. Moreover, sustaining natural processes in areas that are not formally protected is hardly optional, not only in the survival interests of biodiversity but also of humanity. A more hopeful outlook sees progress to date as an exercise in defining the complexity and scope of the challenge (Adams and Hulme, 2001), which is colossal and has been persistently underestimated.

TOWARD LANDSCAPE CONSERVATION IN NORTHERN KENYA

Despite media-generated impressions of teeming wildlife, Kenya is not exceptional in that most of its wildlife populations have been declining, and their habitats fragmenting, for decades (Box 2). These trends and their causes have been documented at both local (e.g., Lamprey

BOX 2. Trends and status of wildlife in Kenya since 1977.

The dynamics of large-bodied (>20 kg) herbivore species have been monitored throughout Kenya's rangelands since 1977 by the Department of Resource Surveys and Remote Sensing (DRSRS, formerly the Kenya Rangeland Ecological Monitoring Unit, KREMU). Using mostly aerial sampling methods (Norton-Griffiths, 1978) and repeatedly surveying entire districts at a time, results are sufficient to measure coarse changes over vast areas. There have been several summaries of overall trends, all showing net declines in most areas (Figure 4). Grunblatt et al. (1996) concluded that wildlife in Kenya's rangelands declined by 33% between 1977 and 1994. Further analyzing results of de Leeuw (1998), Western et al. (2009) concluded that wildlife abundance in 17 districts declined by 38% between 1977 and 1997. A separate analysis by Ojwang' et al. (2006) showed declining wildlife trends in Kajiado District to continue into the early 2000s (excepting plains zebra and elephants). At these rates, and assuming a linear trend, the overall decline by 2011 is projected to be about 60%.

Supplementing data from additional sources, Western et al. (2009) showed that trends inside protected areas were also mainly downward. Between 1977 and 1997 wildlife declined in most protected areas, precipitously in Tsavo and Meru National Parks. In the 1990s steep declines were recorded in Nairobi, Nakuru, and Amboseli National Parks. In areas adjacent to protected areas, wildlife declined sharply around Tsavo National Park and the Masai Mara National Reserve (Western et al., 2009; see also Ottichilo et al., 2000; Homewood et al., 2001; Thompson and Homewood, 2002).

There have been some notable exceptions. Steeply declining elephant and rhino numbers in the 1970s and 1980s were reversed in the 1990s. For elephants, this was achieved by an international ban on ivory trading and stringent enforcement within Kenya. For black rhinos, a well-organized collaboration between national wildlife authorities and private landowners has allowed numbers in small but heavily guarded sanctuaries to increase.

Perhaps most promising, wildlife numbers in private conservation areas have remained steady or even tended to increase in recent decades (Western et al., 2009). In Laikipia District (the southwestern sector of the Ewaso ecosystem), wildlife increases between 1977 and the early 1990s were largely due to a resurgence of plains zebra and elephants. Since 1990, declines in some prey species, especially on properties investing in conservation, were ultimately found to signal a further conservation success: the restoration of predators in that region (Georgiadis et al., 2007a).

Today, the largest proportion of Kenya's wildlife, about 40%, is found on private and communally owned land (Western et al., 2009). An additional 25% is scattered at low density across vast stretches of dry rangeland, much of it held in trust by local governments. Of the 35% remaining within formally protected areas, fully two-thirds are in the Masai Mara Reserve, with Amboseli and Nakuru National Parks holding most of the rest. The future of Kenya's wildlife depends on the success of conservation on private and communally owned lands that lack formally protected status.

and Reid, 2004) and national levels. Habitat loss and fragmentation due to expanding settlement, land subdivision, and spread of incompatible land uses such as cultivation, clearing of woodland for charcoal production, consumption of bushmeat, displacement by livestock, proliferation of firearms, and local outbreaks of the rinderpest virus (today eradicated globally) are widely recognized to be the proximate causes. There is broad agreement that transformative policy measures are needed to arrest, preferably to reverse, these trends, but consensus is lacking as to what those measures should be. Projecting these seemingly irresistible trends forward, it is hard to conclude other than that Kenya's wildlife, its wilderness image, and its tourism sector have a bleak outlook.

The primary challenge is to justify enough space for wildlife so that large-scale ecological processes that ensure their survival, such as seasonal migration by elephants, can continue as before. Toward these ends, much effort and donor funding have been spent in Kenya, attempting to engage landholders in wildlife conservation, to some effect. Stable or increasing wildlife trends on some private and group-owned properties provide rare exceptions to nationally declining trends (Box 2).

The most substantial progress toward landscape conservation has been made in the Ewaso region of northern Kenya (Figure 1, Box 1). In its southwestern sector (Laikipia District), wildlife was once suppressed to promote beef production on large-scale ranches. Following the switch from ranching to conservation and ecotourism, which began in the 1980s, wildlife abundance increased dramatically and today is exceeded only in Kenya's premier reserve, the Masai Mara (which is much larger and wetter, and therefore more productive). The region holds more endangered mammals than anywhere else in the nation, including the world's largest remaining concentrations of Grevy's zebra and reticulated giraffe. More than 30 ecotourism ventures and community enterprises based on natural products have sprouted. Seven rhino sanctuaries

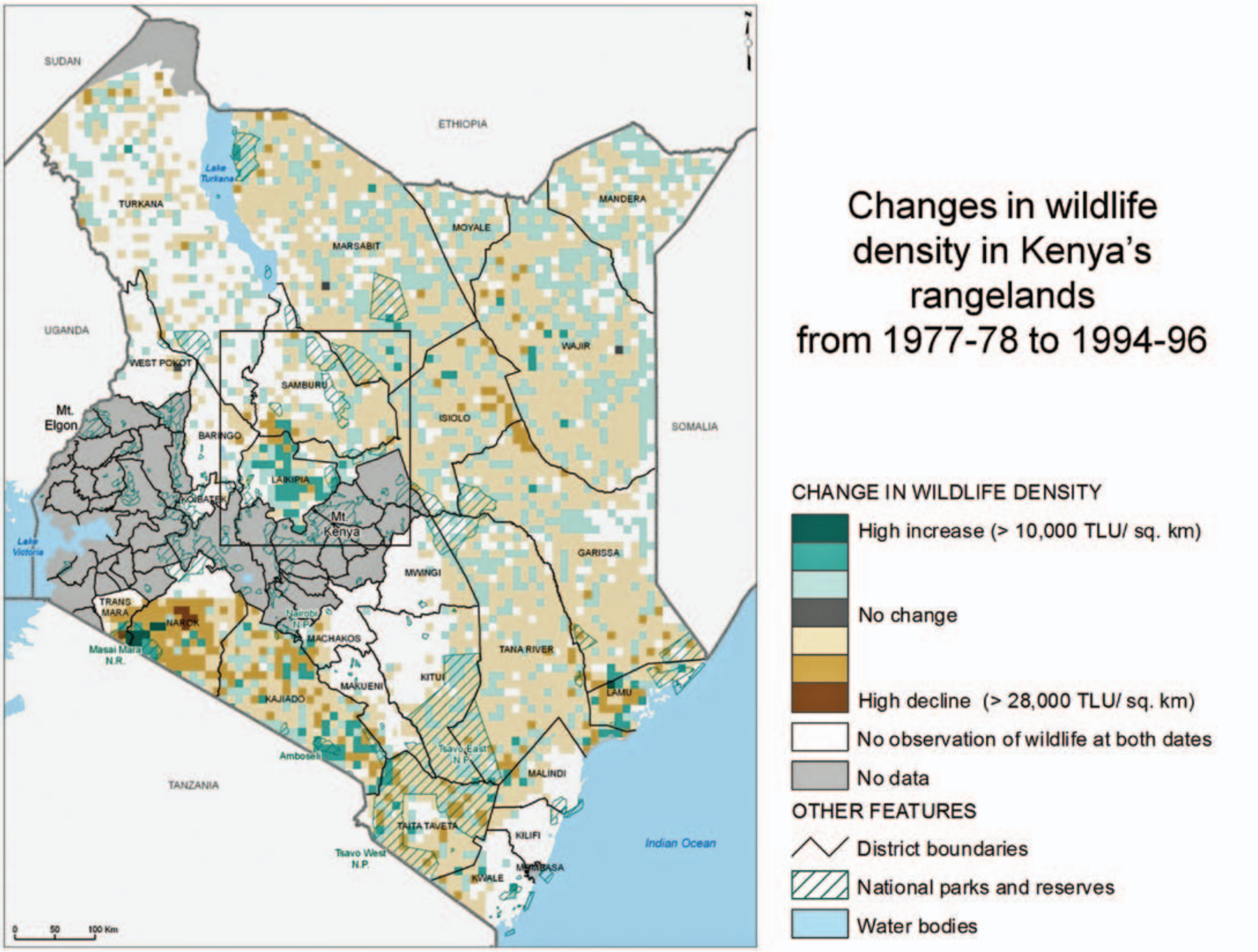

FIGURE 4. Declines and increases in wildlife densities in each 10 km grid square across Kenya's rangelands between 1977 and 1996. The Ewaso ecosystem is outlined by the rectangle. Declines predominate nationally, but the southwestern sector (Laikipia District) of the Ewaso region was one of few areas in which wildlife abundance increased (source: World Resources Institute, 2007).

have been established. Furthermore, an initial strategic conservation plan for the landscape has been drafted.

The importance of this region is that wildlife share most of the largely unfenced landscape with varying densities of people and livestock. Only about 5% of the total land area of around 40,000 km^2 has formally protected status, with an additional 1% set aside exclusively for wildlife in (private) fenced reserves. Land uses and management practices have varied widely as landownership and attitudes toward wildlife among landholders have changed over the last century. The result is a mosaic of properties with contrasting histories, land uses, management practices, ownership attitudes, and densities of livestock and wildlife (Georgiadis et al., 2007b). Such diversity over time and space provides a microcosm of the variability in land use existing across much of dryland Africa, and an instructive model system for large-mammal conservation in human-occupied landscapes.

Conservation success in the Ewaso region has spawned new problems, including aggravated conflict between humans and wildlife in some areas. However, necessity, in turn, is breeding creative solutions to these problems. Solutions have emerged from original research, based largely at Mpala Research Centre, from engagement with communities, through the Laikipia Wildlife Forum, Lewa Wildlife Conservancy, Northern Rangeland Trust, and others, and from a strong entrepreneurial spirit among many of the landholders themselves. Although the collaboration that produced these advances is likely to remain unique, many of the emerging solutions are applicable, with appropriate adaptation, elsewhere.

THE PAPERS

The papers in this volume document approaches, tools, and practices that have led to conservation advances in the Ewaso region. They add to the record of progress in ways intended to promote conservation in this and other unprotected landscapes like it. The targeted readership is landholders and land users, wildlife authorities, the donor and investment sectors, and conservation communities in similar landscapes elsewhere. The rationale and focus of each of the papers in this collection are sketched below.

In the paper following this introduction, Lane begins by outlining the pre-Colonial history of human occupation in the Ewaso region, describing interactions between pastoralist and foraging communities, and interpreting evidence for continuity and change in patterns of settlement.

In the third paper, Georgiadis et al. address the challenge of monitoring wildlife and the human attributes that compete with wildlife for space and resources in unprotected landscapes. Aerial sample surveys, a method widely applied to census wildlife and livestock in Africa, are reassessed in the context of meeting needs for finer-grained information at a time of escalating costs.

In the fourth paper, Pringle et al. review results of long-term studies that examine the *indirect* ecological effects of large herbivorous mammals, including cattle, on less charismatic species that share the landscape, including small mammals, reptiles, invertebrates, and soil microbes. These studies paint a clearer portrait of how humans and livestock modify natural systems and what conservationists mean when they refer to maintaining or restoring "ecological integrity."

In the fifth paper, Augustine et al. synthesize research on rangelands in central Laikipia, highlighting *positive* interactions between cattle and wild herbivores. They describe how livestock management practices can benefit wildlife through soil nutrient redistribution and how native browsers can enhance forage production for grazers.

The sixth and seventh papers focus on how humans and predators live with each other in this landscape. Frank's studies reveal how management of both livestock and lions can be adapted to enhance coexistence between them. Romañach et al. assess attitudes toward predators by landholders and land users in the Ewaso region and their tolerance of livestock losses to predators, relative to socioeconomic factors.

In the eighth paper, Gitahi and Fitzgerald describe the legal framework for landownership in Kenya, highlighting existing and proposed mechanisms for conserving wildlife habitat on private land, such as easements and leases. These tools are not yet widely used, but they present some of the most promising mechanisms for providing the space wildlife will require to survive outside of protected areas.

Finally, Didier et al. describe the results of a strategic planning exercise for conserving the Ewaso landscape, the first of its kind in Kenya. More than 40 researchers and conservationists collaborated to define and prioritize conservation and investment needs for specific biodiversity and development objectives in a spatially explicit manner.

OUTLOOK

Kenya formally recognized the importance of conserving ecosystem processes in 1995 and was one of the first countries in the world to adopt an objective, systematic approach to mapping and prioritizing landscapes and seascapes for conservation at the national level. The policy was abandoned after only a year, and institutional turmoil prevented readoption of an ecosystem conservation agenda until 2005. In the interim, with no clearly defined strategy to guide conservation action, the nation's biodiversity continued to dwindle. Today, national policy and political will are still insufficiently aligned with this ecosystem imperative to effect the changes that are necessary to conserve Kenya's biodiversity. The principal challenge is to justify enough space for wide-ranging species like elephants and large predators to persist in ecologically viable populations. Given human population demands for land, that nonhuman land users do not vote politicians into office, and that economic returns from wildlife are typically lower than from competing interests, the likelihood of meeting this challenge for many areas is low. We hope this volume will help to propagate awareness about the importance and threatened status of Kenya's ecosystems and promote confidence that a policy can be crafted that will reverse their decline.

REFERENCES

Adams, W. M., and D. Hulme. 2001. If Community Conservation is the Answer in Africa, What is the Question? *Oryx,* 35:193–200.

Barrow, E., and M. Murphree. 2001. "Community Conservation: From Concept to Practice." In *African Wildlife and Livelihoods: The Promise and Performance of Community Conservation*, ed. D. Hulme and M. Murphree, pp. 24–37. Oxford: James Currey.

Child, B., ed. 2004. *Parks in Transition: Biodiversity, Rural Development and the Bottom Line*. London: Earthscan.

Child, B., and B. Jones. 2006. Practical Tools for Community Conservation in Southern Africa. *Participatory Learning and Action,* 55:6–12.

Child, B., S. Ward, and T. Tavengwa. 1997. *Zimbabwe's CAMPFIRE Programme: Natural Resource Management by the People.* IUCN-ROSA Environmental Issues Series, No. 2. , Harare, Zimbabwe: Regional Office for Southern Africa, International Union for Conservation of Nature.

Daily, G. C., ed. 1997. *Nature's Services: Societal Dependence on Natural Ecosystems.* Washington, D.C.: Island Press.

de Leeuw, J. 1998. Interpretation of DRSRS Animal Counts (1977–1997) in the Rangeland Districts of Kenya. Nairobi: Department of Resource Surveys and Remote Sensing.

Egoh, B., M. Rouget, B. Reyers, A. T. Knight, R. M. Cowling, A. S. van Jaarsveld, and A. Welz. 2007. Integrating Ecosystem Services into Conservation Assessments: A review. *Ecological Economics*, 63:714–721.

Fabricius, C., E. Koch, H. Magome, and S. Turner, eds. 2004. *Rights, Resources and Rural Development: Community-Based Natural Resource Management in Southern Africa*. London: Earthscan.

Georgiadis, N. J., F. Ihwagi, N. Olwero, and S. S. Romañach. 2007a. Savanna Herbivore Dynamics in a Livestock-Dominated Landscape: II. Ecological, Conservation and Management Implications of Predator Restoration. *Biological Conservation,* 137:473–483.

Georgiadis, N. J., N. Olwero, G. Ojwang', and S. S. Romañach. 2007b. Savanna Herbivore Dynamics in a Livestock-Dominated Landscape: I. Dependence on Land Use, Rainfall, Density, and Time. *Biological Conservation,* 137:461–472.

Ghazoul, J. 2007. Recognising the Complexities of Ecosystem Management and the Ecosystem Service Concept. *GAIA,* 16:215–221.

Grumbine, E. R. 1994. What Is Ecosystem Management? *Conservation Biology,* 8:27–38.

———. 1997. Reflections on "What is Ecosystem Management?". *Conservation Biology*, 11:41–47.

Grunblatt, J., M. Said, and P. Waragute. 1996. DRSRS National Rangelands Report: Summary of Population Estimates for Wildlife and Livestock in Kenyan Rangelands 1977–1994. Nairobi: Department of Resource Surveys and Remote Sensing, Ministry of Planning and National Development.

Hanks, J. 2003. Trans-frontier Conservation Areas (TFCAs) in Southern Africa: Their Role in Conserving Biodiversity, Socioeconomic Development and Promoting a Culture of Peace. *Journal of Sustainable Forestry*, 17:127–148.

Heath, B. 2000. Ranching: An Economic Yardstick. In *Wildlife Conservation by Sustainable Use*, ed. H. H. T. Prins, J. G. Grootenhuis, and T. T. Dolan, pp. 21–34. Boston: Kluwer Academic Publishers.

Homewood, K., E. F. Lambin, E. Coast, A. Kariuki, I. Kikula, J. Kivelia, M. Said, S. Serneels, and M. Thompson. 2001. Long-Term Changes in Serengeti-Mara Wildebeest and Land Cover: Pastoralism, Population, or Policies? *Proceedings of the National Academy of Sciences of the United States of America,* 98:12,544–12,549.

Hutton, J., W. M. Adams, and J. C. Murombedzi. 2005. Back to Barriers? Changing Narratives in Biodiversity Conservation. *Forum for Development Studies*, 2:341–370.

Keough, H. L., and D. L. Blahna. 2006. Achieving Integrative, Collaborative Ecosystem Management. *Conservation Biology,* 20:1373–1382.

Kock, R. 1995. Wildlife Utilization: Use It or Lose It—A Kenyan Perspective. *Biological Conservation,* 4:241–256.

Kroeger, T., and F. Casey. 2007. An Assessment of Market-Based Approaches to Providing Ecosystem Services on Agricultural Lands. *Ecological Economics*, 64:321–332.

Lamprey, R. H., and R. S. Reid. 2004. Expansion of Human Settlement in Kenya's Maasai Mara: What Future for Pastoralism and Wildlife? *Journal of Biogeography*, 31:997–103.

Logan, B. I., and W. G. Moseley. 2000. The Political Ecology of Poverty Alleviation in Zimbabwe's Communal Areas Management Programme Indigenous Resources. *Geoforum*, 33:1–14.

Mburu, J., and R. Birner. 2002. Analyzing the Efficiency of Collaborative Wildlife Management: The Case of Two Community Wildlife Sanctuaries in Kenya. *International Journal of Organization Theory and Behavior*, 5:259–297.

Munthali, S. M. 2007. Transfrontier Conservation Areas: Integrating Biodiversity and Poverty Alleviation in Southern Africa. *Natural Resources Forum*, 31:51–60.

Newmark, W. 1996. Insularization of Tanzanian Parks and the Local Extinction of Large Mammals. *Conservation Biology*, 10:1549–1556.

———. 2008. Isolation of African Protected Areas. *Frontiers in Ecology and the Environment*, 6:321–328.

Newmark, W. D., and J. D. Hough. 2000. Conserving Wildlife in Africa: Integrated Conservation and Development Projects and Beyond. *BioScience,* 50:585–592.

Norton-Griffiths, M. 1978. *Counting Animals.* Nairobi: African Wildlife Foundation.

Norton-Griffiths, M., and C. Southey. 1995. The Opportunity Costs of Biodiversity Conservation in Kenya. *Ecological Economics*, 12:125–139

Ottichilo, W. K., J. de Leeuw, A. K. Skidmore, H. H. T. Prins, and M. Y. Said. 2000. Population Trends of Large Non-migratory Wild Herbivores and Livestock in the Masai Mara Ecosystem, Kenya, between 1977 and 1997. *African Journal of Ecology*, 38:202–216.

Pirot, J.-Y., P. J. Meynell, and D. Elder. 2000. *Ecosystem Management: Lessons from Around the World. A Guide for Development and Conservation Practitioners.* Gland, Switzerland: International Union for Conservation of Nature.

Soulé, M. E., B. A. Wilcox, and C. Holtby. 1979. Benign Neglect: Model of Faunal Collapse in the Game Reserves of East Africa. *Biological Conservation*, 15:259–272.

Spiteri, A., and S. K. Nepal. 2006. Incentive-Based Conservation Programs in Developing Countries: A Review of Some Key Issues and Suggestions for Improvements. *Environmental Management*, 37:1–14.

Thompson, M., and K. Homewood. 2002. Entrepreneurs, Elites, and Exclusion in Maasailand: Trends in Wildlife Conservation and Pastoralist Development. *Human Ecology*, 30:107–138.

Walpole, M. J., and C. R. Thouless. 2005. "Increasing the Value of Wildlife Through Non–consumptive Use? Deconstructing the Myths of Ecotourism and Community-Based Tourism in the Tropics." In *People and Wildlife: Conflict or Coexistence?*, ed. R. Woodroffe, S. J. Thirgood, and A. Rabinowitz, pp. 122–139. Cambridge, UK: Cambridge University Press.

Weaver, L. C., and P. Skyer. 2003. "Conservancies: Integrating Wildlife Land-Use Options into the Livelihood, Development, and Conservation Strategies of Namibian Communities." Paper presented at the "Vth World Parks Congress to the Animal Health and Development (AHEAD)" Forum, Durban, South Africa.

Western, D. 1982. Amboseli National Park: Enlisting Landowners to Conserve Migratory Wildlife. *Ambio*, 11:302–308.

———. 1989. "Conservation without Parks: Wildlife in Rural Landscapes." In *Conservation for the Twenty-First Century*, ed. D. Western and M. M. Pearl, pp. 158–165. New York: Oxford University Press.

Western, D., and H. Gichohi. 1993. Segregation Effects and the Impoverishment of Savanna Parks: The Case for Ecosystem Viability Analysis. *African Journal of Ecology,* 31:269–281.

Western D., S. Russell, and I. Cuthill. 2009. The Status of Wildlife in Protected Areas Compared to Non-Protected Areas of Kenya. *PLoS ONE,* 4(7):e6140. doi: 10.1371/journal.pone.0006140.

Western, D., and J. Ssemakula. 1981. The Future of Savanna Ecosystems: Ecological Islands or Faunal Enclaves. *African Journal of Ecology*, 19:7–19.

Western, D., and R. M. Wright. 1994. *Natural Connections: Perspectives in Community-Based Conservation.* Washington, D.C.: Island Press.

Wolmer, W. 2003. Transboundary Conservation: The Politics of Ecological Integrity in the Great Limpopo Transfrontier Park. *Journal of Southern African Studies*, 29:261–278.

Woodroffe, R., S. J. Thirgood, and A. Rabinowitz. 2005. *People and Wildlife: Conflict or Coexistence?* Cambridge, UK: Cambridge University Press.

An Outline of the Later Holocene Archaeology and Precolonial History of the Ewaso Basin, Kenya

Paul Lane

ABSTRACT. Drawing on a range of archaeological, paleoenvironmental, linguistic, ethnographic, and historical data, this chapter outlines what is currently known about the trajectories of pastoralism in the Ewaso Basin from its initial appearance some 4000 years ago until the early twentieth century, by which time new systems of land use and tenure had been established within the context of British colonial rule. Overall, the evidence indicates that many different groups have occupied parts of this area at different times in the past, and that these have encompassed both hunter-gatherer and pastoralist communities and speakers of various Nilotic, Cushitic, and Bantu languages, among others. There is also good evidence to suggest that the boundaries between different "ethnic," "subsistence," and even linguistic groups have been fairly fluid and that cultural intermixing as well as interaction through exchange and other social mechanisms was common. Additionally, at least four broad phases of pastoralist practices can be identified for the period prior to the twentieth century. These phases entailed different forms and levels of mobility, including population migration and seasonal movements, and had diverse environmental consequences, some of which appear to have enhanced biodiversity and ecological resilience whereas others initiated significant changes to the structure of the vegetation mosaic and may have even resulted in localized rangeland degradation.

INTRODUCTION

The primary aim of this article is to outline what is currently known about the trajectories of pastoralism in the Ewaso Basin from its initial appearance some 4,500 years ago until the early twentieth century, to develop a better understanding of the changing nature of different pastoralist societies over this time period. Before considering this evidence in detail, it is worth noting that in contrast to some other areas of East Africa (such as the Central Rift Valley), the Ewaso Basin has not been subject to intensive archaeological research until recently. Consequently, the archaeological record concerning the trajectory of pastoralism is both patchy and partial. Surviving archaeological traces nevertheless include a combination of rock shelters and open sites with surface scatters of flaked stone,

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pottery, iron slag, and iron smelting furnaces. Several of the rock shelters also contain rock paintings. The ceramics can be linked to regional archaeological typologies, with occurrences of Pastoral Neolithic (PN) Nderit, Elmenteitan, Marangishu, and Akira ceramic types all being reported, as well as a ceramic tradition known as "Kisima Ware" (Siriäinen, 1984), which is believed to be associated with post AD 800 Pastoral Iron Age (PIA) communities (Table 1). At least five different types of stone cairn are also known, some of which were definitely used for human burial (Lane et al., 2007). On the basis of oral traditions among different ethnic groups that have a history of utilizing parts of Laikipia and Leroghi plateaus, however, others may have been used as markers for stock routes, as cenotaphs for fallen warriors, as markers associated with captured (or recaptured) cattle, and even simply as meat stores.

The available historical sources indicate that from ca. AD 1750 to the early twentieth century, various pastoral, Maa-language-speaking Iloikop sections (including Laikipiak, Samburu (Burkeneji), Mumonyot, LeUaso, and Purko Maasai communities) coexisted alongside scattered groups of other peoples that included hunter-gatherers (notably, Dikirri Dorobo and Mukogodo); the area probably also included pockets of Oromo-speaking Warra Daaya and possibly Turkana and Rendille along the northern fringes and various Bantu language speakers (including Meru and Kikuyu) along the more southern boundaries (Kenya Land Commission, 1934; Cronk, 1989, 2004; Lamphear, 1993; Sobania, 1993).

In 1904, a large portion of the Laikipia and Leroghi plateaus was designated part of the Northern Maasai Reserve, and in 1911, following pressure from various quarters, a new agreement was signed between Maasai elders and the British East Africa (BEA) protectorate administration, under the terms of which Maasai occupying the Northern Reserve were to be relocated to the Southern Reserve and some 4,500 square miles (approx. 11,655 sq. km) of land handed over to the BEA protectorate for European settlement (Hughes, 2005, 2006). At the time of this move, the Maa-speaking population of Laikipia was estimated to have numbered around 10,000 and was dominated by members of the Purko, Keekonyukie, and Il Dalalekutuk sections, following their defeat of the Laikipiak Maasai (who belonged to a different moiety) during the intersectional Iloikop wars in the 1870s (Weatherby, 1967; Waller, 1979; Sobania, 1993). The bulk of the Maa-speaking population was moved from the designated area between 1911 and 1913, along with up to approximately one million sheep and goats and 175,000 cattle (Hughes, 2006:50), and the area became part of the "White Highlands" set aside for European settlement.

After the First World War, soldier settlement schemes started to bring European settlers to Laikipia, gradually creating an export-oriented economy, with land use strategies being transformed so as to maximize levels of production. Settlement took off in the early 1920s, with the number of settlers in occupation of their farms increasing from 18 in March 1920 to 42 in March 1921. Not

TABLE 1. Approximate dates of Pastoral Neolithic (PN) and Pastoral Iron Age (PIA) pottery traditions for historically documented ethnic groups (based on Gifford-Gonzalez, 1998, 2000; Karega-Mũnene, 2002). Abbreviations not defined below: LSA, Later Stone Age; MIA, Middle Iron Age.

Age BP (kyr)	Archaeological periodization	Selected LSA stone tool industries	LSA, PN, and PIA ceramic traditions	Iron age ceramic traditions
1	Later Iron Age (LIA), Pastoral IA (PIA)		Kisima, ca. Cal AD 1200–1750; Lanet/Sirikwa, ca. Cal AD 750–1600	MIA and LIA regional variants, from ca. Cal AD 1000
2	Early Iron Age, overlaps with PN and LSA	Elmenteitan	Akira, ca. Cal AD 100–800; Maringishu, ? to ca. Cal AD 350; Elmenteitan, ca. 1600 Cal BC to Cal AD 700; Narosura, ca. 1000 Cal BC to Cal AD 620	Kwale, ca. Cal AD 150–1000; Urewe, ca. 650 Cal BC to Cal AD 1000
4.5	PN, overlaps with later LSA	Eburran 5, ca. 3000 Cal BC to Cal AD 750; LSA "bone harpoon" sites, ca. 8100–2500 Cal BC	Nderit and Ilert, ca. 3800–1800 Cal BC (PN)	
6	Late LSA	Kansyore; Eburran 4	Kansyore, ca. 6300 Cal BC to Cal AD 700	

all the land was immediately taken into productive use, however. Some prospective settlers simply visited but left soon afterward, finding the land either waterless or too stony or bushy for their liking, such that even in 1922, 200 alienated farms still had to be taken up. Even as late as 1937, there were still substantial areas of unoccupied surveyed land in the east of the district (see Waller, 2004, and Vaughan, 2005, for further detail concerning colonial land use history of Laikipia District). With independence in 1963 and a policy of Africanization, several, but not all, Europeans sold their ranches, a number of which were subdivided and settled by small-scale farmers originating in the densely populated Kikuyu areas located south of the district (Carey Jones, 1965; Kohler, 1987). The sale of large-scale commercial ranches to cooperatives and land-buying companies continued at least into the 1990s, and as a consequence, approximately one-third of the original large-scale ranches have now been subdivided. Today, Laikipia District comprises a mosaic of different land use types, including large-scale ranching, small-scale arable farming, traditional pastoralism, and forestry, with ~8.4% under cultivation, mostly concentrated in West Laikipia and around Nanyuki, even though only 1.7% of the district is classified as having high agricultural potential (Huber and Opondo, 1995; Kiteme et al., 1998). These and related events transformed earlier systems of land use and management, replacing them with a largely market-oriented system of production and land tenure, albeit in a piecemeal fashion drawn out over several decades. Pastoralists have nevertheless remained in this landscape and are still a significant presence in some areas of the Ewaso Basin, especially on the Leroghi Plateau. Moreover, when taken together and despite its limitations, the available archaeological evidence provides a good indication of the antiquity of pastoralism in the area, confirmation of a long history of interaction between pastoralist and foraging communities, and a record of continuity and changes in settlement practices, local environments, and material culture traditions, and it is these aspects that are reviewed in detail in the following sections.

LATER STONE AGE HUNTER-GATHERERS AND THE BEGINNINGS OF PASTORALISM

The final phase of the Later Stone Age (LSA) in central Kenya dates from ca. 4400 Cal[1] BC to Cal AD 300 and is associated with "Eburran Phase 5" stone tool flaking technologies (Ambrose, 1985) and, in its initial phases at least, with a purely hunting and gathering subsistence economy. Evidence from several excavated rock shelter and cave sites in the Central Rift Valley, most notably the site of Enkapune ya Muto, indicates that these LSA hunter-gatherer groups were fairly mobile populations who exploited a range of medium- to large-sized animals and participated in wide-ranging exchange networks that gave them access to different lithic raw materials, such as obsidian and chert (Ambrose, 1998; Kusimba and Kusimba, 2005). The evidence also suggests that there were different adaptations to highland and lowland environments, with the groups utilizing the former tending to select caves and rock shelters situated close to the boundary between montane forest and grassland habitats, whereas the latter generally occupied open-air sites on the savannas.

Four rock shelter sites on the Laikipia Plateau have thus far been investigated in some detail, and exploratory investigations have been carried out at a sample of other similar locations. Of the four key sites, those at Shulumai and Kakwa Lelash close to Dol Dol in the Mukogodo Hills (see Figure 1 for map) provide long, dated sequences that span terminal phases of the Middle Stone Age (MSA), the subsequent development of the LSA, and the appearance of PN ceramics and stone tool industries. Additionally, the upper levels at Shulumai contained extensive faunal and other evidence concerning more recent transitions from foraging subsistence to pastoralism among Mukogodo (Mutundu, 1999). The earliest horizon at Shulumai is dated to around 45,000 Cal BC and so represents the final phases of the MSA. The MSA horizon is overlain by successive deposits containing microblades and other lithic materials considered typical of the LSA in East Africa, spanning a date range from ca. 40,000 to ca. 3,000 Cal BC toward the upper levels (Dickson and Gang, 2002). There is a gradual increase in the percentage of nonlocal raw materials through the LSA levels. An even more marked increase in the use of chert and obsidian is evident from the excavated LSA levels at the nearby rock shelter of Kakwa Lelash (Kuehn and Dickson, 1999; Gang, 2001; Dickson and Gang, 2002). This increased use of nonlocally available raw materials is generally regarded as evidence for increased patterns of mobility or, at least, the exploitation of larger territories. Similar trends toward greater mobility and more widely ranging exchange networks have been noted for the LSA at sites around Lukenya Hill in Kenya (Kusimba, 2001) and elsewhere in the region, although the date of this transition is quite variable geographically (Kusimba and Kusimba, 2005). Although there remain some uncertainties with regard to the dating of the sequences at Kakwa Lelash, it is evident that by 20,000 Cal BC, and probably considerably earlier, LSA

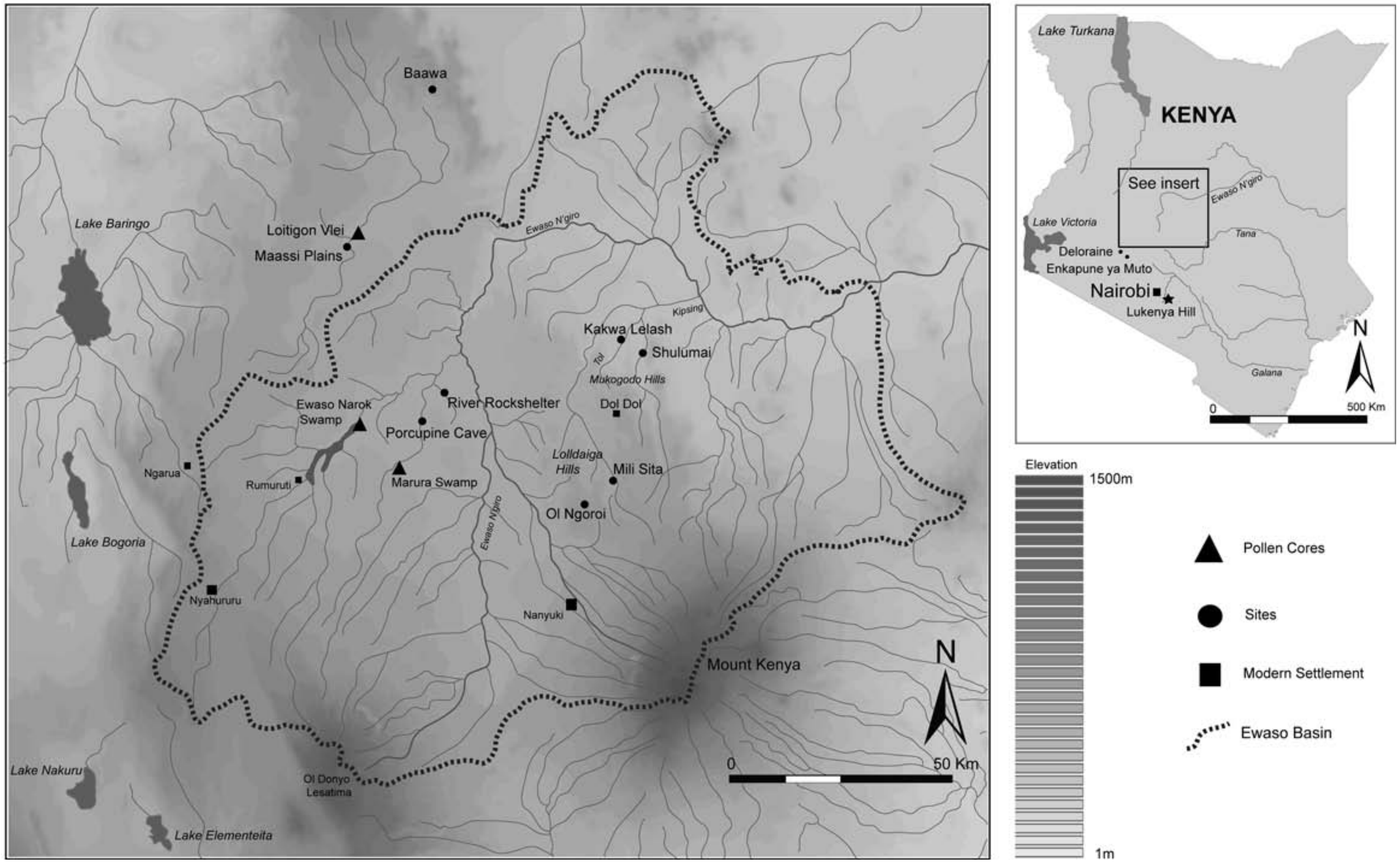

FIGURE 1. Map of the Ewaso Basin showing location of main Pastoral Neolithic and Pastoral Iron Age sites mentioned in the text. Prepared by Tim Evans.

hunter-gatherers occupying Laikipia possessed a complex and sophisticated lithic technology, were relatively residentially mobile with extended territories, and were linked with other hunter-gathering groups in the Central Rift by long-distance exchange that provided access to high-quality lithic raw materials (Dickson and Gang, 2002:19–20; Dickson et al., 2004).

Excavations at a limited number of other rock shelters on the Laikipia Plateau by Jacobs (1972a) and more extensive investigations at Porcupine Cave and two other rock shelters (KFR-A4 and A12) on Kisima Ranch by Siiriäinen (1977, 1984) suggest the first appearance of domestic stock in the Ewaso Basin was between 2000 and 1000 Cal BC. These dates are broadly consistent with the current evidence from other parts of the region, which tends to suggest that there was a gradual southward spread characterized by a series of stops and starts, with the transition to generalized, mixed cattle (*Bos taurus* L.) and caprine (*Ovis* sp.) pastoralism occurring in some parts of the northern lowlands bordering Lake Turkana by ca. 3800 Cal BC (Barthelme, 1985), by ca. 2000–1400 Cal BC in different parts of highland central, southern, and western Kenya (Robertshaw, 1989; Karega-Mũnene, 2002; Marean, 1992; Marshall, 2000), and by ca. 1800 Cal BC in the Tsavo region of southeastern Kenya (Wright, 2005, 2007). By ca. 1000 Cal BC, PN traditions were present across much of eastern Africa.

Archaeological and genetic evidence indicates that the initial introduction of livestock into East Africa was due in part to the southward expansion of small groups of herders from Sudan, Ethiopia, and possibly Somalia (Bower, 1991; Marshall, 2000; Hoelzmann et al., 2001; Hanotte et al., 2002). The diffusion of livestock, knowledge of herding practices, material culture traditions, and technological styles is also likely to have contributed to the southward spread of pastoralist systems of food production and their archaeological signatures. The historical linguistic evidence suggests that these early pastoralists may have been speakers of proto-Southern Cushitic languages (Ehret, 1998). Their southward expansion from the Sahara was probably stimulated (and also facilitated[2]) by the onset of a mid-Holocene dry phase; however, this phase of hyperaridity may have constrained early PN groups to the Lake Turkana Basin until climatic amelioration sometime after ca. Cal AD 0. The uptake farther south was certainly by no means rapid, and many of the earliest dated occurrences of domestic stock come from sites and contexts more closely associated with LSA hunter-gatherers (e.g., Barthelme, 1985; Bower and Chadderdon, 1986; Marean, 1992; Ambrose, 1998). The reasons for this initially slow uptake of herding may have been the relative abundance of wild animals and plants as alternative food sources in many areas and, probably, the spatial distribution of livestock diseases, including trypanosomiasis, foot and mouth, and malignant catarrhal fever, that were endemic to forested areas (Gifford-Gonzalez, 1998, 2000).

It is also important to stress that although the southward spread of pastoralism almost certainly involved some population migration, once herding economies had become established in a particular area, it is highly likely that some of the autochthonous hunter-gatherer communities gained access to livestock and may have ultimately changed their subsistence strategies. This change certainly seems to have been the case in at least some areas of the Ewaso Basin, given that Siiriäinen (1984) found considerable typological continuity in the stone tool assemblages at the sites he excavated spanning levels dated ca. 1000 Cal BC to the twelfth century AD and perhaps even up to the fifteenth century AD. He also found a wide range of different PN pottery types represented at the sites he investigated, with no single type dominating until the emergence of Kisima Ware during the second millennium AD. Both observations would be consistent with a view that the rock shelters were occupied by hunter-gatherer communities that gradually made the transition to food production, although it is possible that PN pastoralists were also utilizing rock shelters, as has been documented in the Central Rift.

The limited information on the faunal assemblages of these sites, which contain a mix of wild and domestic taxa (Siiriäinen, 1984:88), nevertheless indicates that hunting remained an important aspect of the subsistence strategies of these early herding communities. Similarly, at Kakwa Lelash and Shulumai, the upper levels, dated to ca. Cal AD 900 (Gang, 2001:14, 16), contained assemblages of PN and historic pottery associated with worked stone and wild and domestic fauna. Detailed analysis of the faunal remains from this horizon at Shulumai indicates that the assemblage was dominated by remains of wild animals, with a preference for small species such as hyrax, dik-dik, and bushpig, with only small numbers of domestic cattle and sheep or goats (Mutundu, 1999:50–56). Although this pattern of resource use may have been influenced by the ecological conditions in the immediate vicinity of these rock shelters, Mutundu argued that the characteristics of the assemblage are fairly typical of specialized hunter-gatherers with relatively restricted settlement mobility in the process of adopting food production.

The results from recent excavations at Ol Ngoroi rock shelter on Lolldaiga Hills Ranch, undertaken as part of a British Institute in Eastern Africa (BIEA) research project during 2002–2006, lend support to these arguments. Specifically, despite relatively shallow deposits, excavations revealed the presence of domestic livestock remains associated with wild fauna, a microlithic stone tool assemblage on obsidian, and in situ hearth deposits. A charcoal sample from the lowest of these hearths, of which there were seven in all, produced an AMS radiocarbon date of around 2700 Cal BC. Although sheep or goat bones were present, the bulk of the identifiable elements in the faunal assemblage is of wild fauna, and the range of the taxa reflects the structure of the habitats proximal to the site today, with hyraxes and small bovids predominating (Mutundu, 2005). In broad terms, the composition of the assemblage resembles that recovered from the upper levels at Shulumai rock shelter in the Mukogodo Hills, which is known to have been occupied by Mukogodo groups during a period of transition from hunting and gathering to a herding subsistence strategy (Mutundu, 1999). However, until open-air sites associated with diagnostic early PN ceramic and/or lithic assemblages are investigated, the processes whereby the transition to pastoralism occurred across the Ewaso Basin will only be partially understood (as discussed below, locating such sites has been challenging despite systematic survey). It is worth noting here that the Ol Ngoroi shelter, which looks out across the flat plateau land to the west of the Lolldaiga Hills, contains several well-preserved panels of white, geometric rock art (Figure 2). This art is similar in design to that recorded at Lukenya Hill south of Nairobi and is generally attributable to Maasai meat-feasting or initiation rituals (Gramly, 1975; Smith et al., 2004). Several other rock shelters with similar art are known elsewhere in the Ewaso Basin (Chamberlain, 2006), and many appear to have remained important places in the ritual landscapes of Laikipia and Leroghi. The artifactual and faunal remains from

FIGURE 2. Example of white geometric pastoralist art, Ol Ngoroi rock shelter, Lolldaiga Ranch, Laikipia Plateau. Photo ©Paul Lane, BIEA.

the upper levels at Ol Ngoroi are consistent with the later use of the site by pastoralist communities and have yielded a date of ca. Cal AD 1260.

CONSOLIDATION OF PASTORALISM

Recent judgmental and systematic transect surveys undertaken as part of the BIEA research project between 2002 and 2006 on Lolldaiga Hills, Mugie, and Borana Ranches, supplemented by information collected during rock art surveys on Mpala, Jessels, and Chololo Ranches, have located more than 250 previously unrecorded sites (Lane, In press). More than 50% of these sites are stone cairns or complexes of stone cairns (Figure 3), and another 5% are rock art sites. Of the remaining sites, roughly six times as many (29% compared to 5%) probably date to the PIA compared to those associated with the earlier PN. Although this probably reflects a steady increase in human activity and presence on Laikipia during the second millennium AD, it is also possible that a proportion of the older sites have yet to be detected because they lie buried beneath colluvial and alluvial sediment that has accumulated along valley floors over the millennia. Scatters of PN Elmenteitan and SPN (Savanna Pastoral Neolithic) pottery associated with flaked obsidian and other worked lithic material have recently been reported from Lolldaiga (Causey, 2008:316, 2010) and are also known to occur on Kisima and Mpala Ranches and in the vicinity of Baawa on Leroghi Plateau. Since these have yet to be dated or intensively investigated, little can be said at present about the later phases of the PN. Far more evidence is available concerning pastoralist activities in the Ewaso Basin during the PIA.

Current evidence suggests that the adoption of iron manufacturing technologies among pastoralist communities of the Central Rift occurred around Cal AD 800–900 (Collett and Robertshaw, 1983). Archeologists term this phase the Pastoral Iron Age. One of the earliest dated occurrences of this transition comes from the Deloraine "main site," near Rongai to the northwest of Lake Nakuru (Ambrose, 1984). This site contains abundant remains of cattle as well as evidence of cereal processing and the manufacture and use of iron implements. The ceramics may well represent a development of earlier PN Elmenteitan traditions (Sutton, 1993a:123). The ensuing centuries witnessed the consolidation of PIA economies along the Central Rift and adjacent highlands, out of which many of the ethnic identities and linguistic clusters that characterize these areas today were formed.

The BIEA surveys were supplemented by excavations and test excavations at 12 different sites, selected to provide evidence from a range of sites of different ages and dates. Of particular importance to the discussion here of the archaeology of pastoralism in the Ewaso Basin are the results from excavations at the Mili Sita open settlement site in the Lolldaiga Hills and the Maasai Plains site on Mugie Ranch, aspects of which are discussed below. More detailed excavation reports on both sites will be published elsewhere.

FIGURE 3. Stone cairn on Mugie Ranch, Laikipia Plateau, prior to excavation. Photo ©Paul Lane, BIEA.

PASTORAL IRON AGE SETTLEMENTS

Both the Mili Sita and Maasai Plains sites are large, open-air pastoralist settlements that contain a pottery type known as Kisima Ware, which has been tentatively associated with the Laikipiak (Siiriäinen, 1984), although whether the Laikipiak made the pottery themselves or they obtained it through exchange with neighboring communities (possibly hunter-gatherer groups) for other products is not clear (see below), and it should not be assumed (rather than demonstrated) that a particular pottery style can be equated in a straightforward manner with ethnicity. Of the two open-air sites thus far excavated, the Maasai Plains site on Mugie is the older one, and on the basis of available radiocarbon dates it was occupied around Cal AD 1400–1480. The site is situated in an area of open grassland surrounded by woody vegetation, about 1.5 km to the west of Loitigon Vlei, which has been sampled for pollen and other environmental remains (Taylor et al., 2005). The Maasai Plains site consists of three concentric and roughly circular arrangements of low ash mounds between ~0.35 and 1.0 m high, covering an area ~750 m in diameter, with a pair of mud wallows, or shallow waterholes, in the center (Figure 4). The mounds, although not

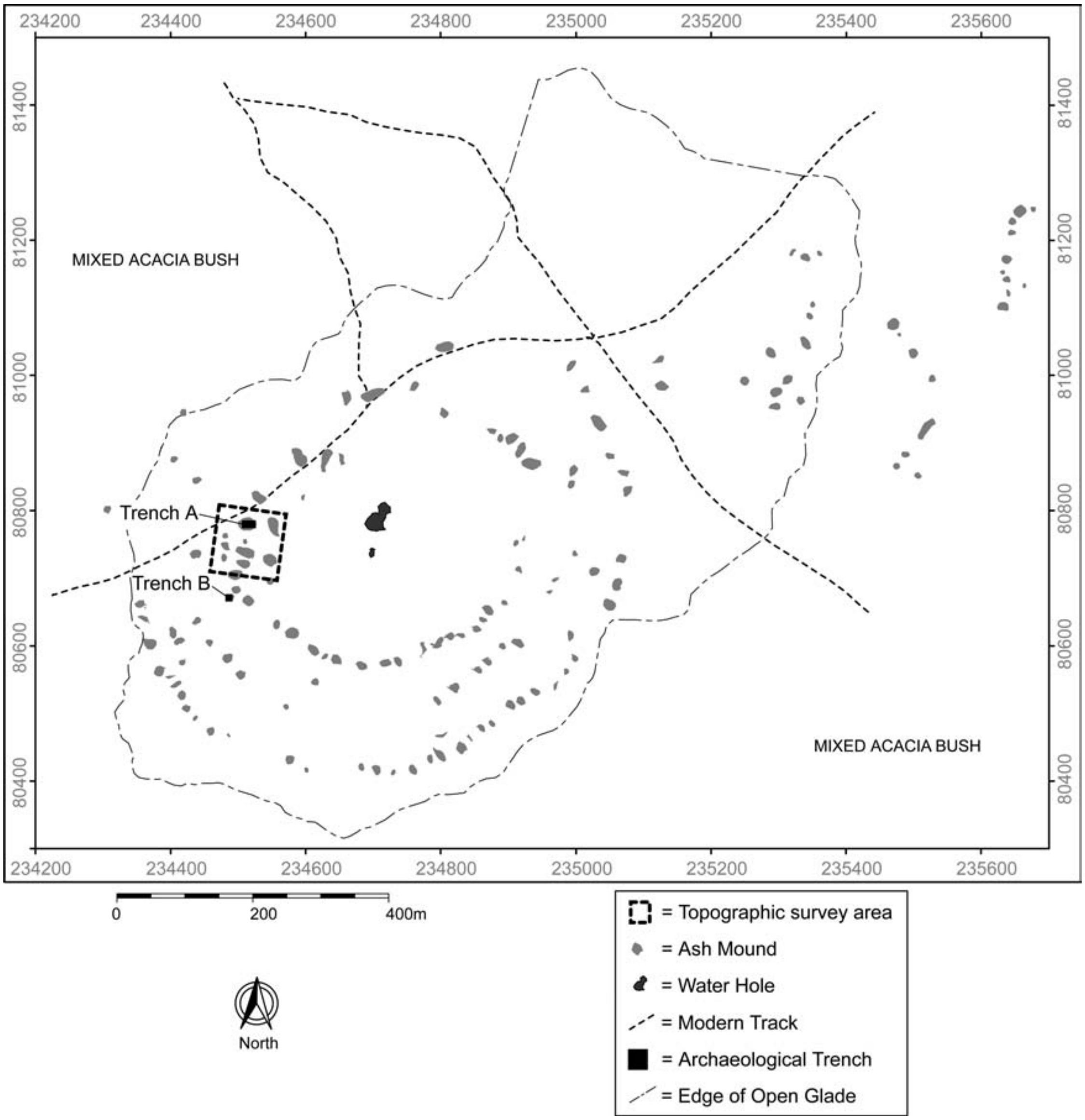

FIGURE 4. Maasai Plains site plan, showing concentric arrangement of low ash mounds, Mugie Ranch, Laikipia. Prepared by Guy Hopkinson and Dave Pinnock from BIEA data.

especially distinctive on the ground, show up as darker patches on vertical aerial photographs and even on moderately low resolution satellite images (see below). Two of the mounds have been examined by excavation, as have some of the level areas between these mounds. The results of these excavations indicate that the mounds comprise a series of interleaved layers of ashy soil, containing pottery and bone fragments and occasional flaked stone artifacts. In terms of the composition of the lithic assemblage, modified blades and outils écaillés dominate, pointing to links with the earlier Elmenteitan, with the main raw materials being obsidian, chert, and quartz. Traces of burnt dung, charcoal, and other organic materials also occur. Preliminary analysis of the faunal remains indicates that the assemblage is dominated by domestic stock (almost equally cattle and small stock), although a few wild fauna are also represented (Kennedy Mutundu, Kenyatta University, personal communication 2006). Sampling for paleobotanical remains was also undertaken at the site, but the results are as yet unavailable. Phytolith evidence recovered from soil samples and charred seed material may help confirm whether crops were cultivated in the vicinity. Isotopic analysis of human remains recovered from burials at Baawa, ~50 km to the north, and also from the single burial thus far recovered at Mili Sita might also indicate whether C_4-based plants, such as millet and sorghum, formed part of their diet (for details of these burials, see Lane et al., 2007; unfortunately, although three cairns at Mugie have been excavated, none have produced any human remains). Moreover, although current rainfall regimes make cultivation in the general vicinity a risky undertaking, slightly higher rainfall, as is documented regionally for the main period of the site's occupation (see below), could have made farming a viable subsistence strategy.

In terms of their form, composition, stratigraphic structure, and contents, these mounds closely resemble the dung-and-trash heaps commonly observed outside modern Samburu homesteads (*nkan'g*; in Maa, *enkang*), formed by the regular cleaning of dung from animal kraals and the discarding of household waste (Figure 5). No house remains have yet been located in the areas between the mounds to confirm this theory, although the presence of low-density mixed artifact and faunal scatters in these areas would be consistent with the kind of debris generated around a living area (Causey, 2008:185–267). The regular patterning of the mounds and the obvious clear area at the center of the site suggest that at a minimum, the mounds making up at least one "ring" were created at the same time, and given the layering in the mounds, each mound was probably built up progressively. The extent of the site is much larger than any other recorded archaeological pastoralist site in the region, and it covers an area even larger than most ethnographically documented Maasai *enkang*. It is entirely possible, however, that other rings were created at different times and that not all mounds relate to separate houses. It is also possible that the site was only occupied for short periods at a time and was perhaps reoccupied on several occasions; it is even possible that it was used for ceremonial purposes similar to those of ethnographically documented Maasai manayatta, which it resembles in terms of its formal spatial organization.

The Mili Sita site is located on a low col toward the end of a northward-trending ridge in the Lolldaiga Hills, and like the Maasai Plains site, it appears to have been used as

FIGURE 5. Example of a dung midden outside a contemporary Samburu homestead, Laikipia, 2005, which is possibly analogous to the ash mounds at Maasai Plains. Photo ©Paul Lane, BIEA.

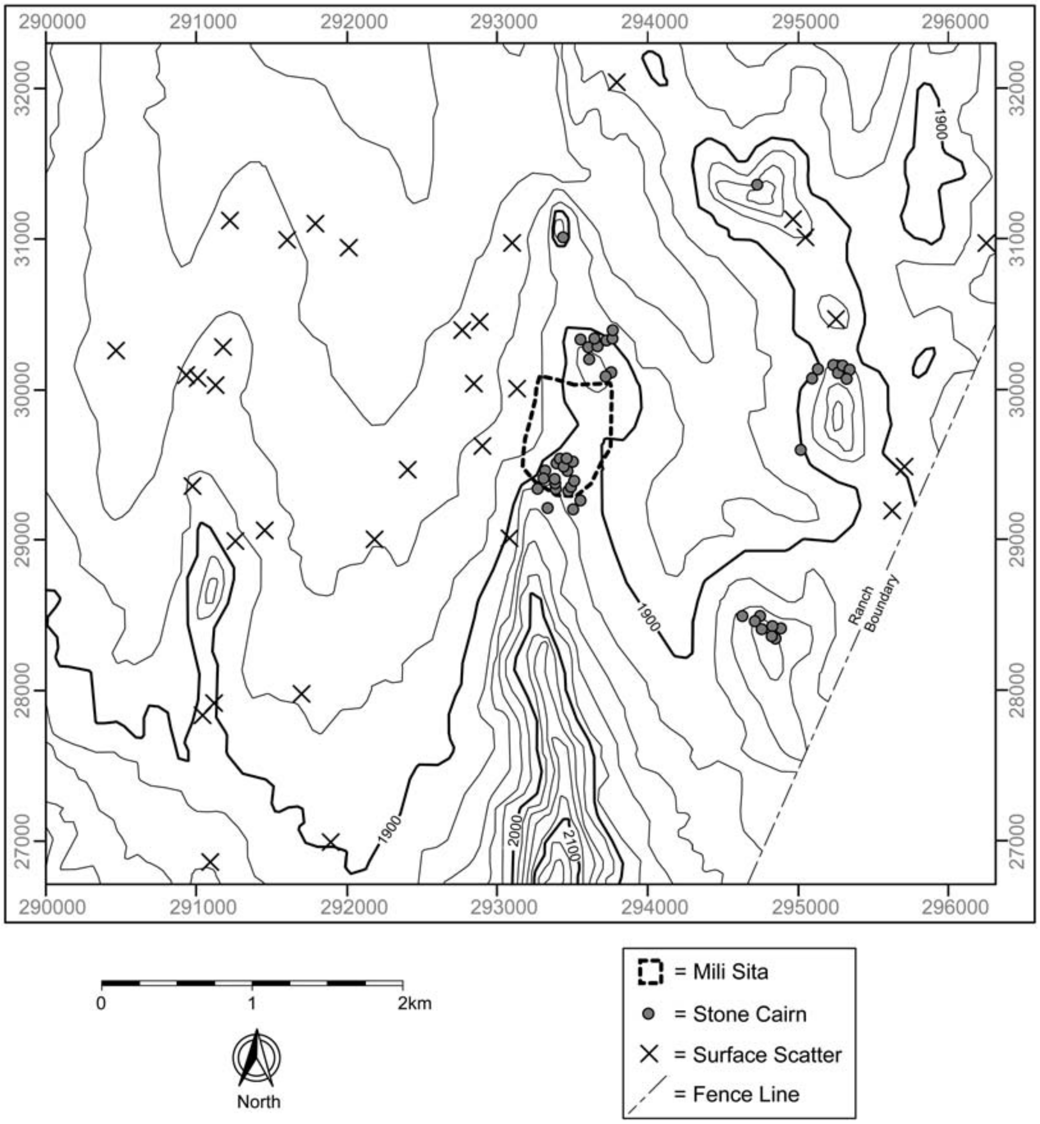

FIGURE 6. Mili Sita site plan, Lolldaiga Hills, Laikipia. Prepared by Michael Causey and Dave Pinnock from BIEA data.

an area of pastoralist settlement (Figure 6). On either side of the ridge, gentle to moderate slopes run roughly east and west to alluvial valley floors. At the center of the col is a large grass-covered area (Figure 7) with several discrete concentrations of archaeological material, including later variants of Kisima Ware that are similar but not identical to those from the Maasai Plains site. Some scatters appear to represent the remains of rubbish dumps, whereas others have been shown by excavation to mark the sites of former dwellings or stock enclosures. As at the Maasai Plains site, provisional assessment of the faunal remains indicates a subsistence economy largely orientated to herding cattle and small stock, which is also confirmed by provisional fungal spore data from the site. Interestingly, preliminary analysis of phytoliths recovered from different contexts also indicates that domestic crops were present throughout the occupation of the site, although these never exceed ~20% of the entire phytolith assemblage (Veronica Muiruri, National Museums of Kenya, personal communication, 2009). Additional research on these samples and equivalent material from the Maasai Plains site is ongoing.

About 300 m northeast of this area, on the upper slopes of the ridge, there is a heavily eroded area nearly bare of grass cover and with only a sparse covering of low

FIGURE 7. View looking south across Mili Sita, 2005. Photo ©Paul Lane, BIEA.

acacia thorn trees. Scattered across this area are numerous distinct scatters of iron slag mixed with tuyere fragments and the remains of several smelting furnaces (Iles and Martinón-Torres, 2009). To the south of the main settlement area there are at least 55 stone cairns, one of which has been excavated and has been shown to have been used for human burial (see Lane et al., 2007:43). Close by are two flat stone slabs, each with parallel rows of small ground hollows, similar to known variants of mankala or bao gaming boards. There is also a line of cairns running at right angles to the ridge at its northern end. On the basis of the available radiocarbon dates, the site appears to have been occupied around Cal AD 1640–1730, which on the basis of available oral histories of the region, could suggest an association with the Laikipiak.

LAIKIPIAK ORIGINS

One current major uncertainty is precisely when Laikipiak entered the Ewaso ecosystem. Most scholars now consider Laikipiak to have been speakers of an Eastern Nilotic language similar to Maa, although Jacobs (1965:66) initially suggested that they may have been Galla originally, a term generally used to refer to speakers of Eastern Cushitic languages, such as Oromo and Borana. If Siiriäinen's (1984) association of Kisima Ware pottery with Laikipiak is correct, then on the basis of the available dates for its occurrence on the Maasai Plains site, Laikipiak were already using the plateau by the mid-fifteenth century AD. However, there are various reasons to be cautious about making such a direct correlation between the ceramics and past identities. First, over the last three decades archaeological research across the globe has shown that variations in material culture forms and styles are influenced by a wide range of different factors, and such variations can signal a multitude of different meanings and identities, not just those related to ethnicity (see, e.g., Jones, 1997; Conkey, 2006). Second, it is possible that pots were obtained via exchange with neighboring groups (including Bantu language speakers to the south and the various pockets of hunter-gatherers known to have coexisted with

Maa-speakers on the Laikipia and Leroghi plateaus) for much the same reasons as have been proposed with reference to PIA Sirikwa pottery and the Okiek groups of central Kenya (Blackburn, 1973). Additionally, differences in scholarly opinion over when the first Maa speakers in general arrived in the rift and adjacent highlands further complicate the picture. Arguing from the position of historical linguistics, Sommer and Vossen (1993:25) suggest that the ancestors of modern Maa speakers reached the Rift Valley "by the end of the ninth century" AD, whereas Galaty (1993) has argued that these represent "early Maa speakers" who can be distinguished from "later Maasai," who represent another expansionary phase of pastoral genesis in the area stretching from Lake Baringo to Lake Natron from which they spread in a spiral fashion (see also Sutton, 1993b). In this model the Laikipiak only attained dominance over the Ewaso Basin around the nineteenth century.

Maasai Purko oral traditions, on the other hand, refer to the Laikipiak arriving from the northeast sometime prior to AD 1600, encountering a group of people (the Il Tatua, or Tatoga) already inhabiting Laikipia. According to these traditions, the latter were driven away by the newcomers (Jacobs, 1972b:82). Some support for these Purko traditions is provided by the fact that although the language (Yaaku) originally spoken by Mukogodo hunter-gatherers (who might well be descended from the autochthonous LSA hunter-gatherers on Laikipia) is considered to belong to Eastern Cushitic (Heine, 1974–1975), it also contains Southern Cushitic loanwords (Ehret, 1974). These loanwords could have entered Yaaku as a result of prolonged interaction with a Southern Cushitic population, such as the Il Tatua. The evidence from rock shelter excavations at Ol Ngoroi, Shulumai, and possibly Porcupine Cave also supports a model of forager-herder interaction. However, if the Laikipiak did indeed enter the area around AD 1600, one would expect to see a noticeable change in pottery and other artifact styles dating to this period. No such marked changes are evident in the available archaeological data, however, and there is no evidence to support a model of population replacement over this time period. Moreover, although the Il Tatua are believed to have been speakers of a proto-Southern Cushitic language (which would be consistent with them being descended from the initial phase of pastoralists entering eastern Africa), it is now generally believed that they lived farther south in the Crater Highlands rather than in the Ewaso Basin. Clearly, further research is required before these issues might be resolved.

Regardless of the precise origins of the Laikipiak, the available historical sources do indicate that from ca. AD 1750 to the early twentieth century pastoral Maa-speaking communities, including Laikipia and Samburu, coexisted on Laikipia and Leroghi with scattered groups of other peoples that included hunter-gatherers (notably, Dikirri Dorobo and Mukogodo). Furthermore, their communities probably also encompassed pockets of Maa-speaking Mumonyot and LeUaso, Oromo-speaking Warra Daaya, and possibly Rendille along the northern fringes together with various Bantu language speakers, including Meru and Kikuyu, along the southern boundaries (Kenya Land Commission, 1934; Herren, 1987; Cronk, 1989, 2004; Sobania, 1993). These ethnicities were not necessarily permanently fixed entities, and in fact, there seems to have been widespread ethnic shifting among different groups within the region that often corresponded to (or resulted in) changes in subsistence strategy (see, e.g., Galaty, 1982, 1986; Schlee, 1989; Waller and Sobania, 1994:55–63; Cronk, 2002). Individuals, rather than entire communities, may also have shifted identity as a result of marriage or some other reason, as has been well documented elsewhere, including more recently in Isiolo, where individuals of Turkana descent subsequently formed the Ilgira section of the Samburu (Hjort, 1981). It is also known that certain times in the past were politically unstable and were characterized by increased levels of intercommunity violence and warfare, especially during the Iloikop wars of the 1840s–1880s, which resulted in the defeat of the Laikipiak Maasai and the penetration of the area by Purko Maasai (Weatherby, 1967; Waller, 1985; Galaty, 1993; Sobania, 1993). Maasai oral traditions place the defeat of the Laikipiak as having taken place during the last Iloikop war during the time of the Laimer age set (1866–1886) (Jennings, 2005:1130). However, this defeat did not result in the complete disappearance of Laikipiak, as is often commonly believed and was seemingly implied by Joseph Thomson, one of the earliest European explorers in the area. Thomson (1968:243) claimed that following the Purko defeat of Laikipiak, "not a man in the entire land" was left. In fact, many Laikipiak families were absorbed by other neighboring groups, including Turkana (Lamphear, 1993), Il Chamus around Baringo (Little, 1998), Samburu on Leroghi (Bilinda Straight, Western Michigan University, personal communication, 2006), and Meru and Kikuyu to the south (Waller, 1985); others temporarily became "Dorobo" or Mukogodo hunter-gatherers, and others still were assimilated into the Purko (Hughes, 2005). The oral traditions of various groups to the north of Laikipia, including those of Rendille, Turkana, Borana, and Samburu, also attest to a continuing presence of Laikipiak as a distinct entity—as exemplified by numerous cattle raids—until at least the last decade of the nineteenth century (Sobania, 1993).

Various external events and historical processes are also known to have had repercussions within northern "Maasailand," such as the southward expansion of the Boran into areas around Marsabit, the extension of Somali territory to include Wajir and sections of the Tana River emanating from the rise of Ethiopian imperialism during the nineteenth century (Fratkin, 2001), and Turkana incursions into the Samburu grasslands after ca. AD 1900 (Lamphear, 1993). Moreover, from the mid-nineteenth century there was a significant expansion of the caravan trade in the region, fed partly by an increase in demand in Europe and North America for ivory, encouraging greater penetration of the interior by traders, hunters, and porters from the Swahili coast and the Bantu-speaking heartlands. The large-scale removal of elephants from the Ewaso Basin as a consequence of this expansion could have also had major ecological consequences, at least over the short term, and potentially much longer (Håkansson, 2004). The East African region was also heavily impacted by a combination of epizootics, famine, and epidemics in the latter part of the nineteenth century, which included widespread famine between 1890 and 1891, smallpox outbreaks during 1883–1890, and rinderpest and bovine pleuropneumonia in the 1880s. These events are likely to have had significant repercussions for local demography and economic productivity (Kjekshus, 1977), as did the enclosure of commons, the restructuring of the tenets of landownership and property, and changes in the approaches to disease control that accompanied the establishment of British colonial rule (Waller, 2004).

EVIDENCE FOR HUMAN-INDUCED ENVIRONMENTAL CHANGE

In common with other parts of the region, the vegetation of the Ewaso Basin has undergone considerable change during the last 5,000–6,000 years. The main shift has been from dry evergreen upland forest dominated by cedar (*Juniperus procera*) and African olive (*Olea africanus*), which still survives in some areas, to savanna vegetation communities of various types. Evidence for these changes is provided by the results from recent paleoenvironmental investigations of swamp soils and sediments at Loitigon vlei on Mugie Ranch in the northern part of Laikipia and research on sediment cores collected from Ewaso Narok swamp just north of Rumuruti and Marura Swamp along the Mutara River adjacent to Ol'Pejeta Ranch (Muiruri, 2008). The data from Loitigon vlei, for example, suggest that there was a marked decline in the extent of Afromontane forest in the catchment at around 100 Cal BC and that this decline coincided with a pulse of biomass fires, as evidenced by an abundance of large-sized fragments of charcoal in the sediments (Taylor et al., 2005). At Marura, there is limited evidence for vegetation disturbance at the base of the record dated to around Cal 200 BC. Fossil pollen at this level is overwhelmingly from montane rainforest taxa (such as *Podocarpus, Olea,* and *Juniperus,* with scattered secondary species that included *Croton, Rapanea,* and *Cyathea*), suggesting a densely wooded environment. This conclusion is further supported by the presence of fungal spores associated with forest conditions (such as *Trichoglossum* cf. *hirsutum* and *Glomus* sp.) at these levels. Microscopic charcoal is also relatively scarce, suggesting a low incidence of fires. From ca. Cal AD 300, there is a marked decline in montane forest taxa and a corresponding increased abundance of Poaceae. An increase in forest fires is also indicated by the dramatic rise in the overall amount of charcoal and by the size of fragments, suggesting that fires were locally abundant (Muiruri, 2008).

Paleoclimatic factors such as drought cannot be fully ruled out as several of the larger lakes in the region experienced low-stands around this time, e.g., Lake Tanganyika, ca. 200 Cal BC (Alin and Cohen, 2003); Lake Edward, ca. Cal AD 0 (Russell et al., 2003); and Lake Victoria, ca. 700–500 Cal BC (Stager et al., 2003). Nevertheless, these changes on Laikipia seem more likely to have been related to an expansion of herding and human-induced bush clearance, especially as evidence from nearby Mount Kenya indicates that the period from ca. 900 Cal BC to Cal AD 100 was one of heavy convective rainfall, enhanced soil erosion, neoglacial ice advances, and forest expansion, rather than contraction, as documented on Laikipia (Barker et al., 2001). Further increases in burning are implied by an increased abundance of the largest-sized fraction of charcoal in the Loitigon sediments from ca. Cal AD 300 to 1300, and according to the pollen and $d^{13}C_{bulk}$ data, the *Acacia* bushland was replaced by fire-adapted C_4 grassland. Rather similar trends are evident in the Marura and Ewaso Narok cores, which document a steady replacement of Afromontane vegetation by woodland and bushland taxa (including *Capparis, Acacia,* and *Grewia*), indicative of open disturbed savannah becoming widely established in these catchments between ca. Cal AD 300 and 850. There is also a marked rise in the proportions of the spores of the dung-colonizing fungi *Cercophora* after Cal AD 1300 in these cores. This rise is probably indicative of an increase in the overall numbers of herbivores (which could include domestic stock), as might be expected following a shift to more open habitats (Muiruri, 2008).

When taken together, the changes in vegetation structure, increased evidence for local as well as regional fires, and the fungal spore evidence suggest that the period between ca. 200 Cal BC and Cal AD 300 (coinciding with the later stages of the PN) witnessed a marked expansion of human activity on Laikipia that included widespread forest clearance through the use of fires aimed at improving and extending grazing. This interpretation is only partially consistent with the available archaeological data since only limited traces of PN activity have been documented thus far. This apparent gap in the archaeological record may be due more to the limited extent and specific geographical distribution of archaeological research and/or various taphonomic processes that have either buried or eroded PN sites, than to a genuine absence of pastoralist activity in the Ewaso Basin at this time. However, it must be noted that the first few centuries AD were a period of considerable climatic variability across the region and especially increased unpredictability of rainfall (Alin and Cohen, 2003). Thus, settlements may have been more transient as pastoralist groups became more mobile and populations dispersed during the dry-season months. It is interesting to note, nonetheless, that the apparent date of occupation of the Maasai Plains site at around Cal AD 1400 coincides with evidence from Lake Naivasha for a brief high-stand, possibly indicative of a period of increased precipitation (Verschuren et al., 2000; Lamb et al., 2003), which could have facilitated a phase of settlement and population aggregation across the Ewaso Basin.

High-resolution environmental records from various locations throughout the region also indicate that the period from the late AD 1500s through the late 1700s appears to have been characterized by long intervals when levels of effective precipitation in eastern Africa were much reduced relative to the present (Taylor et al., 2000; Verschuren et al., 2000; Alin and Cohen, 2003; Robertshaw et al., 2004). Yet as the records from Lake Naivasha and elsewhere indicate, against this general drying trend there were periodic wet episodes interspersed with periods of very low rainfall and ensuing drought, some of which are remembered in various local oral traditions. It is also clear from the most recent work that there have been several massive, supraregional droughts within the last millennium (Verschuren et al., 2000; Verschuren, 2004; Holmgren and Öberg, 2006). Of these, an interdecadal drought dated to ca. Cal AD 1760–1840 (Bessems et al., 2008), which Verschuren et al. (2000) describe as much more serious than any of the twentieth century droughts, may have been particularly instrumental in triggering a variety of economic and settlement changes. Among other things, this severe climate event led to the complete desiccation of Lakes Baringo and Nakuru (Verschuren et al., 2000; Kiage and Liu, 2009) and had profound consequences for vegetation (Lamb et al., 2003; Bessems et al., 2008).

Nevertheless, paleoecological evidence from the same area also suggests that swamp formation around Lakes Baringo and Bogoria was both extensive and rapid during wetter climatic phases, with relatively abrupt shifts between C_3 dry scrubland (mixed warm-season grasses and *Acacia*) and C_3 wetland (dominated by *Typha*) vegetation mosaics (Driese et al., 2004). Moreover, it has been shown that droughts and other climate-induced stresses were not experienced uniformly across the region (Russell et al., 2007). There is also plentiful geomorphological evidence to suggest that rainfall regimes have fluctuated widely across the Ewaso Basin over the millennia. In commenting on the results of recent surveys in the Kipsing and Tol River watersheds in the Mukogodo Hills area immediately north of Lolldaiga, Pearl and Dickson (2004) noted that archaeological site distributions in these areas have been heavily affected by erosion and often reburied beneath recent alluvia. In all, Pearl and Dickson identified five stratigraphic units in this area, which related to different depositional events dated to between ca. 35,000 Cal BC and Cal AD 1550. Of particular interest is the evidence for a major episode of floodplain aggradation after ca. 6500 Cal BC and the subsequent formation of a paleosol near the top of the sequence under cooler and moister conditions than prevail today around Cal AD 600. After a period of relative stability, erosion resumed during the last 400–500 years (Pearl and Dickson, 2004:571–576).

Whether this erosion was induced by grazing pressure generally across Laikipia and Leroghi has yet to be established. Nevertheless, preliminary evidence from around the Mili Sita site in the Lolldaiga Hills suggests that there was a phase of severe soil erosion here before and/or concurrent with the use the site around Cal AD 1640, which would imply that overgrazing and/or the creation of deep drove ways by frequent cattle movements may have contributed to severe degradation in at least some catchments. Elsewhere, in contrast, pastoralist activities also had major beneficial effects on the transfer and local concentration of soil nutrients, with long-term consequences for vegetation patterns. An example is at the Maasai Plains site on Mugie, where concentrated pastoralist activity has resulted in the formation of stable, less-erodible, and fertile soils, with a number of possible positive consequences for local wildlife populations resulting from the formation of long-lived grassland glades within the wider mosaics of *Acacia*-dominated low-tree and shrub savanna and bushland.

More specifically, glades are a common feature of African savanna environments, and researchers from several disciplines have sought to understand their origin and dynamics, both from an ecological perspective and in relation to the implications for environmental management (e.g., Dublin et al., 1990; Reid and Ellis, 1995; Young et al., 1995; Augustine, 2003; Augustine and McNaughton, 2004a). This ecological research has confirmed that some glades represent nutrient-enriched patches related to abandoned pastoralist enclosure settlements ("bomas") that become dominated by nutrient-rich grass species that are particularly palatable to wild grazing ungulates and also enhance local biodiversity more generally. On parts of Laikipia glades have been shown to be dominated by *Cynodon plectostachyus* and the annual forb *Tribbalus terrestris* (Augustine and McNaughton, 2004b:831), whereas on the Athi Plains in southern Kenya, *Cynodon nlemfuensis* is the dominant grass (Stelfox, 1986). In the Amboseli Basin, Kenya, longitudinal study of abandoned bomas has indicated that recolonization of these sites by different plant species tends to follow a distinct sequence, culminating in the overall dominance of *Acacia tortilis* (Muchiru et al., 2008, 2009). Glades are perpetuated in the landscape by browsing and grazing activities that act to suppress the invasion of tree and shrub seedlings, and different studies have shown that glades may survive for periods up to at least 100 years. Numerous factors, including changes in management regime, climate change, fire history, periodic fluctuations in herbivore populations, and the effects of large herbivores such as elephants and giraffes, are known to influence the ecology of glades, and it is likely that different glades have had quite different histories.

Comparison between the Mili Sita and Maasai Plains archaeological sites lends support to such an argument but also indicates that some glades may be much older than currently estimated. Specifically, both sites survive in the landscape today as distinct areas of open grassland, against a broader context of expanding bushland, and both exhibit signs of intensive use for human settlement by pastoralist communities. The Maasai Plains site on Mugie Ranch dates to around Cal AD 1450 and is ~200–250 years older than the Mili Sita site. This site is surrounded by *Acacia*-dominated low-tree and shrub savanna on relatively fertile Chromic Luvisols that exhibit little evidence of soil erosion. Analysis of time series aerial photography and satellite imagery of several glades on Mugie Ranch indicates that changes in their spatial extent since 1950 (the date of the earliest available aerial photograph coverage) have been variable and that bush encroachment has been influenced by a range of anthropogenic and natural processes (Causey, 2008:157–184). Surveys of a sample of these indicate that some but not all of the existing glades contain traces of archaeological material indicative of former pastoralist settlement activity, although the cultural and temporal attributions of this material were variable (Causey, 2008). Of all the glades studied, the greatest decrease in open area was at the Maasai Plains site (31.7% since 1950). Nevertheless, the glade has continued to persist within this landscape as a nutrient "hot spot" that originated directly as a consequence of pastoralist activity some 750 years ago.

The soils around Mili Sita on Lolldaiga Hills Ranch are also Chromic Luvisols, but unlike those in the vicinity of the Maasai Plains site, they are rarely more than 40 cm in depth, usually lack a well-developed A horizon, and frequently have been stripped, leaving only quartz lag deposits. All soils across the col and down the flanks show signs of having been severely eroded in the past, despite the lack of steep rocky slopes that could have generated significant runoff during heavy rainstorms. Both sides of the ridge to the south of Mili Sita are cut by substantial erosion gullies that are in places well over 6 m deep. In light of this evidence for erosion, the persistence of a large expanse of grassland across the col is probably due to the effects of the presence of pastoralist settlement here over a significant period of time. Soil test pits excavated along transects across the col seem to confirm this, as the results showed that the soil here had higher organic carbon levels than the truncated Chromic Luvisols around the Mili Sita ridge (see Payton, 2005). The soil pH was also always neutral and supported by elevated base saturation measurements of 100% and strong enrichment of exchangeable calcium and exchangeable potassium. Both factors lend support to the hypothesis that the soils have been enriched even though their morphology and physical characteristics indicate that the col had been severely eroded *prior to* settlement and the use of the area for penning livestock in the seventeenth century AD. Whether there were earlier phases of settlement on Mili Sita that might have initiated this erosion or whether it arose from climate change (the period from ca. Cal AD 1250 to the late 1500s, for instance, is believed to have been characterized across the region by relatively humid conditions; see Alin and Cohen, 2003) or a combination of factors remains to be established. Nevertheless, it would still appear that although overgrazing might have contributed to severe degradation in the surrounding catchment, pastoralist activities also had a major effect on the transfer and local concentration of soil nutrients in the degraded soils on the Mili Sita ridge, with long-term consequences for vegetation patterns. In contrast to the situation at Mili Sita, at the Maasai Plains site on Mugie the contrasting environment of the phonolite plateau has resulted in the formation of more-stable, less-erodible, and more-fertile soils located in a landscape of low relief. Even with similar land use and grazing pressures to those at Mili Sita, these soils would probably resist soil erosion.

Elsewhere on Lolldaiga, Causey's research has shown that the majority of PIA sites located during the BIEA transect surveys fell within open grassy glades and typically on sloping ridge tops (Causey and Lane, 2005), indicating a settlement location preference similar to what has been recorded among contemporary Maa speakers (e.g., Western and Dunne, 1979), although some settlement activity in the valley floors and open plains also took place. Causey's transect surveys of the lowlands toward the northern end of the ranch, however, found much more evidence for PN activity than encountered during the BIEA surveys. These sites are all smaller in extent than the later PIA examples and occur on slightly sloping ridge tops, but their distribution does not correlate closely with the distribution of open glades (Causey, 2008:294–311, 2010).

In summary, these provisional results suggest that the patterns of soil erosion and deposition and bush encroachment are highly variable in space and time. Further, and of greater significance to contemporary environmental narratives, these results also suggest that pastoralist activity, although a cause of land degradation under some circumstances, can have the potential to encourage local stabilization and a reversal of degradation processes even in those areas where it had acted previously as a catalyst for erosion. In other words, the links between grazing patterns, herd sizes, range quality, and soil erosion appear more complicated than is implied by many current environmental narratives, whether these see pastoralists as the root cause of land degradation and biodiversity loss or as the traditional guardians of an Edenic wilderness. Far more integrated cross-disciplinary research on this topic is, nevertheless, needed to clarify certain human–environment relationships.

SUMMARY

Archaeological, historical, and ethnographic information concerning the Ewaso Basin indicate that many different groups have occupied parts of this area at different times in the past and that these groups have encompassed both hunter-gatherer and pastoralist communities and speakers of various Nilotic, Cushitic, and Bantu languages, and possibly others as well. There is also good evidence to suggest that at least in the recent past, the boundaries between different "ethnic," "subsistence," and perhaps even linguistic groups were fairly fluid and that cultural intermixing as well as interaction through exchange and other social mechanisms was common. All of these factors make it likely that the archaeological traces that survive in the landscape were the product of multiple social groups at different times in the past, with multiple meanings and social significance. Similarly, the available data caution against making simplistic correlations between, for example, a particular cairn or artifact type and either the linguistic or ethnic affiliation of their makers. Problems with dating and uneven preservation further complicate the interpretation of this evidence.

However, on the basis of the combined results of recent work on Laikipia taken together with the broader regional evidence and with the proviso that elements of the sequence and specific details may change as more research is completed, four broad phases of pastoralist practices in the Ewaso Basin can be proposed for the period prior to the establishment of colonial rule, spanning the last ~4000 years. The first three of these are still rather speculative and need to be tested by further research; the evidence for the last phase, however, is more comprehensive. The proposed phases are as follows:

1. An initial "moving frontier" of pastoralism ca. 2700–1000 Cal BC.
2. The formation of a "static frontier" and emergence of specialized pastoralism ca. 1000 Cal BC to Cal AD 100.
3. A shift to more mixed herding-hunting economies and fluid ethnic boundaries ca. Cal AD 100–800.
4. The reappearance of specialized pastoralism and the creation of Maa identities ca. Cal AD 800–1900.

These phases entailed different forms and levels of mobility that at times may have incorporated both population migration and seasonal movements and perhaps even genuine nomadism. At others times, such as between ca. 2000 BC and AD 100, the patterns of mobility may have been characterized more by a system of seasonal transhumance between relatively clearly defined and stable territories. It is also evident that the boundaries between "pastoralists" and nonpastoralists, including both hunter-gatherers and agriculturalists, have at times been more fluid and negotiable than at others, and hence "identity" mobility and not just spatial mobility was at times constrained and at others much less restricted. Other processes and events also acted to stimulate or reduce mobility, all of which would have had rather different effects on local environments and vegetation mosaics.

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NOTES

1. Owing to fluctuations in the ratio of ^{14}C to ^{12}C in the atmosphere over the millennia, largely as a result of changes in the solar magnetic field, "raw" radiocarbon dates do not correspond directly with calendar years. These raw dates can be calibrated by using calibration curves produced by systematic dating of materials of known absolute date (such as tree rings), and comparing the differences between the actual calendar age of the material and its radiocarbon age. Whereas raw radiocarbon dates are conventionally reported in "radiocarbon years BP," calibrated dates are reported in calendar years in the form Cal BC or AD.

2. Although increased aridity in parts of Ethiopia and Sudan may have made these areas more marginal for pastoralism, it would have had the reverse effect in, for example, the Central Rift Valley, where reduction in rainfall and a fall in lake levels would have encouraged the retreat of forest margins to higher altitudes, allowing the expansion of grasslands more suited to grazing (Ambrose and Sikes, 1991; Marean, 1992).

REFERENCES

Alin, S. R., and A. S. Cohen. 2003. Lake-Level History of Lake Tanganyika, East Africa, for the Past 2500 Years Based on Ostracod-Inferred Water-Depth Reconstruction. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 199:31–49.

Ambrose, S. H. 1984. Excavations at Deloraine, Rongai, 1978. *Azania*, 19:79–104.

———. 1985. Excavations at Masai Gorge Rockshelter, Naivasha. *Azania*, 20:29–67.

———. 1998. Chronology of the Later Stone Age and Food Production in East Africa. *Journal of Archaeological Science*, 25:377–392.

Ambrose, S. H., and N. E. Sikes. 1991. Soil Carbon Isotope Evidence for Holocene Habitat Change in the Kenya Rift Valley. *Science*, 253:1402–1405.

Augustine, D. J., 2003. Long-Term, Livestock Mediated Redistribution of Nitrogen and Phosphorus in an East African Savanna. *Journal of Applied Ecology*, 40:137–149.

Augustine, D. J., and S. J. McNaughton. 2004a. Regulation of Shrub Dynamics by Native Browsing Ungulates on East African Rangeland. *Journal of Applied Ecology*, 41:45–58.

———. 2004b. Temporal Asynchrony in Soil Nutrient Dynamics and Plant Production in a Semiarid Ecosystem. *Ecosystems*, 7:829–84.

Barker, P. A., F. A. Street-Perrott, M. J. Leng, P. B. Greenwood, D. L. Swain, R. A. Perrott, R. J. Telford, and K. J. Ficken. 2001. A 14,000-Year Oxygen Isotope Record from Diatom Silica in Two Alpine Lakes on Mt. Kenya. *Science*, 292:2307–2310.

Barthelme, J. 1985. *Fisher-Hunters and Neolithic Pastoralists in East Turkana, Kenya*. BAR International Series 254, Cambridge Monographs in African Archaeology 23. Oxford: B.A.R.

Bessems, I., D. Verschuren, J. Russell, J. Hus, F. Mees, and B. Cumming. 2008. Paleolimnological Evidence for Widespread Late 18th Century Drought across Equatorial East Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 259:107–120.

Blackburn, R. H. 1973. Okiek Ceramics: Evidence for Central Kenya Prehistory. *Azania*, 8:55–70.

Bower, J. R. F. 1991. The Pastoral Neolithic of East Africa. *Journal of World Prehistory*, 5:49–82.

Bower, J. R. F., and T. J. Chadderdon. 1986. Further Excavations of Pastoral Neolithic Sites in Serengeti. *Azania,* 21:129–133.

Carey Jones, N. S. 1965. The Decolonization of the White Highlands of Kenya. *Geographical Journal*, 131:186–201.

Causey, M. 2008. Delineating Pastoralist Behaviour and Long-Term Environmental Change: A GIS Landscape Approach on the Laikipia Plateau, Kenya, Ph.D. diss., School of Archaeology, University of Oxford, Oxford.

———. 2010. New Archaeological Discoveries from the Laikipia Plateau, Kenya. *Azania*, 45:112–136.

Causey, M., and P. Lane. 2005. GIS and Landscape Archaeology: Delineating the Possible Long-Term Environmental Effects of Pastoralism on the Laikipia Plateau, Kenya. *Nyame Akuma,* 64:24–32.

Chamberlain, N. 2006. Report on the Rock Art of South West Samburu District, Kenya. *Azania*, 41:139–157.

Collett, D., and P. T. Robertshaw. 1983. Problems in the Interpretation of Radiocarbon Dates: The Pastoral Neolithic of East Africa. *African Archaeological Review*, 1:57–74.

Conkey, M. W. 2006. “Style, Design and Function.” In *Handbook of Material Culture*, ed. C. Tilley, W. Keane, S. Küchler, M. Rowlands, and P. Spyer, pp. 355–372. London: Sage.

Cronk, L. 1989. From Hunters to Herders: Subsistence Change as a Reproductive Strategy among the Mukogodo. *Current Anthropology*, 30:224–234.

———. 2002. From True Dorobo to Mukogodo Maasai: Contested Ethnicity in Kenya. *Ethnology*, 41:27–49.

———. 2004. *From Mukogodo to Maasai: Ethnicity and Cultural Change in Kenya*. Boulder, Colo.: Westview Press.

Dickson, D. B., and G.-Y. Gang. 2002. Evidence of the Emergence of “Modern” Behaviour in the Middle and Later Stone Age Lithic Assemblages at Shurmai Rockshelter (GnJm1) and Kakwa Lelash Rockshelter (GnJm2) in the Mukogodo Hills of North-Central Kenya. *African Archaeological Review*, 19:1–26.

Dickson, D. B., F. B. Pearl, G.-Y. Gang, S. Kahinju, and S. Wandibba. 2004. Site Reconnaissance in the Kipsing and Tol River Watersheds of Central Kenya: Implications for Middle and Later Stone Age Land-Use Patterns. *African Archaeological Review,* 21:153–191.

Driese, S. G., G. M. Ashley, Z.-H. Lia, V. C. Hover, and R. B. Owen. 2004. Possible Late Holocene Equatorial Palaeoclimate Record Based upon Soils Spanning the Medieval Warm Period and Little Ice Age, Loboi Plain, Kenya. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 213:231–250.

Dublin, H., A. R. E. Sinclair, and J. McGlade. 1990. Elephants and Fire as Causes of Multiple Stable States in the Serengeti-Mara Woodlands. *Journal of Animal Ecology*, 59:1147–1164.

Ehret, C. 1974. *Ethiopians and East Africans: The Problem of Contacts*. Nairobi: East African Publishing House.

———. 1998. *An African Classical Age: Eastern and Southern Africa in World History, 1000 B. C. to A. D. 400*. Oxford: James Currey.

Fratkin, E. 2001. East African Pastoralism in Transition: Maasai, Boran, and Rendille Cases. *African Studies Review*, 44:1–25.

Galaty, J. 1982. Being “Maasai”; Being “People-of-Cattle”: Ethnic Shifters in East Africa. *American Ethnologist*, 9:1–20.

———. 1986. East African Hunters and Pastoralists in Regional Perspective: An Ethnoanthropological Approach. *Sprache und Geschichte in Afrika*, 7(1):105–131.

———. 1993. “Maasai Expansion and the New East African Pastoralism.” In *Being Maasai: Ethnicity and Identity in East Africa*, ed. T. Spear and R. Waller, pp. 61–86. London: James Currey.

Gang, G.-Y. 2001. *The Middle and Later Stone Ages in the Mukogodo Hills of Central Kenya*. BAR International Series 964. Oxford: Archaeopress.

Gifford-Gonzalez, D. 1998. Early Pastoralists in East Africa: Ecological and Social Dimensions. *Journal of Anthropological Archaeology*, 17:166–200.

———. 2000. Animal Disease Challenges to the Emergence of Pastoralism in Sub-Saharan Africa. *African Archaeological Review*, 17:95–139.

Gramly, R. M. 1975. Meat-Feasting Sites and Cattle Brands: Patterns of Rock-Shelter Utilization in East Africa. *Azania*, 10:107–121.

Håkansson, N. T. 2004. The Human Ecology of World Systems in East Africa: The Impact of the Ivory Trade. *Human Ecology*, 32:561–591.

Hanotte, O., D. G. Bradley, J. W. Ochieng, Y. Verjee, E. W. Hill, and J. E. O. Rege. 2002. African Pastoralism: Genetic Imprints of Origins and Migrations. *Science,* 296:336–339.

Heine, B. 1974–1975. Notes on the Yaaku Language (Kenya). *Afrika und Übersee*, 58:27–61, 119–138.

Herren, U. 1987. The People of Mukogodo Division, Laikipia District: A Historical and Anthropological Baseline. *Laikipia–Mount Kenya Reports 9*. Berne: Institute of Geography, University of Berne.

Hjort, A. 1981. Ethnic Transformation, Dependency and Change. *Journal of Asian and African Studies*, 16:50–67.

Hoelzmann, P., B. Keding, H. Berke, S. Kropelin, and H. J. Kruse. 2001. Environmental Change and Archaeology: Lake Evolution and Human Occupation in the Eastern Sahara during the Holocene. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 169:193–217.

Holmgren, K., and H. Öberg. 2006. Climate Change in Southern and Eastern Africa during the Past Millennium and Its Implications for Societal Development. *Environment, Development and Sustainability*, 8:185–195.

Huber, M., and C. J. Opondo, eds. 1995. *Land Use Change Scenarios for Subdivided Ranches in Laikipia District, Kenya. Laikipia–Mount Kenya Reports 19*. Berne: Institute of Geography, University of Berne.

Hughes, L. 2005. Malice in Maasailand: The Historical Roots of Current Political Struggles. *African Affairs*, 104:207–224.

———. 2006. *Moving the Maasai: A Colonial Misadventure*. Basingstoke: Palgrave Macmillan.

Iles, L., and M. Martinón-Torres. 2009. Pastoralist Iron Production on the Laikipia Plateau, Kenya: Wider Implications for Archaeometallurgical Studies. *Journal of Archaeological Science*, 36:2314–2326.

Jacobs, A. 1965. The Traditional Political Organization of the Pastoral Masai. Ph.D. thesis, University of Oxford, Oxford.

———. 1972a. New Archaeological Sites in the Mukogodo Area, Laikipia District. Master’s thesis, Institute of African Studies, University of Nairobi, Nairobi.

———. 1972b. “Appendix A: The Discovery and Oral History of the Narosura Site.” *In* Excavations at Narosura, a Stone Bowl Site in the Southern Kenya Highlands, K. Odner, *Azania*, 7:79–87.

Jennings, C. C. 2005. Scatterlings of East Africa: Revisions of Parakuyo Identity and History. Ph.D. thesis, University of Texas at Austin, Austin.

Jones, S. 1997. *The Archaeology of Ethnicity: Constructing Identities in the Past and Present*. London: Routledge.

Karega-Mũnene. 2002. *Holocene Foragers, Fishers and Herders of Western Kenya*. BAR International Series 1037, Cambridge Monographs in African Archaeology 54. Oxford: Archaeopress.

Kenya Land Commission. 1934. *Kenya Land Commission Evidence*. Volume 2. London: His Majesty’s Stationery Office.

Kiage, L. M., and K. B. Liu. 2009. Palynological Evidence of Climate Change and Land Degradation in the Lake Baringo Area, Kenya, East Africa, since AD 1650. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 279:60–72.

Kiteme, B. P., U. Wiesmann, E. Künzi, and J. M. Mathuva. 1998. A Highland–Lowland System under Transitional Pressure: A Spatio-temporal Analysis. *Eastern and Southern Africa Geographical Journal*, 8:45–53.

Kjekshus, H. 1977. *Ecology, Control and Economic Development in East African History*. London: James Currey.

Kohler, T. 1987. *Land Use in Transition. Aspects and Problems of Small Scale Farming in a New Environment: The Example of Laikipia District, Kenya*. African Studies Series A5. Berne: Geographica Bernensia.

Kuehn, D. D., and D. B. Dickson. 1999. Stratigraphy and Noncultural Site Formation at the Shurmai Rockshelter (GnJm1) in the Mukogodo Hills of North-Central Kenya. *Geoarchaeology*, 14:63–85.

Kusimba, C. M., and S. B. Kusimba. 2005. "Mosaics and Interactions: East Africa, 2000 B. P. to the Present." In *African Archaeology: A Critical Introduction*, ed. A. B. Stahl, pp. 392–419. Oxford: Blackwell Publishing.

Kusimba, S. B. 2001. The Early Later Stone Age in East Africa: Excavations and Lithic Assemblages from Lukenya Hill. *African Archaeological Review*, 18:77–123.

Lamb, H., I. Darbyshire, and D. Verschuren. 2003. Vegetation Response to Rainfall Variation and Human Impact in Central Kenya During the Past 1100 Years. *The Holocene*, 13:285–292.

Lamphear, J. 1993. "Aspects of 'Becoming Turkana': Interactions and Assimilation between Maa- and Ateker-Speakers." In *Being Maasai: Ethnicity and Identity in East Africa*, ed. T. Spear and R. Waller, pp. 87–104. London: James Currey.

Lane, P. J., ed. 2005. Landscape and Environmental Change in Semi-arid Regions of East & Southern Africa: Developing Interdisciplinary Approaches. Summary of Results on Laikipia, Kenya. Report. Nairobi: British Institute in Eastern Africa.

———. In press. The Later Holocene Archaeology of Laikipia Plateau, Kenya, and Evidence for Environmental Change. In *Proceedings of the 12th Congress of the Pan African for Prehistory and Related Studies*, ed. P. A. Tsheboeng and A. K. Segobye. Gaborone: Pula Press.

Lane, P. J., B. Straight, and C. Hilton. 2007. Excavations at Baawa, Samburu District, Kenya: Preliminary Report on the 2006 Season. *Nyame Akuma,* 68:34–46.

Little, P. D. 1998. Maasai Identity on the Periphery. *American Anthropologist*, 100:444–457.

Marean, C. W. 1992. Hunter to Herder: Large Mammal Remains from the Hunter-Gatherer Occupation at Enkapune ya Muto Rockshelter. *African Archaeological Review*, 10:65–127.

Marshall, F. B. 2000. "The Origins and Spread of Domestic Animals in East Africa." In *The Origins and Development of African Livestock: Archaeology, Genetics, Linguistics and Ethnography*, ed. R. M. Blench and K. C. MacDonald, pp. 191–221. London: UCL Press.

Muchiru, A. N., D. J. Western, and R. S. Reid. 2008. The Role of Abandoned Pastoral Settlements in the Dynamics of African Large Herbivore Communities. *Journal of Arid Environments*, 72:940–952.

———. 2009. The Impact of Abandoned Pastoral Settlements on Plant and Nutrient Succession in an African Savanna Ecosystem. *Journal of Arid Environments*, 73:322–331.

Muiruri, V. M. 2008. Detecting Environmental Changes and Anthropogenic Activities on the Laikipia Plateau, Kenya. MSc. thesis, Department of Botany, University of the Free State, Bloemfontein, South Africa.

Mutundu, K. K. 1999. *Ethnohistoric Archaeology of the Mukogodo in North Central Kenya*. BAR International Series 775, Cambridge Monographs in African Archaeology 47. Oxford: Archaeopress.

———. 2005. Faunal Remains from Ol Ngoroi Rockshelter. Report. Nairobi: British Institute in Eastern Africa.

Odner, K. 1972. Excavations at Narosura, a Stone Bowl Site in the Southern Kenya Highlands. *Azania*, 7:25–92.

Payton, R. W. 2005. "Soils, Land Degradation and Landscape History in Laikipia District." In Landscape and Environmental Change in Semi-arid Regions of East & Southern Africa: Developing Interdisciplinary Approaches. Summary of Results on Laikipia, Kenya, ed. P. J. Lane, pp. 45–59. Report. Nairobi: British Institute in Eastern Africa.

Pearl, F. B., and D. B. Dickson. 2004. Geoarchaeology and Prehistory of the Kipsing and Tol River Watersheds in the Mukogodo Hills Region of Central Kenya. *Geoarchaeology,* 19:565–582.

Reid, R. S., and J. E. Ellis. 1995. Impacts of Pastoralists on Woodlands in South Turkana, Kenya: Livestock-Mediated Tree Recruitment. *Ecological Applications*, 5:978–992.

Robertshaw, P. T. 1989. "The Development of Pastoralism in East Africa." In *The Walking Larder: Patterns of Domestication, Pastoralism and Predation*, ed. J. Clutton-Brock, pp. 207–212. London: Unwin Hyman.

Robertshaw, P., D. Taylor, S. Doyle, and R. Marchant. 2004. "Famine, Climate and Crisis in Western Uganda." In *Past Climate Variability Through Europe and Africa*, ed. R. Battarbee, F. Gasse, and C. Strickey, pp. 535–550. Amsterdam: Kluwer.

Russell, J. M., T. C. Johnson, K. R. Kelts, T. Lærdal, and M. R. Talbot. 2003. An 11000-year Lithostratigraphic and Paleohydrologic Record from Equatorial Africa: Lake Edward, Uganda-Congo. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 193:25–49.

Russell, J. M., D. Verschuren, and H. Eggermont. 2007. Spatial Complexity of 'Little Ice Age' Climate in East Africa: Sedimentary Records from Two Crater Lake Basins in Western Uganda. *The Holocene*, 17:183–193.

Schlee, G. 1989. *Identities on the Move: Clanship and Pastoralism in Northern Kenya*. Manchester: Manchester University Press.

Siiriäinen, A. 1977. Later Stone Age Investigation in the Laikipia Highlands, Kenya: A Preliminary Report. *Azania*, 12:161–186.

Siiriäinen, A. 1984. *Excavations in Laikipia: An Archaeological Study of the Recent Prehistory in the Eastern Highlands of Kenya*. Helsinki: Suomen Muinais-muistoyhdistksen Aikakauskirja Finska Fornminnesförenengens Tidskrift.

Smith, B. W., S. Mguni, and W. Steyn. 2004. The Rock Art of Laikipia District, Rift Valley Province, Kenya. Report. Nairobi: British Institute in Eastern Africa.

Sobania, N. 1993. "Defeat and Dispersal: The Laikipiak and Their Neighbours in the Nineteenth Century." In *Being Maasai: Ethnicity and Identity in East Africa*, ed. T. Spear and R. Waller, pp. 105–119. London: James Currey.

Sommer, G., and R. Vossen. 1993. "Dialects, Sectiolects, or Simply Lects? The Maa Language in Time Perspective." In *Being Maasai: Ethnicity and Identity in East Africa*, ed. T. Spear and R. Waller, pp. 25–37. London: James Currey.

Stager, J. C., B. F. Cumming, and L. D. Meeker. 2003. A 10,000-year High-Resolution Diatom Record from Pilkington Bay, Lake Victoria, East Africa. *Quaternary Research*, 59:172–181.

Stelfox, J. B. 1986. Effects of Livestock Enclosures (Bomas) on the Vegetation of the Athi Plains, Kenya. *African Journal of Ecology*, 24:41–45.

Sutton, J. E. G. 1993a. Deloraine: Further Excavation, and the Iron Age Sequence of the Central Rift. *Azania* 28:103–125.

———. 1993b. "Becoming Maasailand." In *Being Maasai: Ethnicity and Identity in East Africa*, ed. T. Spear and R. Waller, pp. 38–60. London: James Currey.

Taylor, D., P. Robertshaw, and R. A. Marchant. 2000. Environmental Change and Political-Economic Upheaval in Precolonial Western Uganda. *The Holocene*, 10:527–536.

Taylor, D., P. J. Lane, V. Muiruri, A. Ruttledge, R. Gai McKeever, T. Noland, P. Kenny, and R. Goodhue. 2005. Holocene Vegetation Dynamics on the Laikipia Plateau, Kenya. *The Holocene*, 15:837–846.

Thomson, J. 1968. *Through Masai Land*. Reprint. London: Frank Cass. [Original publication 1885.]

Vaughan, C. 2005. "Changing Patterns of Land Use during the Colonial Era." In Landscape and Environmental Change in Semi-arid Regions of East & Southern Africa: Developing Interdisciplinary Approaches. Summary of Results on Laikipia, Kenya, ed. P. J. Lane, pp. 12–25. Report. Nairobi: British Institute in Eastern Africa.

Verschuren, D. 2004. Decadal and Century-Scale Climate Variability in Tropical Africa during the Past 2000 Years. *Developments in Paleoenvironmental Research*, 6:139–158.

Verschuren, D., K. R. Laird, and B. R. Cumming. 2000. Rainfall and Drought in Equatorial East Africa during the Past 1,100 Years. *Nature*, 403:410–414.

Waller, R. D. 1979. The Lords of East Africa: The Maasai in the mid-Nineteenth Century (c. 1840–1880). Ph.D. thesis, University of Cambridge, Cambridge.

———. 1985. Ecology, Migration and Expansion in East Africa. *African Affairs*, 84:347–370.

———. 2004. "Clean" and "Dirty": Cattle Disease and Control Policy in Colonial Kenya, 1900–40. *Journal of African History*, 45:45–80.

Waller, R., and N. W. Sobania. 1994. Pastoralism in Historical Perspective. In *African Pastoralist Systems: An Integrated Approach*, ed. E. Fratkin, K. A. Galvin, and E. A. Roth, pp. 45–68. London: Lynne Rienner Publishers.

Weatherby, J. M. 1967. Nineteenth Century Wars in Western Kenya. *Azania*, 2:133–144.

Western, D., and T. Dunne, 1979. The Location of Maasai Settlements in Relation to Geomorphology, Hydrology and Vegetation. *Human Ecology*, 7:75–98.

Wright, D. K. 2005. New Perspectives on Early Regional Interaction Networks of East African Trade: A View from Tsavo National Park, Kenya. *African Archaeological Review*, 22:111–140.

———. 2007. Tethered Mobility and Riparian Resource Exploitation Among Neolithic Hunters and Herders in the Galana River Basin, Kenyan Coastal Lowlands. *Environmental Archaeology*, 12:25–47.

Young, T. P., N. Partridge, and A. Macrae. 1995. Long-Term Glades in Acacia Bushland and their Edge Effects in Laikipia, Kenya. *Ecological Applications*, 5:97–108.

Reassessing Aerial Sample Surveys for Wildlife Monitoring, Conservation, and Management

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ABSTRACT. Concerns about the cost-effectiveness of conservation monitoring prompt a reassessment of systematic aerial sample surveys, which have been widely applied to census wildlife and livestock in African savannas for more than 30 years. First, we use results from high-resolution sample surveys in Laikipia District (northern Kenya) to directly compare results from aerial total and sample surveys, showing few systematic differences in their estimates of wildlife abundance but great differences in cost and scope. Second, we quantify how the precision of population estimates is affected by survey resolution and species density. Results suggest that lower survey resolutions widely used in the past to census wildlife and livestock resources have been insufficient to reliably estimate all but the most abundant species. Third, we describe how sample survey data can be used to map the potential for human–wildlife conflict across large landscapes. High-resolution sample surveys in Laikipia have revealed causes and consequences of ecosystem change, advanced our understanding of ungulate population dynamics, guided wildlife management and conservation action, and increased confidence in sample survey methodology. However, further refinements in sample survey methods are needed to improve cost-effectiveness.

INTRODUCTION

There is a growing need to inventory and monitor wildlife resources as well as threats to those resources, for several reasons. One is to track the status of threatened and endangered species: Are they dwindling or recovering? Another is to ensure that exploited species are harvested sustainably. There is also a need to map the changing human "footprint" across landscapes since this is typically the principal threat to the extent and integrity of wildlife habitat. Finally, there is a need to evaluate the success of measures designed to achieve specific conservation targets (Stem et al., 2005). Judging how best to allocate limited funds either to direct conservation actions or to monitoring the success of those actions is not

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straightforward (Tear et al., 2005). Within this context of enhancing conservation efficiency, we reassess aspects of the utility and role of systematic aerial sample surveys as a tool for conservation monitoring.

Aerial sample surveys originated in Serengeti National Park in the early 1970s as an affordable way to monitor the rapidly growing wildebeest population (Sinclair and Norton-Griffiths, 1982). The method was later refined to estimate the abundance of all large herbivores, both wild and domestic, and to map their distributions across vast regions (Norton-Griffiths, 1978). For more than 30 years this monitoring method has been widely applied in African savannas to track wildlife and livestock dynamics (see Box 1 in the Introduction to this volume: Georgiadis, 2011:2).

A reassessment of systematic sample surveys was prompted by several concerns. Increasing costs have sharpened questions about affordability and cost-effectiveness. Declining numbers and distributions of many wildlife populations call for data at ever increasing levels of spatial resolution, prompting questions about the precision of sample survey estimates and when precision is sufficient for specific conservation and management applications. Cutting costs by reducing survey resolution seems counterproductive, given its attendant penalties of diminished precision and spatial resolution. Another option is to increase resolution but limit the spatial extent of surveys to areas of particular concern. A compromise is to stratify surveys, covering different areas at different resolutions. A final option is to abandon aerial surveys entirely. Other than some initial attention to these issues (International Livestock Centre for Africa, 1981; Redfern et al., 2002), little quantitative information has been published that helps us choose among available options.

We address these issues empirically, using results from high-resolution sample surveys that have guided the conservation and management of large herbivores in Laikipia District (northern Kenya) for more than two decades. We begin with a direct comparison of results from aerial total and sample counts of wildlife in Laikipia District, discussing their strengths and weaknesses. We then show how the precision of population estimates from sample surveys is affected by survey resolution and species density, inferring thresholds at which density may be too low to yield reliable results. Finally, we describe a simple but instructive application of sample survey data, in which the spatial proximity of wildlife and human attributes is used to map the potential for human–wildlife conflict. Further refinements in sample survey methods are suggested to improve cost-effectiveness and conservation applications.

COMPARING RESULTS FROM TOTAL AND SAMPLE COUNTS, AND SEASONAL EFFECTS ON VISIBILITY BIAS

Sample surveys have provided an unparalleled record of wildlife and livestock dynamics in Kenya since 1977 (Georgiadis, 2011, this volume:2 [Box 1]). However, reservations about the reliability of sample surveys have persisted, resulting from several surveys that appeared to yield wildly inaccurate results. Such reservations prompted a census of wild herbivores in Laikipia District in September 1996 by total aerial counting, a more expensive method, but with greater intuitive expectation among nonscientists to yield accurate results. A high-resolution sample survey covering the same area followed only five months later, in February 1997. The two censuses by different methods were sufficiently close in time for actual changes in wildlife numbers to be minor and for differences in population estimates to be largely due to counting method (elephants were omitted from the comparison as the only species capable of migrating in or out of the study area in the interim). This provided a rare opportunity to directly compare population estimates obtained from total and sample surveys over a relatively large area.

Our “null” expectation was that results from these surveys should not be identical. We expected sample surveys to yield slightly higher estimates than total counts for two reasons. First, searching efficiency by observers should be higher within the narrow (150 m) strip transects of a sample survey than in a total count, in which the effective strip width may be up to 1000 m wide. Second, in a total aerial count there is always a strip underneath the aircraft that is obscured, contributing further to an undercount. Consequently, more individuals should be missed in a total count than a sample survey.

Given that the total count took place during a wet phase and the sample survey took place during a dry phase, seasonal factors such as background foliage density and color may also have biased the results because of changes in observer visibility (Redfern et al., 2002). An opportunity to test the effect of season on visibility, without the confounding influence of different survey methods, was afforded by an identical sample survey conducted in June 1997, just five months after the dry season sample survey in February 1997. This coincided with the wettest El Niño event on record. Since Laikipia District is effectively a closed system for wild herbivores (excepting elephants), differences in population estimates between February and June 1997 would more likely reflect a seasonal visibility bias than actual population changes.

Total Counting Method: Over three days in September 1996, numbers of wild ungulate species were counted over an area of about 7,000 km^2 within Laikipia District, using 10 aircraft, all but one provided and crewed by local landowners (Kenya Wildlife Service provided one aircraft, and the U.S. Agency for International Development (USAID) provided fuel). To cut costs, areas with little or no wildlife (partially cultivated land in southwestern Laikipia) were omitted from the survey zone. Counting was organized by dividing the survey zone into three sections, with one section counted per day. Within each section, daily counting blocks of 200–500 km^2 were allocated to each aircraft. Counting began at around 0700 local time and ended before 1030 in the morning, and it took place again between 1530 and 1830 in the evening. Blocks were searched systematically, using transects separated by 1–2 km from a height of 75–122 m above ground. Flight paths were tracked using Trimble GPS, and the locations of all herds were recorded as numbered waypoints (Figure 1, top left, bottom left). Flight paths and waypoint maps were printed out immediately upon landing and handed back to crews for checking and annotation so that overlaps and double counts between adjacent blocks could be identified and corrected.

Sample Survey Method: Aerial sample surveys of Laikipia District were carried out using one or two high-wing, twin-engine Partenavia P68s, each with a crew of four, consisting of the pilot, a front seat observer (FSO), and two rear seat observers (RSO). Topographic sheets of scale 1:250,000 were used in preflight planning to define the survey area boundary and the location of parallel transects, oriented north–south, each separated by a fixed distance (5 km for a low-resolution survey or 2.5 km for a high-resolution survey). Flying at about 190 km/h and at a height above the ground of 122 m (using a radar altimeter), the pilot navigated transects oriented north–south using GPS. Observers counted animals that fell within narrow strips of known width (150 m) on either side of the aircraft, defined by rods attached to the wing struts. Both wild and domestic herbivore species were counted, including cattle, donkeys, camels, and sheep and goats, the latter two treated as a single "species" because they cannot be distinguished from the air. Herds of 10 or fewer animals were counted directly. Herds exceeding 10 animals were estimated and obliquely photographed using 35 mm digital cameras for subsequent counting. Since the sampling fraction is known (about 6.25% of the area for transects separated by 5 km or 12.5% for 2.5 km transect spacing), population estimates within the entire survey zone can be extrapolated from densities estimated within strip transects. Transects were subdivided into 5 km sections using GPS, defining survey subunits of 2.5 × 5 km or 5 × 5 km. Human dwellings were also counted, and the presence of cultivation was recorded, the spread of both indicative of human population trends and loss of wildlife habitat. The spatial location of all observations within a given subunit was assigned to the center point of the subunit (Figure 1, top right, bottom right).

Although the sample survey covered the entirety of Laikipia District, the total count omitted parts with low or zero wildlife densities. To allow a direct comparison with total count results, sample survey results were adjusted such that the same zone was covered in both counts.

Results: Population estimates from sample and total counts differed by <23% for all but two species (Figure 2a; dotted line is $x = y$; solid line is the least squares regression: $\ln(y) = 0.93.\ln(x)+0.69$; $r^2 = 0.94$, $n = 11$). Estimates for oryx and Grant's gazelle differed by 89% and 67%, respectively. As expected, estimates for all but one species (Thompson's gazelle) were greater from the sample survey than from the total count, an outcome unlikely to be caused by chance ($P = 0.01$). However, this bias was not great, yielding a regression with a slope not significantly different from unity and an intercept not significantly greater than zero ($P > 0.33$, $n = 11$).

Comparing results from dry and wet season sample surveys, population estimates were again in fair agreement (Figure 2b; bars denote standard errors; solid line is least squares regression: $\ln(y) = 0.96.\ln(x)+0.32$; $r^2 = 0.97$, $n = 11$), differing by <23% for all species except eland (31.2%) and buffalo (37.1%). Once again, there was no overall bias, in that neither the regression slope nor intercept differed significantly from 0 or 1, respectively ($P > 0.63$, $n = 11$). However, this agreement could have resulted from opposing biases for individual species canceling each other out.

Discussion: Neither total nor sample surveys necessarily yield accurate population estimates. Both methods tend to yield undercounts, with bias varying among species, observers, and habitats (Caughley, 1974; East, 1999; Redfern et al., 2002). For example, underestimates of more than 50% are not uncommon for impala in woodland (their preferred habitat). In this comparison, undercounting bias appeared to be slightly greater in the total count than the sample survey, as expected, but on average, differences were not large. However, comparison of additional factors, such as cost and the scope of information provided, revealed huge differences in favor of sample surveys. Compared to total counts, for example, costs of sample surveys diminish by a factor related

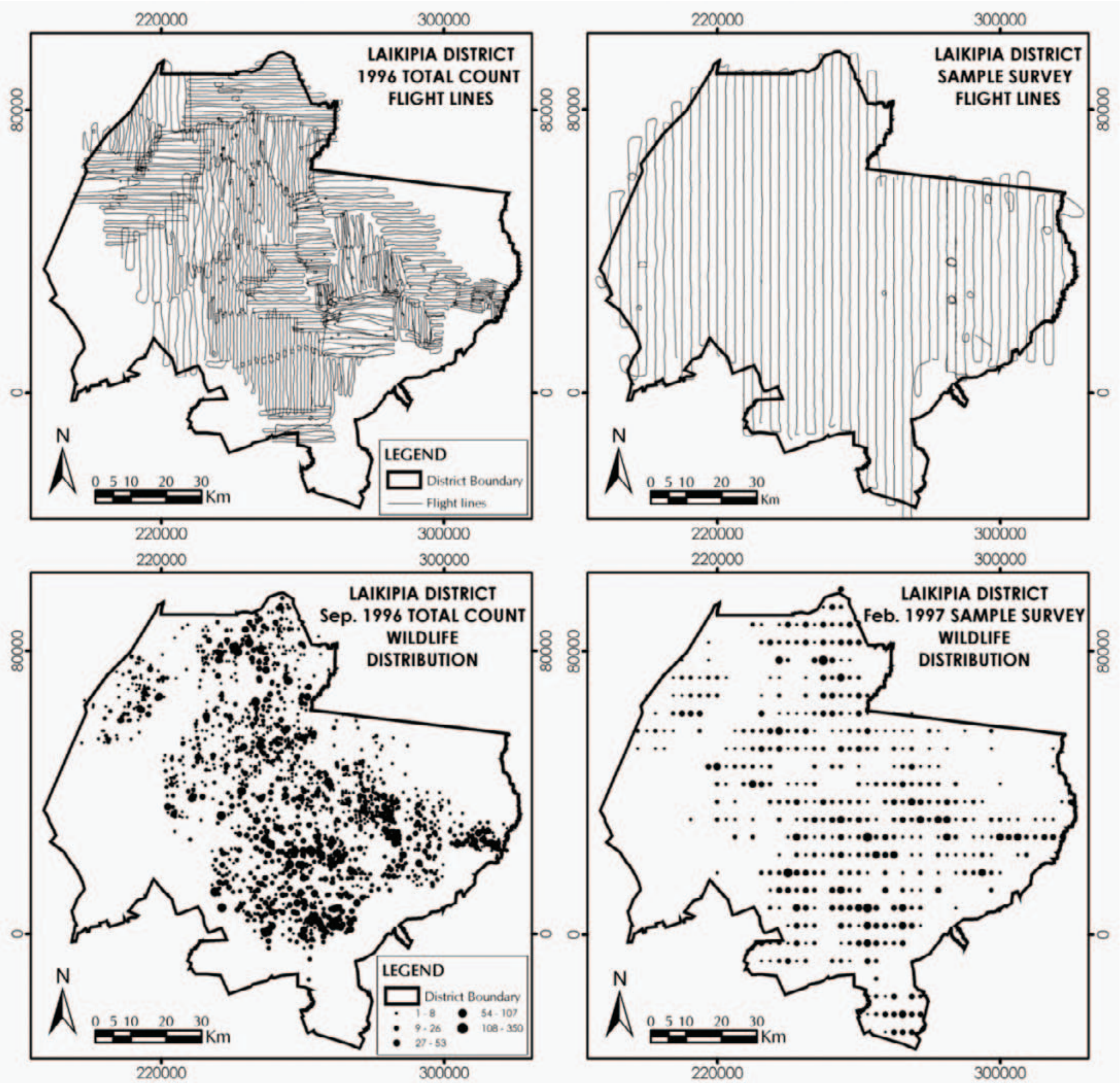

FIGURE 1. Comparison of results from a total count and a sample survey of wild herbivores in Laikipia District. Top left: Combined flight paths of 10 aircraft involved in the total count of herbivores in September 1996, transects spaced 1–2 km apart (low-density areas omitted). Top right: Flight path of the single aircraft used to conduct a high-resolution sample survey in February 2007, transects spaced 2.5 km apart (only the restricted zone in vicinity of Nanyuki Air Force Base in southeast was excluded). Bottom left: Relative size and distribution of herbivore herds resulting from the total count. Bottom right: Impression of herbivore relative abundance and distribution from the sample survey. In the latter, animals are featured only if they were observed within strip transects having a combined width of 300 m. The sample survey yielded a realistic impression of wildlife distribution at less than half the cost of the total count.

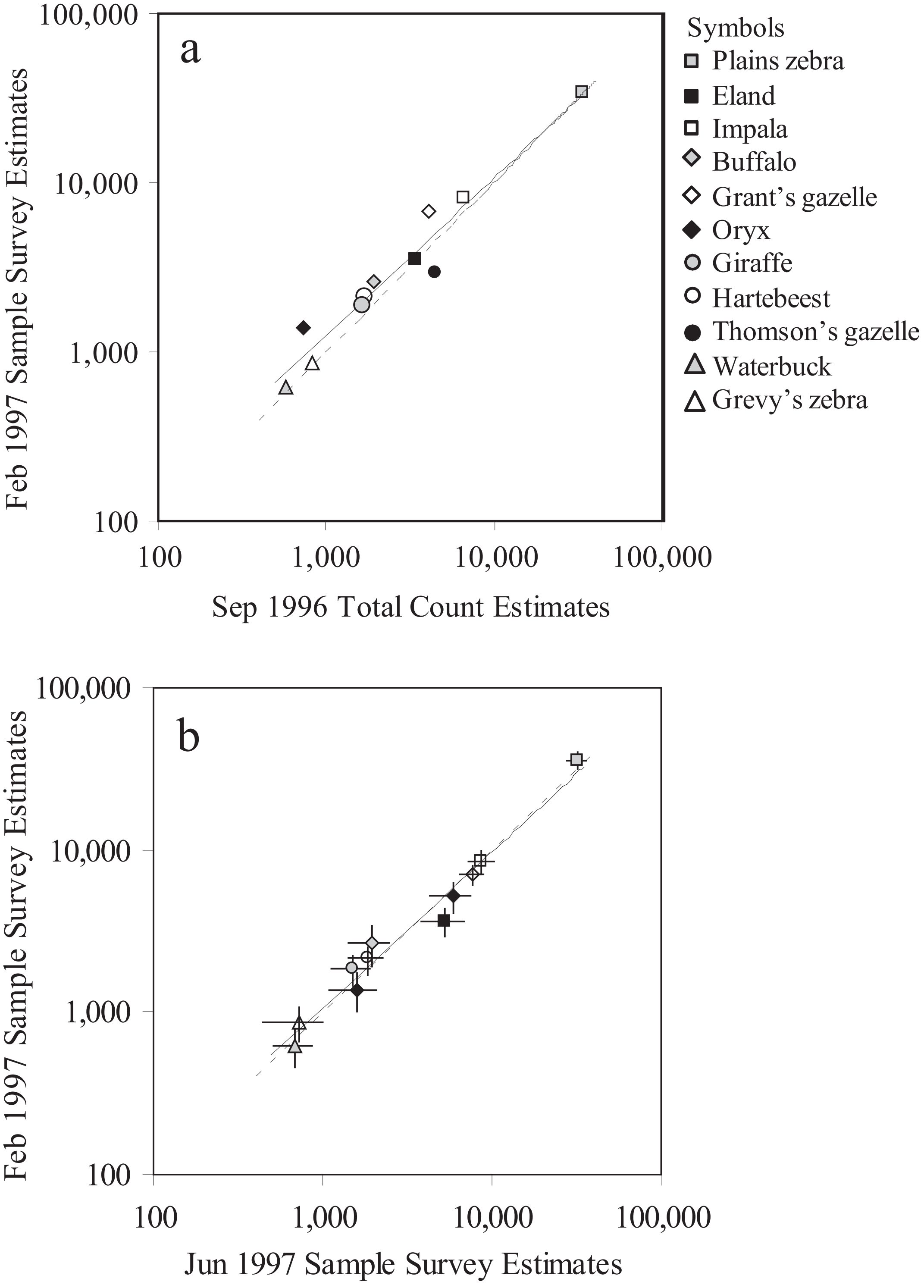

FIGURE 2. Comparison of population estimates for 11 herbivore species in Laikipia District. (a) Total count in September 1996 (*x* axis) versus a high-resolution sample count in February 1997 (*y* axis; axes are log-transformed). (b) High-resolution sample surveys in June 1997 (*x* axis; wet season) versus February 1997 (*y* axis; dry season). Symbols in legend apply to both graphs.

to transect spacing (e.g., by about 60% for a survey with 2.5 km transect spacing, as in this case). Perhaps most importantly, whereas only wildlife species can typically be censused in a total count, livestock, human settlement of various kinds, cultivation, and many other variables can also be censused in a sample survey. For wildlife conservation in nonprotected landscapes, tracking human and livestock attributes is vital because they present the principal conservation threats (see below).

At least for abundant herbivore species, these comparisons should enhance confidence that total counts and sample surveys yield population estimates that do not differ greatly or in unexpected ways, at least for abundant species. In many ways, aerial total counts can be viewed as a special kind of sample survey, with narrowly spaced transects and wide counting strips, but lacking any estimate of precision. Focusing on sample surveys for the remainder of this chapter, we highlight the importance of this omission.

Optimizing Sample Survey Resolution

Population estimates from sample surveys are often used to guide conservation and management actions. Rarely, however, is the precision of those estimates assessed as to its adequacy for a given application. Precision is especially important when census results are used to set harvesting rates, as they were in Laikipia from 1997 to 2003, because periodic overestimates due to random sampling errors can lead to overharvesting, even if population estimates are unbiased (Milner-Gulland et al., 2001). However, the tendency for sample surveys to yield underestimates reduces the likelihood that harvest rates based on sample survey results will lead to overharvesting. Precision is also important when seeking trends in low-density species, for which variances associated with population estimates are inevitably high. In this section we describe an empirical approach used to assess the precision of population estimates for ungulates in Laikipia District. Specifically, we show how precision varies with survey resolution (transect spacing) and animal abundance (density).

Methods: Data were used from seven high-resolution sample surveys (2.5 km transect spacing) across the entirety of Laikipia District. The first survey was in 1991; there were two in 1997 (discussed in the section above) and others in 1999, 2001, 2003, and 2004. In each case, a second set of population estimates was generated as if they were from low-resolution surveys (5 km transect spacing) simply by omitting alternating transects from the high-resolution data.

Results: A way to visualize how population estimates vary with survey resolution is to plot, for each species in each survey, the ratio of estimates made at low and at high resolution against estimated density at high resolution (Figure 3a). The overall pattern shows this ratio varying widely at low densities but converging on unity at higher densities. This is the expected pattern, given the inflation in sampling error for low-density species. At least in Laikipia, estimates made at high and low resolution can diverge markedly (by >40%) for species with densities less than about 1 individual per km^2. This threshold density was exceeded only by the three most abundant species (sheep and goats, cattle, and plains zebra).

At low resolution, a density of 1 individual per km^2 corresponds to a proportional standard error of, on average, about 20%, a subjective threshold commonly considered to be a working limit for management purposes (Figure 3b). The density associated with this level of precision at high resolution was, on average, 0.17 km^{-2} (Figure 3b). Doubling the survey resolution from 5 to 2.5 km between transects therefore improved by more than fivefold the threshold density at which relatively stable population estimates could be expected.

Discussion: This assessment of precision served to validate the Laikipia Wildlife Forum's choice of higher-resolution sample surveys to guide the conservation and management of wild herbivores in Laikipia District. In addition to the one wild species abundant enough to be reliably censused at low resolution (plains zebra), eight additional species had mean densities exceeding the lower threshold afforded by high-resolution surveys. Estimates for impala, Grant's and Thomson's gazelles, buffalo, and eland were used to set harvesting quotas. Estimates for giraffe, hartebeest, and waterbuck revealed declining trends (Georgiadis et al., 2007b). Estimates for species with mean densities <0.17 km^2 (Grevy's zebra, warthog, kudu, oryx, and gerenuk) were considered to vary too widely to guide conservation action reliably.

The choice of high-resolution surveys was further validated by modeling analyses based on sample survey data, which provided mechanistic insights into the causes of observed herbivore population dynamics and guidelines for harvesting. For example, a simulation model established that plains zebra dynamics in Laikipia District were driven by an interaction between annual rainfall and zebra density (Figure 4; details in Georgiadis et al., 2003). Best fit solutions were fit to data from 1985 to 1999 for two alternative models, one purely rainfall dependent (RD; thin line) and the other rainfall mediated, density dependent (RMDD; thick line). Both were able to reconstruct the population history from 1985 to 1999 reasonably well.

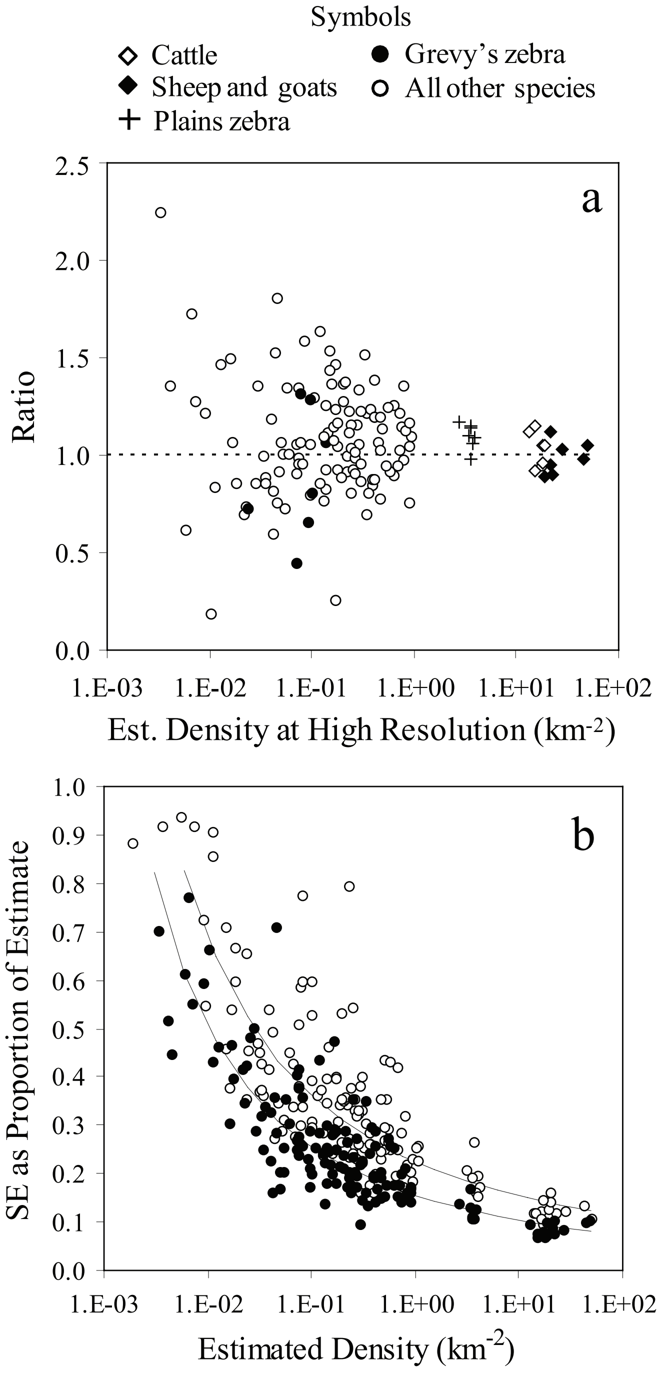

FIGURE 3. Variation of precision with sample survey resolution. (a) Ratio of population density estimates at low survey resolution (5 km transect spacing) to high resolution (2.5 km transect spacing), plotted against density estimates at high resolution for 21 species in Laikipia District. Data are from 7 surveys conducted between 1997 and 2004. Dotted line is $y = 1$. The x axis is log-transformed. (b) Decline of the standard error of population estimates with increasing density for 21 species from 7 sample surveys at low resolution (white circles) and high resolution (black circles). Standard errors are expressed as a proportion of the density estimate. The x axis is log-transformed.

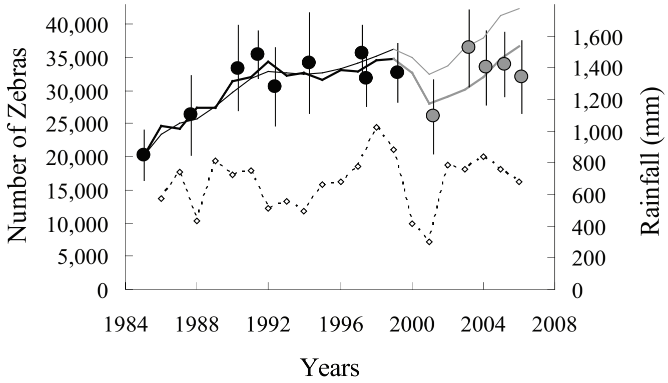

FIGURE 4. Time series of Laikipia zebra population estimates (large dots; vertical bars are standard errors), with best fit solutions for two alternative models (solid lines; see details in text). Dotted line is mean annual rainfall as measured from five gauges scattered around Laikipia.

However, when both models were projected beyond 1999 (gray dots and lines), with census estimates and model predictions independent of each other, the RD model deviated progressively from the census series (thin gray line), but the RMDD model continued to perform quite well (thick gray line). The RMDD model suggests how "equilibrial" (density-related) and "nonequilibrial" (rainfall-related) factors interact in the bottom-up control of a savanna ungulate population.

Linear modeling also implicated rainfall or population density in the dynamics of other abundant species, and predators were implicated in the decline of less-abundant species (Georgiadis et al., 2007a, 2007b). To our knowledge, this was the first time that results of sample surveys have been used to suggest causality in the dynamics of an ungulate community.

Mapping the Potential for Human–Wildlife Conflict

Human–wildlife conflict (HWC) is not only a liability to people, most of whom cannot afford crop or livestock losses to wildlife, it is also a severe threat to conservation. Where they are opposed, human interests almost invariably prevail over wildlife interests over the long term. Understanding and reducing HWC is therefore a conservation priority in human-occupied landscapes. In this section we show how a snapshot of the potential for HWC can be mapped across a landscape using sample survey data and a few simple assumptions. Our first assumption was that conflict (or at least the potential for conflict) increases with geographical proximity between wildlife and one or more of the human-related elements of conflict, namely, livestock, cultivation, and habitation. For example, co-occurrence of wild herbivores with cultivation in the same subunit raises the potential for crop raiding or signals loss of wildlife habitat. Likewise, co-occurrence of wildlife with human habitation implies conflicting land use and loss of habitat. Finally, co-occurrence of wild herbivores with livestock implies competition for forage or the presence of predators that could prey on livestock. This approach was used to map the potential for different types of HWC on different types of land use in Laikipia District and to record how patterns of potential conflict changed over time.

METHODS: Presence or absence of wildlife, livestock, habitation, and cultivation in each survey subunit (2.5 × 5 km) from six high-resolution sample surveys conducted between 1991 and 2003 were used for this analysis. Within each survey, three principal land use types were distinguished. *Pro-wildlife* properties are large-scale, private holdings on which wildlife is actively favored, often as the basis for ecotourism. *Group ranches* are large-scale holdings communally owned by a registered group of families, mostly practicing pastoralism. *Transitional* properties were formerly large-scale farms or ranches that have been subdivided into small plots (1–10 ha), with titles sold to thousands of smallholders, only some of which have been occupied and cultivated when rainfall permits. Where not occupied by the owner, many transitional properties are grazed by pastoralists. Larger properties that either only tolerate or actively discourage wildlife were included in this category. For each survey, co-occurrences within each subunit of wildlife with other elements of HWC (livestock, cultivation, and settlement) were tallied using geographic information systems (GIS).

RESULTS: The potential for different types of conflict varied markedly across the landscape and among different land uses in Laikipia (Figure 5a, Table 1). By definition, there was little or no potential for HWC wherever wildlife was rare or absent, as in southwest Laikipia, or where wildlife was abundant and conflicting human attributes relatively uncommon, as on the pro-wildlife properties. The potential for crop raiding (co-occurrence of wildlife with cultivation) was prevalent in sectors of southern Laikipia where wildlife is still present and cultivation is possible in wet seasons. In contrast, the potential for predation on or competition with livestock (co-occurrence of wildlife with livestock) was more prevalent in drier areas, especially on group ranches and transitional areas adjacent to pro-wildlife properties.

The potential for HWC tended to decline between 1991 and 2003, particularly between wildlife and livestock on all property types (Table 1; also compare results for the first and last survey in Figure 5). At first impression, this decline may appear to signal a conservation success, but closer scrutiny of changing distribution patterns for each of the components of conflict showed the cause to be a steady shrinking of wildlife distribution, significantly so on transitional and group ranches (see wildlife-only column in Table 1). Agriculture, settlement, and especially livestock tended to increase over time on transitional properties, but wildlife declined markedly. On pro-wildlife and group ranch properties a different pattern of change was evident over the same period, in that not only wildlife but also livestock tended to decline, although not significantly (Table 1).

DISCUSSION: Data routinely collected in aerial sample surveys were used to derive a plausible impression of the potential for HWC in Laikipia District and how it has changed over space and time. Validation of this impression was provided by an independent study of the actual incidence of HWC in Laikipia, in which the location and type of incident (livestock predation, crop raiding, infrastructure damage, etc.) were systematically recorded in a dedicated database, known as the Ewaso Incident Reporting System. The potential for HWC was in fair agreement with the observed distribution of incidents, with livestock predation occurring largely on group ranches adjacent to pro-wildlife properties and crop-raiding incidents scattered mostly across transitional properties in southern and western Laikipia (compare Figure 5b and 5c). The only exception was a cluster of crop-raiding incidents around Rumuruti forest in southwestern Laikipia. These incidents were caused by elephants that inhabited the forest during the day and raided crops in adjacent fields at night. This pattern did not feature in the potential HWC map because elephants were not detected under the forest canopy during sample surveys.

Opposing trends in the spatial prevalence of livestock on transitional and pro-wildlife ranches suggest different factors contributed to declines in wildlife abundance on different land use types. Increasing livestock abundance, particularly of sheep and goats, probably displaced wildlife on transitional properties over the last decade (Georgiadis et al., 2007b). In contrast, the most likely cause of wildlife decline on pro-wildlife properties and, to a lesser extent, on adjacent group ranches as well turned out to be the restoration of predators (Georgiadis et al., 2007a).

This validated example enhances confidence that sample survey data, especially at high resolution, can provide a reliable impression of the potential for and distribution of human–wildlife conflict. A more exacting spatial analysis using actual figures rather than presence/absence data may provide further insights into spatial and temporal dynamics of potential conflict wherever wildlife share the landscape with humans and livestock.

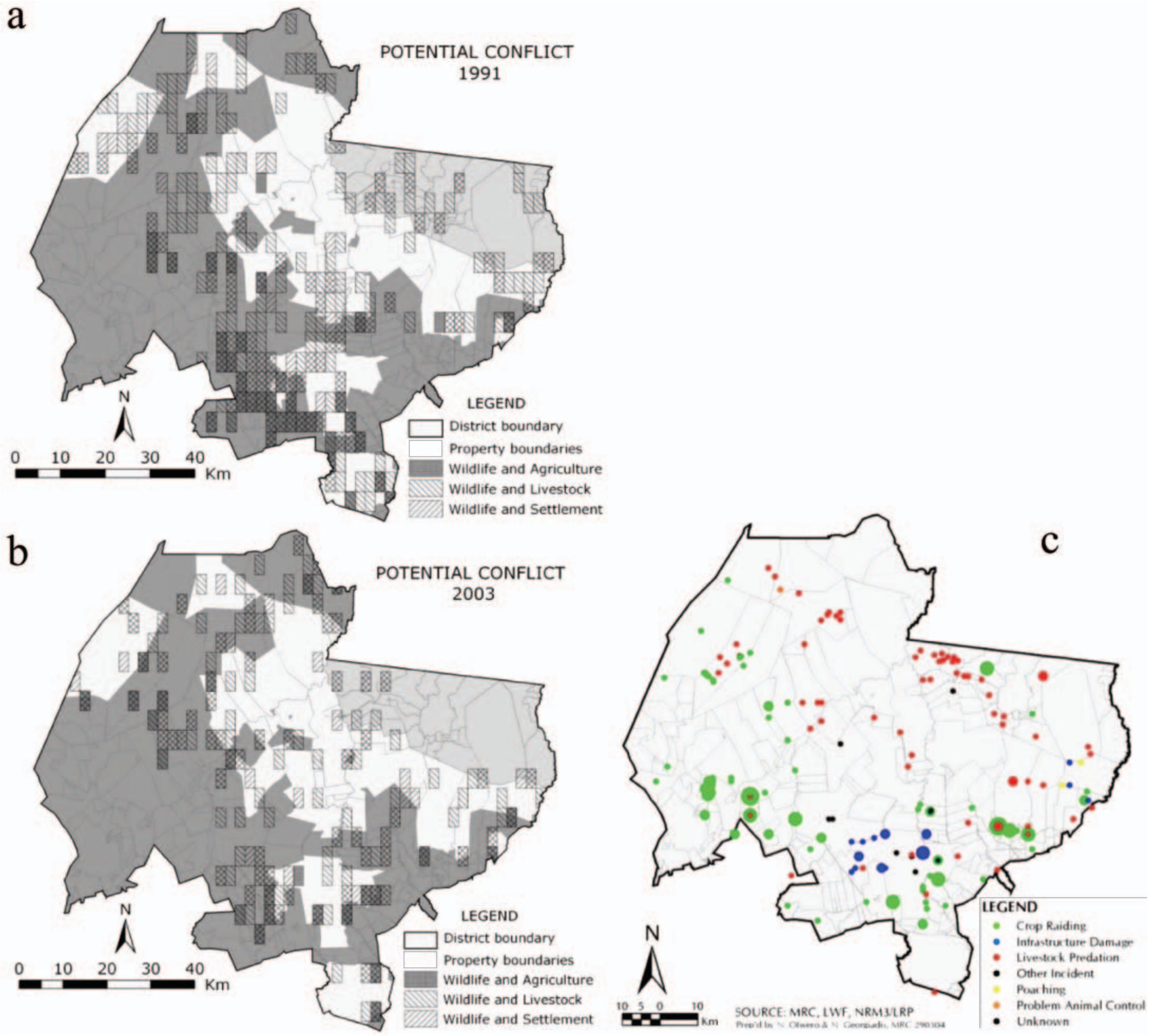

FIGURE 5. Potential for human–wildlife conflict is mapped across three principal land use types in Laikipia District (group ranches in light gray, private ranches in white, and transitional properties in dark gray) by the spatial co-occurrence of wildlife with agriculture, livestock and settlement in survey subunits (described in the text). Visual comparison of the distribution of potential HWC in (a) February 1991 and (b) February 2003 shows the apparent decline in potential for human–wildlife conflict. (c) Recorded distribution of human–wildlife conflict incidents between June 2003 and February 2004, showed fair correspondence with potential for conflict in (b). Source: Ewaso Incident Reporting System, unpublished report, 2005.

CONCLUSIONS AND RECOMMENDATIONS

We used data collected in Laikipia District over two decades to assess the utility of aerial sample surveys for monitoring wildlife and human attributes across large landscapes, understanding wildlife dynamics, and guiding conservation action. A direct comparison between results from sample surveys and total counts showed relatively minor differences in population estimates but great reductions in cost and a substantial increase in the scope and

TABLE 1. Proportion of the total number of survey subunits in which the elements of human–wildlife conflict were observed in high-resolution sample surveys of Laikipia District between 1991 and 2003, partitioned by three principal land use types.[a] Trends over time in the incidence of these elements of human–wildlife conflict are indicated by correlation coefficients (r) between these percentages and survey date (proportional data were root/arcsine-transformed for analysis; $n = 6$ in all cases; an asterisk (*) denotes significance at $\alpha = 0.05$; a dash denotes statistic is not applicable).

Land use type	Survey date, statistic	Wildlife (W)	Agriculture (A)	Livestock (L)	Settlement (S)	W+A	W+L	W+S	W+A+L+S
Transitional	Nov 1991	42.0%	36.3%	70.2%	53.4%	7.1%	26.4%	15.0%	6.4%
	Feb 1997	43.0%	39.4%	73.5%	67.6%	6.9%	27.1%	22.9%	5.5%
	Jun 1997	39.1%	47.3%	73.1%	55.6%	8.3%	23.7%	11.1%	6.9%
	Feb 1999	34.2%	43.7%	79.0%	65.9%	4.5%	21.3%	15.1%	4.3%
	Feb 2001	34.3%	40.0%	79.9%	54.1%	7.4%	20.9%	10.4%	5.2%
	Feb 2003	28.1%	41.6%	78.7%	64.4%	4.0%	18.1%	12.4%	3.1%
	Correlation, r	–0.856*	0.396	0.897*	0.373	–0.509	–0.863*	–0.351	–0.751
Pro-wildlife	Nov 1991	53.4%	3.8%	24.2%	11.8%	2.4%	18.9%	8.9%	1.6%
	Feb 1997	54.8%	3.4%	21.5%	16.1%	2.6%	16.3%	13.3%	1.1%
	Jun 1997	50.7%	4.8%	20.2%	10.6%	2.7%	14.8%	6.7%	2.1%
	Feb 1999	45.4%	4.0%	24.1%	12.0%	1.6%	16.0%	7.2%	1.6%
	Feb 2001	47.9%	4.8%	21.1%	12.4%	3.9%	13.8%	6.9%	2.3%
	Feb 2003	43.8%	4.1%	20.9%	12.0%	2.0%	11.4%	8.4%	1.7%
	Correlation, r	–0.793	0.345	–0.547	–0.031	0.076	–0.943*	–0.267	0.343
Group ranch	Nov 1991	7.8%	0.0%	15.4%	5.9%	0.0%	5.5%	2.4%	0.0%
	Feb 1997	7.9%	0.0%	15.3%	11.5%	0.0%	6.0%	4.2%	0.0%
	Jun 1997	6.3%	0.0%	11.2%	6.6%	0.0%	3.6%	1.3%	0.0%
	Feb 1999	5.0%	0.3%	14.9%	10.1%	0.0%	3.2%	2.2%	0.0%
	Feb 2001	5.6%	0.5%	11.7%	4.6%	0.0%	2.0%	0.8%	0.0%
	Feb 2003	3.4%	0.0%	12.4%	8.3%	0.0%	1.7%	1.2%	0.0%
	Correlation, r	–0.859*	0.397	–0.571	0.086	–	–0.844*	–0.483	–

[a] For example, on transitional properties in November 1991, wildlife was recorded in 42.0% of survey subunits, agriculture in 36.3% of subunits, livestock in 70.2%, and settlement in 53.4%. Both wildlife and agriculture were observed in 7.1% of subunits, wildlife and livestock in 26.4%, etc.

utility of variables that can be monitored with sample surveys. An assessment of precision suggested that survey resolutions widely used in the past to census wildlife and livestock resources in Kenya have been high enough to estimate reliably only the most abundant species or combinations of species, such as “all wildlife.” This, in turn, suggests that persistent reservations about the reliability of sample surveys are largely due to a tendency to accept population estimates at face value, without accounting for degrees of precision. Finally, we described how sample survey data can provide a useful impression of the spatial incidence of different types of human–wildlife conflict across a landscape. Overall, data from higher-resolution sample surveys in Laikipia have advanced our understanding of ungulate population dynamics, revealed causes and consequences of ecosystem change, provided a quantitative basis for consumptive management of wild ungulates, and guided conservation action (Georgiadis et al., 2003, 2007a, 2007b). This assessment should improve confidence in the validity and utility of sample surveys.

Conservation challenges in Laikipia District are echoed across much of Kenya’s rangelands, where, in theory at least, regular high-resolution sample surveys would likewise yield sufficient information for conservation and management purposes. However, costs of monitoring all of Kenya’s rangeland districts at higher resolution would be prohibitive, particularly with escalating fuel prices. Survey costs in Laikipia were largely born by donors and will continue to be for the foreseeable future. It is unlikely that survey costs somehow could be met from income generated by wildlife enterprises, landholders, or conservation authorities in this or any other region.

The analysis suggests several changes in monitoring methodology would enhance the utility of sample surveys. First, a more precise record of change would be generated by a shift from lower-resolution surveys done relatively frequently to higher-resolution surveys done less frequently. Second, sample survey methods should be tailored to conservation needs in nonprotected areas, where awareness about the distribution, activities, and impact of humanity is vital to conservation. In particular, tasks assigned to the FSO in sample surveys should be reviewed and revised. For example, we have found that subjective estimates of woody vegetation cover by the FSO are not reliable (comparing woody cover estimates for individual subunits over time, there was no correspondence from one survey to the next). Instead, the FSO could collect more refined data on human activities, especially the type and spatial extent of habitation and cultivation. Third, a further improvement at no added cost would be to double survey resolution by dividing 2.5 × 5 km subunits in half to yield a 2.5 × 2.5 km grid, a logistical problem involving doubling the frequency of GPS readings. Fourth, electronic advances are available that could greatly increase the amount of imaging information collected automatically along transects, for example, with vertically and obliquely mounted digital cameras taking georeferenced images.

Finally, an ongoing collaboration between the Department of Resource Surveys and Remote Sensing and Mpala Research Centre aims to add distance sampling methodology (Buckland et al., 2001) to aerial sample surveys (M. Kinnaird, Mpala Research Centre, personal communication, 2007). Application of this relatively recent method could improve both precision and accuracy of population estimates from sample surveys while reducing costs. Distance sampling differs from the method currently used primarily by quantifying, and correcting for, the decline in visibility of counted objects with distance from the observer (that is, the ability of the observer to detect and count objects). In distance sampling, therefore, accuracy of the population estimate is improved by applying an empirically derived "detection function," which allows a correction for individuals missed by the observer. Ideally, different detection functions are applied for different habitat types (e.g., open grassland versus woodland) and even different species. Precision may be improved with this approach because sampling strip width is increased, allowing a greater fraction of the survey area to be sampled. Costs are reduced because fewer transects can be flown for the same degree of precision. To map areas of human–wildlife conflict, survey stratification may be necessary, such that rapidly changing areas would be covered at higher resolution. Initial capital investment for refining these enhancements would be high, not least because both types of survey would have to be run simultaneously in order to compare them directly. However, this cost would be justified by the improved quality of information gathered thereafter.

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REFERENCES

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford, UK: Oxford University Press.

Caughley, G. 1974. Bias in Aerial Survey. *Journal of Wildlife Management,* 38:921–933.

East, R. 1999. African antelope database 1998. IUCN/SSC Antelope Specialist Group, pp. 91–92. Gland, Switzerland and Cambridge, UK: IUCN.

Georgiadis, N. J. 2011 (this volume). "Introduction: Conserving Wildlife in Kenya's Ewaso Landscape." In *Conserving Wildlife in African Landscapes: Kenya's Ewaso Ecosystem*. ed. N. J. Georgiadis. Smithsonian Contributions to Zoology, No. 632:1–10. Washington, D.C.: Smithsonian Institution Scholarly Press.

Georgiadis, N. J., M. Hack, and K. Turpin. 2003. The Influence of Rainfall on Zebra Population Dynamics: Implications for Management. *Journal of Applied Ecology*, 40:125–136.

Georgiadis, N. J., F. Ihwagi, N. Olwero, and S. S. Romañach, 2007a. Savanna Herbivore Dynamics in a Livestock-Dominated Landscape: II. Ecological, Conservation and Management Implications of Predator Restoration. *Biological Conservation,* 137:473–483.

Georgiadis, N. J., N. Olwero, G. Ojwang', and S. S. Romañach. 2007b. Savanna herbivore dynamics in a livestock-dominated landscape: I. Dependence on land use, rainfall, density, and time. *Biological Conservation,* 137:461–472.

International Livestock Centre for Africa. 1981. *Low-Level Aerial Survey Techniques*. ILCA Monograph 4. Addis Ababa: ILCA.

Milner-Gulland, E. J., K. Shea, H. Possingham, T. Coulson, and C. Wilcox. 2001. Competing Harvesting Strategies in a Simulated Population under Uncertainty. *Animal Conservation,* 4:157–167.

Norton-Griffiths, M. 1978. *Counting Animals*. Nairobi: African Wildlife Foundation.

Redfern, J. V., P. C. Viljoen, J. M. Kruger, and W. M. Getz. 2002. Biases in Estimating Population Size from an Aerial Census: A Case Study in the Kruger National Park, South Africa. *South African Journal of Science*, 98:455–461.

Sinclair, A. R. E., and M. Norton-Griffiths, eds. 1979. *Serengeti: Dynamics of an Ecosystem*. Chicago: University of Chicago Press.

Stem, C., R. Margoluis, N. Salafsky, and M. Brown. 2005. Monitoring and Evaluation in Conservation: A Review of Trends and Approaches. *Conservation Biology*, 19:295–309.

Tear, T. H., P. Kareiva, P. L. Angermeier, P. Comer, B. Czech, R. Kautz, L. Landon, D. Mehlman, K. Murphy, M. Ruckelshaus, J. M. Scott, and G. Wilhere. 2005. How Much Is Enough? The Recurrent Problem of Setting Measurable Objectives in Conservation. *BioScience*, 55:835–849.

Ecological Importance of Large Herbivores in the Ewaso Ecosystem

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ABSTRACT. Large ungulate herbivores are widely considered to be functionally important components of African savannas, but this belief is based largely on what is known about their direct interactions (as consumers of plants and food for predators). Their indirect interactions, both as key consumers within food webs and as "engineers" of habitat structure, are less well understood. Here we review the results of nearly 15 years of experimental research at Mpala Research Centre (Laikipia, Kenya), focusing primarily on the indirect effects of ungulates on the abundance, distribution, and diversity of other species. We highlight several broad conclusions: (1) ungulate exclusion increases densities of plants and many small consumers; (2) the strength of these indirect effects is context dependent and may vary systematically along environmental gradients; (3) impacts of different ungulate species vary both quantitatively and qualitatively. Although some of the observed effects of ungulate exclusion were predictable, others were surprising. These insights are obliquely relevant to management, but there remains a mismatch between the kinds of information most interesting to academics on the one hand and most useful to land mangers on the other. We conclude by identifying some areas of likely convergence between questions of basic and applied importance.

INTRODUCTION

Much early research on African savanna ecosystems focused on the natural history and population dynamics of particular wildlife species. Pioneering work on conspicuous species such as elephants (Laws et al., 1975), buffalo (Sinclair, 1977), lions (Schaller, 1972), and hyenas (Kruuk, 1972) helped lay the foundation for studies that illuminated relationships between herbivores and plants and between predators and prey (e.g., McNaughton, 1976, 1978; Hilborn and Sinclair, 1979). Recently, synthetic works have drawn on this knowledge to paint more complete pictures of entire ecosystems (Scholes and Walker, 1993; Sinclair and Arcese, 1995; du Toit et al., 2003).

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As a result, we now know a great deal about the biology of large mammals in African savannas: what they eat, how they eat it, what eats and what parasitizes them, and, increasingly, how their activities affect vegetation communities and other key landscape attributes. Most of these processes fall into the category of what ecologists call direct interactions—immediate physical contact and/or exchanges of energy between species. But such direct exchanges represent only a fraction of the total number of interspecific interactions in an ecosystem since each direct interaction creates the potential for numerous indirect interactions. Indirect effects occur when a direct interaction between two species influences a third species in some meaningful way (Abrams et al., 1996). One well-known example from African ecosystems involves the Serengeti ungulate migrations, where grazing by wildebeest (*Connochaetes taurinus*) prevents grass senescence, enhances productivity, and therefore determines the subsequent pattern of grazing by Thomson's gazelles (*Gazella thomsonii*) (McNaughton, 1976).

Typically, however, indirect interactions are difficult or impossible to observe in real time. To take just one example, detecting system-wide indirect effects of lions on grasses via their suppressive effects on grazers might require years of observation and experimentation. Partly for this reason, indirect effects remain poorly understood relative to direct ones. Nevertheless, ecological studies over the past 40 years have shown repeatedly that indirect interactions are powerful determinants of the abundance, distribution, and diversity of organisms in many types of ecosystems and that they are frequently even more important in these respects than direct interactions (Paine, 1966, 1980; Wootton, 1994; Menge, 1995; Abrams et al., 1996; Schmitz et al., 2000; Ripple and Beschta, 2004).

Thus, we cannot understand any ecosystem or predict the likely consequences of perturbing it without characterizing the most important interaction chains within it. Indirect interactions help define the emergent patterns and properties of all ecosystems, including how many species it supports, how many individuals of each species, where these individuals occur, and how they behave. Indirect interactions can also define characteristics of savannas at very broad scales, such as the relative balance of trees and grasses and the amount of carbon stored in the ecosystem (Holdo et al., 2009). Even seemingly straightforward direct interactions, such as the impact of ungulates on plants, are often mediated by cryptic indirect effects (as we will describe below) (Goheen et al., 2010).

Studying the indirect effects of large mammals in African rangelands is appealing for several reasons, some esoteric and some more pragmatic: it allows us to test general hypotheses about ecological organization; it may enable us to predict the consequences of wildlife declines and extinctions (or, conversely, wildlife translocations and reintroductions); and at least in theory, it can provide insights about how best to manage landscapes simultaneously for wildlife conservation and livestock production.

Many advances in our understanding of the functional importance of large mammals in savanna landscapes have emerged from the past 15 years of research at the Mpala Research Centre and Conservancy in Laikipia, Kenya (an area under constant but relatively low-intensity human use). Much of this work has utilized a series of large-scale (0.5–4 ha) experimental plots that employ electric fences of different designs to selectively exclude different kinds of large mammals, allowing investigators to assess the responses of plant and small-animal communities. There are two ways to view this research. One is as an effort in experimental "community disassembly" for the purpose of basic understanding. The other is as a simulation of extinction: if the declining trends in many wildlife populations continue, what are the likely consequences for biodiversity and ecosystem functioning? In the remainder of this chapter, we summarize salient findings from this body of work and discuss ways in which future research might speak more directly to conservationists and land managers.

METHODS

Mpala Research Centre supports several large-mammal exclusion experiments ("exclosures"). The oldest is the Kenya Long-term Exclosure Experiment (KLEE), located in the southwestern corner of Mpala Ranch on black-cotton vertisol ("clay") soils (Young et al., 1998). This experiment was established in 1995 and uses electric wires at different heights along with visual barriers to selectively exclude cattle, "megaherbivores" (elephants and giraffes), and all other large ungulates (>15 kg) from three replicated sets of 4 ha plots, allowing researchers to isolate the impacts of each of these groups. The high clay content of these recent volcanic soils impedes infiltration and drainage and causes pronounced shrinking and swelling with changes in water content. At least partly for these reasons, the clay soils of Mpala are highly productive but low in diversity and evenness of almost every group of organisms *except* large mammals: a single tree (the whistling thorn, *Acacia drepanolobium*) makes up ~97% of the overstory (Young et al., 1997), five dominant grasses constitute ~90% of the understory (Riginos and Young, 2007), the pouched mouse (*Saccostomus mearnsi*) represents 75% of all rodent captures (Keesing, 1998), etc.

Another experiment, comprising only two treatments (total exclusion plots surrounded by 3 m tall electric fences along with unfenced "control" plots), was established by David Augustine in 1999 (Augustine and McNaughton, 2004). This experiment is located in red sand soil and includes three replicated sets of exclusion (70 × 70 m) and control plots in ordinary bushland and another three in nutrient-rich treeless glades (abandoned cattle enclosures called "bomas"; Young et al., 1995). The sand soils are older and coarser and contain fewer nutrients than the clay soils; they are less productive but support more heterogeneous and diverse biotic communities than the clay soils. Further details on the design of these experiments and the sampling strategies of studies conducted within them can be found in the original sources cited throughout this chapter.

RESULTS

INFLUENCE OF UNGULATES ON POPULATION DENSITIES OF OTHER SPECIES

Perhaps the most straightforward prediction from these experiments was that standing plant biomass would increase in the absence of ungulates. In general, this prediction has been supported, although the net effects of ungulates on plants are not straightforward (Figure 1). In sand soil bushland, woody plants responded rapidly and dramatically to ungulate exclusion: after three years, *Acacia* leaf density and biomass were lower by 60% and 80%, respectively, in unfenced plots relative to ungulate exclosures (Augustine and McNaughton, 2004). Likewise, live aboveground grass and herb biomass was greater in ungulate exclusion than control plots in both bushland and glade sites, although these effects were contingent on rainfall: in a low-rainfall year grazers reduced aboveground productivity regardless of soil nutrient availability, whereas in a wetter year grazers reduced productivity in bushland but *increased* productivity in nutrient-rich glades (Augustine, 2002).

Plant responses to ungulate exclusion in black-cotton clay soils have been more muted. After a decade, plots without wildlife exhibited no substantial increases in the density, cover, or biomass of the whistling thorn tree (*Acacia drepanolobium*) (Okello, 2007; Pringle et al., 2007; Ogada et al., 2008; Augustine et al., 2011 [this volume]). Changes in grass and forb cover materialized slowly, with no appreciable difference between the experimental treatments during the first two years of the experiment (Keesing, 1998). By the sixth year of the experiment, grass density was 28% greater in cattle exclusion plots than in plots with cattle, while forb density was 8% greater in plots from which only megaherbivores had been excluded (this latter change is attributable to elephants since giraffes do not eat forbs) (Young et al., 2005).

There are several potential explanations for this difference in plant community response between the two soil types, and these factors might be operating singly or in conjunction with one another. The greater productivity in clay soils relative to sands might contribute to this result because, with all else equal, plants in high-productivity environments can compensate more rapidly for each unit of production lost to herbivores (Chase et al., 2000; Pringle et al., 2007). Differential ungulate activity levels across soil types would also influence the relative magnitude of effects in different sites. Moreover, some of the dominant plants in clay soils are exceptionally well defended, most notably the whistling thorn, which is protected by both large thorns and symbiotic ants. Recent research by Goheen and Palmer (2010) shows that ants effectively defend trees against elephants, which reduces the impact of elephants on tree density at the landscape scale. Moreover, the removal of large herbivores precipitates a shift in the structure of this ant community; specifically, an ant species that weakly defends its host trees gains dominance over a more aggressively defending species (Palmer et al., 2008). Because trees occupied by the poorly defending species are more likely to die, the shift toward this species in the absence of ungulates may, counterintuitively, increase tree mortality. Finally, the removal of large mammals causes a dramatic increase in the density of rodents (see below). Rodents are efficient predators upon whistling thorn seeds and seedlings (Figure 1), which means that reduction in browsing of *Acacia* by large mammals (which largely affects resilient mature trees) is offset by increased mortality of juvenile tree stages due to mice (Goheen et al., 2010). Thus, although more seeds are produced by trees in the absence of large browsing mammals (Goheen et al., 2007; Young and Augustine, 2007), fewer are able to establish.

A second set of predictions involved the responses of small consumers. Since many small mammals consume vegetation, Keesing (1998, 2000) tested the hypothesis that rodent populations would be released from competition and increase in plots without large herbivores. Years of trapping within the clay soil KLEE plots have shown a sustained doubling of the dominant rodent species in the black-cotton community, the pouched mouse, *S. mearnsi* (Keesing, 1998, 2000; Goheen et al., 2004; McCauley et

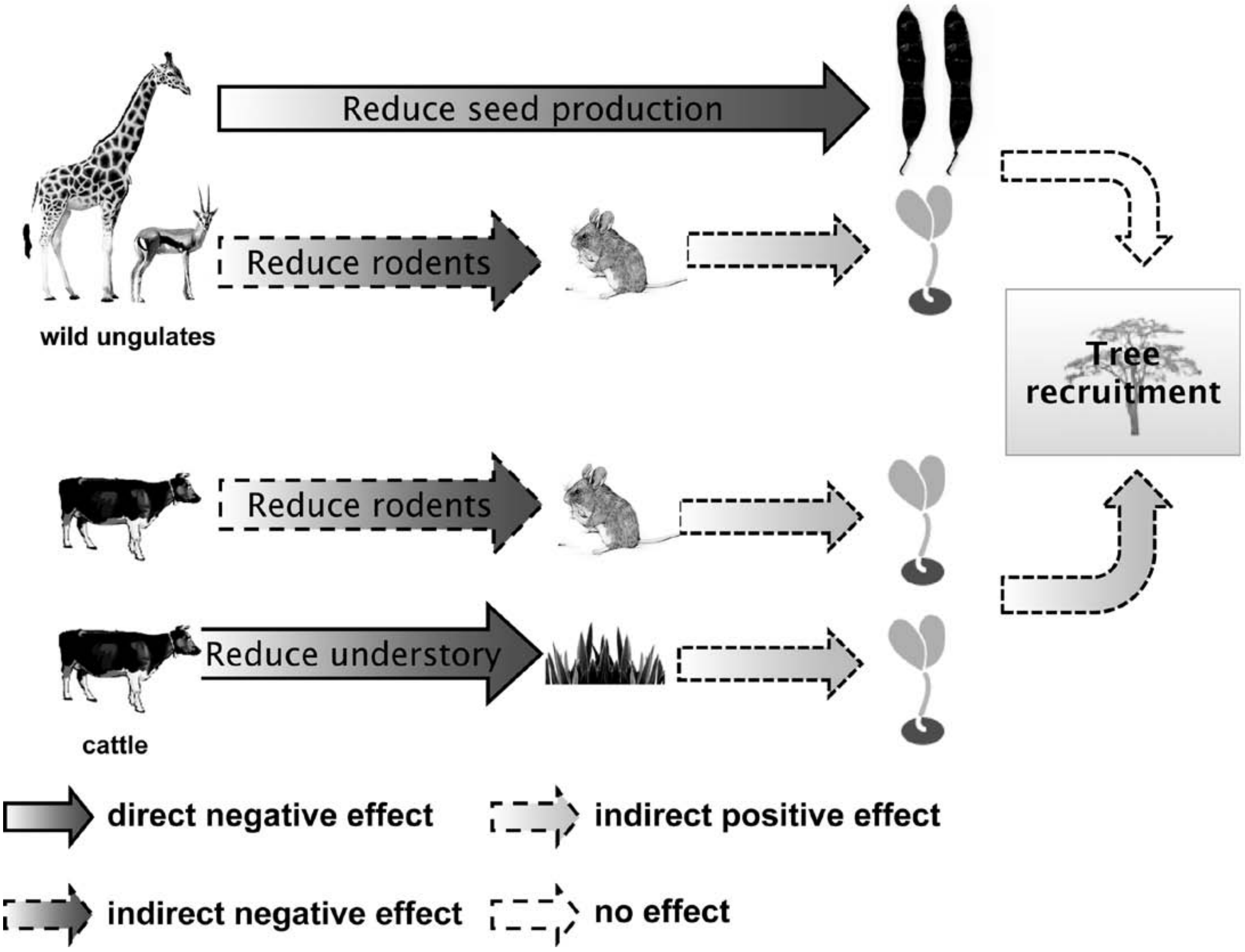

FIGURE 1. Direct and indirect effects of wild and domestic ungulates on *Acacia* establishment. Browsers such as giraffes and gazelles (pictured) directly suppress seed production. However, this negative effect is cancelled by the positive indirect effects of browsers' suppressing rodents, which depredate seedlings. Cattle, in contrast, suppress rodents and grasses, leading to positive net effects on tree establishment. Reprinted, with permission, from Goheen et al., 2010.

al., 2006). This increase occurred before any detectable difference in the amount of grass cover (Keesing, 1998), suggesting two things. First, it is unlikely that mice became more abundant simply because they were better concealed from predators, a conclusion further supported by the fact that mouse survivorship rates were similar in areas with and without large herbivores (Keesing, 2000). Second, as discussed above, mice might be consuming plant biomass in ungulate removal plots before it can accumulate, providing one explanation for the relatively mild shifts in vegetation cover documented in KLEE. Consistent with this interpretation, Keesing (2000) installed small rodent exclosures within the larger ungulate exclosures and found that plant biomass in these smaller ungulate- and rodent-free plots increased by 50%.

Predators and parasites of mice have also responded to ungulate removal. Nineteen months of sampling in KLEE's total-exclusion and control plots revealed that rodent-eating sand snakes (*Psammophis mossambicus*) were roughly twice as abundant within the exclosures (McCauley et al., 2006). The number of fleas (Siphonaptera) that parasitize mice increased as a linear function of mouse density, also leading to a near doubling, on average, of flea density in ungulate exclusion plots (McCauley et al., 2008).

In contrast to the consistent results for mice and their predators and parasites, studies of free-living insect populations have yielded variable results that defy easy explanation. Ogada et al. (2008) sampled arthropods within the clay soil KLEE plots and found that cattle suppressed grass-dwelling arthropods (captured in sweep nets) whereas megaherbivores (elephants and giraffes only) suppressed ground-dwelling arthropods (captured in pitfall traps). Goheen et al. (2004) used both pitfall traps and sweep nets and found that true bugs (Hemiptera) increased more than twofold in total-exclusion plots but that beetles (Coleoptera) and grasshoppers (Orthoptera) did not respond detectably. Several years later, Pringle et al. (2007) used the same sampling methods in both KLEE and the sand soil exclusion plots and found that only beetles increased significantly following ungulate removal, again by nearly twofold on average, but with much stronger responses in sand soils than clay soils (Figure 2). Thus, insect responses, when detected, tend to be in the same direction (greater in the absence of ungulates), but the responses are not always detected and vary spatially, temporally, and taxonomically. The lack of clarity regarding the impacts of large herbivores on insect populations may stem in part from inadequate taxonomic resolution in these studies (in which insects were identified only to order) and/or from insufficient sampling duration or repetition. It is also possible that arthropod populations respond much more strongly to abiotic climatic variables such as precipitation than to shifts in the biotic variables influenced by large mammals.

Among the arboreal fauna, Pringle et al. (2007) found that densities of the Kenya dwarf gecko (*Lygodactylus keniensis*) increased in the absence of ungulates, by about 60% on average, because of increases in the availability of both prey (insects) and habitat (trees). As was the case with the beetles and trees studied by Pringle et al. (2007), the response of geckos to ungulate exclusion was more dramatic in sand soil than clay soil habitats (Figure 2). One potential explanation, as mentioned above, is that this variability in effect size was related to productivity, with stronger effects in lower-productivity areas (i.e., where rainfall is low or soils are poor). Although this hypothesis is consistent with evidence that grassland plants are more sensitive to herbivory in low-productivity areas (Chase et al., 2000), the existence of multiple confounding factors across the two soil types means that further testing is required. A novel ungulate exclusion experiment (UHURU, see below), which is replicated across a rainfall gradient, is now underway and will shed light on the context dependence of ungulate effects.

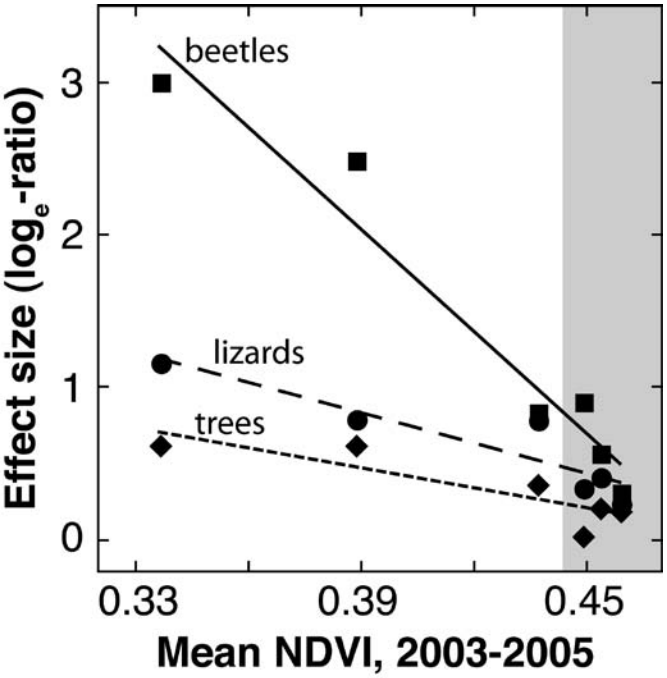

FIGURE 2. Spatial variation in the strength of ungulate effects across six pairs ungulate exclusion and control plots. The strength of the experimental effect of ungulate exclusion on the densities of trees (diamonds), beetles (squares), and lizards (circles) is negatively related to the normalized difference vegetation index (NDVI), a commonly used proxy for primary productivity. Effect size is calculated as the natural logarithm of the ratio of each variable in the exclosure versus the control plot at each site. White background indicates three relatively low-productivity sites on red sand soils, and gray indicates three relatively high-productivity sites on black clay soils. Redrawn from data in Pringle et al. (2007).

Intriguingly, the negative indirect effects of ungulates on geckos in general concealed a positive effect of elephants in particular. Elephant browsing alters tree structure, often creating splintered crevices, which geckos use for shelter (Pringle, 2008). As a result, geckos were most abundant where there were no ungulates whatsoever, but where ungulates were present, geckos were more numerous in areas with elephant-damaged trees. This finding underscores the importance of physical, "ecosystem-engineering" effects on habitat structure and illustrates two additional points: not all ungulates are equivalent in the effects that they exert on other species, and some species may simultaneously exert positive and negative indirect effects on other species via distinct pathways. Thus, in making difficult management decisions about individual wildlife species—for example, whether to reduce or augment elephant populations—comparisons of treatments that exclude *all* ungulates versus open-access controls may not be particularly informative, since they do not allow experimenters to discern the impacts of individual species.

EFFECTS ON BIODIVERSITY

Many fewer studies have addressed how ungulate removal influences community composition and biodiversity. Theoretical arguments suggest that forces promoting disturbance and habitat heterogeneity, such as large herbivores, should enhance diversity (Ritchie and Olff, 1999), but there are currently insufficient data to allow a compelling test of this proposition in the Ewaso ecosystem.

The few studies that have compared community composition across different ungulate exclusion treatments have revealed complex and context-dependent effects. Huntzinger (2005) studied grasshoppers. In sand soil glade habitats, grasshopper biomass increased dramatically following the exclusion of ungulates from red soil glade habitat. In the clay soil KLEE plots, total grasshopper biomass did not differ between plots with and without cattle, but the number of grasshopper individuals was actually slightly *higher* where cattle were present. This seemingly counterintuitive result arose from differential responses within the grasshopper community: two small-bodied species increased in abundance while a medium-sized species decreased. Hence, cattle facilitate some grasshopper species while suppressing others, which may result from structural impacts of cattle on the architecture of the herbaceous layer.

Invertebrate predators also exhibited subtle responses to changes in the large-mammal community. Warui et al. (2005) sampled spiders in the KLEE plots and found that native ungulates did not influence total spider diversity. Cattle, however, decreased the diversity of the spider community as well as the abundance of the three most common species. One species of jumping spider (Salticidae), in contrast, increased in abundance where cattle were present. Because cattle decreased herbaceous cover and because spider diversity was positively correlated with relative vegetation cover, Warui et al. (2005) proposed that cattle indirectly affect spiders via their effects on vegetation structure. It is also possible that spiders suffered from reductions in their insect prey (Goheen et al., 2004; Pringle et al., 2007; Ogada et al., 2008). However, these studies of grasshoppers and spiders seem to suggest that for many arthropod communities the structural attributes of the grass layer may be at least as important as food availability.

Finally, Ogada et al. (2008) showed that elephants and giraffes significantly reduced total bird activity and the diversity of insectivorous birds in the 4 ha KLEE plots, whereas native ungulates in general depressed the diversity of granivorous birds. Again, multiple causality is likely: removal of elephants and giraffes increased the canopy area of subdominant tree species (i.e., species other than *A. drepanolobium*), providing a greater number of perches and less exposure to predators, whereas enhanced seed production in ungulate-free plots may have attracted granivores.

IMPLICATIONS FOR MANAGED LANDSCAPES

Several studies have revealed effects of ungulate exclusion that may be relevant for the maintenance of productive rangelands. For example, Sankaran and Augustine (2004) showed that ungulates indirectly suppressed the abundance of microbial decomposers in red soil glade and bushland habitats by decreasing the input of plant matter to the soils. Because these decomposers play a pivotal role in the breakdown of organic matter such as dead plants, dung, and animal carcasses, reductions in ungulate biomass could reduce rates of nutrient cycling, a key ecosystem function with important economic ramifications.

Another example involves behavioral interactions among native and domestic ungulates. Grazing wildlife such as zebra may sometimes compete with cattle for food (Odadi et al., 2007). As described above, the KLEE plots independently manipulate the presence of cattle, megaherbivores, and all other wildlife. Young et al. (2005) reported data suggesting that the strength of competition between cattle and zebra depended upon whether elephants were present. The presence of cattle caused zebra to forage elsewhere (but not vice versa). However, this effect was significantly weaker in plots accessible to elephants, perhaps because of changes in the composition of the herbaceous layer. Cattle feed readily on certain forbs, and elephants reduced forb cover by 33% in this experiment. Young et al. (2005) hypothesized that cattle may feed less in plots accessible to elephants because of lower forb availability, which may then make these plots more attractive to grazing zebra.

Evidence from other African savanna systems suggests that ungulates are an important link between the biosphere and the climate. In the Serengeti ecosystem of northern Tanzania, vaccination of cattle against the rinderpest virus in the late 1950s led to the eradication of the disease among the native grazers of Serengeti National Park (Dobson, 1995). The resulting four- to fivefold expansion of the wildebeest population between 1960 and

1980 reduced fuel loads and fires, which, in turn, increased woody cover. This shift from an open grassland to a more heterogeneous savanna doubled the amount of carbon stored in trees, switching the Serengeti from a net source of carbon to the atmosphere to a net sink (Holdo et al., 2009). Thus, this chain of indirect effects involving large herbivores determines a key ecosystem function with major implications for climatic change.

DISCUSSION

CONCLUSIONS AND GAPS IN BASIC KNOWLEDGE

The work summarized above helps to illuminate the ecological structure of the Ewaso ecosystem and suggests several broad conclusions. In general, the removal of large herbivores has a net positive effect on the densities and/or activity levels of other populations, although not all species respond. Taxa increasing in density, biomass, or local habitat usage following removal of large ungulates include woody and herbaceous plants, small mammals, lizards, snakes, and at least some species of birds and arthropods. The ecological interpretation of these results seems straightforward: the large-mammal guild represents a very large warm-blooded biomass, which is maintained by the consumption of vast quantities of plant material. The reduction or elimination of large mammals from the system frees that primary production for use by other consumers (and, by extension, the consumers of those consumers), either as energy or as habitat.

However, the mechanisms underlying these net effects may be complex and counterintuitive, necessitating some caution in extrapolating the results. For example, although tree density is higher on average in ungulate exclusion plots than in control plots, ungulates actually *facilitate* tree seedling establishment and survival by suppressing herbivorous rodents and competing grasses (Goheen et al., 2004, 2010; Riginos, 2009). In the special case of the whistling thorn tree, aggressive ant defenders also limit the impacts of mammalian herbivory. Likewise, arboreal geckos are suppressed by the ungulate community at large but facilitated by structural impacts of elephant on trees (Pringle et al., 2007; Pringle, 2008). Indeed, most of the experimental effects documented to date are likely to have multiple causes, although only for trees have these been systematically and experimentally untangled (Goheen et al., 2004, 2010; Riginos and Young, 2007; Riginos, 2009).

An obvious conclusion, but one whose implications may often be overlooked, is that different large-herbivore species are not ecologically equivalent. A thousand kilograms of zebra does not equal a thousand kilograms of elephant or a thousand kilograms of cattle. Each species eats different sets of plants in different ways, and each therefore exerts a unique impact on the broader system. The distinction between predominantly grazing and predominantly browsing species is one example, but there are many ecologically important differences between species within these loosely defined guilds: body size, water requirements, and, in the case of elephants, the ability to uproot mature trees. The effects of altering livestock density are likely to be particularly pronounced, in part because humans shield domestic animals from many factors that control wildlife populations: drought, food shortage, and predation (Hairston et al., 1960). Thus, livestock may continue to exert strong ecological influence even at times when other large-herbivore populations are declining and in circumstances (e.g., drought) when the rest of the community may be least resilient to their impacts.

Finally, the relative ecological importance of large herbivores is variable in space. Pringle et al. (2007) showed that the indirect effects of ungulates on the densities of trees, beetles, and arboreal geckos varied in strength across a gradient in soil type and rainfall. Because the magnitude of these effects were negatively related to productivity (Figure 2), the authors hypothesized that productivity may modulate the strength of herbivore impacts. Studies elsewhere (Larson et al., 2008; Asner et al., 2009) have yielded at least partial support for this notion. However, multiple factors confounded the comparison of effects across soil types.

To better understand both the modulating influence of environmental context and the differential effects of different native ungulate species, J. R. Goheen, R. M. Pringle, and T. M. Palmer (unpublished) initiated a novel ungulate exclusion experiment in September 2008. Ungulate Herbivory Under Rainfall Uncertainty (UHURU) was designed to focus on the effects of three particularly abundant and influential wildlife species: dik-dik (*Madoqua kirkii*), impala (*Aepyceros melampus*), and elephant (*Loxodonta africana*). Thus, the experiment includes a treatment that excludes all mammals larger than hares (*Lepus* spp.), another that allows dik-dik but excludes impala and all larger species, and a third that excludes elephant and giraffes only. A fourth treatment is unfenced and accessible to all wildlife (but not to livestock, which are kept out by herders). Each plot is 1 ha (100 × 100 m), and each type of plot is replicated three times in the northern, central, and southern parts of the Mpala Conservancy (all on red sand soils), with precipitation increasing ~80% from north to south. This experiment will reveal potential interactions between herbivory and precipitation regimes, and planned warming treatments may also reveal how important ecosystem variables like soil carbon storage will vary as global temperature increases.

What is most striking in reviewing these studies is how much we still do not know. It is odd how few studies have addressed the effects of ungulate exclusion on community diversity, especially with respect to grass and forb communities. There is a similar paucity of data about the influence of large herbivores on basic ecosystem functions such as decomposition and nutrient-cycling rates. Even the influence of ungulates on primary productivity has received little study, and no attempt has been made to understand how the impacts of herbivores on plants scale up to determine levels of carbon sequestration and storage (cf. Holdo et al., 2009). The role of predators is likewise poorly understood. Studies in the Yellowstone ecosystem of North America have shown that the reintroduction of wolves in the mid-1990s has profoundly affected the landscape by altering the behavior and physiology of elk (Ripple and Beschta, 2004; Creel et al., 2007). Similar processes may be at work in the Ewaso ecosystem, with the apparent recent recovery of many predator species on properties in Laikipia since the 1990s (Georgiadis et al., 2007a, 2007b), but no data exist with which to evaluate this possibility. Finally, there has thus far been a bias in this research toward questions that are academically interesting but dubiously useful from the perspective of day-to-day landscape management, an issue that we address in the following section.

Reconciling Basic and Applied Interests

At the most ethereal level, it can be argued that preserving any complex system in working order—from automobiles to ecosystems—requires a functional understanding of how that system works and what its different parts actually do. The studies that we synthesize above, which paint an increasingly complex picture of how ungulates shape the abundance, distribution, and diversity of other species in savannas, are certainly an effort in this direction. On a slightly more pragmatic level, the information generated by these studies should be considered when managing large-herbivore populations. Harvesting, culling, contraception, translocation, and reintroduction of ungulates are all common practices (van Aarde et al., 1999; Georgiadis et al., 2003; Tambling and du Toit, 2005; Druce et al., 2006; Hayward et al., 2007a, 2007b; Whitman et al., 2007). These actions are always expensive and often contentious (e.g., Landeman, 1978; Pimm and van Aarde, 2001), and it therefore seems prudent to know how such deliberate manipulations are likely to affect biodiversity and ecosystem processes. Understanding the direct and indirect effects of elephants in particular (i.e., how ecosystem properties change as a function of elephant abundance) may inform the emotionally charged issue of elephant management. The indirect effects of elephants have received little formal study. Given the high stakes of elephant management and control programs, this is an area where rigorous experimental data are surprisingly few.

These issues aside, very different imperatives drive academic science, on the one hand, and land management, on the other. The reward structures in most parts of academia (including the large grants necessary to finance major research efforts) demand advances at the “forefront” of scientific theory (wherever that might be at the time). Many rangeland management issues are widely considered (rightly or wrongly, and with definite exceptions) to fall outside the narrow boundaries of modern ecology’s leading edge. This situation can lead to frustration on behalf of both local stakeholders (“Why are researchers spending so much time and money on projects with no immediate practical benefit?”) and researchers (“Why won’t managers and community members look at the ‘big picture’ of interconnected parts?”).

From the perspective of the research community, there are at least two ways to help resolve this dilemma. One is to identify research questions that simultaneously meet both needs: to extend the frontiers of ecology and to address issues that genuinely matter to managers and pastoralists. (This suggestion is not to diminish the importance of research questions that are more purely basic or more purely applied but merely to point out that all of these things are compatible.) Each of the concerns most commonly cited by those who raise livestock or manage multiuse landscapes in the Ewaso ecosystem dovetails in some way with issues currently considered exciting by academic ecologists and ecological economists: the relationship between climate and plant (i.e., forage) production, the potential for competition between native and domestic herbivores, the behavior and population dynamics of large carnivores, the transmission and management of infectious diseases, the determinants of range quality, the market price of livestock, and strategies for generating alternative revenue streams, such as from tourism.

We provide just a few examples relevant to the topic of this chapter. As discussed above, early research in KLEE showed that small mammals and their potentially disease-bearing ectoparasites doubled in the absence of ungulates. The logical next steps, some of which are currently under investigation by McCauley, Keesing, and colleagues, are to understand whether this shift actually alters the prevalence of disease in humans and domestic animals and to what extent this is true in landscapes where livestock have completely replaced native ungulates. The effort to address these questions links recent intensive efforts in disease ecology with very real problems encountered in managed landscapes. Another example, being addressed by Goheen's research group, is to understand how both wild and domestic ungulates might be better managed to limit predation on the latter (or similarly, how common wild ungulates might be managed to minimize depredation of rare ones). This research fuses long-standing academic interest in issues such as apparent competition (Holt, 1977) with the goal of enabling coexistence of people and predators and/or the stabilization of rare and declining wildlife species such as hartebeest (Georgiadis et al., 2007a, 2007b). Rangeland quality, from the perspective of livestock production, is largely a product of factors that have long intrigued basic biologists and that are determined in part by the abundance and community composition of ungulates, such as the relative abundance of trees and grasses. Along similar lines, an ecological-economic quantification of how the relative abundance of native wildlife influences per hectare profitability of single-use and multiuse landscapes would be warmly received both by managers and by academics in the thriving hybrid discipline of ecosystem services. Finally, there is enormous interest within academia in projecting the biological impacts of ongoing climatic change. Such changes, including shifts in rainfall regime, will determine the quantity, quality, and spatial distribution of forage over the coming century, but they remain poorly understood.

None of these research efforts, however conclusive their results might be, will yield the desired objective of linking basic science to conservation without another element, which is to aggressively disseminate results and their implications to nonscientists while simultaneously being forthright about the limits of current knowledge in informing range management. Experimental results are unlikely to be applied if they remain confined to scientific journals; of equal importance, but perhaps easier to forget, is that nothing diminishes respect for science more efficiently than hypotheses passed off as certainties in an effort to be relevant.

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REFERENCES

Abrams, P. A., B. A. Menge, G. G. Mittelbach, D. A. Spiller, and P. Yodzis. 1996. "The Role of Indirect Effects in Food Webs." In *Food Webs: Integration of Patterns and Dynamics*, ed. G. A. Polis and K. O. Winemiller, pp. 371–395. New York: Chapman and Hall.

Asner, G. P., S. R. Levick, T. Kennedy-Bowdoin, D. E. Knapp, R. Emerson, J. Jacobson, M. S. Colgan, and R. E. Martin. 2009. Large-scale impacts of herbivores on the structural diversity of African savannas. *Proceedings of the National Academy of Sciences of the United States of America*, 106:4947–4952.

Augustine, D. J. 2002. Large Herbivores and Process Dynamics in a Managed Savanna Ecosystem. Ph.D. diss., Syracuse University, Syracuse, N.Y.

Augustine, D. J., and S. J. McNaughton. 2004. Regulation of Shrub Dynamics by Native Browsing Ungulates on East African Rangeland. *Journal of Applied Ecology*, 41:45–58.

Augustine, D. J., K. E. Veblen, J. R. Goheen, C. Riginos, and T. P. Young. 2011 (this volume). "Pathways for Positive Cattle–Wildlife Interactions in Semiarid Rangelands." In *Conserving Wildlife in African Landscapes: Kenya's Ewaso Ecosystem*, ed. N. J. Georgiadis. Smithsonian Contributions to Zoology, No. 632:55–71. Washington, D.C.: Smithsonian Institution Scholarly Press.

Chase, J. M., M. A. Leibold, A. L. Downing, and J. B. Shurin. 2000. The Effects of Productivity, Herbivory, and Plant Species Turnover in Grassland Food Webs. *Ecology*, 81:2485–2497.

Creel, S., D. Christianson, L. S. Liley, and J. A. Winnie. 2007. Predation Risk Affects Reproductive Physiology and Demography of Elk. *Science*, 315:960.

Dobson, A. 1995. "The Ecology and Epidemiology of Rinderpest Virus in Serengeti and Ngorongoro Conservation Area." In *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem*, ed. A. R. E. Sinclair and P. Arcese, pp. 485–505. Chicago: University of Chicago Press.

Druce, H., K. Pretorius, D. Druce, and R. Slotow. 2006. The Effect of Mature Elephant Bull Introductions on Resident Bull's Group Size and Musth Periods: Phinda Private Game Reserve, South Africa. *South African Journal of Wildlife Research*, 36:133–137.

du Toit, J., K. H. Rogers, and H. C. Biggs, eds. 2003. *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Washington, D.C.: Island Press.

Georgiadis, N., M. Hack, and K. Turpin. 2003. The Influence of Rainfall on Zebra Population Dynamics: Implications for Management. *Journal of Applied Ecology*, 40:125–136.

Georgiadis, N. J., F. Ihwagi, J. G. N. Olwero, and S. S. Romanach. 2007a. Savanna Herbivore Dynamics in a Livestock-Dominated Landscape. II: Ecological, Conservation, and Management Implications of Predator Restoration. *Biological Conservation*, 137:473–483.

Georgiadis, N. J., J. G. N. Olwero, G. Ojwang, and S. S. Romanach. 2007b. Savanna Herbivore Dynamics in a Livestock-Dominated Landscape: I. Dependence on Land Use, Rainfall, Density, and Time. *Biological Conservation*, 137:461–472.

Goheen, J. R., F. Keesing, B. F. Allan, D. L. Ogada, and R. S. Ostfeld. 2004. Net Effects of Large Mammals on Acacia Seedling Survival in an African Savanna. *Ecology*, 85:1555–1561.

Goheen, J. R., and T. M. Palmer. 2010. Defensive plant-ants stabilize megaherbivore-driven landscape change in an African savanna. *Current Biology*, 20:1768–1772.

Goheen, J. R., T. M. Palmer, F. Keesing, C. Riginos, and T. P. Young. 2010. Large Herbivores Facilitate Savanna Tree Establishment via Diverse and Indirect Pathways. *Journal of Animal Ecology*, 79:372–382.

Goheen, J. R., T. P. Young, F. Keesing, and T. M. Palmer. 2007. Consequences of Herbivory by Native Ungulates for the Reproduction of a Savanna Tree. *Journal of Ecology*, 95:129–138.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community Structure, Population Control, and Competition. *American Naturalist*, 94:421–425.

Hayward, M. W., J. Adendorff, L. Moolman, G. J. Hayward, and G. I. H. Kerley. 2007a. The Successful Reintroduction of Leopard *Panthera pardus* to the Addo Elephant National Park. *African Journal of Ecology*, 45:103–104.

Hayward, M. W., J. Adendorff, J. O'Brien, A. Sholto-Douglas, C. Bissett, L. C. Moolman, P. Bean, A. Fogarty, D. Howarth, R. Slater, and G. I. H. Kerley. 2007b. The Reintroduction of Large Carnivores to the Eastern Cape, South Africa: An Assessment. *Oryx*, 41:205–214.

Hilborn, R., and A. R. E. Sinclair. 1979. "A Simulation of the Wildebeest Population, Other Ungulates, and Their Predators." In *Serengeti: Dynamics of an Ecosystem*, ed. A. R. E. Sinclair and M. Norton-Griffiths, pp. 287–309. Chicago: University of Chicago Press.

Holdo, R. M., A. R. E. Sinclair, A. P. Dobson, K. L. Metzger, B. M. Bolker, M. E. Ritchie, and R. D. Holt. 2009. A Disease-Mediated Trophic Cascade in the Serengeti and its Implications for Ecosystem C. *PLoS Biology,* 7:e1000210, doi:10.1371/journal.pbio.1000210.

Holt, R. D. 1977. Predation, Apparent Competition, and Structure of Prey Communities. *Theoretical Population Biology*, 12:197–229.

Huntzinger, M. 2005. How Do Distantly Related Herbivores That Share Food Resources Interact? Ph.D. diss., University of California, Davis.

Keesing, F. 1998. Impacts of Ungulates on the Demography and Diversity of Small Mammals in Central Kenya. *Oecologia*, 116:381–389.

———. 2000. Cryptic Consumers and the Ecology of an African Savanna. *BioScience*, 50:205–215.

Kruuk, H. 1972. *The Spotted Hyena: A Study of Predation and Social Behavior*. Chicago: University of Chicago Press.

Landeman, M. 1978. Is Culling Necessary? Is Culling Cruel? Is the National Parks Board Killing Elephants for Profit? *African Wildlife*, 32:6–8.

Larson, A. J., J. A. Lutz, R. F. Gersonde, J. F. Franklin, and F. F. Hietpas. 2008. Potential Site Productivity Influences the Rate of Forest Structural Development. *Ecological Applications*, 18:899–910.

Laws, R. M., I. S. C. Parker, and R. C. B. Johnstone. 1975. *Elephants and Their Habitats*. Oxford: Oxford University Press.

McCauley, D. J., F. Keesing, T. P. Young, B. F. Allan, and R. M. Pringle. 2006. Indirect Effects of Large Herbivores on Snakes in an African Savanna. *Ecology*, 87:2657–2663.

McCauley, D. J., F. Keesing, T. Young, and K. Dittmar. 2008. Effects of the Removal of Large Herbivores on Fleas of Small Mammals. *Journal of Vector Ecology*, 33:263–268.

McNaughton, S. J. 1976. Serengeti Migratory Wildebeest: Facilitation of Energy Flow by Grazing. *Science*, 191:92–94.

———. 1978. Serengeti Ungulates: Feeding Selectivity Influences Effectiveness of Plant Defense Guilds. *Science*, 199:806–807.

Menge, B. A. 1995. Indirect Effects in Marine Rocky Intertidal Interaction Webs: Patterns and Importance. *Ecological Monographs*, 65:21–74.

Odadi, W. O., T. P. Young, and J. B. Okeyo-Owuor. 2007. Effects of Wildlife on Cattle Diets in Laikipia Rangeland, Kenya. *Rangeland Ecology and Management*, 60:179–185.

Ogada, D., M. E. Gadd, R. S. Ostfeld, T. P. Young, and F. Keesing. 2008. Impacts of Large Herbivores on Bird Diversity and Abundance in an African Savanna. *Oecologia*, 156:387–397.

Okello, B. D. 2007. Effects of herbivores, fire and harvesting on the population dynamics of *Acacia drepanolobium* Sjoestedt in Laikipia, Kenya. Ph.D. diss., University of KwaZulu-Natal, Pietermaritzburg, South Africa.

Paine, R. T. 1966. Food Web Complexity and Species Diversity. *American Naturalist*, 100:65–75.

———. 1980. Food Webs: Linkage, Interaction Strength and Community Infrastructure—The 3rd Tansley Lecture. *Journal of Animal Ecology*, 49:667–685.

Palmer, T. M., M. L. Stanton, T. P. Young, J. R. Goheen, R. M. Pringle, and R. Karban. 2008. Breakdown of an Ant-Plant Mutualism Follows the Loss of Large Mammals from an African Savanna. *Science*, 319:192–195.

Pimm, S. L., and R. J. van Aarde. 2001. Population Control: African Elephants and Contraception. *Nature*, 411:766–766.

Pringle, R. M. 2008. Elephants as Agents of Habitat Creation for Small Vertebrates at the Patch Scale. *Ecology*, 89:26–33.

Pringle, R. M., T. P. Young, D. I. Rubenstein, and D. J. McCauley. 2007. Herbivore-Initiated Interaction Cascades and Their Modulation by Productivity in an African Savanna. *Proceedings of the National Academy of Sciences of the United States of America*, 104:193–197.

Riginos, C. 2009. Grass Competition Suppresses Savanna Tree Growth Across Multiple Demographic Stages. *Ecology*, 90:335–340.

Riginos, C., and T. P. Young. 2007. Positive and Negative Effects of Grass, Cattle, and Wild Herbivores on *Acacia* saplings in an East African Savanna. *Oecologia*, 153:985–995.

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the Ecology of Fear: Can Predation Risk Structure Ecosystems? *BioScience*, 54:755–766.

Ritchie, M. E., and H. Olff. 1999. Spatial Scaling Laws Yield a Synthetic Theory of Biodiversity. *Nature* 400:557–560.

Sankaran, M., and D. J. Augustine. 2004. Large Herbivores Suppress Decomposer Abundance in a Semiarid Grazing Ecosystem. *Ecology*, 85:1052–1061.

Schaller, G. B. 1972. *The Serengeti Lion: A Study of Predator-Prey Relations*. Chicago: University of Chicago Press.

Schmitz, O. J., P. A. Hamback, and A. P. Beckerman. 2000. Trophic Cascades in Terrestrial Systems: A Review of the Effects of Carnivore Removals on Plants. *American Naturalist*, 155:141–153.

Scholes, R. J., and B. H. Walker. 1993. *An African Savanna: Synthesis of the Nylsvley Study*. Cambridge: Cambridge University Press.

Sinclair, A. R. E. 1977. *The African Buffalo*. Chicago: University of Chicago Press.

Sinclair, A. R. E., and P. Arcese, eds. 1995. *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem*. Chicago: University of Chicago Press.

Tambling, C. J., and J. T. du Toit. 2005. Modelling Wildebeest Population Dynamics: Implications of Predation and Harvesting in a Closed System. *Journal of Applied Ecology*, 42:431–441.

van Aarde, R., I. Whyte, and S. Pimm. 1999. Culling and the Dynamics of the Kruger National Park African Elephant Population. *Animal Conservation*, 2:287–294.

Warui, C. M., M. R. Villet, T. P. Young, and R. Jocque. 2005. Influence of Grazing by Large Mammals on the Spider Community of a Kenyan Savanna Biome. *Journal of Arachnology*, 33:269–279.

Whitman, K. L., A. M. Starfield, H. Quadling, and C. Packer. 2007. Modeling the Effects of Trophy Selection and Environmental Disturbance on a Simulated Population of African Lions. *Conservation Biology*, 21:591–601.

Wootton, J. T. 1994. The Nature and Consequences of Indirect Effects in Ecological Communities. *Annual Review of Ecology and Systematics*, 25:443–466.

Young, T. P., and D. J. Augustine. 2007. Interspecific Variation in the Reproductive Response of Acacia Species to Protection from Large Mammalian Herbivores. *Biotropica*, 39:559–561.

Young, T. P., B. Okello, D. Kinyua, and T. Palmer. 1998. KLEE: A Long-Term Multi-species Herbivore Exclusion Experiment in Laikipia, Kenya. *African Journal of Range and Forage Science*, 14:92–104.

Young, T. P., T. M. Palmer, and M. E. Gadd. 2005. Competition and Compensation among Cattle, Zebras, and Elephants in a Semi-arid Savanna in Laikipia, Kenya. *Biological Conservation*, 122:351–359.

Young, T. P., N. Patridge, and A. Macrae. 1995. Long-Term Glades in *Acacia* Bushland and Their Edge Effects in Laikipia, Kenya. *Ecological Applications*, 5:97–108.

Young, T. P., C. H. Stubblefield, and L. A. Isbell. 1997. Ants on Swollen Thorn Acacias: Species Coexistence in a Simple System. *Oecologia*, 109:98–107.

Pathways for Positive Cattle–Wildlife Interactions in Semiarid Rangelands

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ABSTRACT. Livestock-wildlife interactions in rangelands are often viewed in terms of competition, but livestock and native ungulates can also benefit each other through long-term modifications of rangeland habitats. Here we synthesize research on rangelands in central Laikipia focusing on two types of cattle-wildlife interactions that have implications for their long-term coexistence. The first interaction occurs via redistribution of soil nutrients within the ecosystem, which is a consequence of the use of bomas (temporary corrals) to manage livestock. Our studies on two different soil types show that rotational boma management creates hectare-scale patches in the landscape that are enriched in soil and plant nutrients and persist for decades to centuries. In both of the predominant soil types in Laikipia, forage phosphorus content is low relative to ungulate demands during peak lactation. Nutrient-rich boma sites (hereafter referred to as glades) provide a key wet-season forage resource of nutritional sufficiency for lactation. Our studies further show that a wide range of native ungulates selectively use glades relative to surrounding nutrient-poor habitats. Impala (*Aepyceros melampus*) in particular show intensive use of glades on sandy soils and are rare in portions of the landscape lacking glades. A second important pathway for cattle-wildlife interaction occurs through the influence of native browsing ungulates on woody vegetation. Shrub and tree cover has been increasing in Laikipia over the past century, followed by increases in native browsers in recent decades on ranches where wildlife are allowed to coexist with cattle. Our exclosure experiments in central Laikipia indicate that native browsers suppress shrub encroachment on both dominant soil types. However, the strength of browser effects are three to seven times greater on sandy soils, where two browsers, dik-dik and elephants, are both abundant, compared to heavy clay soils, where elephants are the only dominant browser. In the clay soils, native browsers still exert a significant influence on dynamics of the dominant tree, *Acacia drepanolobium*, and suppress encroachment by subdominant shrub species. Browser effects on woody vegetation likely enhance forage production for cattle and maintain open habitats favored by native grazers for predator avoidance. Taken together, our studies indicate that boma rotation and browser control of shrub encroachment are key interaction pathways that promote cattle-wildlife coexistence in the Ewaso ecosystem.

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INTRODUCTION

In East Africa, most native ungulate populations still occur on rangelands outside of formally protected areas, and long-term coexistence of livestock and native species is critical if wildlife is to be conserved in the region (Western, 1989; Prins et al., 2000). Negative relationships between wildlife and livestock on some pastoral rangelands in Kenya have been attributed to poaching and harassment by humans associated with livestock, rather than direct competition for forage (de Leeuw et al., 2001). However, where such direct human effects are removed and livestock are maintained at moderate stocking rates, the magnitude of competition between livestock and native herbivores is a concern for the production of livestock and the conservation of the native fauna. Livestock-wildlife interactions in rangelands are often viewed in terms of competition because herbivores with overlapping habitat and diets have obvious potential for competition. However, multiple pathways of interaction are possible in diverse herbivore communities. Prins (2000) provided a comprehensive review of negative pathways, including direct resource competition, apparent competition, diffuse competition, predation, and competition through habitat modification. He suggested that despite considerable resource overlap between wildlife and cattle, competition is largely asymmetrical and diffuse, with cattle having a competitive effect on some wildlife species, but wildlife often having little or no net competitive effect on cattle (Prins, 2000). Several recent large-scale experiments have demonstrated competition between cattle and native grazers in grasslands under controlled conditions, but the magnitude of competition is often less than expected on the basis of diet overlap (Hobbs et al., 1996; Young et al., 2005; Derner et al., 2006; Odadi et al., 2009).

The relationship between livestock and cattle can also be positive (Arsenault and Owen-Smith, 2002). Prins (2000) discussed two modes of positive cattle-wildlife interactions: facilitation of forage quality or accessibility and facilitation through habitat modification. In diverse herbivore communities, the existence and strength of facilitation can determine the net effect of cattle and wildlife on one another and hence are important to long-term cattle-wildlife coexistence. Facilitation of forage quality or accessibility is usually defined as a short-term effect that bulk-feeding herbivores can have on forage for smaller herbivores (Bell, 1971; Gordon, 1988; Verweij et al., 2006). Facilitation through habitat modification involves long-term effects of different herbivore species on soil nutrient distribution and plant community composition (Arsenault and Owen-Smith, 2002). Our studies in the Ewaso ecosystem have addressed trophic interactions among soils, plants, and herbivores and identified two types of facilitation through habitat modification that have implications for the coexistence of livestock and native ungulates. The first interaction occurs through redistribution of soil nutrients within the landscape, which is a consequence of the use of bomas (temporary livestock corrals) to manage livestock. Boma-derived nutrient redistribution, in turn, has substantial long-term effects on the heterogeneity of forage nutrient content within the landscape, with potential benefits to both cattle and native herbivores. The second interaction is the ecosystem service that native browsers provide by suppressing and reversing shrub encroachment into grasslands, with implications for wildlife and livestock use of the landscape. In addition, the old boma sites are themselves treeless and attract increased wildlife use for this reason as well as for their nutrient-rich grasses. Here we synthesize studies examining these interaction pathways on two widely distributed soil types in the Ewaso ecosystem.

In central Laikipia, the Ewaso ecosystem encompasses a transition in soils, elevation, and vegetation, where gently undulating plains dominated by grassland and *Acacia drepanolobium* savanna switch to a more dissected lower plateau on Precambrian metamorphic rocks dominated by *Acacia mellifera*, *A. etbaica*, and *A. brevispica* bushland with a discontinuous grass understory (Ahn and Geiger, 1987; Taiti, 1992; Augustine, 2003b). Black cotton soils (Pellic Vertisols) occur on the plains in the south and west, whereas red sandy loams (Ferric and Chromic Luvisols) occur at lower elevations to the north and east (Ahn and Geiger, 1987). These soils differ dramatically in texture, with black cotton containing, on average, 50% clay and 24% sand (Young et al., 1998) and red sands containing 15% clay and 74% sand (Augustine, 2003a). The Mpala Research Centre (MRC) spans this transition zone, which occurs at elevations of 1740–1800 m above sea level. Although these two soils support distinctly different assemblages of plants, native herbivores, and other biota (Table 1), we show that on both of these soil types, herbivore-mediated nutrient heterogeneity and shrub control are important pathways through which cattle and wildlife benefit each other.

LIVESTOCK MANAGEMENT AND NUTRIENT HETEROGENEITY

Tropical rangelands are notoriously poor in mineral nutrients, such that mineral supplementation is recommended

TABLE 1. Comparison of plant and herbivore communities on two widespread soil types in Laikipia, Kenya.

Variable	Red Sands Habitat	Black Cotton Habitat
Soil texture	74% sand, 15% clay	24% sand, 50% clay
Dominant grasses	*Digitaria milanjiana, Cynodon dactylon, Pennisetum stramineum*	*Pennisetum stramineum, Bracharia lachnantha, P. mezianum, Themeda triandra*
Dominant shrubs and trees	*Acacia mellifera, A. etbaica, A. brevispica*	*Acacia drepanolobium*
Dominant native ungulates	Impala, dik-dik, elephant	Plains zebra, Grant's gazelle, hartebeest, giraffe
Less abundant native ungulates	Plains zebra, Grevy's zebra, eland, waterbuck, giraffe	Elephant, Grevy's zebra, eland, buffalo, oryx

as a standard practice for tropical livestock (McDowell, 1985). Wild herbivore biomass is also strongly affected by large-scale variation in geology and soil nutrient availability (Bell, 1982; Fritz and Duncan, 1994). Furthermore, spatial heterogeneity in soil and plant nutrients in African rangelands can strongly influence the distribution of wild herbivores at multiple spatial scales (McNaughton, 1988, 1990; Blackmore et al., 1990; Ben-Shahar and Coe, 1992; Murray, 1995; Muchiru et al., 2008). Natural sources of soil nutrient heterogeneity include termites (Brody et al., 2010; Fox-Dobbs et al., 2010) and tree canopies (Riginos et al., 2009). Here we discuss a major anthropogenic source of landscape heterogeneity: livestock corrals.

Abandoned livestock corrals, or bomas, are a widespread feature of African rangelands. Bomas are temporary structures consisting of a dense ring of thorn scrub branches that contain and protect livestock overnight from theft and predation for periods ranging from weeks to years. A major consequence of boma use is the concentration of large quantities of dung and urine within a small area, where livestock excrete and redistribute nutrients from the surrounding savanna. Following abandonment, boma sites often support a nutrient-enriched plant community and potentially alter the spatial pattern of nutrient cycling within the ecosystem. Recently abandoned boma sites in East Africa support unique herbaceous plant communities with nutrient enrichment both in soils and grasses (Stelfox, 1986; Augustine, 2003a; Treydte et al., 2006; Muchiru et al., 2009). Studies in South Africa even suggest that plant communities on abandoned sites of human occupation can persist in a nutrient-enriched state for centuries (Blackmore et al., 1990).

Soil and Grass Nutrients on Red Sands Versus Black Cotton Soil

For increased nutrient heterogeneity to benefit wild herbivores, forage nutrients must be limiting to herbivores in all or a portion of the landscape during part of the year. Previous studies on nutrient limitations to savanna ecosystem processes and herbivore abundances have primarily relied upon geology or cation exchange capacity as general indices of soil fertility at broad spatial scales (Bell, 1982; Fritz and Duncan, 1994; Olff et al., 2002). We used direct measures of soils and grasses to examine forage nutrient availability on black cotton soils, red sands, and a transition zone between them at MRC in central Laikipia. On the basis of the previous discussion of nutrient limitations to ungulates in Africa, we focus here on N, P, and Ca.

We sampled soil and grass leaf blades at 100 locations within MRC during the wet season in August 2001. We randomly selected 60 locations within the red sands soil type that underlies the majority of MRC, 20 locations within a region of transitional soils between 1740 and 1800 m elevation, and 20 locations within the black cotton soil type above 1800 m elevation in the southwestern portion of MRC. At each location, we sampled 30–40 of the youngest, fully expanded grass leaves from a 1 m^2 plot dominated by any of the dominant grasses (red sands: *Digitaria milanjiana, Cynodon dactylon, Pennisetum mezianum, Pennisetum stramineum, Enteropogon macrostachyus, Cymbopogon pospischilii, Themeda triandra, Sporobolus ioclados, Harpachne schimperi,* or *Chloris roxburghiana*; transitional soils: *Digitaria milanjiana, Pennisetum stramineum, Themeda triandra, Cymbopogon pospischilii, Pennisetum mezianum,* and *Cenchrus ciliaris*; black cotton soils: *Pennisetum stramineum, Themeda triandra, Pennisetum mezianum, Brachiaria lachnantha, Setaria sphacelata*, and *Lintonia nutans*.

Leaves were analyzed for N, P, and Ca content following McNaughton (1988). At each location, we also collected a soil core (15 cm depth). Cores were stored at 5°C at the MRC laboratory, and within 48 hours of collection, a 15 g subsample was extracted with 1 M KCl to measure NH_4^+ and NO_3^- content, and a 2.5 g subsample was extracted with Mehlich-3 solution to measure extractable P and Ca (Mehlich, 1984). Another 15 g subsample from each core was dried and analyzed for total soil N, P, Ca, and Na following McNaughton (1988). For extractable soil nutrient pools, we report geometric means because of high variability within soil types. Post hoc, pairwise comparisons among soil types were tested using Tukey's honestly significant difference (HSD), and all letters in figures indicate significant differences at the $P < 0.05$ level.

Black cotton soils contain greater concentrations of N and Ca compared to red sands (Figure 1A,C; $F_{2,97} > 9.41$, $P < 0.0002$ for one-way analysis of variance (ANOVA)), but both soils have similar total P concentration (Figure 1B; $F_{2,97} = 2.37$, $P = 0.10$). Mean soil C concentration is more than twice as high in black cotton soils compared with red sands (mean ± 95% confidence interval = 2.44 ± 0.35% versus 1.12 ± 0.13%), and soil C:N ratios are also higher in black cotton compared to red sands (17.3 ± 2.4 versus 10.1 ± 0.2). Extractable soil nutrient pools mirrored patterns for total soil nutrients, with inorganic Ca significantly lower on the red sands ($F_{2,97} = 43.9$, $P < 0.0001$; Figure 1F) and inorganic N only marginally lower on red sands ($F_{2,97} = 2.50$, $P = 0.087$; $P > 0.05$ for all pairwise comparisons; Figure 1D). Extractable soil P was similar on red sands and black cotton and lower for the transitional soils ($F_{2,97} = 12.8$, $P < 0.0001$; Figure 1E).

Grass P content was relatively consistent ($F_{2,97} = 1.1$, $P = 0.34$; Figure 1H) and low across the different soil types, reflecting a similar pattern for total and extractable soil P. In contrast to soil nutrient patterns, grass N content was significantly greater on red sands relative to black cotton ($F_{2,97} = 5.2$, $P = 0.007$; Figure 1G). Grass Ca content did not vary across soil types ($F_{2,97} = 0.5$, $P = 0.59$; Figure 1J), even though black cotton soils contain significantly more total and extractable Ca.

Variation in grass nutrient content across soil types has clear implications for large herbivores. Most notably, wet-season forage P content is lower than estimated demands for lactating ruminants on both red sands and black cotton soils (Figure 1H). For example, Murray (1995) estimated minimum forage P content of 3,900 mg/kg dry weight necessary for lactating wildebeest (*Connochaetes taurinus*), and recommendations for lactating cattle are in the range of 3,100–4,000 mg/kg (McDowell, 1985). Despite considerable differences in parent material and properties of red sands versus black cotton soil, our results indicate that forage P content is likely to affect growth rates and distribution of wild grazers in both habitats. Calcium can also be a critical nutrient for large herbivores in tropical grasslands (McNaughton, 1988, 1990; Murray, 1995), but in the Ewaso ecosystem, grass calcium content is relatively constant across soil types, insensitive to variation in soil Ca availability, and sufficient to meet demands of grazing ungulates (Figure 1F,J).

Nitrogen content of grasses during the wet season on both the red sands and black cotton soils also appears sufficient to meet the protein requirements of ungulate grazers. For example, grasslands in the Serengeti ecosystem supporting high wet-season ungulate densities contain leaves with 2.2%–2.6% N dry weight (Murray, 1995), similar to grass leaf N content on black cotton soil (mean = 2.3%, 1 standard error (SE) = 0.1%) and lower than grass leaf N content on red soil (mean = 2.9%, 1 SE = 0.1%). For high-yielding dairy cattle and actively growing beef cattle, optimum N content in the diet is typically in the range of 2.1%–3.2% dry weight (McDowell, 1985; Whitehead, 1995). We note that our analysis does not address dry-season N limitations, when forage N content below 1% N can limit rumen microbes (Van Soest, 1994). Although our results emphasize P as a critical limiting nutrient for ungulates in Laikipia, the significantly lower N content in black cotton grasses compared to red sands suggests that future studies in the black cotton habitat should consider factors influencing seasonal and spatial variation in grass protein content.

INFLUENCE OF ABANDONED BOMAS ON LANDSCAPE NUTRIENT HETEROGENEITY

In the Ewaso ecosystem, shortgrass and shrub-free lawns on the order of 0.2–1 ha in size are a widespread and conspicuous feature of the landscape. These shortgrass lawns are derived from abandoned livestock bomas, contain nutrient-enriched soil, and support a unique plant community dominated primarily by the stoloniferous grass *Cynodon plectostachyus* (Young et al., 1995; Augustine, 2003a). In the red sands habitat, abandoned boma sites can persist in this shrub-free, shortgrass state for at least four decades and likely for centuries (Augustine, 2003a). In the black cotton soils, *Cynodon* lawns usually develop to a *Pennisetum stramineum*–dominated but still shrub-free stage over one to three decades and likely remain in the latter state many decades more (Veblen and Young, 2010). Hereafter, we refer to all of these nutrient-enriched, shrub-free communities that have developed on abandoned boma sites as "glades." In some of our studies, we used aerial photographs from the 1960s to determine ages of abandoned boma sites, and we examined soils, plant nutrients, and herbivore distribution in relation to glades created by boma abandonment during the past four decades (young glades) versus those

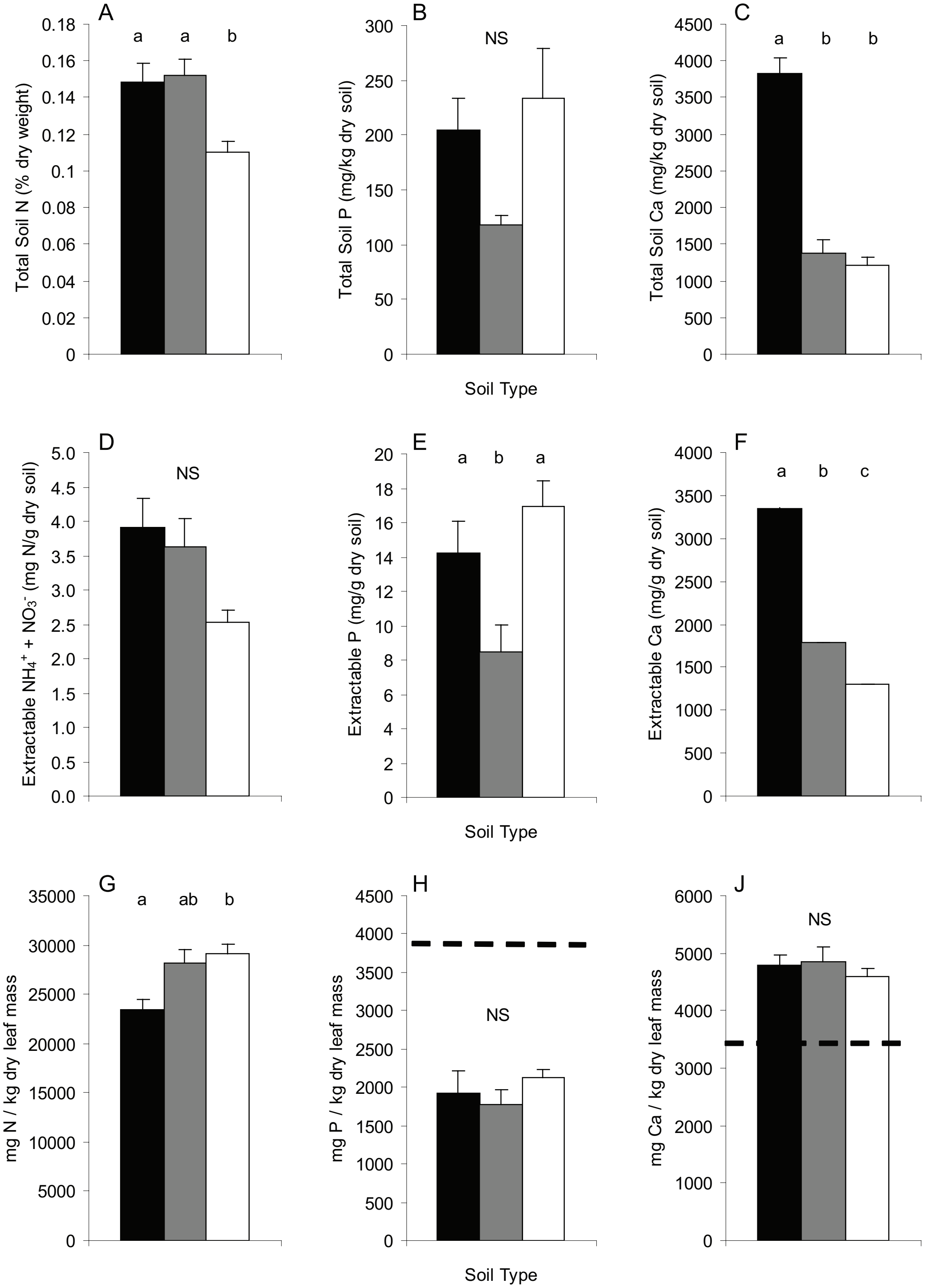

FIGURE 1. Variation in concentrations of N, P, and Ca in (A–C) the total soil pool, (D–F) inorganic soil pool, and (G, H, J) wet-season grass leaves across soil types (n = 60 red soil sampling locations, 20 transition soil locations, and 20 black cotton soil locations) at the Mpala Research Centre in central Laikipia. Dashed lines in (H) and (J) show forage phosphorus and calcium requirements for lactating wildebeest (Murray, 1995).

derived from bomas abandoned more than 40 years ago (old glades).

In the red sands habitat, soil nutrient content is substantially enriched on abandoned boma sites relative to the surrounding landscape and also varies in relation to the age of abandoned boma sites. Over the first four decades following boma abandonment, soil carbon and nitrogen decline relatively rapidly, while soil phosphorus is more tightly retained; old glades contain 1.9 times more N and 7.4 times more P than surrounding soils (Augustine, 2003a). Analysis of soil phosphorus availability using the Mechich-3 extractant (Mehlich, 1984) from soil cores (0–15 cm depth) collected at four glades and four paired bushland sites revealed 27 times more extractable phosphorus in glade versus bushland soils (Figure 2, left; paired $t_3 = 4.82$, $P = 0.02$). In the black cotton habitat, soil cores (0–30 cm depth) collected from nine glades and nine black cotton sites showed 1.84 times more total soil N in glades, whereas phosphorus availability measured using the Olsen-P extractant (Olsen and Sommers, 1982) revealed 20 times more extractable phosphorus in black cotton glades compared to nonglade soil (nitrogen: $t_8 = 4.47$, $P = 0.0002$; phosphorous: $t_8 = 3.48$, $P = 0.008$; Figure 2, right). Although the Olsen extraction appears to provide lower estimates of soil P availability compared to the Mehlich extraction, both methods revealed the ≥20-fold larger soil P pools in glade compared to nonglade soils.

A study of grass nutrient content in the red sands habitat during the wet season evaluated variation associated with glades, topography, and plant species (Augustine, 2004). Results from this study, combined with previous analyses of spatial variation in grass species distributions (Augustine, 2003b), illustrate the variation in forage P content that a selectively foraging impala could experience in the red sands habitat (Figure 3). Mineral requirements specific to impala have not been evaluated; hence, we rely upon previously discussed requirements on the order of 3100–4000 mg P/kg dry matter for wildebeest and cattle (McDowell, 1985; Murray, 1995). Although a selectively foraging ungulate moving through the red sands habitat experiences substantial small-scale variation in forage P content among grass species and topographic positions, access to P-rich forage in glades is clearly important for meeting dietary demands (Figure 3). Within the nutrient-poor red sands habitat, P content of grasses is similar to grasslands in the Serengeti ecosystem of Tanzania, which

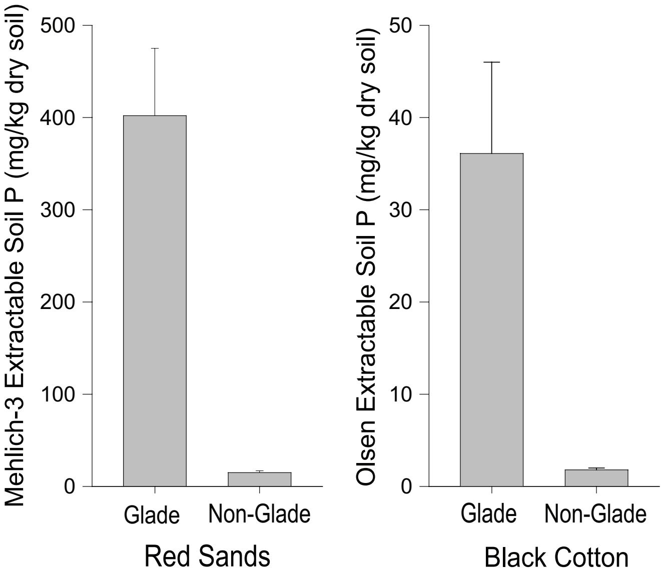

FIGURE 2. Differences in extractable soil phosphorus content of glade and surrounding nonglade soils for the red sands (four glade versus four paired nonglade sites; paired $t_3 = 4.82$, $P = 0.02$) and black cotton soil (nine glade versus nine paired nonglade sites; $t_8 = 3.48$, $P = 0.008$) at Mpala Research Centre in central Laikipia.

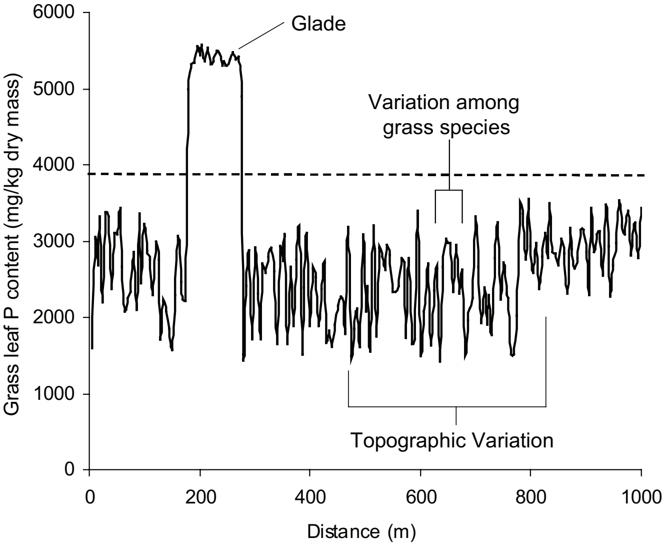

FIGURE 3. Spatial representation of variation in forage phosphorus content that an herbivore in the red sands landscape of Laikipia, Kenya, might encounter while traveling along a 1 km transect beginning at a ridge, passing through a glade, and ending in a drainage, based on forage P content analyses (Augustine, 2004) and grass species distributions in the red sands habitat (Augustine, 2003b). Variation at scales of 5–15 m results from the patchy distribution of dominant grasses. The dashed line shows the forage P requirement measured for lactating wildebeest (Murray, 1995).

migratory ungulates are only able to use during the dry season, outside of calving and peak lactation periods. In contrast, P content in glades is similar to the shortgrass Serengeti plains to which ungulate herds migrate in the wet season for calving (McNaughton, 1990). Phosphorus content in glade grasses at MRC is also similar to grassland "hot spots" in the Serengeti ecosystem that support high concentrations of resident herbivores, including impala (McNaughton, 1988). If a selectively foraging impala were able to acquire a dietary intake of 2800 mg P/kg forage from the red sands bushland habitat, for example, by foraging in lowlands and feeding on red sands grasses such as *Cynodon dactylon* and *Pennisetum stramineum*, the impala would still need to acquire an estimated 42% of its forage from glades in order to achieve an overall dietary P content of 3900 mg P/kg.

Similar measures of grass nutrient content in black cotton glades have not yet been conducted. However, the soil P and N enrichment documented in black cotton glades combined with low grass P content found in grasses on the background black cotton soil suggests that (1) grasses on black cotton glades are likely to be enriched in N and P and (2) the level of P enrichment may be important for meeting nutritional requirements of wild grazers. Quantitative measures of how grass nutrient content varies in the black cotton habitat in relation to glades versus other factors such as seasonality, termite mounds, topography, and plant community composition are clearly needed.

INFLUENCE OF ABANDONED BOMAS ON UNGULATE DISTRIBUTION

On the basis of the previous findings for forage nutrient content, it is not surprising that in the landscape encompassing both black cotton and red sands habitats, some native ungulate species exhibit preferential use of abandoned bomas. In both habitats, we used dung group surveys of transects in abandoned bomas compared to the surrounding background vegetation to quantify these patterns. In the red sands habitat, we measured dung group densities in December 1999 at (1) all known glades abandoned between 10 and 40 years ago ($n = 38$), (2) glades abandoned >40 years ago ($n = 16$), and (3) a grid of transects distributed systematically across all bushland habitat at MRC ($n = 46$). Dung groups were counted within three randomly located 20 m transects using a 2 m width for impala dung and a 4 m width for all other species at each glade site and within a 50 × 4 m area for each bushland transect. Cattle dung group counts could possibly include cape buffalo dung, but direct counts of both species indicated that buffalo were extremely rare (65 times less abundant than cattle) in the study area (D. J. Augustine, unpublished). Data were analyzed by standard one-way ANOVA, with Tukey's HSD for pairwise comparisons.

In the black cotton habitat, we measured dung group densities in August 2003 at five glades abandoned <42 years ago and five glades abandoned >42 years prior to sampling. Inside each of the 10 glade sites we identified and counted all herbivore dung within two 400 m^2 blocks (except at one site where we had only one block). We also sampled dung group densities outside of each of the 10 glade sites along two 4 × 100 m transects, one located 100 m away from the boma site and one located 200 m away. Data were analyzed as a split-plot ANOVA, treating glade age as the main plot effect and location (inside, 100 m or 200 m) as the subplot effect. Pairwise comparisons were made with planned orthogonal independent contrasts testing (1) inside versus outside and (2) 100 m versus 200 m.

In the red sands habitat, impala dung group densities were 21–35 times greater in old and young glades compared with surrounding bushland habitat (Figure 4; $F_{2,95} = 28.2$, $P < 0.0001$). For zebra (*Equus burchelli* and *E. grevyi* combined), dung group densities were four to five times greater in glades compared with surrounding bushland (Figure 4; $F_{2,95} = 11.98$, $P < 0.0001$). For eland (*Taurotragus oryx*), densities were four times greater in young glades versus bushland habitat, with intermediate densities in old glades (Figure 4; $F_{2,95} = 11.82$, $P < 0.0001$). For cattle, densities were three times greater in glades compared to surrounding bushland habitat (Figure 4; $F_{2,95} = 29.6$, $P < 0.0001$). Waterbuck (*Kobus ellipsiprymnus*) did not show significant selection for glades ($F_{2,95} = 2.19$, $P = 0.12$). The two browsers (elephant, *Loxodonta africana*, and giraffe, *Giraffa camelopardalis*) also did not select glades ($F_{2,95} < 0.65$, $P > 0.53$).

In the black cotton habitat, dung group densities of hartebeest (*Alcelaphus buselaphus*) and Grant's gazelles (*Gazella granti*) were three to seven times higher inside boma sites of both age classes relative to surrounding bushland (Figure 5; inside versus outside, hartebeest: $F_{1,16} = 5.56$, $P = 0.03$; Grant's gazelles: $F_{1,16} = 8.75$, $P = 0.01$). Cattle densities were three times higher in young glades (new: in versus out, $F_{1,16} = 3.92$, $P = 0.07$), whereas oryx (*Oryx beisa*) densities were six times higher in old glades (old: in versus out, $F_{1,16} = 8.10$, $P = .01$). Eland showed an inconsistent response to black cotton glades (location, $F_{2,16} = 0.54$, $P = 0.59$). In contrast to the red sands habitat, elephant dung density was six times higher in newer (<42 years) boma sites in black cotton habitat (new: in versus

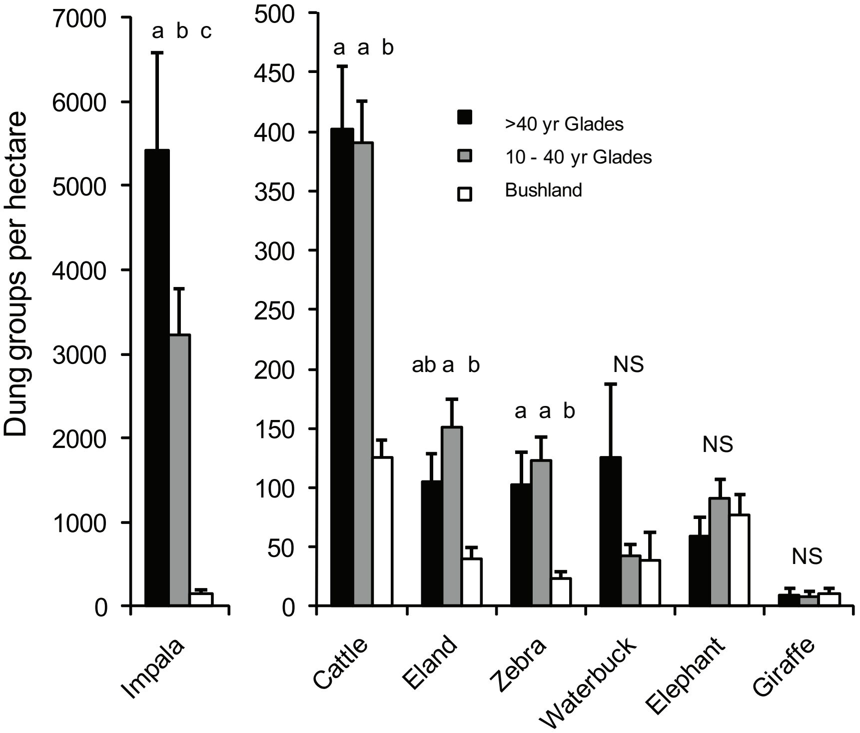

FIGURE 4. Red Soils: Selection of old glades (>40 years since boma abandonment, *n* = 16 sites) and young glades (10–40 years since boma abandonment, *n* = 38 sites) relative to surrounding bushland habitat (*n* = 44 sites) for ungulates in the red sands landscape in central Laikipia, Kenya, as indexed by dung group densities. "Zebra" includes both plains and Grevy's zebra. Error bars show 1 SE above the mean. For each species, bars with different letters indicate significant ($P < 0.05$) differences between the three habitats, and NS indicates species with no significant differences among the three habitats.

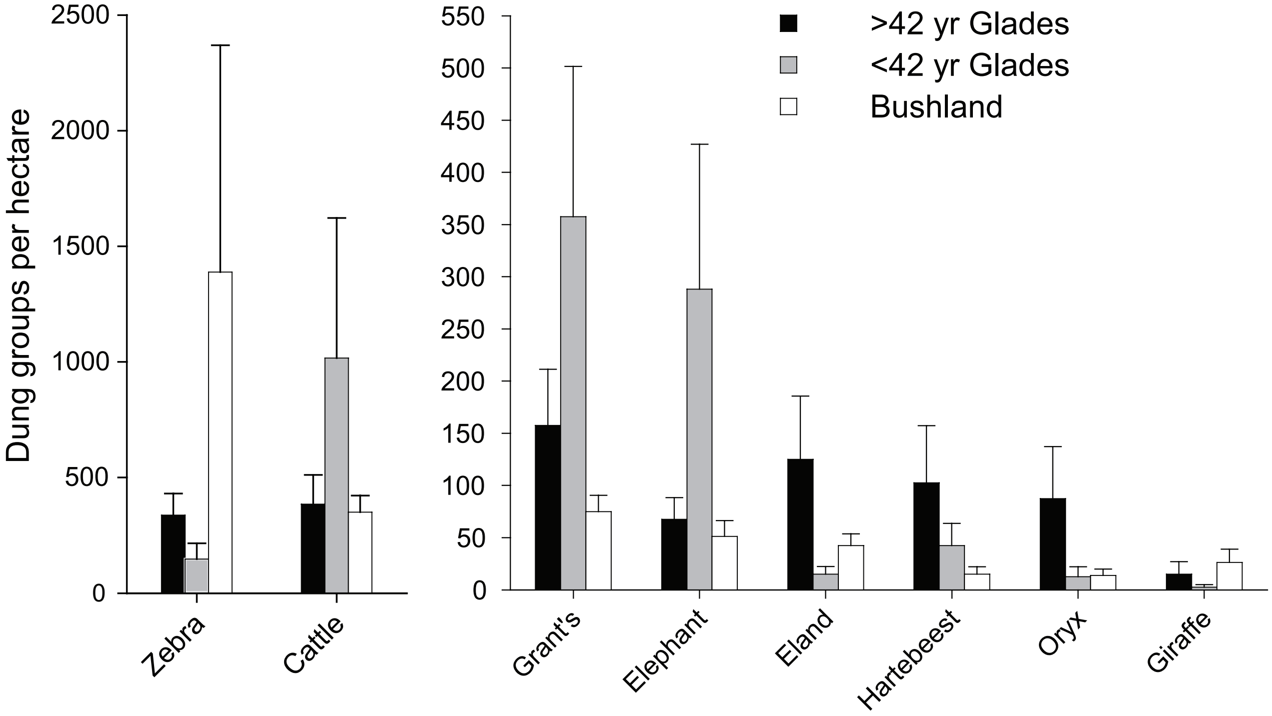

FIGURE 5. Black Soils: Selection of old glades (>42 years since boma abandonment, *n* = 5 sites) and young glades (<42 years since boma abandonment, *n* = 5 sites) relative to surrounding savanna habitats (100–200 m distant from glades, *n* = 10 sites) on black cotton soil in central Laikipia, Kenya, as indexed by dung group densities. "Zebra" includes both plains and Grevy's zebra. Error bars show 1 SE. For each species, bars with different letters indicate significant ($P < 0.05$) differences between the three habitats, and NS indicates species with no significant differences among the three habitats.

out, $F_{1,16} = 5.62$, $P = 0.03$). Giraffe avoided boma sites (in versus out, $F_{1,16} = 7.67$, $P = 0.06$). Likewise, zebra densities were not elevated inside black cotton glades and instead showed a nonsignificant trend toward avoidance of glades relative to woodland (location, $F_{2,16} = 1.52$, $P = 0.25$).

We have also used infrared camera monitors to conduct more detailed analyses of how glades influence seasonal and spatial distribution of impala in the red sands habitat (Augustine, 2004). Camera monitors showed that impala preferentially used glades compared to surrounding bushland in both wet and dry seasons but increased glade use ninefold during wet compared to dry seasons (Figure 6A). Furthermore, impala density was highly correlated with the distance to the nearest glade or abandoned boma (Figure 6B), with impala density declining to extremely low levels in areas where glades were more than 600 m distant.

Overall, our studies demonstrate that across diverse soil types, the management of livestock via bomas creates nutrient hot spots within the landscape. These hot spots have a strong influence on wild ungulate distribution and potentially influence overall carrying capacity. Our work on impala showed that (1) glades are critical for meeting wet-season phosphorus requirements, (2) impala show strong preferential use of glades, especially during the wet season, and (3) portions of the landscape distant from glades support few impala. Fine-scale distribution analyses have not been conducted for other wild herbivores, but many species show clear preferential use of glades (Figures 4 and 5). Our surveys have also documented some notable differences between red sands and black cotton habitats, especially with zebra and elephant use of glades. Factors such as differences in grazing pressure or in the structure and composition of the plant communities in the two habitat types may be involved and merit future research attention.

Our studies also suggest that anthropogenic glades can contribute to the viability of ungulate species of conservation concern in the Ewaso ecosystem. Although species such as plains zebra and Grant's gazelles may be adaptable to livestock-dominated landscapes, others such as impala, hartebeest, eland, waterbuck, and buffalo may require deliberate management efforts (Georgiadis et al., 2007a). The hartebeest population in Laikipia is the largest of only three distinct populations of *A. buselaphus* remaining in Kenya that are hybrid between two morphotypes (*A. b. cokei* and *A. b. lelwel*), the remainder having been extirpated by human activities. Hartebeest have been declining in Laikipia over the past decade and serve as one of several focal species for conservation efforts in the region (Georgiadis et al., 2007b). In the black cotton habitat, hartebeest are strongly attracted to glades, especially

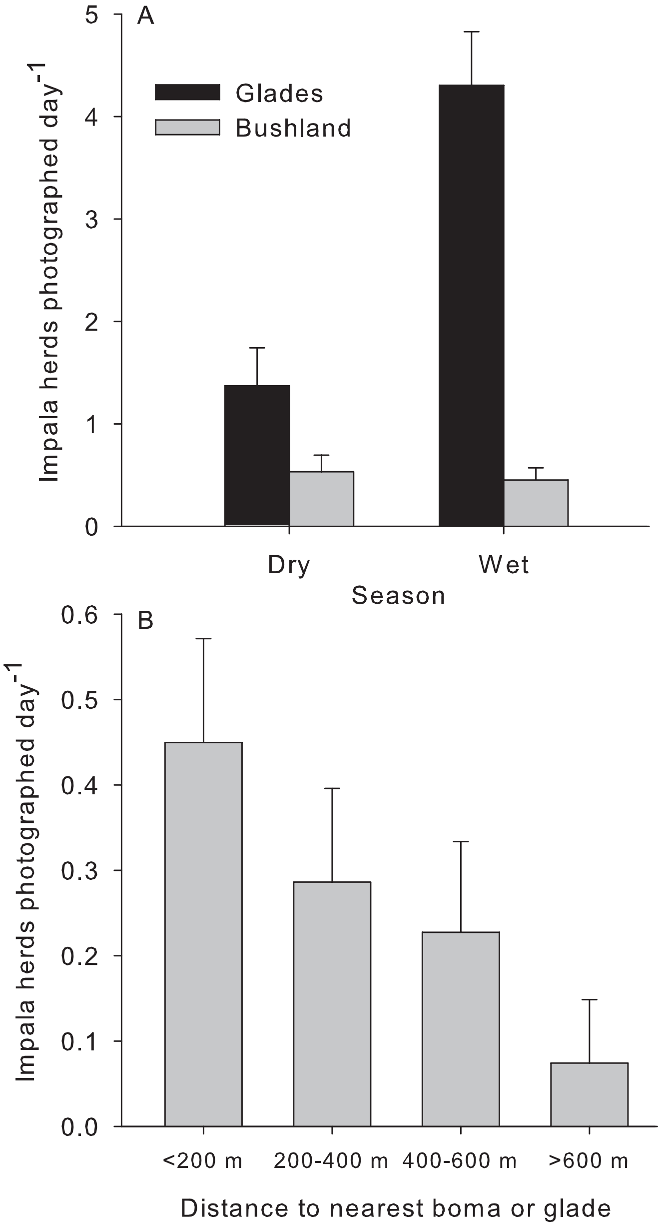

FIGURE 6. (A) Seasonal variation in the abundance of impala in glades versus adjacent red sands bushland habitat and (B) spatial variation in wet-season impala abundance within bushland habitat as a function of the distance to the nearest glade or abandoned boma in Laikipia, Kenya, 2001–2002. Impala herds were present in glades at a significantly higher rate during wet versus dry seasons (season × habitat interaction: $F_{1,27} = 23.96$, $P < 0.001$). Error bars show 1 SE above the mean, and the number above each bar in (B) shows the number of locations sampled within each distance class. Reprinted from Augustine (2004) with permission; © The Wildlife Society.

younger glades (Figure 5). Hartebeest also preferentially forage on abandoned bomas in southern Kenyan rangelands (Stelfox, 1986). Hartebeest are primarily associated with open, treeless grasslands; provision of nutrient-rich glades in combination with such open areas may be one important means to enhance habitat for the species.

The Grevy's zebra is another rare and declining species, with much of the remaining population found in the Ewaso ecosystem (Williams, 2002). Grevy's zebra at MRC are primarily found in the red sands and adjacent transitional habitats dominated by *Acacia* bushland. Grevy's zebra habitat use at MRC differs for lactating versus nonlactating mares, with lactating mares selecting the shortest, greenest grass swards in the landscape (Sundaresan et al., 2008). Abandoned bomas are the primary source of these shortgrass swards. Use of glades by Grevy's zebra may be constrained by availability of drinking water (which lactating females require frequently) and the locations of active bomas (which Grevy's zebra avoid; Sundaresan et al., 2008). Although Grevy's zebra avoid areas with herders and cattle in the short term, they also appear to benefit from long-term consequences of boma rotation. Consideration of how water sources and shrub density interact with glade distribution could assist in boma placement and rotation planning to provide critical habitat for such declining wildlife species.

Long-Term Glade Persistence

Glades in the Ewaso ecosystem persist for at least four decades and could potentially persist for centuries, as reported for nutrient-enriched patches in a southern African savanna (Blackmore et al., 1990). During 1961–2000 at MRC, bomas in the red sands habitat were abandoned at a mean rate of 1.15 per year, while long-term glades (i.e., those present in 1961) were invaded by *Pennisetum* at a rate of only 0.08 per year (Augustine, 2003a). In other words, glade density in the landscape was increasing during this four-decade period primarily because existing glades persisted in a nutrient-enriched, *Cynodon*-dominated state for well beyond 40 years. Soil nitrogen can be lost from glades over time via several pathways, including leaching, denitrification, and volatilization, such that long-term glade persistence likely depends upon nitrogen inputs to replenish these losses. Detailed analysis of glade nitrogen budgets at MRC showed that during dry seasons, impala bed within glades (Figure 6) while foraging in adjacent bushland, causing a substantial net input of nitrogen via dung and urine deposition (Augustine et al., 2003). This N input may facilitate long-term glade persistence in the *Cynodon*-dominated state and represents a pathway by which impala benefit all ungulate grazers that make use of glades, including livestock.

In the black cotton soils, there is more rapid transition from *Cynodon*-dominated glades to glades dominated by *Pennisetum stramineum* (in as few as 20–30 years), but the latter also persist for a minimum of 40 years, and probably much longer. In these black cotton soils, the long-term persistence of glades may be associated with increased termite activity (not seen in the red soil glades), which not only enriches soil fertility but also changes soil texture and reinforces the treelessness of glades. Another factor may be the length of time a boma is occupied by livestock, which in black cotton soils can be limited by rainy-season accessibility. In addition, a recent study of multiple proximate glades in black cotton soils in Laikipia (Porensky, in press) has shown that the areas between glades within 150 m of each other have elevated tree densities and concomitant low use by herbivores, perhaps because of low predator visibility (see below). This result suggests that although bomas can be useful in enhancing wildlife habitat, details of boma density, configuration, and persistence can produce emergent patterns that will also need to be considered.

Taken together, our studies have several implications for boma and nutrient management in this ecosystem. First, boma rotation is key to glade formation and hence ungulate hot spots, indicating boma placement can be used as a tool to attract wild ungulates into particular locations in the future. Fertilization at the hectare scale, particularly with phosphorus, may also be a means to induce herbivore hot spots in desired locations. Sedentarization of bomas or elimination of boma use may have negative long-term consequences for wildlife species such as impala, hartebeest, Grevy's zebra, eland, and Grant's gazelle. Long-term persistence of glades may also be contingent on use by wild ungulates. In bushlands on red soils, where shrub-free glades attract herbivores year-round, dung and urine inputs from native ungulates such as impala can prevent long-term nitrogen loss from glades and hence can maintain them in a shortgrass, *Cynodon*-dominated state (Augustine et al., 2003). In purely grassland habitats, soil and plant nitrogen in glades may decline, and *Pennisetum* cover may increase over time. However, enriched P content in glade grasses is likely to persist for decades in all soil types and to be an important wet-season forage resource for native ungulates.

NATIVE BROWSERS AND RANGELAND SHRUB ENCROACHMENT

Worldwide, rangeland ecosystems are experiencing increases in woody plant abundance and associated declines in their suitability for cattle production (Scholes and Archer, 1997; Van Auken, 2000). Shifts from grassland to shrubland may be related to changes in climate (Polley et al., 1997; Morgan et al., 2007), fire frequency and grazing intensity (Dublin et al., 1990; Roques et al., 2001; Tobler et al., 2003), and browsing pressure (Dublin et al., 1990). In some areas of Africa, woodlands have declined in protected areas coincident with a concentration of elephants into these areas (e.g., Laws, 1970; Dublin et al., 1990; Van de Vijver et al., 1999). Conversely, woodland expansion is often observed in African rangelands managed for cattle production (Scholes and Archer, 1997; Oba et al., 2000; Roques et al., 2001; Tobler et al., 2003). A consequence of lowered tree or shrub densities may be increased availability of understory nutrients (Treydte et al., 2007), whereas increased densities of trees and shrubs can negatively affect grass productivity (Scholes and Archer, 1997; Smit and Rethman, 2000). High densities of spinescent *Acacia* shrubs can also physically impede cattle access to the understory, effectively reducing forage availability.

Our studies in Laikipia have addressed the effects of native browsers on woody plant dynamics on rangelands where native fauna coexist with cattle. Here we first present baseline information on the abundance of native browsers in the red sands and black cotton landscapes and the history of woody plant dynamics in the district. We then synthesize results of exclosure studies in both red sands and black cotton soils, addressing the effect of native browsers on woody plant dynamics. Finally, we discuss the long-term implications for both cattle and wildlife.

Historic Trends in Shrubs and Browsers in the Ewaso Ecosystem

The distribution of woody vegetation and elephants across the Ewaso ecosystem has changed substantially since settlement by European ranchers in Laikipia began in 1912. As reviewed by Thouless (1995), none of the early European explorers, hunters, and ivory traders who traveled through the Ewaso ecosystem during 1880–1910 found elephants in central Laikipia, and this area consisted mostly of open grass plains. Laikipia is now dominated by *Acacia* bushland on red soils and contains extensive areas of *A. drepanolobium* woodland on black cotton soils (Taiti, 1992; Young et al., 1998; Augustine, 2003b; Table 1). As recently as a few decades ago, much of Laikipia was open grassland on both the red and black soils (Heady, 1960; T. P. Young, personal communications with living ranch owners and herders).

Early in the twentieth century, elephants in this region were found only in Samburu district to the north of Laikipia, but by the 1950s elephants were increasing and expanding their range toward Laikipia (Thouless, 1995). Heavy poaching during the 1970s and 1980s strongly affected elephant numbers and distribution in Samburu. By the 1990s, telemetry studies identified a significant population of elephants (estimated at ~800 individuals) that regularly migrated 80–100 km between pastoral rangelands in Samburu and the commercial ranches in Laikipia (Thouless, 1995). Our studies have examined savanna dynamics on the commercial rangelands in Laikipia utilized by this migratory elephant population. Our own surveys of ungulate densities at MRC during 2000–2002 (distance sampling of 93 km of ground transects in the red sands habitat at 6 month intervals; densities calculated following Thomas et al., 1998) show a continued migration of substantial numbers of elephants into this region during June–October each year (Table 2). In addition, the *Acacia* bushland habitat on the red soils supports high densities of dik-dik, a small antelope that forages predominantly on woody vegetation (Table 2). Dik-dik were unlikely to have been abundant in grasslands that dominated Laikipia early in the twentieth century. Rather, the high abundance of dik-dik and migratory elephants are likely a response, in part, to increases in woody vegetation. Other browsing species also likely to have increased as the density of woody species has increased include giraffe, eland, steinbuck, and kudu.

Current landscape-scale estimates of shrub and tree cover in central Laikipia are approximately 28% for the red sands (Augustine, 2003b) and 31% for the black cotton soils (Riginos et al., 2009). A continental-scale analysis of woody cover in African savannas predicts that in the long-term absence of disturbances (i.e., no browsers or

TABLE 2. Densities of dik-dik and elephant (number/km^2) in the red sands habitat at Mpala Research Centre during dry seasons (March) and wet seasons (August) of 2000–2002. CI, confidence interval.

	Dik-dik		**Elephant**	
Season	**Mean density**	**95% CI**	**Mean density**	**95% CI**
2000 dry season	130	(99, 170)	0.0	(0.0, 0.0)
2000 wet season	140	(102, 194)	5.2	(1.4, 19.8)
2001 dry season	139	(106, 182)	0.04	(0.01, 0.39)
2001 wet season	139	(119, 164)	2.9	(1.3, 6.4)
2002 dry season	145	(121, 173)	0.3	(0.1, 1.7)
Five-survey mean	139	(124, 156)	1.7	(0.8, 3.4)

fire), the rainfall-limited bound for woody cover on both soil types in central Laikipia based on 500 mm mean annual precipitation is approximately 56% (Sankaran et al., 2005). Continued increases in shrub and tree abundance toward this maximum could have at least two negative effects on herbivores. First, high densities of shrubs and trees can substantially suppress grass production (Smit and Rethman, 2000; Smit, 2004) and hence reduce forage for cattle. In the black cotton habitats, sites with a low density of trees were found to have double the grass production as sites with a high density of trees (Riginos et al., 2009). Further research is needed to quantify the effects of tree density on grass productivity in the red sands habitat. Second, woody encroachment is likely to directly affect some native wild herbivores by reducing the quality of the habitat available to them. In the black cotton habitat, a recent study examined patterns of herbivore use in *A. drepanolobium* woodland habitats that varied from 240 to 2,784 trees per hectare, or 6 to 45% canopy cover. All but the largest herbivore species (elephants) spent significantly more time in areas with low tree density and avoided areas with high tree density (Riginos and Grace, 2008). This preference was independent of grass cover or species composition. Rather, herbivore habitat preference was strongly related to visibility; in more open habitat with low tree density and cover, predators are more visible, making those areas favorable for vulnerable herbivore species. Thus, areas with high tree density represent lower-quality habitat for small- and medium-sized herbivores, including the declining hartebeest. Areas with high tree density, in contrast, actually attracted elephants and experienced more damage per tree (Riginos and Grace, 2008). These relationships suggest that elephants and other native browsers can have important feedbacks on landscape-scale woody vegetation dynamics, with potential benefits to native grazers and cattle alike.

EFFECTS OF NATIVE BROWSERS ON SHRUB AND TREE DYNAMICS IN LAIKIPIA

Two large-scale herbivore exclusion experiments at MRC have demonstrated the effects of native browsers on shrubs and trees. In 1999, a set of exclosures was established in the red sands habitat to examine effects of browsers on bushlands dominated by *A. mellifera*, *A. etbaica*, and *A. brevispica* (Augustine and McNaughton, 2004). Exclusion of browsers for just three years led to rapid shrub encroachment, measured in terms of shrub cover, density, and biomass (see Table 4). This response was due to the effects of two vastly different native species. First, high densities of dik-dik (*Madoqua kirkii*) strongly suppressed growth of shrubs less than 0.5 m high; exclusion of dik-dik led to rapid recruitment of shrubs into taller height classes, which was the primary determinant of increases in shrub density. Second, browsing elephants focused mainly on large (>2.5 m high) shrubs, significantly suppressing rates of change in shrub cover and aboveground biomass (Augustine and McNaughton, 2004).

On the black cotton soils, the Kenya Long-term Exclusion Experiment (KLEE), initiated in 1995, has examined browser effects on woodland dynamics (Young et al., 1998). Studies at this site have confirmed that cattle do not eat the dominant woody plant, *Acacia drepanolobium* (Odadi et al., 2007), whereas native browsers regularly feed on this species. We used three measurements from the KLEE plots to examine how the exclusion of native browsers has affected woodland encroachment in this ecosystem. First, we monitored annual changes in size of *A. drepanolobium* in KLEE plots from which all large herbivores have been excluded and in KLEE plots to which all large herbivores have access. Briefly, we measured crown breadth, diameter at breast height, and height of all *A. drepanolobium* trees in two 150 × 10 m strip transects at each plot each year during 2004–2007 (see Goheen et al., 2007). We use this data set to quantify differences in canopy cover of adult *A. drepanolobium* (>1 m) between the ninth and twelfth year of large-herbivore exclusion and also changes in height of large trees (>2.5 m) during this time. Second, we measured the height, diameter at 30 cm above ground, and location for every tree >1 m tall within the central hectare of plots exposed to large herbivores and plots from which large herbivores had been excluded. We use these data to compare differences in density and biomass of *A. drepanolobium* stemming from the 10 year exclusion of large herbivores. Third, we measured the cover of all shrub species other than *A. drepanolobium* in the KLEE plots in 2001, which we use to quantify effects of herbivores on the rare shrub species after six years of herbivore exclusion. We used mixed-model ANOVA to analyze these measurements, treating large-herbivore exclusion as a fixed factor and replicate as a random factor.

Large herbivores reduced the density of tall (>1.0 m) *A. drepanolobium* by 32% ($F_{1,2}$ = 16.14, P = 0.06), reduced mean canopy cover by 28% ($F_{1,2}$ = 2.54, P = 0.25), and reduced woody biomass of *Acacia drepanolobium* by 29% ($F_{1,2}$ = 5.88, P = 0.14; Figure 7). Even more dramatic was the increase in canopy cover of the several species of subordinate trees and shrubs, which accounted for a relatively small fraction of total woody abundance (Table 3). Density of subordinate species was not affected by the exclosure treatment, but established plants that had been suppressed by constant browsing were released when

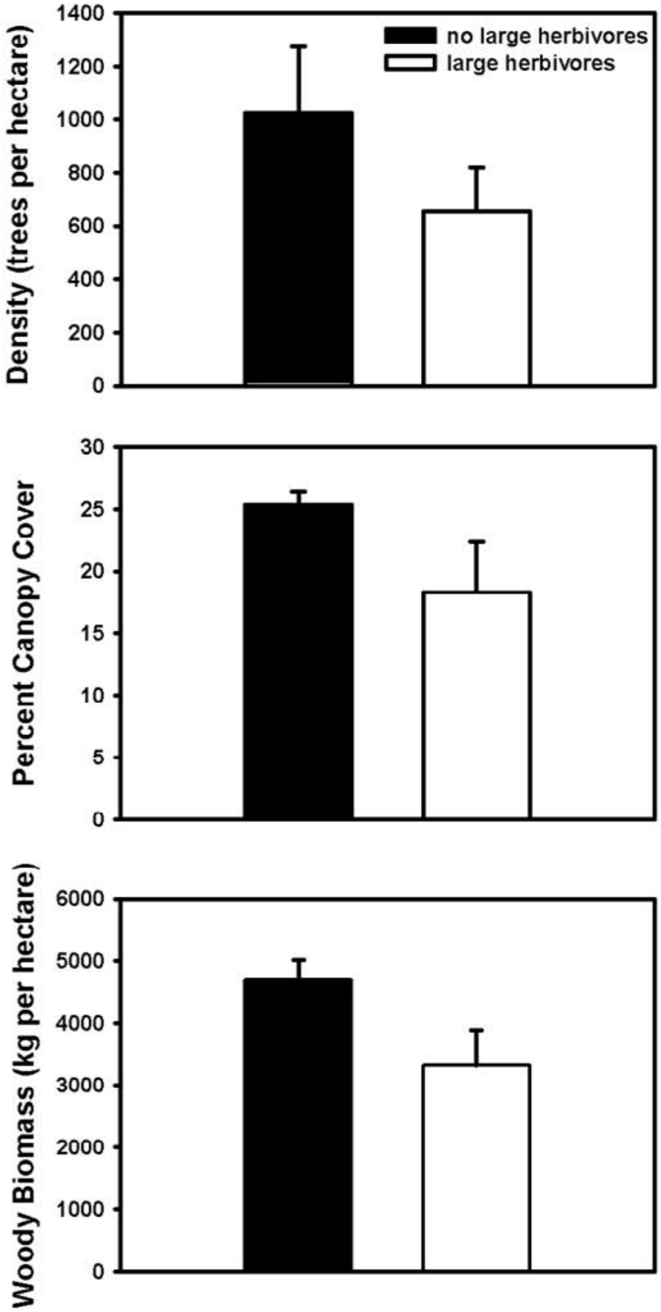

FIGURE 7. Effects of removing large herbivores on the density of tall (>1.0 m) individuals, percent canopy cover, and woody biomass of *Acacia drepanolobium* in the Kenya Long-term Exclusion Experiment. Error bars show 1 SE above the mean; *n* = 3 exclosures and 3 paired control sites for each comparison.

protected from herbivory. The mean canopy sizes of some species increased by as much as twentyfold, and the percent contribution to woody cover across all these species was 12.8% in exclosures compared to 3.8% in the presence of browsers (Table 3).

Our studies have shown that browsers strongly influence woody vegetation dynamics in both soil types, and they also highlight differences in the strength of browser effects (Table 4). Following the experimental removal of native browsers, the cover, density, and biomass of shrubs have been increasing on both soils, but at three to seven times greater rates on red sands compared to black cotton soils (Table 4). One potential factor underlying these rate differences may be high dik-dik densities combined with substantial elephant browsing pressure in the red sands, compared to elephants being the only high-density browser in the black cotton habitat.

A second important factor influencing shrub encroachment rates may be differences in herbivore resistance traits of the dominant *A. drepanolobium* on black cotton soils compared to the dominant *Acacia* species in the red sands. Results for the subdominant shrub species on the black cotton soil, which showed a fourfold increase in cover over just six years (Table 3), also indicate that browsers exert less control over *A. drepanolobium* compared to other co-occurring woody species. Ant symbionts that occur on *A. drepanolobium* effectively protect host trees and greatly reduce browse intake by elephants (Goheen and Palmer, 2010). In addition, subordinate species in the black cotton habitat may experience low rates of growth and reproduction on black cotton soils relative to red soils and therefore may not be able to compensate after being browsed by large herbivores (Harper, 1969; Holt and Lawton, 1994). Fire is another management tool that has substantial potential to influence shrub dynamics and interact with the effects of browsing ungulates (Dublin et al., 1990). There is widespread belief among ranchers, pastoralists, herders, and ecologists that fire, and probably intentional burning, was once far more frequent and widespread in Laikipia in previous centuries and that it suppressed woody plant densities. Fire effects may be stronger in the black cotton habitat because of the continuous understory grass cover, but grass cover in the red sands would likely have been great enough in at least some years to carry a fire. In addition, there can be synergistic effects of fires and herbivores. In a recent study in the black cotton habitat at MRC, burnt *A. drepanolobium* trees were found to survive the fires themselves but later to succumb to increased browsing pressure in the burned areas (Okello et al., 2008). Using ground and satellite-derived measurements of canopy cover, we estimate that although shrub cover on unburned KLEE plots accessible to native wild herbivores was 18% (Figure 7), the combination of fire and native herbivore presence reduced average canopy cover to 13%. These findings emphasize the need to understand herbivore responses to

TABLE 3. Differences in canopy cover of nine subdominant shrub species in the black cotton habitat after six years of large-herbivore exclusion. Although these species are typically rare within the plant community, following browser exclusion, they exhibited more rapid rates of increase than the dominant woody species, *Acacia drepanolobium*. For three species, there was insufficient sample size for reliable statistical analysis. Here n.a. denotes statistic is not applicable.

	Mean Percent Canopy Cover				
Species	Herbivores excluded	Herbivores present	Ratio	*F*	*P*
Cadaba farinosa	3.36	1.42	2.4	15.5	0.0002
Balanites aegyptiaca	4.23	1.06	4.0	36.4	<0.0001
Acacia mellifera	2.95	0.89	3.3	4.59	0.038
Lycium europaeum	0.86	0.36	2.4	n.a.	n.a.
Rhus natalensis	0.92	0.04	22.0	2.72	0.14
Grewia spp.	0.17	0.02	6.9	7.80	0.019
Boscia angustifolia	0.15	0.03	4.4	3.67	0.07
Acacia brevispica	0.14	0.01	10.6	n.a.	n.a.
Lippia javanica	0.05	0.004	12.5	n.a.	n.a
Total	**12.82**	**3.84**	**3.3**	n.a.	n.a.

fires in semiarid rangelands in order to take full advantage of burning as a management tool.

CONCLUSIONS

Two themes in African wildlife conservation have emerged over the past decade. The first is the underlying importance of habitat heterogeneity across multiple spatial scales in sustaining biodiversity (du Toit et al., 2003; Cromsigt and Olff, 2006). The second is the critical role of nonprotected lands, especially managed rangelands, in sustaining Africa's large mammalian fauna (Prins et al., 2000). These themes are related, in that protected areas of Africa often do not encompass sufficient heterogeneity across scales to maintain the range of habitats that sustain diverse and abundant mammalian communities. Our studies show that facilitation via habitat modification is an important pathway for cattle-wildlife interactions in semiarid rangelands. First, nutrient-enriched patches created by abandoned cattle bomas can persist for decades to centuries and provide a key source of nutrient-rich forage for both native and domestic grazers. Nutrient-rich glades that develop from abandoned bomas in the red sands habitat not only sustain local impala abundance but are also maintained as glades by nitrogen inputs from impala (Augustine et al., 2003). Such feedbacks and interactions among cattle bomas, soil and plant nutrients, and wild ungulates indicate that ranch managers can influence the long-term distribution and abundance of wild ungulates though the placement and rotation of current bomas. Second, although cattle can directly compete with native grazers for forage (Young et al., 2005), native browsing ungulates can provide an important compensatory benefit to cattle by controlling shrub encroachment. There is even evidence that the ability of elephants to reduce forb cover may interact with effects of cattle grazing in a manner that reduces competition between cattle and zebra (Young et al., 2005). Soils have a strong influence on the structure of woody plant communities and rates of shrub encroachment, but the influence of native browsers appears to be robust across such variation.

To directly measure the importance of such facilitation through habitat modification, we would ideally compare ranches with dynamic boma management and the presence of native fauna to ranches where bomas are not rotated and native fauna are excluded. An example of the latter is provided by a large ranching enterprise in the coastal savannas of Tanzania. There the 462 km^2 Mkwaja ranch was managed for cattle production using a system of permanent paddocks where cattle were kept at night; native ungulates were rare throughout the property (Tobler et al., 2003; Treydte et al., 2006). Over a 48 year period, this intensive, cattle-only ranching operation proved to be economically and ecologically unsustainable, primarily because of severe bush encroachment that developed in

TABLE 4. Summary of the effects of native browsing ungulates on woody plant dynamics at the Mpala Research Centre in central Laikipia, Kenya. Browser effects in the red sands habitat are from Augustine and McNaughton (2004) and Young and Augustine (2007). Browser effects in the black cotton habitat are derived from Gadd et al. (2001), Goheen et al. (2007), Riginos and Young (2007), and this chapter (see Figure 7).

Dynamic	Red sands (*A. etbaica* and *A. mellifera*)	Black cotton (*A. drepanolobium*)
Seed production	No effect	Reduced by half in the presence of browsers
Twig growth rate	Annual twig growth rates negative or zero in the presence of dik-diks; positive and rapid in the absence of dik-diks; no detectable browser effects above dik-dik foraging height	Simulated giraffe browsing resulted in compensatory twig regrowth (i.e., no negative short-term effect on twig biomass), but this may occur at the expense of long-term growth and/or seed production
Sapling recruitment	Recruitment into 0.5–1.5 m height class reduced sixfold by browsers, primarily due to effects of dik-dik	Enhanced in the presence of large herbivores, despite suffering greater browse damage; enhanced recruitment likely due to reduced density of conspecific adult trees
Shrub growth in large size class	Browser presence reduced canopy volume and height for shrubs >2.5 m tall, primarily due to elephant damage	Browser presence reduced vertical growth by 49% over three years for trees >2.5 m tall, primarily due to elephant damage
Net browser effect on woody plant abundance		
Change in shrub density	No change in the presence of browsers; rapidly increasing (+137 individuals ha^{-1} yr^{-1}) with browser removal	Adult trees >1.0 m increasing (+37 individuals ha^{-1} yr^{-1}) with browser removal
Change in shrub cover	Shrub cover increasing rapidly with browser removal (+1.92% per year) and declining (–0.75% per year) in the presence of browsers	*A. drepanolobium* cover increasing slowly with browser removal (+0.7% per year); cover of other shrub species three times greater after six years of browser exclusion.
Woody biomass accumulation	Near zero (–26 kg ha^{-1} yr^{-1}) in the presence of browsers; rapidly increasing (+962 kg ha^{-1} yr^{-1}) with browser removal.	Increasing with browser removal (+137 kg ha^{-1} yr^{-1})

wide bands around the permanent paddocks (Tobler et al., 2003). Similarly in Laikipia, ranches intolerant of browsing wildlife are often characterized by greater tree densities. Although numerous ecological factors differ between coastal savanna and the Ewaso ecosystem, the long-term patterns observed in these rangelands illustrate the potential importance of boma rotation and browsing ungulates in sustaining the Ewaso ecosystem.

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REFERENCES

Ahn, P. M., and L. C. Geiger. 1987. Kenya Soil Survey: Soils of Laikipia District. Kabete, Kenya: Ministry of Agriculture, National Agricultural Laboratories.

Arsenault, R., and N. Owen-Smith. 2002. Facilitation versus Competition in Grazing Herbivore Assemblages. *Oikos*, 97:313–318.

Augustine, D. J. 2003a. Long-Term, Livestock-Mediated Redistribution of Nitrogen and Phosphorous in an East African Savanna. *Journal of Applied Ecology*, 40:137–149.

———. 2003b. Spatial Heterogeneity in the Herbaceous Layer of a Semi-arid Savanna Ecosystem. *Plant Ecology,* 167:319–332.

———. 2004. Influence of Cattle Management on Habitat Selection by Impala on Central Kenyan Rangeland. *Journal of Wildlife Management*, 68:916–923.

Augustine, D. J., and S. J. McNaughton. 2004. Regulation of Shrub Dynamics by Native Browsing Ungulates on East African Rangeland. *Journal of Applied Ecology,* 41:45–58.

Augustine, D. J., S. J. McNaughton, and D. A. Frank. 2003. Feedbacks between Soil Nutrients and Large Herbivores in a Managed Savanna Ecosystem. *Ecological Applications,* 13:1325–1337.

Bell, R. V. H. 1971. A Grazing Ecosystem in the Serengeti. *Scientific American,* 224:86–93.

———. 1982. "The Effect of Soil Nutrient Availability on Community Structure in African Ecosystems." In *Ecology of Tropical Savannas*, ed. B. J. Huntley and B. H. Walker, pp. 193–216, New York: Springer-Verlag.

Ben-Shahar, R., and M. Coe. 1992. The Relationships between Soil Factors, Grass Nutrients and the Foraging Behaviour of Wildebeest and Zebra. *Oecologia,* 90:422–428.

Blackmore, A. C., M. T. Mentis, and R. J. Scholes. 1990. The Origin and Extent of Nutrient-Enriched Patches within a Nutrient-Poor Savanna in South Africa. *Journal of Biogeography*, 17:463–470.

Brody, A. K., T. M. Palmer, K. Fox-Dobbs, and D. F. Doak. 2010. Termites, Vertebrate Herbivores, and the Fruiting Success of *Acacia drepanolobium*. *Ecology,* 91:399–407. (doi:10.1890/09-0004.1).

Cromsigt, J., and H. Olff. 2006. Resource Partitioning Among Savanna Grazers Mediated by Local Heterogeneity: An Experimental Approach. *Ecology,* 87:1532–1541.

de Leeuw, J., M. Waweru, O. Okello, M. Maloba, P. Nguru, M. Said, H. Aligula, I. Heitkonig, and R. Reid. 2001. Distribution and Diversity of Wildlife in Northern Kenya in Relation to Livestock and Permanent Water Points. *Biological Conservation,* 100:297–306.

Derner, J., J. Detling, and M. Antolin. 2006. Are Livestock Weight Gains Affected by Black-Tailed Prairie Dogs? *Frontiers in Ecology and the Environment,* 4:459–464.

Dublin, H., A. Sinclair, and J. McGlade. 1990. Elephants and Fire as Causes of Multiple Stable States in the Serengeti-Mara Woodlands. *Journal of Animal Ecology,* 59:1147–1164.

du Toit, J. T., K. H. Rogers, and H. C. Biggs, eds. 2003. *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Washington, D.C.: Island Press.

Fritz, H., and P. Duncan. 1994. On the Carrying Capacity for Large Ungulates of African Savanna Ecosystems. *Proceedings of the Royal Society of London, Series B,* 256:77–82.

Fox-Dobbs, K., D. F. Doak, A. K. Brody, and T. M. Palmer. 2010. Termites Create Spatial Structure and Govern Ecosystem Function by Affecting N2 Fixation in an East African Savanna. *Ecology,* 91:1296–1307.

Gadd, M., T. Young, and T. Palmer. 2001. Effects of Simulated Shoot and Leaf Herbivory on Vegetative Growth and Plant Defense in *Acacia drepanolobium*. *Oikos,* 92:515–521.

Georgiadis, N., F. Ihwagi, J. Olwero, and S. Romanach. 2007b. Savanna Herbivore Dynamics in a Livestock-Dominated Landscape. II: Ecological, Conservation, and Management Implications of Predator Restoration. *Biological Conservation*, 137:473–483.

Georgiadis, N., J. Olwero, G. Ojwang, and S. Romanach. 2007a. Savanna Herbivore Dynamics in a Livestock-Dominated Landscape: I. Dependence on Land Use, Rainfall, Density, and Time. *Biological Conservation,* 137:461–472.

Goheen, J. R., and T. M. Palmer. 2010. Defensive Plant-Ants Stabilize Megaherbivore-Driven Landscape Change in an African Savanna. *Current Biology*, 20(19):1768–1772.

Goheen, J. R., T. P. Young, F. Keesing, and T. M. Palmer. 2007. Consequences of Herbivory by Native Ungulates for the Reproduction of a Savanna Tree. *Journal of Ecology*, 95:129–138.

Gordon, I. J. 1988. Facilitation of Red Deer Grazing by Cattle and Its Impact on Red Deer. *Journal of Applied Ecology,* 25:1–10.

Harper, J. L. 1969. The Role of Predation in Vegetational Diversity. *Brookhaven Symposia in Biology,* 22:48–62.

Heady, H. F. 1960. *Range Management in East Africa.* Nairobi: Kenya Department of Agriculture.

Holt, R. D., and J. H. Lawton. 1994. The Ecological Consequences of Shared Natural Enemies. *Annual Review of Ecology and Systematics,* 25:495–520.

Hobbs, N. T., D. L. Baker, G. D. Bear, and D. C. Bowden. 1996. Ungulate Grazing in Sagebrush Grassland: Effects of Resource Competition on Secondary Production. *Ecological Applications*, 6:218–227.

Laws, R. M. 1970. Elephants as Agents of Habitat and Landscape Change in East Africa. *Oikos,* 21:1–15.

McDowell, L. R. 1985. *Nutrition of Grazing Ruminants in Warm Climates*. New York: Academic Press.

McNaughton, S. J. 1988. Mineral Nutrition and Spatial Concentrations of African Ungulates. *Nature*, 334: 343–345.

———. 1990. Mineral Nutrition and Seasonal Movements of African Migratory Ungulates. *Nature,* 345:613–615.

Mehlich, A. 1984. Mehlich 3 Soil Test Extractant: A Modification of Mehlich 2 Extractant. *Communications in Soil Science and Plant Analysis*, 15:1409–1416.

Morgan, J. A., D. G. Milchunas, D. R. LeCain, M. West, and A. R. Mosier. 2007. Carbon Dioxide Enrichment Alters Plant Community Structure and Accelerates Shrub Growth in the Shortgrass Steppe. *Proceedings of the National Academy of Sciences of the United States of America*, 104:14,724–14,729.

Muchiru, A. N., D. J. Western, and R. S. Reid. 2009. The Impact of Abandoned Pastoral Settlements on Plant and Nutrient Succession in an African Savanna Ecosystem. *Journal of Arid Environments*, 73:322–331.

———. 2008. The Role of Abandoned Pastoral Settlements in the Dynamics of African Large Herbivore Communities. *Journal of Arid Environments*, 72:940–952.

Murray, M. 1995. "Specific Nutrient Requirements and Migration of Wildebeest." In *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem,* ed. P. Arcese and A. Sinclair, pp. 231–256. Chicago: University of Chicago Press.

Oba, G., E. Post, P. Syvertsen, and N. Stenseth. 2000. Bush Cover and Range Condition Assessments in Relation to Landscape and Grazing in Southern Ethiopia. *Landscape Ecology*, 15:535–546.

Odadi, W. O., T. P. Young, and J. B. Okeyo-Owuor. 2007. The Effects of Wild Herbivores on Cattle Diet in Laikipia Rangeland, Kenya. *Rangeland Ecology and Management*, 60:179–185.

———. 2009. The Effects of Wild Herbivores on Cattle Intake and Movement Rates in Laikipia Rangeland, Kenya. *Applied Animal Behaviour Science,* 116:120–125.

Okello, B. D., T. P. Young, C. Riginos, D. Kelly, and T. O'Connor. 2008. Short-Term Survival and Long-Term Mortality of *Acacia drepanolobium* after a Controlled Burn in Laikipia, Kenya. *African Journal of Ecology,* 46:395–401.

Olff, H., M. Ritchie, and H. Prins. 2002. Global Environmental Controls of Diversity in Large Herbivores. *Nature,* 415:901–904.

Olsen, S. R., and L. E. Sommers. 1982. "Phosphorus." In *Methods of Soil Analysis*: *Part 2. Chemical and Microbiological Properties*, ed. A. L. Page, pp. 403–430. Agronomy Monograph 9. 2nd ed. Madison, Wis.: American Society of Agronomy and Soil Science Society of America.

Polley, H., H. Mayeux, H. Johnson, and C. Tischler. 1997. Viewpoint: Atmospheric CO_2, Soil Water, and Shrub/Grass Ratios on Rangelands. *Journal of Range Management,* 50:278–284.

Porensky, L. M. In press. When Edges Meet: Interacting Edge Effects in an African Savanna. *Journal of Ecology*.

Prins, H. H. T. 2000. "Competition between Wildlife and Livestock in Africa." In *Wildlife Conservation by Sustainable Use,* ed. H. H. T. Prins, J. G. Grootenhuis, and T. T. Dolan, pp. 5–80. Boston: Kluwer Academic Publishers.

Prins, H. H. T., J. G. Grootenhuis, and T. T. Dolan, eds. 2000. *Wildlife Conservation by Sustainable Use*. Boston: Kluwer Academic Publishers.

Riginos, C., and J. B. Grace. 2008. Savanna Tree Density, Herbivores, and the Herbaceous Community: Bottom-up vs. Top-down Effects. *Ecology,* 89:2228–2238.

Riginos, C., J. B. Grace, D. J. Augustine, and T. P . Young. 2009. Local versus Landscape-Scale Effects of Savanna Trees on Grasses. *Journal of Ecology,* 97:1337–1345.

Riginos, C., and T. P. Young. 2007. Positive and Negative Effects of Grasses and Wild and Domestic Herbivores on *Acacia* Saplings. *Oecologia*, 153:985–995.

Roques, K., T. O'Connon, and A. Watkinson. 2001. Dynamics of Shrub Encroachment in an African Savanna: Relative Influences of Fire, Herbivory, Rainfall and Density Dependence. *Journal of Applied Ecology*, 38:268–280.

Sankaran, M., N. P. Hanan, R. J. Scholes, J. Ratnam, D. J. Augustine, B. S. Cade, J. Gignoux, S. I. Higgins, X. Le Roux, F. Ludwig, J. Ardo, F. Banyikwa, A. Bronn, G. Bucini, K. K. Caylor, M. B. Coughenour, A. Diouf, W. Ekaya, C. J. Feral, E. C. February, P. G. H. Frost, P. Hiernaux, H. Hrabar, K. L. Metzger, H. H. T. Prins, S. Ringrose, W. Sea, J. Tews, J. Worden, and N. Zambatis.2005. Determinants of Woody Cover in African Savannas. *Nature,* 438:846–849.

Scholes, R., and S. Archer. 1997. Tree-Grass Interactions in Savannas. *Annual Review of Ecology and Systematics*, 28:517–544.

Smit, G. N. 2004. An Approach to Tree Thinning to Structure Southern African Savannas for Long-Term Restoration from Bush Encroachment. *Journal of Environmental Management*, 71:179–191.

Smit, G. N., and N. F. G. Rethman. 2000. The Influence of Tree Thinning on the Soil Water in a Semi-arid Savanna of Southern Africa. *Journal of Arid Environments,* 44:41–59.

Stelfox, J. B. 1986. Effects of Livestock Enclosures (Bomas) on the Vegetation of the Athi Plains, Kenya. *African Journal of Ecology*, 24:41–45.

Sundaresan, S., I. Fischhoff, H. Hartung, P. Akilong, and D. Rubenstein. 2008. Habitat Choice of Grevy's Zebras (*Equus grevyi*) in Laikipia, Kenya. *African Journal of Ecology,* 46:359–364, doi:10.1111/j.1365-2028.2007.00848.x.

Taiti, S. W. 1992. The Vegetation of Laikipia District, Kenya. *Laikipia-Mount Kenya Papers B-2*. Bern, Switzerland: Laikipia Research Programme, University of Nairobi and University of Bern,.

Thomas, L., J. Laake, J. Durry, S. Buckland, D. Borcher, D. Anderson, K. Burndam, S. Strindberg, S. Hedley, M. Burt, F. Marques, J. Pollard, and R. Fewster. 1998. DISTANCE 3.5. Research Unit for Wildlife Population Assessment. St. Andrews, U.K.: University of St. Andrews.

Thouless, C. R. 1995. Long Distance Movements of Elephants in Northern Kenya. *African Journal of Ecology,* 33:321–334.

Tobler, M. W., R. Cochard, and P. J. Edwards. 2003. The Impact of Cattle Ranching on Large-Scale Vegetation Patterns in a Coastal Savanna in Tanzania. *Journal of Applied Ecology,* 40:430–444.

Treydte, A. C., S. M. Bernasconi, M. Kreuzer, and P. J. Edwards. 2006. Diet of the Common Warthog (*Phacochoerus africanus*) on Former Cattle Grounds in a Tanzanian Savanna. *Journal of Mammalogy* 87:889–898.

Treydte, A. C., I. M. A. Heitkonig, H. H. T. Prins, and F. Ludwig. 2007. Trees Improve Grass Quality for Herbivores in African Savannas. *Perspectives in Plant Ecology, Evolution and Systematics*, 8:197–205.

Tuttle, E. M., L. Wulfson, and T. Caraco. 1990. Risk-Aversion, Relative Abundance of Resources and Foraging Preference. *Behavioural Ecology and Sociobiology,* 26:165–172.

Van Auken, O. W. 2000. Shrub Invasions of North American Semiarid Grasslands. *Annual Review of Ecology and Systematics,* 31:197–215.

Van de Vijver, C., C. Foley, and H. Olff. 1999. Changes in the Woody Component of an East African Savanna during 25 Years. *Journal of Tropical Ecology,* 15:545–564.

Van Soest, P. J. 1994. *Nutritional Ecology of the Ruminant*. Ithaca, N.Y.: Cornell University Press.

Veblen, K. E., and T. P. Young. 2010. Contrasting Effects of Cattle and Wildlife on the Vegetation Development of a Savanna Landscape Mosaic. *Journal of Ecology*, 98:993–1001.

Verweij, R. J. T., J. Verrelst, P. E. Loth, I. M. A. Heitkonig, and A. M. H. Brunsting. 2006. Grazing Lawns Contribute to the Subsistence of Mesoherbivores on Dystrophic Savannas. *Oikos,* 114:108–116.

Western, D. 1989. "Conservation without Parks: Wildlife in the Rural Landscape." In *Conservation for the Twenty-First Century*, ed. D. Western and M. C. Pearl, pp. 158–165. New York: Oxford University Press.

Whitehead, D. C., 1995. "Consumption, Digestion and Excretion of Nitrogen by Ruminant Livestock." In *Grassland Nitrogen*, pp. 59–81. Oxon, U.K.: CAB International.

Williams, S. D. 2002. Status and Action Plan for the Grevy's zebra (*Equus grevyi*). In *Equids: Zebras, Asses, and Horses: Status Survey and Conservation Action Plan*, ed. P. D. Moehlman, pp. 11–27. Gland, Switzerland: International Union for Conservation of Nature.

Young, T. P., and D. J. Augustine. 2007. Interspecific Variation in the Reproductive Response of *Acacia* Species to Protection from Large Mammalian Herbivores. *Biotropica*, 39:559–561.

Young, T. P., B. Okello, D. Kinyua, and T. M. Palmer. 1998. KLEE: A Long-Term, Multi-species Herbivore Exclusion Experiment in Laikipia, Kenya. *African Journal of Range and Forage Science,* 14:92–104.

Young, T. P., T. M. Palmer, and M. E. Gadd. 2005. Competition and Compensation among Cattle, Zebras, and Elephants in a Semi-arid Savanna in Laikipia, Kenya. *Biological Conservation*, 122:351–359.

Young, T. P., N. Partridge, and A. Macrae. 1995. Long-Term Glades in *Acacia* Bushland and Their Edge Effects in Laikipia, Kenya. *Ecological Applications,* 5:97–108.

Living with Lions: Lessons from Laikipia

Laurence Frank

ABSTRACT. Lion numbers are in steep decline in Africa. Lions have been eliminated from agricultural areas, and pastoralists have lost tolerance for predators; ready availability of cheap and effective poison poses a critical threat to their survival in Kenya outside of the largest national parks. However, lions still thrive on the commercial ranchlands of Laikipia District, where landowners use traditional low-cost African methods of livestock husbandry to effectively protect domestic stock from predators. Thus, Laikipia has been an ideal laboratory in which to investigate the ecology of predators living in human-dominated landscapes and factors in management of both livestock and lions which allow coexistence between them. Although socioeconomically unrepresentative of most African rangelands, the Laikipia experience shows that it is easy to raise livestock in the presence of viable populations of large carnivores if people have incentive and motivation to take basic, traditional measures to keep them apart. The current lack of financial incentives for rural Kenyans to tolerate wildlife, however, may limit the usefulness of the Laikipia model to privately owned lands.

INTRODUCTION

Laikipia District is unusual in many ways, but unique in one: it is the only place in the world where commercial ranchers actively conserve large predators and go to significant lengths to coexist with them. In Europe, North America, and Asia, humans have eliminated large carnivores to protect livestock, but at a time when Africa's great predators are also rapidly disappearing, the Laikipia example shows that carnivore extinction is not a necessary consequence of livestock production and rural development. Nor does carnivore conservation require resources beyond traditional methods available and familiar to pastoralists throughout East Africa. Laikipia ranchers have found that the ancient techniques which traditionally allowed humans to rear livestock in natural ecosystems are still highly effective at protecting domestic animals from predators.

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In 1995 wolves (*Canis lupus*) were reintroduced into the northern Rocky Mountains despite the vehement and nearly universal opposition of the livestock ranchers of Wyoming, Montana, and Idaho. In 2005, the entire 71,600 km^2 Yellowstone ecosystem lost 13 cattle and 71 sheep to wolves (Defenders of Wildlife, 2006); in spite of full monetary compensation and prompt removal of the offending wolves, the great majority of U.S. ranchers are still intensely opposed to wolf recovery. By comparison, in 1995–1996, the average (132 km^2) ranch in Laikipia lost 10.6 cattle and 52.3 sheep to predators (Frank, 1998). Ranchers there are not compensated for their losses, and many make little money from tourism, yet few advocate the elimination of predators. Unlike American ranchers, most accept costs of livestock protection measures and occasional livestock losses as a part of doing business.

STATUS OF LIONS IN AFRICA

Ten thousand years ago, the lion (*Panthera leo*) was the most widely distributed mammal on earth, ranging across most of Europe, Asia, Africa, and North and South America (Turner and Anton, 1997; Yamaguchi et al., 2004). It was eliminated from the New World at the end of the Pleistocene and from Europe and nearly all of Asia in historical times. In Africa, it has been eliminated from 83% of its historic range since European colonization, but only in the last few years have conservationists come to realize how serious the situation has become: the best current estimate is that fewer than 30,000 lions exist in the wild, and nearly half of those are in Tanzania (Chardonnet, 2002; Bauer and van der Merwe, 2004; IUCN, 2006). Most of the rest are in small and isolated national parks, vulnerable to stochastic events such as disease and political upheaval.

Only six protected or managed areas are large enough to ensure long-term survival of lions and other wide-ranging mammals (IUCN, 2006); three of those are in Tanzania and one, the Tsavo complex, is in Kenya. Given Africa's history of political instability and rapid human population growth, lion populations may soon come to resemble tiger populations: scattered among small parks, few of which are sufficiently large and interconnected to maintain a viable metapopulation. It is a truism of population biology that small, isolated populations cannot survive indefinitely without gene flow among them (Harcourt et al., 2001). Because human population growth and land pressures make creation of new large protected areas unlikely, maintaining viable populations of large mammals outside and between national parks is critical to their conservation.

STATUS OF LIONS IN KENYA

European settlement of Kenya at the turn of the twentieth century had a major impact on wildlife generally and predators in particular. Because they readily prey on livestock, large carnivores were considered vermin, and settlers exterminated them from farming and ranching areas. As an example of the zeal with which lions were killed, safaris to the Serengeti area in the early 1900s sometimes shot over 100 lions (Turner, 1987), and clients of just one Nairobi safari company killed 700–800 lions in 1911 alone (Herne, 1999:78–89). In 1908, over 150 lions were killed "on license" in Laikipia District (Playne, 1909). This scale of slaughter was not exclusive to the early days of settlement: between 1946 and 1952, one Laikipia game warden shot 434 lions "on control" (Herne, 1999), and several individuals killed over 300 lions apiece in the course of ranching in other parts of Kenya in the 1970s and 1980s (Anonymous individuals, personal communications).

Much of this killing took the form of "sport" but was motivated primarily by the perceived need to protect domestic animals. Although ranchers in East Africa used traditional African cattle husbandry methods that effectively minimized losses (see below), western practice was to eliminate predators rather than try to live with them. Poison (strychnine and organochlorine cattle dips) was widely used on East African ranches, continuing well into the latter half of the twentieth century (Denney, 1972). At least until recently, both the Kenya Wildlife Service and the Kenya Veterinary Department poisoned and shot spotted hyenas (*Crocuta crocuta*) on a wide scale, affecting lions and other scavengers as well (Mwaniki, 1997; L. Frank, personal observation, 1991).

In Kenya, lions were eliminated from settled agricultural areas in the last century, and today they persist only in national parks and reserves and on some rangelands. Extrapolating from known numbers in a few areas, we estimate a current Kenya population of less than 2,000 individuals (Frank et al., 2006); there are no data upon which to base estimates for earlier periods. Until quite recently, they were still widespread in Masailand of southern Kenya and throughout much of northern Kenya (covering roughly half of Kenya's land area), but that has changed dramatically in the past 20 years. Although there are no data available for the north, it seems clear that overgrazing and ubiquitous firearms have largely eliminated most wildlife, including lions. Again, there are no historical data for lion numbers in southern Kenya, but they were still abundant in much of Masailand until the current century, which has seen a dramatic decline due to spearing and poisoning (Ogutu et al., 2005; Frank et al., 2006).

LIVING WITH LIONS: THE LAIKIPIA PREDATOR PROJECT

In spite of its overwhelming importance in modern lion conservation, there has been remarkably little research on lion-human conflict. Laikipia ranchers' commitment to conservation, including tolerance of predators, has made this an ideal laboratory in which to study all aspects of carnivore-livestock interactions and to improve humans' ability to live with lions. Working in central and northern Laikipia, we have identified over 180 lions and radio collared 145 since 1998.

STATUS OF LIONS IN LAIKIPIA

COMMUNAL LANDS

Lions are rare on most communal lands of Laikipia. Overgrazing by domestic livestock has reduced wild ungulate numbers on group ranches, leaving superabundant goats and cattle as the most available and vulnerable prey for carnivores. Incoming lions kill livestock and are then poisoned. Because lions are so rare on communal lands, our community conservation efforts among Laikipia pastoralists have concentrated on reducing losses to spotted hyenas.

Lions avoid community areas, remaining largely within the bounds of commercial ranches by day (Figure 1). Note, however, that most of our data are obtained from radio tracking flights in the early morning; current studies with GPS collars will reveal the extent to which some individuals may use communal areas at night. The cues used by lions to avoid communal areas are not known but may involve low density of wild prey, high density of livestock and humans, or greater experience of persecution in those areas.

Use of poison is widespread in Laikipia's communities. We have records of at least 52 lions being poisoned on communal lands since 2003; 22 of these are known to have originated on commercial ranches but were poisoned when they moved onto community lands. Spotted hyenas are in steep decline as well: at least nine were known to have been poisoned on one Laikipia group ranch in seven months in 2007 (S. Dolrenry, Living With Lions/University of Wisconsin, personal communication, 2007). Much poisoning is meant for hyenas, but lions often die instead; an entire northern Laikipia pride died this way in 2004, and we have had similar reports from eastern Laikipia. Poisoning is not restricted to Laikipia: a minimum of 68 lions have been poisoned in the comparably sized Amboseli-Tsavo ecosystem since 2001 (Frank et al., 2006; L. Hazzah, Living with Lions and University of Wisconsin-Madison, unpublished data). Although shooting can target specific problem animals, poison is indiscriminate and often removes whole prides at once, as well as large numbers of other predators and scavengers.

Although strychnine was identified in one case, a more common agent is carbofuran, sold as Furadan for use in agriculture. Although banned in Europe and North America because of its toxicity to birds and mammals, Furadan is cheap and was widely available in Kenya until 2009, when adverse publicity in the United States caused the American manufacturer to temporarily withdraw it from the Kenya market (Gavshon and Magratten, 2009). Vultures have become noticeably uncommon in most of Kenya, including Laikipia, the victims of poisoned carcasses put out to kill lions, hyenas, and leopards. Bushmeat snaring also affects predators (Hofer et al., 1993), and in some parts of Laikipia a substantial proportion of hyenas and lions bear snare scars.

COMMERCIAL RANCHES

The commercial ranches of Laikipia support one of the few stable population of lions in Kenya and the only one outside a protected area; most other populations are known or thought to be in decline. Most Laikipia lions are wary of humans, staying in dense bush by day, and we have found that they do not respond reliably to call-in census techniques that are useful in protected areas (Mills, 1996; Mills et al., 2001). Thus, it is difficult to obtain precise numbers, but extrapolating from known pride sizes and home ranges, we estimate a stable population of 200–250 of all ages, representing a density of 6–7 adult and subadult lions/100 km^2 on the commercial ranches. In comparison to ecologically comparable bush ecosystems lacking livestock, densities in Kruger National Park varied between 3.3 and 9.6 adult and subadult lions/100 km^2 (Mills, 1995). Creel and Creel (1997) estimated the lion density of the hunted population in the Selous Game Reserve to be between 8 and 13 adults/100 km^2, and Yamazaki (1996) estimated densities of between 5 and 6 adult and subadult pride females/100 km^2, or 12–13 lions/100 km^2 if calculated for all pride members, in a hunted population in Zambia. In Kenya, Patterson et al (2004) estimated about 4 adult females/100 km^2 in the bush country surrounding Tsavo National Park.

Although wild ungulates in Laikipia are outnumbered 10 to 1 by livestock (N. Georgiadis, N. Olwero, and

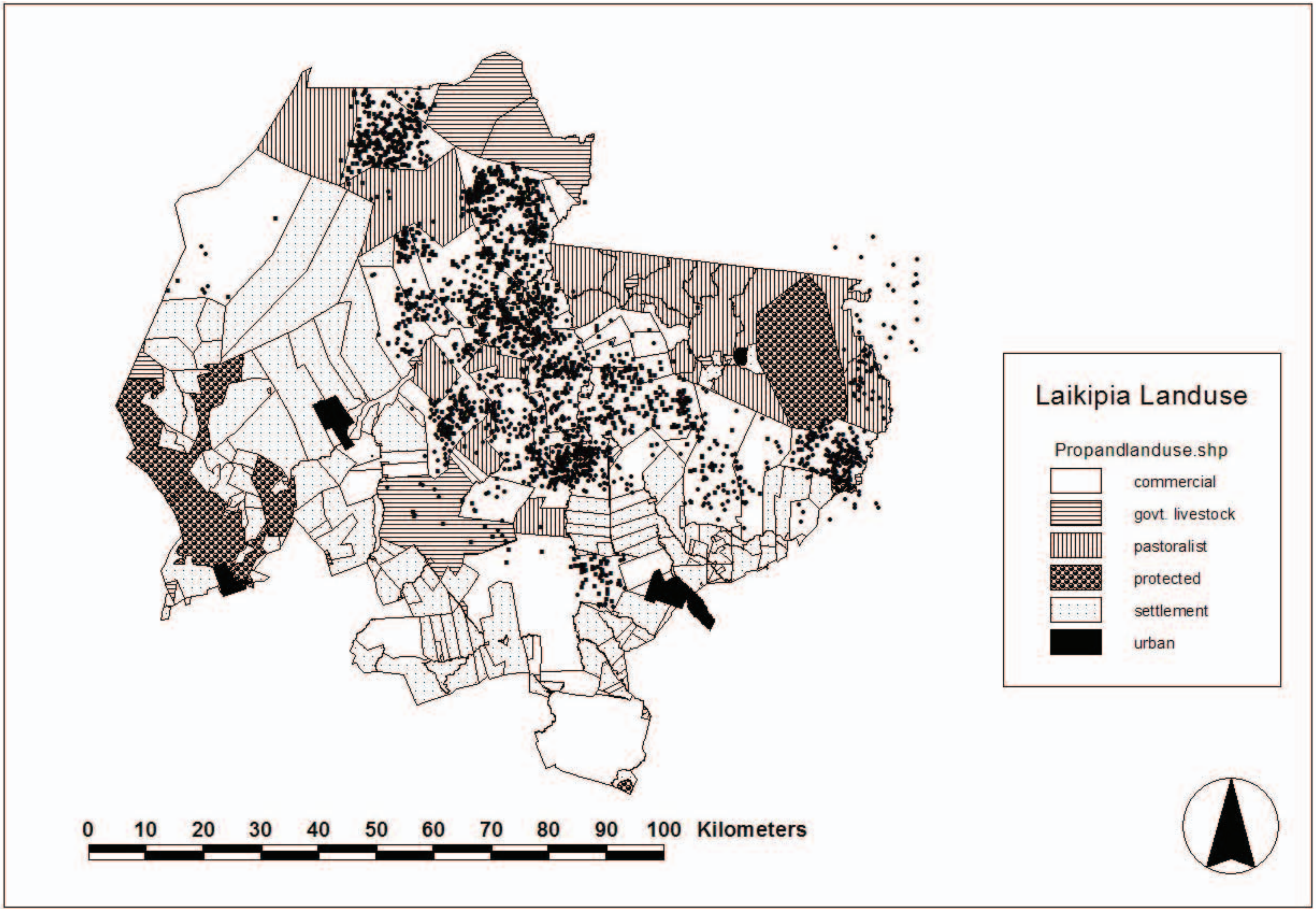

FIGURE 1. Land use map of Laikipia showing that lions remain on commercial ranches by day, avoiding communal pastoralist and settlement areas. Each dot represents an aerial radio tracking fix obtained for an individual lion (n = 3,658 fixes from 136 lions, 1998–2007). The fixes in the northeast are of two female lions collared on Il Ngwesi, one of the few group ranches which had resident lions; they have since been extirpated by poisoning (R. Moller, Lewa Wildlife Conservancy, personal communication).

G. Ojwang', unpublished report, "Numbers and Distributions of Large Herbivores in Laikipia District, Leroghi and Lewa Conservancy," presented at Laikipia Wildlife Forum, Nanyuki, Kenya, 2003), wild prey form the bulk of the lions' diet. Burchell's zebra (*Equus burchelli)* and eland (*Taurotragus oryx)* have been the primary prey of Laikipia lions since 1998 (Living With Lions, unpublished data), but buffalo (*Syncerus caffer)*, which were seriously reduced in the 2000–2001 drought, may become more important as numbers recover. Because smaller prey such as impala are eaten very quickly, their contribution to the lions' diet may be underrepresented in observational data.

COSTS OF LIVING WITH LIONS

In all studies of livestock losses, disease and drought account for a much higher proportion of livestock mortality than do predators (Frank, 1998). However, losses to predators or human raiders elicit a much stronger emotional response from owners.

Both commercial ranchers and Mukogodo Masai pastoralists use traditional African livestock husbandry techniques: cattle, sheep, goats, and camels are closely herded as they graze by day, and at dusk they are brought back into thornbush bomas (corrals or kraals), with people living in huts around them. On the commercial ranches, Frank (1998) found that lions took 0.51% of cattle and 0.27% of sheep annually. In 1996, it cost on average $360 in lost livestock to support a lion on the commercial ranches of Laikipia, or $1.54/head of cattle. However, there was great variation in loss rates among ranches, and losses on most ranches have declined with improved husbandry in subsequent years.

Data from one Laikipia group ranch and one settlement scheme (both communally owned by Mukogodo Masai pastoralists) showed losses of 0.69% of their cattle and 1.40% of sheep and goats annually to predators, largely spotted hyenas. This result may be compared to commercial ranches adjoining Tsavo, which lost 2.2% of cattle to lions annually (Patterson et al., 2004). In one communal area of Zimbabwe, 1.2% of cattle and 3.4% of shoats were taken by predators (calculated from Butler, 2000). On the Mbirikani Group Ranch in Kenyan Masailand, predators took 2.28% of the livestock herd annually, but lions accounted for only 4.4% of those losses, whereas spotted hyenas accounted for 62% (Maclennan et al., 2009). However, lions have been reduced to only about 1.5/100 km^2 on Mbirikani (Frank et al., 2006; Maclennan et al., 2009), a quarter of the density in Laikipia, and the relatively high livestock losses are due to poor herding, as most incidents involve stock left out in the bush at night.

DEPREDATION CIRCUMSTANCES

The great majority of lion depredation occurs at night (Frank, 1998; Hemson, 2003; Ogada et al., 2003). In Kenya, lions most frequently take cattle simply by approaching a boma, causing the cattle inside to panic. If the boma is not sufficiently strong or if it has weak points (most often the "gate," which may be just a bush pulled into the opening), the cattle stampede out of the boma and may then be taken by the lions or by hyenas; rounding them up often takes several men and vehicles most of the next day. Aside from the actual loss of cattle killed, the stress may cause loss of weight and, hence, profit. Depending on the structure of the boma (see below), some lions may learn to leap over the wall, particularly when taking small stock from stone or wicker bomas.

Less commonly, lions take stock by day, which seems to be more opportunistic than taking them from bomas at night and usually occurs when a herd wanders into lions sleeping in the bush. Most ranchers consider this loss to be simply bad luck and do not hunt down the responsible lions. On one ranch that stopped all lion shooting, however, lions learned that they could take stock by day with impunity, and losses rose to 79 cattle in one year (M. Dyer, Borana Ranch, personal communication, 2005).

Data from Laikipia (Frank et al., 2005; Woodroffe and Frank, 2005) and from the Tsavo region (Patterson et al., 2004) support ranchers' and pastoralists' reports that livestock losses are higher during rainy periods. We saw few losses to predators during a severe multiyear drought, but losses skyrocketed when the rains finally came, and many lions were shot in response. We speculate that listless wild prey and ready availability of carcasses during dry periods provide easy meals and that lions are likely to turn to livestock when abundant grass makes wildlife harder to catch because they are well nourished, alert, and energetic. In the Makgadikgadi Pan, Botswana, and Ngorongoro Conservation Area, Tanzania (Hemson, 2003; Ikanda and Packer, 2008), clear seasonal trends in livestock predation were recorded. These were related to wild prey availability: stock raiding decreased when migratory wild prey was present in large numbers and increased when migrant zebra and wildebeest moved to other areas.

In livestock areas, conservative grazing practices and effective control of poaching not only promote wildlife but also probably help minimize depredation losses.

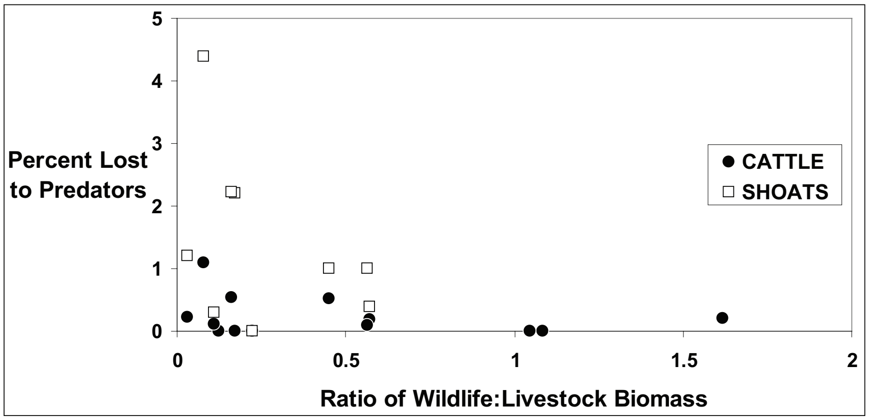

FIGURE 2. Relationship between livestock loss rate in 1995–1996 and wildlife density on individual ranches in Laikipia. (Wildlife data are from N. Georgiadis, N. Olwero, and G. Ojwang', unpublished report, "Numbers and Distributions of Large Herbivores in Laikipia District, Leroghi and Lewa Conservancy," presented at Laikipia Wildlife Forum, Nanyuki, Kenya, 2003.)

Although more data are needed, in Laikipia it seems clear that depredation is strongly affected by the availability of wild prey (Figure 2); lions are more likely to take livestock when other ungulates are in short supply. Thus, when livestock production is coupled with wildlife for ecotourism or sport hunting, losses to predators are reduced. Such "mixed systems" also maximize profit from land that is unsuitable for agriculture (Mizutani et al., 2005; Norton-Griffiths et al., 2006).

LETHAL CONTROL

Although Laikipia ranchers are remarkably tolerant of predators and willing to absorb a certain amount of loss, they do shoot persistent stock raiders, usually by tracking lions from a kill or by "sitting up," waiting for them to return to the carcass of a cow killed the night before. This is highly selective; "innocent" lions are rarely shot. Between 1998 and 2002, an average of 19.4% of the adult population was shot annually, amounting to 30–40 lions per year, divided equally among males and females (Frank, 1998; Woodroffe and Frank, 2005). Although this seems a high mortality rate, lion numbers are capable of rapid recovery; cub survival as high as 78.5% (Hunter et al., 2007) and annual population growth rates of 30%–80% have been documented (Maddock et al., 1996; Kissui and Packer, 2004). In Laikipia, cub survival is high, and the only emaciated lions we have seen have been very old, solitary individuals.

Importantly, lions originally collared in association with livestock kills were four times more likely to be shot in response to subsequent livestock damage than were lions collared on wildlife kills (12.9% versus 49.0%), strongly supporting ranchers' contention that certain individuals or prides are chronic livestock killers and others are not. More generally, ranches with good livestock husbandry rarely lose stock and rarely shoot lions, whereas both livestock and lions are killed at higher rates on ranches with poor practices.

Given that most Laikipia lions move over several ranches (which average 132 km^2 in size), a single ranch that kills many lions serves as a local sink, draining lions from a much larger area (Woodroffe and Frank, 2005). In a recent example, a pride known since 1998 had a home range centered on Ranches C, D, and E, which have excellent cattle husbandry and minimal depredation problems (Figure 3). Only 2.7% of all aerial fixes (n = 300) of the four collared females from this pride were on Ranch F, which does not use bomas for its cattle or tolerate wildlife, yet 9 of the 10 pride members, including five breeding females, were shot there. As we only learn of deaths in collared prides, these represent an unknown fraction of the total killed on this single ranch. A small number of the 25 commercial ranches in Laikipia account for the great majority of lion deaths in the region. Thus, even if a community of landowners wants to support predators, a few with poor husbandry and no interest in conservation can jeopardize the population of an entire region.

Because of the high mortality rate of stock-killing females, those not known to take livestock had four times higher cub production (0.98 cub/female/year versus 0.23 cub/female/year) and 2.7 times higher cub survival than did stock killers. Moreover, this population is producing a skewed cub sex ratio, 69:31 favoring males (Woodroffe and Frank, 2005). It is not known whether this is an effect of excess male mortality or other ecological factors.

SOLUTIONS

Ogada et al. (2003) assessed the efficacy of traditional African methods of livestock husbandry in protecting

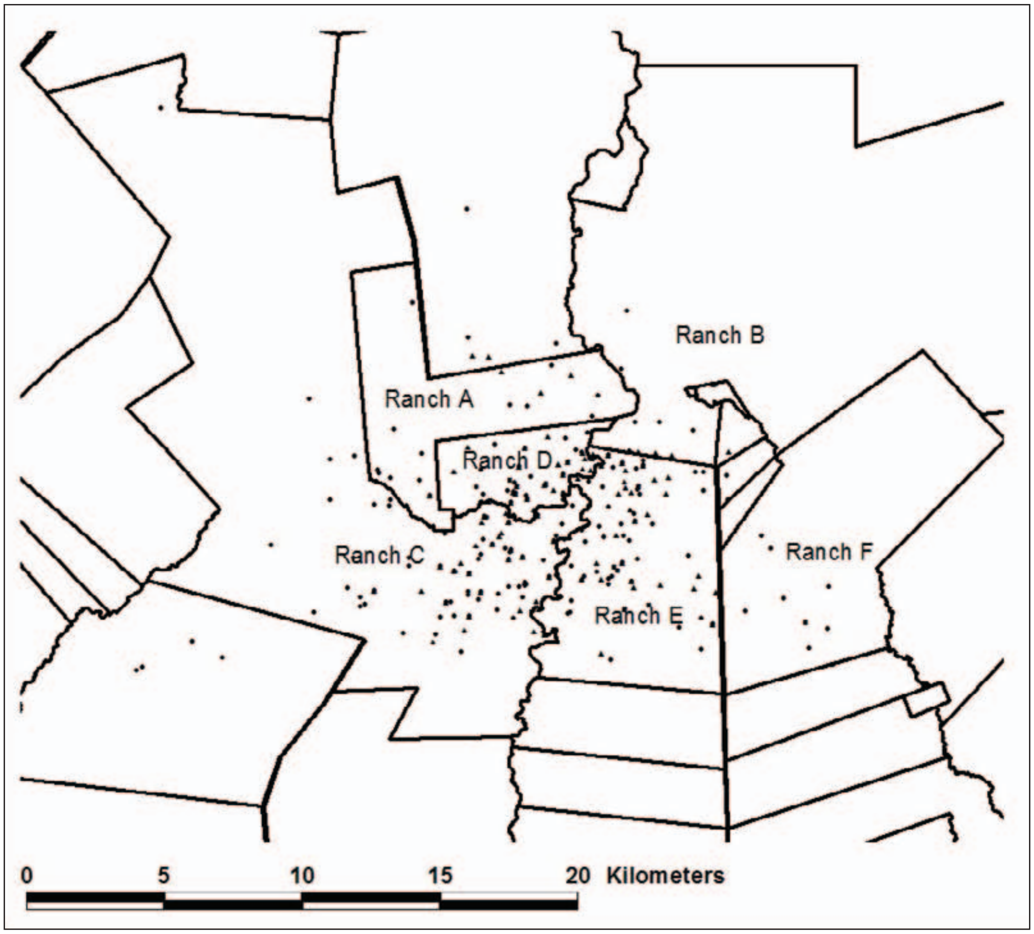

FIGURE 3. Central Laikipia, showing the home range of female lions LF5, LF69, LF85, LF110, and their seven pride mates. These animals were not known to take livestock on Ranches A–E, but nine were shot on Ranch F, which does not use bomas for its cattle.

livestock from predators on commercial ranches. These practices evolved in response to the twin threats of both predators and livestock-stealing humans and are probably similar to those used when pastoralism was first introduced in Africa over 9,000 years ago (Marshall, 2000). Not surprisingly, Ogada et al. (2003) found that ranchers kill significantly more predators on ranches where predators kill more livestock. Thus, implementation of any practice that reduces the vulnerability of livestock is critically important for reducing retaliatory killing of predators.

Seventy-five percent of depredation of cattle, sheep, and goats took place at night, and lions were responsible for over 75% of the total; depredation on Laikipia ranches occurs largely at the boma. Well-built bomas effectively constrain cattle and keep predators out. Bomas in Laikipia are made from native thornbush (Figure 4), stone walls, wooden posts, or wire mesh; of these, thick strong thornbush was most effective at keeping lions out and panicked cattle in. However, thornbush deteriorates over time, and many ranchers are reluctant to keep cutting mature trees to rebuild them. Stone is an excellent building material if there is a fence on top to prevent lions from leaping onto the wall and into the boma. Although most expensive to build, stone bomas last essentially forever and need little maintenance.

Thornbush bomas are most effective if divided into inner “rooms” that make it harder for cattle to reach the main gate, and the gate must be very strong, preferably made from lumber. The normal practice of using a tree or bush as a gate is ineffective, as it does not contain panicked cattle and allows hyenas to enter.

Wire mesh is a poor barrier if not well supported, but John Harris on Suyian Ranch and Giles Prettejohn of

FIGURE 4. Thornbush boma used on commercial ranches in Laikipia. Photo by Laurence Frank.

Ol Pejeta Conservancy have developed modular, moveable bomas made of mesh or old fencing wire welded into panels of interconnecting steel frames that are highly resistant to predators and easily transported (Ol Pejeta Conservancy, 2011). Not only are they predator proof, but they also allow ranchers to move bomas every few days to improve pastures. Although expensive (cattle bomas cost on the order of US$2,000 each), these bomas have proven 100% effective in preventing lion depredation by night and are being rapidly adopted by other Laikipia ranches.

We found that lions are reluctant to approach bomas that are located in close proximity to large numbers of people. However, for security and environmental reasons, some ranches do not allow herders to have their families at the bomas. Of course, in traditional societies bomas usually have large numbers of people and dogs. Dogs are also highly effective deterrents by both day and night (Woodroffe et al., 2007); they do not chase predators but warn herders, who then chase the lions. Again, however, some ranches do not allow dogs, as herders may use them for hunting wild game. Dogs can carry lethal carnivore diseases, but they are such an effective deterrent that vaccinated dogs are an essential component of livestock husbandry. Bright lights or noise-making devices like a shotgun or thunder flash (firecracker) also effectively repel loitering lions.

PROBLEM ANIMAL CONTROL

In the absence of totally reliable methods for protecting livestock from lions, some depredation is inevitable, and some lions will become habitual livestock killers. There is as yet no alternative to lethal removal of chronic offenders through Problem Animal Control (PAC). “Translocating” problem predators to parks is not a humane alternative, as translocated predators often sustain severe tooth and claw damage in the trap, are severely persecuted by residents of the same species where released, and usually end up being killed, often after causing further problems as they try to find their way home (P. Jenkins, Kenya Wildlife Service, 1997; Frank et al., 2003). Because of trauma to the animals and the low likelihood of survival, we strongly recommend against translocation.

Most commercial ranchers are able to deal with problem lions, but small-scale rural farmers and pastoralists usually do not have the means. In Kenya, rural people consistently complain that wildlife authorities do not respond effectively when people report chronic stock raiders, leading to resentment not only against wildlife, but also government, conservation, and tourism. A well-trained and reliable PAC team, able to respond efficiently, effectively, and rapidly, is an essential element of large-carnivore management in livestock areas. In their absence, rural people have little alternative besides such indiscriminate methods as poisoning, which probably poses the most serious threat to predator populations. Problem Animal Control teams should be trained not only in the reliable identification of problem animals and humane removal but also, most importantly, in educating rural people in livestock husbandry techniques that better protect stock.

CONCLUSIONS

Large carnivores are among the most difficult animals to conserve because their feeding habits inevitably bring them into conflict with humans. At the same time, their wide ranging movements and need for substantial prey populations require very large areas, and thus, only the biggest protected or well-managed landscapes currently provide long-term security for viable populations; only six such areas currently exist in Africa.

Conflict with humans over livestock depredation is the single most important factor causing the decline in African lion populations. With growing numbers of people and livestock throughout the continent, conflict mitigation must be implemented on a wide scale if lions are not to become restricted to a few very large protected areas or well-managed hunting blocks. Traditional methods of livestock husbandry are remarkably effective at minimizing conflict, but these are being lost to modernization. Building good bomas and conscientiously tending livestock require time and effort at a time when poison is readily available and spearing lions is the only traditional test of manhood left for young warriors. As pastoralists increasingly engage in a cash economy, they have lost their tolerance of predators and are likely to continue eliminating lions unless lions bring in financial benefits that outweigh costs.

In the 95% of Kenya's rangeland that does not support tourism (Norton-Griffiths et al., 2006), wildlife are only an expensive nuisance to the people who share their habitat: wild animals kill livestock, destroy crops, and occasionally kill and injure humans. Few rural people benefit from tourism revenues, but in combination with poor law enforcement, national policy, which prohibits legal and sustainable consumptive utilization, ensures that the only value for wildlife is as bushmeat, snared or hunted illegally and unsustainably. Thus, current policy in Kenya, essentially determined by foreign animal rights groups with neither interest nor expertise in conservation, effectively makes rural Kenyans resent and eliminate wildlife.

In 2007, tourist hunters in Botswana paid US$140,000 to shoot a lion, $100,000 of which went to the community in which it was taken (J. Rann, Rann Safaris, personal communication, 2006). Given Kenya's romantic history of hunting (Herne, 1999), today's wealthy trophy hunters would probably pay substantially more than that for a Kenyan lion. Laikipia is currently the only nonprotected area in Kenya with a lion population large and stable enough to permit a carefully regulated offtake of several old males per year (Whitman et al., 2004). If equitably distributed and combined with help in preventing depredation losses, this potential income could significantly improve community perceptions of predators and the potential role of wildlife in raising rural living standards. However, many argue that Kenya's pervasive corruption would make it impossible to sustainably manage and regulate a lucrative hunting industry except on privately owned lands.

People will either learn to live with lions or we will lose them. We have shown that ancient livestock husbandry methods effectively protect livestock from lions, but spears, bullets, and poison are always cheaper and easier solutions than managing livestock, lions, or growing rural human populations. Thus, rural people must perceive lions and other wildlife as valuable commodities if they are to accept the burden of living with them: the benefits of wildlife must outweigh the costs. Successful lion conservation must combine effective management of risks with development of viable wildlife-based economies that improve the lives of rural Africans. Traditional peoples and wildlife managers already have most of the techniques necessary to manage depredation, but the greater challenge of managing ecologically sustainable rural development lies in the realm of policy, social science, and politics.

ACKNOWLEDGMENTS

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REFERENCES

Bauer, H., and S. van der Merwe. 2004. Inventory of Free Ranging Lions *Panthera leo* in Africa. *Oryx*, 26–31.

Butler, J. R. A. 2000. The Economic Costs of Wildlife Predation on Livestock in Gokwe Communal Land, Zimbabwe. *African Journal of Ecology,* 38:23–30.

Chardonnet, P. 2002. *Conservation of the African Lion: Contribution to a Status Survey*. Paris: International Foundation for the Conservation of Wildlife and Conservation Force.

Creel, S., and N. M. Creel. 1997. Lion Density and Population Structure in the Selous Game Reserve: Evaluation of Hunting Quotas and Offtake. *African Journal of Ecology, 35*:83–93.

Defenders of Wildlife. 2006. Wolf Compensation Trust. http://www.defenders.org/resources/publications/programs_and_policy/wildlife_conservation/solutions/full_list_of_payments_in_the_northern_rockies_and_southwest.pdf (accessed 8 October 2010).

Denney, R. 1972. Relationships of Wildlife to Livestock on Some Developed Ranches on the Laikipia Plateau, Kenya. *Journal of Range Manage*, 25:415–425.

Frank, L. G. 1998. Living With Lions: Carnivore Conservation and Livestock in Laikipia District, Kenya. Report prepared for U.S. Agency for International Development. Washington, D.C.: DAI.

Frank, L. G., S. M. Maclennan, L. Hazzah, R. Bonham, and T. Hill. 2006. Lion Killing in the Amboseli–Tsavo Ecosystem, 2001–2006, and Its Implications for Kenya's Lion Population. Project report for Living with Lions, Nanyuki, Kenya. http://www.lionconservation.org/AnnualReports/2006-Lion-killing-in-Amboseli-Tsavo-ecosystem.pdf.

Frank, L. G., D. Simpson, and R. B. Woodroffe. 2003. Foot Snares: An Effective Method for Capturing African Lions. *Wildlife Society Bulletin*, 31:309–314.

Frank, L. G., R. B. Woodroffe, and M. Ogada. 2005. "People and Predators in Laikipia District, Kenya." In *The Conservation of Wildlife that Conflicts with Man,* ed. R. B. Woodroffe, S. Thirgood, and A. Rabinowitz, pp. 86–304. Cambridge: Cambridge University Press.

Gavshon, Michael, and Drew Magratten, producers. 2009. "Poison Takes Toll on Africa's Lions." On *60 Minutes*. New York: CBS News/CBS Interactive. http://www.cbsnews.com/stories/2009/03/26/60minutes/main4894945.shtml (accessed 14 February 2010).

Harcourt, A. H., S. A. Parks, and R. B. Woodroffe. 2001. Human Density as an Influence on Species/Area Relationships: Double Jeopardy for Small African Reserves? *Biodiversity and Conservation*, 10:1011–1026.

Hemson, G. 2003. The Ecology and Conservation of Lions: Human–Wildlife Conflict in Semi- arid Botswana. PhD. Thesis. University of Oxford, Oxford, UK.

Herne, B. 1999. *White Hunters*. New York: Henry Holt and Co.

Hofer, H., M. L. East, and K. L. I. Campbell. 1993. Snares, Commuting Hyaenas and Migratory Herbivores: Humans as Predators in the Serengeti. *Symposia of the Zoological Society of London*, 65:347–366.

Hunter, L. T. B., K. Pretorius, L. C. Carlisle, M. Rickleton, C. Walker, R. Slotow, and J. D. Skinner. 2007. Restoring Lions *Panthera leo* to Northern KwaZulu-Natal, South Africa: Short-Term Biological and Technical Success but Equivocal Long Term Conservation. *Oryx,* 41:196–204.

Ikanda, D., and C. Packer. 2008. Ritual vs. Retaliatory Killing of African lions in the Ngorongoro Conservation Area, Tanzania. *Endangered Species Research*, 6:67–74.

International Union for Conservation of Nature (IUCN). 2006. Regional Conservation Strategy for the Lion *Panthera leo* in Eastern and Southern Africa. IUCN, Gland, Switzerland.

Kissui, B. M., and C. Packer. 2004. Top-down Population Regulation of a Top Predator: Lions in the Ngorongoro Crater. *Proceedings of the Royal Society of London B,* 271:1867–1874.

Maclennan, S. D., R. Groom, D. W. Macdonald, and L. G. Frank. 2009. Evaluation of a Compensation Scheme to Bring about Pastoralist Tolerance of Lions. *Biological Conservervation,* 142:2419–2427

Maddock, A., F. Anderson, N. Carlisle, A. Galli, A. James, A. Venster, and W. Whitfield. 1996. Changes in Lion Numbers in Hluluwe-Umfolozi Park. *Lammergeyer,* 44:6–18.

Marshall, F. 2000. "The Origins of Domesticated Animals in Eastern Africa." In *The Origins and Development of African Livestock: Archaeology, Genetics, Linguistics and Ethnography*, ed. R. M. Blench and K.C. MacDonald, pp. 191–221. London: University College London Press.

Mills, M. G. L. 1995. Notes on Wild Dog *Lycaon pictus* and Lion *Panthera leo* Population Trends during a Drought in the Kruger National Park. *Koedoe,* 38:95–99.

———. 1996. "Methodological Advances in Capture, Census, and Food-Habits Studies of Large African Carnivores." In *Carnivore Behavior, Ecology, and Evolution,* Vol. 2, ed. J. Gittleman, pp. 223–242. Ithaca: Cornell University Press.

Mills, M. G. L., J. M. Juritz, and W. Zucchini, 2001. Estimating the Size of Spotted Hyaena (*Crocuta crocuta*) Populations through Playback Recordings Allowing for Non-response. *Animal Conservation,* 4:335–343.

Mizutani, F., E. Muthiani, P. Kristjanson, and H. Recke. 2005. "Impact and Value of Wildlife in Pastoral Livestock Production Systems in Kenya: Possibilities for Healthy Ecosystem Conservation and Livestock Development for the Poor." In *Conservation and Development Interventions at the Wildlife/Livestock Interface: Implications for Wildlife, Livestock and Human Health*, ed. S. A. Osofsky, S. Cleaveland, W. B. Karesh, M. D. Kock, P. Nyhus, L. Starr, and A. Yang, pp. 121–132. Gland, Switzerland: International Union for Conservation of Nature.

Mwaniki, D. 1997. Hyenas as Problem Carnivores: the Mandera/Moyale Experience. Paper presented at *KWS Workshop to Review Management of "Problem" Carnivores in Kenya*. 3 March 1997. Nairobi: Kenya Wildlife Service.

Norton-Griffiths, M., M. Y. Said, S. Serneels, D. S. Kaelo, M. Coughenour, R. H. Lamprey, D. M. Thompson, and R. S. Reid. 2006. "Land Use Economics in the Mara Area of the Serengeti Ecosystem." In *Serengeti III: Human Impacts on Ecosystem Dynamics,* ed. A. R. E. Sinclair, C. Packer, S. A. R. Mduma, and J. M. Fryxell, pp. 379–416. Chicago: Chicago University Press.

Ogada, M., R. B. Woodroffe, N. N. Oguge, and L. G. Frank. 2003. Limiting Depredation by African Carnivores: The Role of Livestock Husbandry. *Conservation Biology,* 17:1521–1530.

Ogutu, J. O., N. Bhola, and R. Reid. 2005. The Effects of Pastoralism and Protection on the Density and Distribution of Carnivores and Their Prey in the Mara Ecosystem, Kenya. *Journal of Zoology,* 265:281–293.

Ol Pejeta Conservancy. *Specification Details for Ol Pejeta's Predator-Proof Bomas.* http://www.olpejetaconservancy.org/sites/default/files/Predator%20Proof%20Boma%20Design%20Specs.pdf (accessed 13 April 2011).

Patterson, B. D., S. M. Kasiki, E. Selempo, and R. W. Kays. 2004. Livestock Predation by Lions *Panthera leo* and Other Carnivores on Ranches Bordering Tsavo National Parks, Kenya. *Biological Conservation,* 119:507–516.

Playne, S. 1909. *East Africa; Its History, People, Commerce, Industries and Resources*. London: Unwin Bros.

Turner, A., and M. Anton. 1997. *The Big Cats and Their Fossil Relatives*. New York: Columbia University Press.

Turner, M. 1987. *My Serengeti Years*. New York: Norton.

Whitman, K., A. M. Starfield, H. S. Quadling, and C. Packer. 2004. Sustainable Trophy Hunting of African Lions. *Nature*, 428:175–178.

Woodroffe, R., and L. G. Frank. 2005. Lethal Control of African Lions (*Panthera leo*): Local and Regional Population Impacts. *Animal Conservation,* 8:91–99.

Woodroffe, R., L. G. Frank, P. A. Lindsey, S. M. K. ole Ranah, and S. Romañach. 2007. Livestock Husbandry as a Tool for Carnivore Conservation in Africa's Community Rangelands: A Case Control Study. *Biodiversity and Conservation,* 16:1245–1260.

Yamaguchi, N., A. Cooper, L. Werdelin, and D. W. Macdonald. 2004. Evolution of the Mane and Group-Living in the Lion (*Panthera leo*): A Review. *Journal of Zoology,* 263:329–342.

Yamazaki, K. 1996. Social Variation of Lions in a Male-Depopulated Area in Zambia. *Journal of Wildlife Management,* 60:490–497.

Attitudes Toward Predators and Options for Their Conservation in the Ewaso Ecosystem

Stephanie S. Romañach, Peter A. Lindsey, and Rosie Woodroffe

ABSTRACT. The act of killing predators over livestock predation has been the principal cause of declining predator populations throughout Africa. Finding solutions for the coexistence of people with predators in the Ewaso region is of great importance for the local tourism industry and for the persistence of Kenya's wildlife outside of protected areas. We report results of an assessment of attitudes toward predators by landholders and land users in the Ewaso region and their tolerance of livestock losses, relative to socioeconomic factors. Although prospects are good for predator conservation on large-scale private ranches, the future of predators on communally owned properties remains uncertain. Prospects would be improved not only by finding solutions to reduce livestock depredation but also by ensuring that individuals tolerating losses from predators receive benefits from having predators on their land. Additionally, policy changes are needed to allow landholders to capitalize on benefits from wildlife, which would encourage their participation in wildlife conservation.

PREDATORS AND PEOPLE

Predators are among the hardest animals to conserve because they range widely, often outside of protected areas and onto land *not* used for wildlife conservation. Predators can become a liability to landholders, who incur financial losses when livestock are killed. As a result, people kill predators, often preemptively. For example, lions (*Panthera leo*) are killed in Kenya because of conflict over livestock (Woodroffe and Frank, 2005). Predators, including wild dogs (*Lycaon pictus*) and cheetahs (*Acinonyx jubatus*), are suppressed on some wildlife ranches in southern Africa where they kill antelopes, which are valuable for ecotourism and trophy hunting (Sillero-Zubiri and Laurenson, 2001; Ogada et al., 2003; Marker et al., 2003; Lindsey et al., 2005). Persecution of predators has resulted in serious declines in the population sizes and distributions of many predator species (Woodroffe and Ginsberg, 1998), and it remains the most important source of their mortality.

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Finding ways to increase tolerance of predators is critical for their survival (Hackel, 1999; Woodroffe, 2000). Strenuous attempts have been made to improve local citizens' attitudes toward predators in rural Africa through community-based conservation projects, education campaigns, and outreach programs (e.g., Painted Dog Research Project, Zimbabwe; Cheetah Conservation Fund, Namibia). Some successful programs have focused on generating income from predators through ecotourism or sport hunting (Adams and Hulme, 2001). For such programs to work, financial returns from wildlife must reach individuals who bear the costs of living with wildlife and must be adequate to offset not only direct costs but also opportunity costs. This prerequisite is difficult to achieve because the benefits any individual can receive from predators are often diluted by the number of community members among whom benefits must be shared (Walpole and Thouless, 2005), whereas costs are accrued individually. Accordingly, predator population sinks can form outside of protected areas, threatening predators both outside and inside of protected areas.

CONSERVATION CHALLENGES IN KENYA

Kenya's national parks and reserves house 35% of the country's wildlife; the remaining populations are found on land that is privately or communally owned or held in trust by local government (Grunblatt et al., 1996; Western et al., 2009). The persistence of wildlife is important for the persistence of Kenya's primary industry, tourism (Ottichilo et al., 2000). Human populations continue to grow, resulting in the movement of people from densely populated areas to Kenya's rangelands to practice subsistence livestock farming, where they overlap with the majority of the country's wildlife (Ottichilo et al., 2000). Over the last decade Kenya's human population has grown nearly 4% per year (Shikwati, 2004). Rising human populations have driven habitat conversion to accommodate subsistence pastoralism and agriculture, resulting in increased conflict between people and wildlife and population declines of many wildlife species (Awere, 1996).

EWASO ECOSYSTEM

Kenya's Ewaso ecosystem is an area dominated by livestock, but it retains the potential to host viable wildlife populations. With six large carnivore species indigenous to the area (cheetahs, lions, leopards [*Panthera pardus*], spotted and striped hyenas [*Crocuta crocuta* and *Hyaena hyaena*], and the endangered African wild dog), reducing conflict between people and predators is essential for the persistence of wildlife in this area. This need is particularly true for predators, which range across a mosaic of land uses, including subsistence pastoralism, patchy small-scale agriculture, large-scale commercial livestock ranches, and wildlife conservation and tourism areas. In this chapter we report results of an assessment of attitudes toward predators by local landholders and land users, and their tolerance of livestock losses, relative to socioeconomic factors. Our goals were to examine the challenges facing people and predators and to identify ways to improve their potential for coexistence in the region.

INTERVIEWS

We interviewed 416 community members and commercial livestock ranchers in the Ewaso ecosystem in 2004–2005 to assess their attitudes toward predators, tolerance for livestock kills, and options for predator conservation (Figure 1). We conducted interviews with 23 commercial ranch managers or owners. Nine local assistants interviewed 393 rural community members who owned livestock, including people from 10 tribes (Maasai and Samburu are the predominant tribes in the area, although people from other tribes, including Borana, Kalenjin, Kikuyu, Merian, Pokot, Rendile, Somali, and Turkana, were also interviewed).

Before each interview, we assessed the respondents' familiarity with predators (e.g., hunting behavior) using an illustrated card with color drawings of each predator (for interview details, see Romañach et al., 2007). The questionnaires were designed to assess respondents' attitudes toward and tolerance for livestock losses from cheetahs, jackals (*Canis mesomelas*), leopards, lions, spotted hyenas, striped hyenas, and wild dogs. We quantified respondents' tolerance for predator attacks on livestock by recording how many livestock (measured as the number of cattle or the combined number of sheep and goats) respondents were willing to lose before trying to kill the predator responsible. Older interviewees were also asked what their tolerance for livestock losses to predators was 20 years ago. Interviewers asked respondents whether they would want predators on their properties if they were to start tourism operations. We asked whether people thought trophy hunting should be legalized again in Kenya, an industry banned in Kenya in 1977 because of poor control and coordination and large-scale poaching (Outoma, 2004). Interviewees were also asked, in an open-ended question,

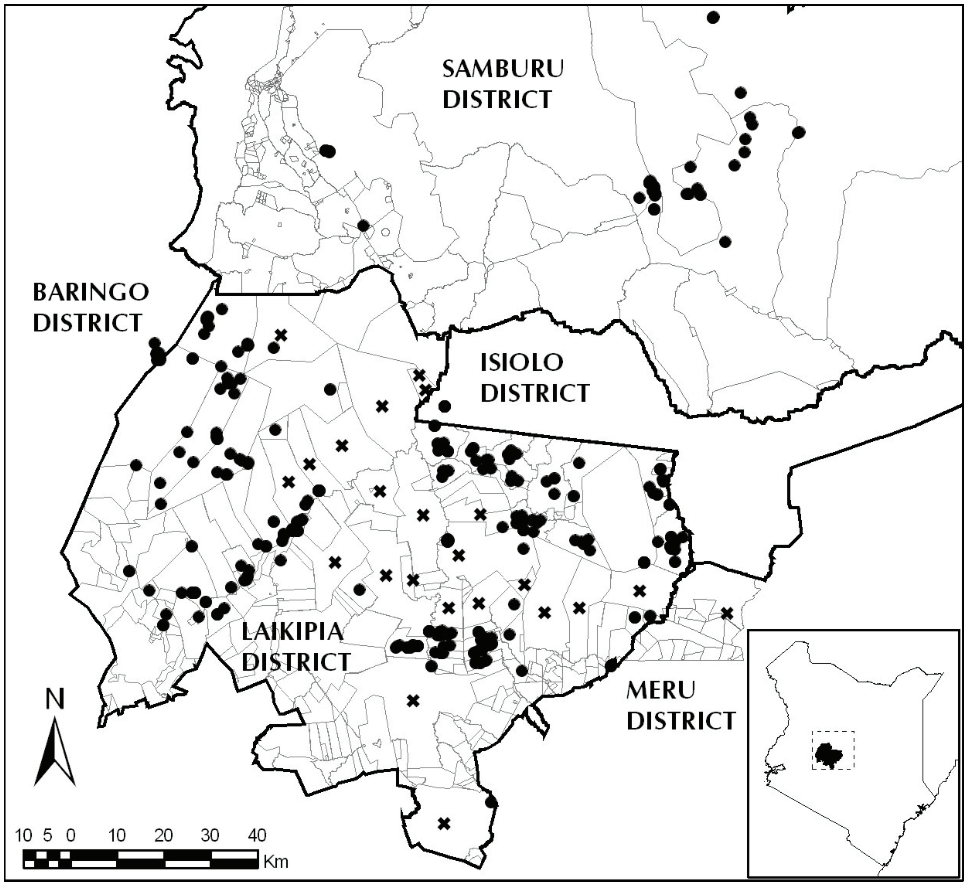

FIGURE 1. Map of locations for commercial rancher interviews (×) and community member interviews (•). (Source: Romañach et al., 2007.)

to provide suggestions for methods to promote coexistence between people and predators.

During each interview, we recorded information on characteristics of the property where the interviewee was living at the time of the interview: land use type (e.g., group ranch, commercial ranch); if the property had wildlife tourism as a form of income at the time of the interview; primary source of property income; benefits received from wildlife (e.g., dams built, communications radios purchased); whether the property had a wildlife conservation area set aside (where livestock did not graze); whether there was an immediate (within two years) plan to start a wildlife conservation area if there was not one at the time of the interview; presence of each predator on the property; and for commercial ranchers, whether ranch activities served as the primary source of income for the ranch owner, compared to having a subsidized income, for example. We recorded personal information about each interviewee: age, gender, number of years of formal education, primary source of household income, and the number of their livestock killed by each predator in the last year.

FINDINGS AND IMPLICATIONS FOR PREDATOR CONSERVATION

Attitudes and Tolerance

More than 90% of commercial ranchers were in favor of having predators on their land (Figure 2). We found that commercial ranchers want to have all predators in question on their land, regardless of the rancher's personal characteristics (e.g., age, education) or the ranch characteristics (e.g., primary source of property income, presence of tourism). Commercial ranchers were also more tolerant of livestock losses from all predators compared to the tolerance of community members.

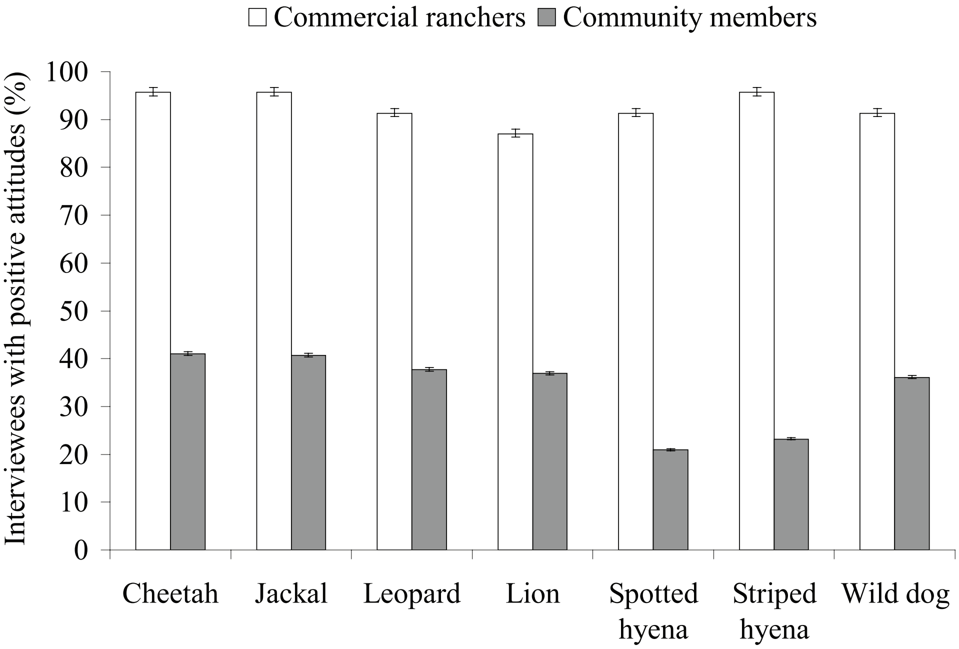

FIGURE 2. Percentages (95% confidence intervals) of commercial ranchers and community members who wanted each predator on their property. (Source: Romañach et al., 2007.)

Community members were less enthused about the presence of predators. For example, only about 20% wanted to have spotted hyenas on their land, and about 40% wanted to have other predator species. Community members were more likely to want predators on their land if benefits from having predators reached the individual, not if benefits were only given to the community as a whole (e.g., dams built). We found that people with more education were more likely not to want predators on their communal land; however, the higher the level of education, the higher interviewees' stated level of tolerance for predators that were on their land. These findings suggest the value of education in conservation of biodiversity in that although people might not like predators, higher levels of education lead to greater tolerance. Another factor contributing to interviewees' increased tolerance was if their community was planning to start a wildlife conservancy in the next two years, as opposed to if they already had a conservancy. Our results also show the danger of false hope brought by the promise of tourism when planning to start a wildlife conservancy if the plan does not come to fruition and also for individuals who are part of a conservancy but who do not personally receive benefits. Distribution of benefits so that they reach individuals, particularly reaching those that tolerate livestock losses, will be important to the future of predators on communal land.

Over half (53%) of all interviewees reported having lost livestock to at least one predator in the year prior to the interview. Lions, leopards, and spotted hyenas were reported to be the most troublesome killers of livestock (Table 1). Lions are thought to be the most problematic of predators and therefore may have the most uncertain future.

Some respondents said they would not kill predators in response to livestock attacks, no matter how many head of stock were lost; this "no-kill" policy was largely for stated tolerance of cheetahs and wild dogs. Conversely, other respondents stated they would kill predators on sight, even if no attack had occurred. Of commercial ranchers, only one rancher held a "kill-on-sight" policy, and it was for spotted hyenas. Of community members, depending on predator species, 77%–88% of interviewees stated having a kill-on-sight policy. Community members were least likely to want to kill wild dogs, which we attributed partially to the belief of Samburu respondents that wild dogs are sacred and partially to the perception that a successful wild dog research and conservation project in the region has provided jobs. This sentiment was particularly notable in areas where full-time field scouts are employed to

TABLE 1. Survey results of commercial ranchers and community members asked to rank predators as worst attacker of livestock and owners who lost livestock to predators in the preceding year. Some respondents did not give a ranking for all predators, and some had livestock killed by multiple predators; thus rows will not necessarily total 100%.

Measurement	Cheetah	Jackal	Leopard	Lion	Spotted hyena	Striped hyena	Wild dog
Commercial ranchers (%)							
Ranking predator worst for cattle attacks	0	0	0	70	30	0	0
Owning cattle killed by predator	0	0	17	78	22	0	0
Ranking predator worst for sheep/goat attacks	9	0	35	9	48	0	0
Owning sheep/goat killed by predator	17	4	48	26	43	0	4
Community members (%)							
Ranking predator worst for cattle attacks	2	5	3	71	9	1	1
Owning cattle killed by predator	1	0.3	24	21	11	1	0.3
Ranking predator worst for sheep/goat attacks	7	6	27	2	35	6	9
Owning sheep/goat killed by predator	14	21	29	5	31	8	4

monitor movement of wild dogs on their community land (e.g., Kijabe Group Ranch). The Samburu-Laikipia Wild Dog Project (SLWDP; headed by Rosie Woodroffe) had been running in the region for three years (since 2001) at the time of the interviews.

Despite the high number of community members reporting a kill-on-sight policy, all native large predator species are at least present over large areas of communal land in the region. Lions are not common on communal lands, however, and are heavily persecuted (L. G. Frank, personal communication, University of California, Berkeley, 2004). Seventy-seven percent of respondents stated a kill-on-sight policy for wild dogs, but none reported having killed wild dogs in the previous year, and only 15% reported having killed any predators in the previous year. Additional data from the study area show that at the time of our interviews, only 2 of 33 (6%) radio-collared wild dogs had been killed by humans (R. Woodroffe, unpublished data, 2005), and the population size of wild dogs continues to increase. This increase is particularly striking given that wild dogs primarily occur on community land in the region (Woodroffe et al., 2004), where they are generally unwelcome. Two of the goals of the SLWDP are to help reduce livestock depredation by wild dogs and to encourage wild dog ecotourism for income. SLWDP has been successful in meeting its goals and, as a result, has been increasingly gaining the support of locals for the protection of wild dogs.

Thirty-one percent of all interviewees (commercial and community) who owned or managed livestock for the last 20 years reported increased tolerance for predators today, and 6% reported being less tolerant of predators today. Commercial ranchers are prepared to lose between four and eight stock (cattle or sheep/goats) before eliminating the responsible predator, which is about twice the tolerance they said they had 20 years ago. Community members were less tolerant and were unwilling to lose more than one head of stock at any time before attempting to eliminate the predator.

LETHAL CONTROL

We found that people (commercial ranchers and community members) who lost livestock to predators in the last year were much more likely to have killed them compared to people who had not experienced livestock losses. This finding emphasizes the importance of improving methods of livestock protection (e.g., stronger corrals) to decrease retribution killings and thus to increase coexistence of people with predators through greater tolerance. Commercial ranchers were more likely to have killed predators in the last year if the income generated by their ranch was the ranch owner's primary source of income (compared to ranches that have subsidized incomes, for example, through foreign investment). This finding highlights the financial difficulty of tolerating livestock losses to predators and the difficultly of coexistence between people and predators even on large-scale ranching areas.

Interviewees were asked how they would kill predators responsible for livestock attacks. Commercial ranchers and community members differed in their preferred means of lethal control. Ranchers who would kill predators would largely shoot them; however, when considering lethal control of spotted hyenas, one respondent would gas them inside of their dens, and another would use general carcass poisoning. No commercial ranchers would set wire snares to kill predators.

Of community members, almost half (47%) would use carcass poisoning to kill predators, and 9% would set wire snares. To kill cheetahs, 60% of respondents would use spears or knives, 13% would use poisoned arrows, 8% would trap the cheetah with no mention what they would do with the animal once trapped, 6% said they would call the government authority (Kenya Wildlife Service) to take care of the problem, 4% would use clubs, 4% would shoot the animal, and 1% would hunt predators with domestic dogs.

COMMUNAL LAND

Communal land makes up 60% of Laikipia District and nearly all of the surrounding districts. It is therefore the land use type of greatest concern—and potential—for conservation. We found that community members living on group ranches (i.e., those with title deeds) were most positive toward predators compared to those on government land and squatters. The Laikipia Wildlife Forum (LWF), African Wildlife Foundation, other nongovernmental organizations, and commercial landowners have been helping communities to gain title deeds to their land in the region. Promoting group landownership could have positive implications for predator conservation over the large areas in Africa. Property rights provide residents with incentives for the sustainable use of natural resources, given that they will have access to those resources in future. Group ranches have the benefit of being a size large enough for holding suitable populations of wildlife species compared to smaller-sized, individually owned land. Such a model is preferable to the subdivision of formerly communally owned land into small privately owned parcels. Such land tenure shifts in parts of Kenya have been demonstrated to be associated with declining diversities and densities of wildlife (Norton-Griffiths, 2007).

Community members who lost livestock to predators in the last year killed more predators than those whose livestock were not attacked. Of community members interviewed, Masais and Samburus were the most positive toward predators. However, Samburus had a relatively high incidence of killing predators in response to livestock attacks. We found no association between livestock lost to a particular predator and likelihood for that specific predator species to be killed. This finding suggests that if people lost livestock to any predator, they were more likely to kill all predators in retaliation.

COMMERCIAL RANCH LAND

Attitudes were most positive and tolerance was greatest among commercial ranchers. These positive attitudes are noteworthy given that 30% of commercial ranchers receive no benefits from tourism and no income subsidies and yet are interested in conserving predators that can have negative effects on their livestock ranching activities. Tolerance for predators among commercial ranchers has improved compared to their tolerance 20 years ago. Most respondents attributed their increased tolerance to realizing the importance of wildlife conservation (citing education from LWF) and, for some, experiencing economic return from wildlife. Commercial ranchers in the Ewaso region hold more positive attitudes than southern African ranchers (Marker et al., 2003; Lindsey et al., 2005), indicating great promise for the Ewaso ecosystem. Although prospects for predator conservation are greatest on commercial ranches, ranches cover only 40% of the Laikipia District and very little to none of the neighboring districts; therefore, great efforts are needed to promote wildlife conservation participation on communal land for wildlife to persist across the mixed land uses.

OPTIONS TO PROMOTE COEXISTENCE BETWEEN PEOPLE AND PREDATORS

When asked as an open-ended question about how attitudes toward predators could be improved, the most common suggestion from all respondents (commercial ranchers and community members) was to give value to predators, with most citing using ecotourism and trophy hunting.

Tourism is the world's fastest growing industry, with ecotourism its fastest growing sector (Gössling, 2000), and developing nations are increasingly popular destinations (Goodwin, 1996; Gössling, 1999). With the number of successful tourism operations in the Ewaso region growing and with visitors increasingly interested in both wildlife and human cultures, tourism should continue to improve attitudes toward predators. There are a number of successful tourism operations in the region, several of which are on community land (e.g., Il Ngwesi Lodge, Sarara Camp, Koija Starbeds), with more lodges in the development stages. The Ewaso ecosystem houses globally important populations of endangered wild dogs and Grevy's zebra (*Equus grevyi*), as well as cheetahs and lions, all of which are of interest to tourists.

The development of tourism operations on communal land in the region would be facilitated through the development of public-private-community partnerships, whereby commercial ranchers form partnerships with adjacent communities in the development of an ecotourism enterprise. A community neighboring Savé Valley Conservancy in Zimbabwe, for example, has voluntarily removed all livestock and incorporated 40 km^2 of their land into the conservancy (Lindsey et al., 2008). This community will receive full financial gains from wildlife as well as become part of wildlife management decision making.

When interviewees were asked directly about their attitudes toward legalizing trophy hunting in Kenya, older community members were generally in favor of trophy hunting, mentioning benefits brought by employment. Younger community members had mixed views, with negativity stemming from the fear that trophy hunters would kill all wildlife and leave nothing to show visitors. Hunting was banned in Kenya in 1977, so most Kenyans lack firsthand experience of tourist hunting, and many are concerned that it would pose a threat to the country's wildlife populations (see Box 1). However, most wildlife species in Kenya have declined significantly since hunting was banned, suggesting that the ban has not been an effective conservation measure (Western et al., 2009). In fact, the hunting ban may have exacerbated the decline by removing a key option for landholders to derive financial benefits from conserving wildlife (Norton-Griffiths, 2007). One of the major challenges with the management of trophy hunting (and ecotourism) is ensuring that a sufficiently large proportion of revenues accrue to communities.

Current government policy in Kenya is such that its citizens would not be able to adequately benefit from trophy hunting as a wildlife land use because wildlife belongs to the state. If trophy hunting were legalized, changes would also be required to grant full user rights over wildlife to private landowners and communities. In Zimbabwe, for example, positive effects for wildlife conservation were seen as a result of the Communal Areas Management Programme For Indigenous Resources (CAMPFIRE), which resulted in devolution of user rights over wildlife from central government to local government (Child, 2000). However, most practitioners believe that CAMPFIRE would be more successful still if user rights over wildlife were devolved further to the community level. Without the devolution of user rights to wildlife, locals cannot benefit adequately from wildlife and therefore lack incentive to protect it.

Predators can pose a cost to people living with or near them, so to conserve these species, conservationists must

BOX 1. Potential for trophy hunting in Kenya.

Reinstating trophy hunting in Kenya would provide incentives for wildlife conservation over a wide area. Hunting and ecotourism are largely complementary land uses; trophy hunting is often conducted in areas not desired by ecotourists, such as areas with low wildlife densities and where people and livestock predominate. Trophy hunting has been successful in creating incentives for conservation on communal lands in other parts of Africa, particularly in Namibia, Botswana, and Zimbabwe. In Namibia, following legislative changes that made provision for communities to obtain user rights over wildlife, income from trophy hunting has been the primary stimulant for the development of a network of communal conservancies now covering more than 126,000 km^2 in which wildlife populations are recovering rapidly (Jones and Weaver, 2008; M. Lamprechts, Trophy Hunting in Namibia from the 1960s to the Present Day, http://www.huntersnamibia.com/Lamprecht_Paper.doc). The Namibian conservancy example clearly illustrates the importance of allocating user rights over wildlife to communities and allowing the option of utilizing wildlife consumptively. Properly managed trophy hunting has potential to offset losses of livestock due to depredation and to create incentives for predator conservation. Visiting hunters pay particularly high prices for opportunities to hunt predators. In southern Africa, hunters pay US$6,000–32,000 in trophy fees per safari to hunt lions in addition to US$1,300–4,000 per day for a minimum of 15–28 days (Booth, 2009). Potential earnings from trophy hunting are particularly high in Kenya because of the presence of a number of species and subspecies that do not occur or are rare elsewhere and because the country is viewed with nostalgia by many hunters as being the original hunting safari destination (Lindsey et al., 2006). There are problems associated with trophy hunting that prevent the industry from benefiting conservation and local development to its potential. For example, there is inadequate regulation of the hunting industry in some areas, and in some cases local communities do not receive an adequate proportion of hunting revenues. However, the net impact of trophy hunting on conservation is almost certainly positive through the creation of financial incentives for the retention and development of wildlife as a land use, especially in areas where alternative income sources such as ecotourism are not viable (Lindsey et al., 2007).

find ways to reduce costs, increase the value of predators, or, preferably, both. If benefits from wildlife are increased, communities might be encouraged to establish wildlife areas on their land, as has occurred elsewhere in southern and eastern Africa. In Zambia, for example, some communities chose to stop agricultural production in favor of forming wildlife areas for trophy hunting for the greater financial benefit (Lewis and Alpert, 1997). The conversion from agriculture- to wildlife-based land use has provided a greater amount of habitat, which is critical for the persistence of wide-ranging species. A key means of reducing the costs of living with predators is reducing livestock losses, for example, through improved livestock husbandry (e.g., Treves and Karanth, 2003; Jackson and Wangchuk, 2004; Woodroffe et al., 2007) and seasonal stocking strategies (Patterson et al., 2004). In another pastoralist area in Kenya, Kruuk (1981) suggested that constructing stronger, less-penetrable corrals should reduce livestock losses, but Ogada et al. (2003) found that corral height and thickness had no effect on livestock losses in Laikipia (see Frank, 2011, this volume, for further discussion on livestock predation). Setting aside conservation areas to conserve wild prey may also reduce livestock losses by increasing the abundance of available wild prey (Woodroffe et al., 2005).

Positive attitudes of community members regarding predators were generally based on the hope of financial gain from wildlife. Our interview results show that community members in the Ewaso region were generally more tolerant of predators if they had tourism on their properties and thus were receiving a benefit. Thirty-five percent of community respondents had tourism operations on their land at the time of our interviews, and an additional 21% had plans to start a wildlife conservancy in the next two years. As a result, a maximum of 56% of respondents should be able to earn income from wildlife tourism in the near future. If the planned tourism schemes come to fruition, community members' attitudes toward predators should improve. However, previous work has shown that when people do not receive expected benefits, their attitudes may ultimately become worse (Western, 1994; Walpole and Goodwin, 2001; Walpole and Thouless, 2005). Although we found that community members' tolerance for wild dogs was greater if some of their household income came from tourism, we found no increased tolerance for predators if benefits were shared among the community as a whole (e.g., schools built). This finding is in keeping with the increasing realization that if benefit-sharing schemes are to succeed, benefits must reach individuals (Walpole and Goodwin, 2001; Walpole and Thouless, 2005).

The best prospects for enhancing predator conservation lie in promoting wildlife-based land uses. Options for communities to benefit financially from predators and other wildlife species would be significantly enhanced if government policies were changed such that user rights to wildlife were granted and consumptive forms of wildlife utilization were permitted.

Among commercial ranchers, increased tolerance for predators compared to 20 years ago is encouraging. Commercial ranchers are considerably wealthier than their communal counterparts, and a significant proportion of them favor wildlife, including predators. On the commercial ranches in the region that favor wildlife, prospects for predator conservation in the Ewaso ecosystem are therefore excellent.

CONCLUSION

Attitudes toward predators have generally improved in Laikipia over the last 20 years, but further improvement is still possible and is necessary to ensure the persistence of predators. Kenya has recently been going through a process to try to improve its wildlife policies for the benefit wildlife and the people living with wildlife. Implementation of policies that allow people to maximize benefits from the wildlife they live with should advance local citizens' interest in expansion of habitat for wildlife conservation.

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REFERENCES

Adams, W. M., and D. Hulme. 2001. If Community Conservation Is the Answer in Africa, What Is the Question? *Oryx*, 35:193–200.

Awere, G. 1996. National Land Use Patterns and Trends. [Final] Report. Nairobi: Kenya Wildlife Service.

Booth, V. R. 2009. *A Comparison of the Prices of Hunting Tourism in Southern and Eastern Africa*. Budapest: Joint publication of FAO and CIC.

Child, B. 2000. "Making Wildlife Pay: Converting Wildlife's Comparative Advantage into Real Incentives for Having Wildlife in African Savannas, Case Studies from Zimbabwe and Zambia." In *Wildlife*

Conservation by Sustainable Use, ed. H. H. T. Prins, J. G. Grootenhuis, and T. T Dolan, pp. 203–218. London: Kluwer Academic Publishers.

Frank, L. 2011 (this volume). "Living with Lions: Lessons from Laikipia." In *Conserving Wildlife in African Landscapes: Kenya's Ewaso Ecosystem,* ed. N. J. Georgiadis. Smithsonian Contributions to Zoology, No. 632:73–83. Washington, D.C.: Smithsonian Institution Scholarly Press.

Gössling, S. 1999. Ecotourism: A Means to Safeguard Biodiversity and Ecosystem Functions? *Ecological Economics*, 29:303–320.

———. 2000. Tourism—Sustainable Development Option? *Environmental Conservation*, 27:223–224.

Grunblatt J., M. Said, and P. Waragute. 1996. Department of Remote Sensing and Resource Surveys (DRSRS) National Rangelands Report. Summary of Population Estimates for Wildlife and Livestock. Kenyan Rangelands 1977–1994. Draft, Ministry of Planning and National Development, DRSRS, Nairobi.

Hackel, J. D. 1999. Community Conservation and the Future of Africa's Wildlife. *Conservation Biology,* 13:726–734.

Jackson, R. M., and R. Wangchuk. 2004. A Community-Based Approach to Mitigating Livestock Depredation by Snow Leopards. *Human Dimensions of Wildlife*, 9:307–315.

Jones, B., and C. Weaver. 2008. "CBNRM in Namibia: Growth, Trends, Lessons and Constraints." In *Evolution and Innovation in Wildlife Conservation: Parks and Game Ranches to Transfrontier Conservation Areas,* ed. H. Suich, B. Child, and A. Spencely, pp. 224–242. London: Earthscan.

Kruuk, H. 1981. The Effects of Large Carnivores on Livestock and Animal Husbandry in Marsabit District, Kenya. *Integrated Project in Arid Lands Technical Report E-4.* Nairobi: United Nations Environment Programme (UNEP)–Man and the Biosphere (MAB).

Lewis, D., and P. Alpert. 1997. Trophy Hunting and Wildlife Conservation in Zambia. *Conservation Biology*, 11:59–68.

Lindsey, P. A., R. Alexander, L. G. Frank, A. Mathieson, and S. S. Romañach. 2006. Potential of Trophy Hunting to Create Incentives for Wildlife Conservation in Africa Where Alternative Wildlife-Based Land Uses May Not Be Viable. *Animal Conservation*, 9:283–291.

Lindsey, P. A., J. T. du Toit, and M. G. Mills. 2005. Attitudes of Ranchers Towards African Wild Dogs *Lycaon pictus*: Conservation Implications for Wild Dogs on Private Land. *Biological Conservation*, 125:113–121.

Lindsey, P. A., R. du Toit, A. Pole, and S. Romañach. 2008. "Savé Valley Conservancy: A Large Scale African Experiment in Cooperative Wildlife Management." In *Evolution and Innovation in Wildlife Conservation: Parks and Game Ranches to Transfrontier Conservation Areas,* ed. H. Suich, B. Child, and A. Spencely, pp. 163–184. London: Earthscan.

Lindsey, P. A., P. A. Roulet, and S. S. Romañach. 2007. Economic and Conservation Significance of the Trophy Hunting Industry in Sub-Saharan Africa. *Biological Conservation*, 134:456–467.

Marker, L. L., A. J. Dickman, M. G. L. Mills, and D. W. Macdonald. 2003. Aspects of the Management of Cheetahs, *Acinonyx jubatus jubatus*, Trapped on Namibian Farmlands. *Biological Conservation*, 114:401–412.

Norton-Griffiths, M. 2007. How Many Wildebeest Do You Need? *World Economics*, 8:41–64.

Ogada, M. O., R. Woodroffe, N. Oguge, and L. G. Frank. 2003. Limiting Depredation by African Carnivores: The Role of Livestock Husbandry. *Conservation Biology*, 17:1521–1530.

Ottichilo, W. K., J. Grunblatt, M. Y. Said, and P. W. Wargute. 2000. "Wildlife and Livestock Trends in the Kenya Rangeland." In *Wildlife Conservation by Sustainable Use,* ed. H. H. T. Prins, J. G. Grootenhuis, and T. T Dolan, pp. 203–218. London: Kluwer Academic Publishers.

Outoma, J. 2004. The Effects of Wildlife-Livestock-Human Interactions on Habitat in the Meru Conservation Area, Kenya. *Land Use Change Impacts and Dynamics*, *Working Paper 39,* Nairobi: International Livestock Research Institute.

Patterson, B. D., S. M. Kasiki, E. Selempo, and R. W. Kays. 2004. Livestock Predation by Lions (*Panthera leo*) and Other Carnivores on Ranches Neighboring Tsavo National Parks, Kenya. *Biological Conservation*, 119:507–516.

Romañach, S. S., P. A. Lindsey, and R. Woodroffe. 2007. Determinants of Attitudes Toward Predators in Central Kenya and Suggestions for Increasing Tolerance in a Livestock Dominated Landscape. *Oryx*, 41:185–195.

Shikwati, J. 2004. Insecurity and Economic Development in Kenya. Report. Inter Region Economic Network, Nairobi.

Sillero-Zubiri, C., and M. K. Laurenson. 2001. "Interactions between Carnivores and Local Communities: Conflict or Coexistence?" In *Carnivore Conservation*, ed. J. L. Gittleman, S. M. Funk, D. W. Macdonald, and R. K. Wayne, pp. 282–312. Cambridge, UK: Cambridge University Press.

Treves, A., and K. U. Karanth. 2003. Human-Carnivore Conflict and Perspectives on Carnivore Management Worldwide. *Conservation Biology*, 17:1491–1499.

Walpole, M. J., and H. J. Goodwin. 2001. Local Attitudes Towards Conservation and Tourism around Komodo National Park, Indonesia. *Environmental Conservation*, 28:160–166.

Walpole, M. J., and C. R. Thouless. 2005. "Increasing the Value of Wildlife through Non–consumptive Use? Deconstructing the Myths of Ecotourism and Community-Based Tourism in the Tropics." In *People and Wildlife: Conflict or Coexistence?,* ed. R. Woodroffe, S. J. Thirgood, and A. Rabinowitz, pp. 122–139. Cambridge, UK: Cambridge University Press.

Western, D. 1994. "Ecosystem Conservation and Rural Development: The Case of Amboseli." In *Natural Connections: Perspectives in Community-Based Conservation*, ed. D. Western and R. M. Wright, pp. 15–52. Washington, D.C.: Island Press.

Western, D., S. Russell, and I. Cuthill. 2009. The Status of Wildlife in Protected Areas Compared to Non-Protected Areas of Kenya. *PLoS ONE,* 4(7): e6140. doi: 10.1371/journal.pone.0006140.

Woodroffe, R. 2000. Predators and People: Using Human Densities to Interpret Declines of Large Carnivores. *Animal Conservation*, 3:65–173.

Woodroffe, R., and L. G. Frank. 2005. Lethal Control of African Lions (*Panthera leo*): Local and Regional Population Impacts. *Animal Conservation*, 8:91–98.

Woodroffe, R., L. G. Frank, P. A, Lindsey, S. ole Ranah, and S. S. Romañach. 2007. Tools for Conserving Large Carnivores in Africa's Community Rangelands: A Case-Control Study of Livestock Husbandry. *Biodiversity and Conservation,* 16:1245–1260.

Woodroffe, R., and J. R. Ginsberg. 1998. Edge Effects and the Extinction of Populations inside Protected Areas. *Science*, 280:2126–2128.

Woodroffe, R., P. A. Lindsey, S. S. Romañach, A. Stein, and S. M. K. ole Ranah. 2005. Livestock Predation by Endangered African Wild Dogs (*Lycaon pictus*) in Northern Kenya. *Biological Conservation*, 124:225–234.

Woodroffe, R., J. W. McNutt, and M. G. L. Mills. 2004. "African Wild Dog *Lycaon pictus*." In *Canids: Foxes, Wolves, Jackals and Dogs, IUCN Status Survey and Conservation Action Plan,* ed. C. Sillero-Zubiri, M. Hoffmann, and D.W. Macdonald, pp. 174–183. Cambridge, UK: IUCN.

Conserving Wildlife on Private Land: The Legal Framework for Landownership and New Tools for Land Conservation in Kenya

Nyokabi Gitahi and Kathleen H. Fitzgerald

ABSTRACT. The threat to wildlife conservation in Kenya continues to escalate, largely because of an increase in habitat fragmentation, land use change, and human population pressure. To maintain viable populations of native wildlife, lands outside protected areas must be conserved through innovative measures. This paper describes the legal framework for landownership in Kenya and existing legal mechanisms used to conserve wildlife habitat and recommends new tools for land conservation on private land. We stress that none of the existing land tenure systems provide an absolute right of use and that most existing legal mechanisms for conservation cannot be relied upon to effectively conserve wildlife habitat outside protected areas. Although environmental statutes such as the Forests Act (Laws of Kenya, 2005) prescribe conservation guidelines, most environmental legislation in Kenya relies upon enforcement and compliance. This approach is not effective because of the lack of institutional capacity to enforce. Because existing measures are not sufficient, other mechanisms such as environmental easements, land purchase, and conservation leases are urgently needed. Even if Kenya's environmental legislation was fully enforced and implemented, environmental easements, land leases, and land purchase would still be vital tools for conservation. Although these tools have great promise, they have not been widely used in Kenya because of legal limitations and lack of precedence. Legislative change and the testing of these tools through existing statutes are required to enable their broader application in Kenya. The Kenya Land Conservation Trust is introduced as an institution providing the framework and structure to utilize conservation mechanisms, such as environmental easements.

INTRODUCTION

The majority of Kenya's large mammals inhabit land outside the network of formally protected national parks, reserves, and forest reserves, which comprise approximately 7.5% of Kenya's land area (Western and Wright, 1994). It is also agreed that the survival of wide-ranging wildlife species found within protected areas depends on seasonal access to surrounding non-protected lands. Large mammals and their access to dispersal areas outside protected areas have been declining in Kenya for decades, creating a severe threat to their viability. Existing

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conservation mechanisms are not adequate to address the threat to wildlife and habitat. New mechanisms are needed. This paper outlines existing and proposed legal provisions and mechanisms for conserving wildlife habitat outside protected areas. In particular, we outline the potential for landholders to conserve wildlife habitat through new legal mechanisms, based on property rights.

LAND RIGHTS IN KENYA

The Constitution of Kenya[1] recognizes and protects the right of individuals to hold and enjoy private property, either individually or in association with others, as one of the Rights and Fundamental Freedoms of the individual. It protects the individual from being arbitrarily deprived of their property without compensation (Laws of Kenya, 2010: section 40). The right to property as used in the Constitution includes property rights in land and is further set out in various statutes that provide for the manner in which property rights in land may be held and transferred. The statutes include Government Lands Act (Laws of Kenya, 1915), Registration of Titles Act (Laws of Kenya, 1920), Land Titles Act (Laws of Kenya, 1908), Land (Group Representatives) Act (Laws of Kenya, 1968c), Trust Land Act (Laws of Kenya, 1970), Registered Land Act (Laws of Kenya, 1963b), Land Acquisition Act (Laws of Kenya, 1968a), and the Land Control Act (Laws of Kenya, 1967). The statutes relating to land will be revised to ensure that they are consistent with the new Constitution of Kenya of 2010 adopted and enacted in a national referendum on 4 August 2010.

The Constitution classifies landownership into three categories: public land; private land, in which individuals or corporate entities hold lease or freehold interests; and community land, in which freehold interests are vested in communities, including registered groups whose lands are referred to as "group ranches," lands registered to a specific community, and lands vested in county governments to hold in trust on behalf of the communities residing within them (Laws of Kenya, 2010: sections 62–64).

Public lands comprise what were formerly Crown Lands under the Crown Land Ordinance of 1915 (Laws of Kenya, 1915) and consist now of unalienated land; that is, land that had not been leased to any other person as of the effective date of the Constitution of Kenya of 2010 (by which date the Commissioner of Lands had not issued any letter of allotment). Public land also includes government forests, game reserves, water catchment areas, national parks, and government animal sanctuaries as well as all minerals and mineral oils, and all rivers and lakes. Ownership of public land is divided between county government and national government as trustees for the people of Kenya. Government forests, government game reserves, national parks, and animal sanctuaries are vested in the national government. A national land commission established in the Constitution administers all public lands on behalf of the national and county governments.

Private land is held by individuals or corporations in the form of freehold or leasehold interests. These interests are established through a process of adjudication, consolidation, and titling of land. The only limitations to absolute proprietorship over land are when there are restrictions registered against the title, such as a right of way, caveats, or use agreements or land use regulations created by law (Laws of Kenya, 1963b, 2010). Absolute proprietorship over land is unlimited in time and can be transferred over generations. Private ownership of land is also achieved through leasehold tenure provided under the Registered Land Act (Laws of Kenya, 1963b). Leaseholds are generally issued for 99 years and are renewable. Foreigners are not permitted to hold free-hold title in Kenya and they can only hold leases for up to 99 years (Laws of Kenya, 2010: Section 65(1)).

Most of the land outside protected areas that is used by wildlife is classified as "agricultural." Ownership of agricultural land in Kenya is controlled by the Land Control Act (Laws of Kenya, 1967). Agricultural land transactions that are subject to the Land Control Act include sale, transfer, lease, mortgage, exchange, partition, or other disposal of or dealing with agricultural land, including shares in a private company or cooperative society that owns agricultural land (Laws of Kenya, 1967: section 6). The Act establishes Land Control Boards whose responsibility is to consider and grant or deny consent to any controlled transaction following application as set out in the Act. The Land Control Act limits dealings with agricultural land to citizens of Kenya, private companies, or cooperative societies whose membership is entirely comprised of Kenyan citizens, group representatives incorporated under the Land Group Representatives Act, or a state corporation established under the State Corporation Act (Laws of Kenya, 1986). Any other individuals or entities that wish to deal in agricultural land are required to seek exemption from the provisions of the Land Control Act, and this exemption can only be granted by the President of the Republic of Kenya following an application for exemption (Laws of Kenya, 1967: section 24). In the absence of an exemption, the Land Control Board is required to refuse consent to persons who do not meet the above criteria, and refusal of consent makes a controlled transaction for which the consent is sought void for all purposes (Laws of Kenya, 1967: section 9(2)). For example, if the African Wildlife Foundation (AWF) wishes to purchase agricultural land in Kenya, because it does not qualify as any of the above, AWF must seek exemption from the Land Control Board to own land. These controls on dealing with agricultural land are expected to change to reflect the provisions of the new Constitution on the rights to own property and the establishment of a national land commission.

Lands held under group ranches and lands vested in county governments in trust for local communities living on the land are categorized as community lands. Group ranches are established under the Land (Group Representatives) Act (Laws of Kenya, 1968c) and apply mainly in the rangeland districts. Most of these rangelands are occupied by Maa-speaking communities that were largely nomadic pastoralists.

In 1968 the Land Adjudication Act (Laws of Kenya, 1968b) and the Land (Group Representatives) Act (Laws of Kenya, 1968c) formalized the conversion of rangelands into group lands to communities with title vested in small groups. No individual group member can dispose of the land. The group members continue to access and use the land communally on the basis of customary laws (Laws of Kenya, 1968c). Group representatives are elected and, upon registration, become a body corporate. Members of the group have a right to vote and participate in decision making through meetings of the group. Over the past decade, many group ranches in southern Kenya have subdivided their land, changing the dynamics of group ranches by vesting ownership within parts of the ranch to individuals. For example, east of Amboseli National Park in southern Kenya, the Kimana Group Ranch has subdivided their land into 60 acre lots that are leased by individuals, who are now free to sell or lease their land for any use permitted by law.

Land vested in county governments to hold in trust for the communities residing within them are referred to as trust lands. These were previously native reserves in the colonial period that were, at independence, vested in local government authorities as trustees for communities ordinarily resident in them (Laws of Kenya, 2010). These lands are now vested in county governments as per the new Constitution (Laws of Kenya, 2010: section 63). The communities residing in trust lands apply African customary law for purposes of land occupation, use, control, disposal, and succession. (Laws of Kenya, 1939: section 69).

COMPULSORY ACQUISITION AND LIMITATION OF LAND RIGHTS

None of Kenya's land tenure systems as previously described grants an absolute right of land use without any limitations on use, nor does any land tenure preclude the government from acquiring such land. The Constitution provides the government two ways to limit property rights: through compulsory acquisition or through land use regulations. The Constitution states that the government may acquire property compulsorily for purposes of public interest and that this may be exercised for the following purposes: defence, public safety, public order, public morality, public health, or land use planning (Laws of Kenya, 2010).

In the case of compulsory acquisition, the landowner is entitled to full and prompt compensation under certain circumstances (Laws of Kenya, 2010: section 40(3)). When determining compensation, the government considers inter alia the market value of the land (Laws of Kenya, 1968a: section 9). The Land Acquisition Act states that land may be acquired for purposes of the government or public body (Laws of Kenya, 1968a: section 6). Once the Minister for Lands makes a decision to acquire land for public purposes, a notice is published in the *Kenya Gazette* and served to the landowner and interested parties.

The power of government to acquire land for purposes of wildlife conservation outside protected areas is also provided for within the Wildlife (Conservation and Management) Act, which empowers the government, through the minister responsible for wildlife, to declare an area a national park (Laws of Kenya, 1976: section 6). In the case of private land the process requires parliamentary approval before the requirements of the Land Acquisition Act (Laws of Kenya, 1968a) can apply. The end result of compulsory acquisition of land is that title is vested in the government free from all encumbrances (Laws of Kenya, 1968a). When all the land has been acquired, documents of prior title are cancelled. When only part of the property has been acquired, the documents of title are amended to reflect the change against the title in the Register of Titles (Laws of Kenya, 1968a: section 20).

Although the potential to protect wildlife habitat through application of eminent domain is theoretically unlimited, any attempt to apply compulsory acquisition today would be met with resistance of a scale highly likely to defeat the objective. Kenya's protected areas were established through a process of compulsory land acquisition largely belonging to communities, resulting in a great deal of bitterness and resentment that persists today. Any attempt to secure conservation land through eminent domain would be fought vigorously by community members and leaders.

Apart from compulsorily acquiring land, the government has power to regulate and limit the rights of landowners to use land for the purpose of conserving wildlife habitat (Laws of Kenya, 2010: section 66). This is done mainly through land use planning and zoning and the use of regulations and sanctions to enhance compliance. The government has no obligation to compensate the landowner for land rights limited as a result of land use regulations.[2] Like eminent domain, forcefully limiting personal rights on land for wildlife conservation will be challenged because of the history of compulsory land acquisition for the creation and management of protected areas in Kenya. Thus, conservation via land use regulations alone is not a viable option for securing land for conservation.

HABITAT CONSERVATION USING EXISTING STATUTES

Kenya has numerous statutes that are designed to conserve natural resources. This section highlights some of these statutes and how they may be used to protect land outside of protected areas. Currently, Kenya is reviewing and redrafting a number of its policies that pertain to natural resource conservation. Any new laws will need to be made fully compatible with the new Constitution.

Provisions of the Water Act (Laws of Kenya, 2002) relating to the protection of water bodies could, if implemented effectively, benefit wildlife habitat. The Act's provisions can be used to ensure availability of clean water for wildlife and protect catchment habitat around water bodies. The Act prohibits various harmful activities relating to water bodies and requires permits for certain activities. For example, the Act criminalizes pollution of water bodies as well as obstruction or diversion of water from any water resource without authority under the Act, with stiff penalties for violations (Laws of Kenya, 2002: section 94).

The Agriculture Act (Laws of Kenya, 1963a) is aimed at promoting and maintaining agricultural production, stimulating the development of good land management and husbandry, developing agricultural land, conserving soil and soil fertility, and preventing soil erosion. "Agricultural land" refers here to all land that is used for purposes of agriculture and excludes any land that is by provision of any law relating to planning, such as the Physical Planning Act, and proposed for use other than agriculture (Laws of Kenya, 1963a: section 2). The term "agriculture" is used broadly under the Agricultural Act and includes cultivation, horticulture, dairy farming, beekeeping, and raising livestock. Much of the land used by wildlife outside of protected areas is arid, agricultural land primarily used by pastoralists. Agricultural land also includes land used for the keeping of game animals and birds as well as breeding and game ranching within the provisions of Kenya's Wildlife (Conservation and Management) Act (Laws of Kenya, 1976: section 2).

The Agriculture Act gives the minister in charge of agriculture authority to issue sanctions to enforce the provisions of the Act. For example, the Minister may require a private landowner to carry out an activity that preserves soil (Laws of Kenya, 1963a: section 51). The Act makes it an offense for any landowner to fail to comply with an order, and if found guilty, the offender is liable to a fine, imprisonment, or the disposal of his land (Laws of Kenya, 1963a: section 60). The Agriculture Act would benefit rangelands by preventing soil degradation; however, like most laws that require enforcement, these sanctions have not been effective because of lack of enforcement capacity.

The Minister of Agriculture has wide powers for ensuring preservation of agricultural land, and these include powers to make regulations and rules for preservation and development of agricultural land (Laws of Kenya, 1963a: sections 51, 64). The Minister has wide powers for enforcing the provisions of the Agriculture Act as well as any regulations made under the Act, including the power to dispossess owners and occupiers of agricultural land and to purchase or compulsorily acquire the land from landowners who fail to comply with any regulations or orders made under the Agricultural Act. The Minister also has power to intervene in issues of land management on any agricultural land if, in the Minister's opinion, the land is inadequately managed or has ceased to be managed; and the Minister can take measures to prevent or delay deterioration of such land, including issuing management orders against the landowner, which allows the Minister to manage the land to the exclusion of the landowner (Laws of Kenya, 1963a: section 187).

The Forests Act (Laws of Kenya, 2005) was intended to provide for conservation and management of Kenya's forest resources. This is another statute that could have potential benefits to wildlife habitat outside protected areas; however, like the Water and Agricultural acts, this Act relies on enforcement and sanctions for compliance (Laws of Kenya, 2005).

The 1999 Environmental Management and Coordination Act (EMCA) provides a legal framework for management of the environment, which is defined to include the physical factors of the surroundings of human beings, including land, water, atmosphere, climate, sound, odor, taste, the biological factors of animals and plants, and the social factor of aesthetics, and includes both the natural and built environments (Laws of Kenya, 1999: section 2). The Environmental Management and Coordination Act contains several provisions that could be used to protect wildlife habitat outside protected areas. These provisions include environmental easements, environmental restoration orders, environmental impact assessment, and environmental impact licenses.

The foregoing examples illustrate that Kenya has several strong statutes intended to protect natural resources and the environment. However, much of Kenya's environmental legislation relies heavily on compliance, implementation, and enforcement. Because of low capacity of enforcing agencies, there is poor enforcement of Kenya's environmental laws. Monitoring for compliance and prosecuting offences are challenging functions, especially where there is widespread default, and most government institutions have insufficient staff for these purposes. With few exceptions, the overall result is a general failure of existing legal measures for conserving wildlife habitat outside of protected areas, thus leaving the wildlife vulnerable to various threats and resulting in a continued decline in wildlife.

MECHANISMS FOR HABITAT CONSERVATION BASED ON PROPERTY RIGHTS

If Kenya's environmental laws were fully enforced and implemented, tools such as environmental easements, land acquisition, and conservation leases would still be necessary to adequately secure Kenya's wildlife and landscapes. Conservation of natural resources is best served by a diversity of tools. Regulation may be appropriate in certain places, whereas different tools may be more appropriate in other areas. In addition, legislation is subject to change, so although Kenya may enjoy strong environmental legislation one year, that may change the following year, which jeopardizes the conservation of natural resources.

Tools such as leases, described below, can provide direct benefit to landowners; otherwise, they may choose alternative land uses that are permitted by law yet are incompatible with wildlife and conservation. For example, Kitengela is a wildlife dispersal area south of Nairobi National Park. Development pressure is significant because of proximity to Nairobi. Much of the land in Kitengela has been subdivided and is held by title; thus, landowners can legally sell their land for development or agriculture. One conservation entity is leasing the land on an annual basis to keep the area open for wildlife movement. This land would have been fragmented by a number of legally permissible uses if not for the lease program. The challenge, however, is how to sustain the lease program as well as compete with escalating market prices. If someone can make four times as much by selling their land than they can from the lease program, they will be very tempted to sell.

The failure of coercive legal measures and existing statues for conserving wildlife habitat outside protected areas and the diversity of conservation needs and challenges call for additional approaches. There is an urgent need for incentive-based mechanisms that provide landowners with opportunities to conserve their land through the voluntary restriction of their property rights. These mechanisms include land purchase, environmental easements, and conservation leases. The successful use of conservation mechanisms based on property rights depends on clearly defined and articulated land rights. A landowner must have secure legal rights over the land and the power to convey rights and interests for the benefit of wildlife conservation in order to take advantage of these tools. Several such mechanisms are described below.

LAND PURCHASE

Typically, when parcels of land come up for sale in Kenya, they are purchased, developed for agriculture, habitation, or other uses that are incompatible with wildlife conservation. These lands can be purchased by entities intending to manage them for conservation. For example, in 2004 a large-scale ranch in Laikipia District that was located in an area strategically important for conservation was purchased by a private company registered in Kenya and funded through an international conservation organization. Today, the land is managed successfully for conservation and wildlife, and it also benefits the surrounding communities. In this case, the provisions and requirements under the Land Control Act as to who can own land in Kenya were met because the purchaser of the above land is a company comprised of Kenyan shareholders. Buying land for conservation purposes, assuming compliance with the Land Control Act and other Kenyan statutes, is an effective tool that can be used by conservation entities to secure critical wildlife habitat. By owning the land, the conservation entity is in control of the land use and can manage specifically for wildlife purposes. The challenges to purchasing land are ensuring clear land rights of the seller, raising the funds to purchase land, and managing the land in the long term.

ENVIRONMENTAL EASEMENTS

An environmental easement is an agreement between a landowner and the holder of the easement, which restricts certain uses of a property to achieve conservation purposes. Easements in Kenya have their origin in English law (Gaunt and Morgan, 1997). They have also been used for non-conservation purposes, such as to create a right of way or grant water rights (Gaunt and Morgan, 1997).

In Kenya, the 1999 EMCA makes provisions for use of easements to conserve wildlife habitat. The aspect of the environment that benefits from the restrictions placed on the land by an easement is called the "benefited environment," and the land subject to the easement is called the "burdened land." The essence of an environmental easement is to conserve target resources such as wildlife, watersheds, and habitat.

Use of environmental easements to conserve wildlife habitat requires landowners to forego certain land use options on their land. Under EMCA, the process operates through the court and is not necessarily voluntary. If the court imposes an environmental easement, the landowner is entitled to compensation commensurate with the lost value of the use of the land (EMCA). The person awarded the easement pays the compensation, unless the court determines a national importance; then the government may be instructed to compensate the landowner. Under EMCA, section 112 (Laws of Kenya, 1999), anyone can hold a conservation easement. This is in contrast to the Land Control Act (Laws of Kenya, 1967), which controls dealings in agricultural land and limits the rights of noncitizens to own agricultural land without the consent of the President of the Republic of Kenya, which may be obtained following an application for exemption from the provisions of the Land Control Act. In a situation where an environmental easement is negotiated, the landowner and the easement holder would agree on the value of compensation due to the landowner. For example, if Mr. M. believes his neighbor's property is important wildlife habitat, under EMCA he can file for an environmental easement. If the court approves the environmental easement, Mr. M. will hold the easement, and as per the recommendation of the court, he will compensate the neighbor. The neighbor has no choice in this matter.

To encourage landowners to place environmental easements on their land, EMCA and/or other legislation in Kenya should be amended to allow for the use of *voluntary* environmental easements without being imposed through judicial process. Imposing an environmental easement through the court presumes an adversarial approach and could be viewed as punitive. Instead, landowners and appropriate organizations should be able to negotiate and agree to voluntary environmental easements. To ensure the long-term sustainability of easements, institutions that can monitor and uphold easements should be the easement holders. Moreover, EMCA makes no provision for determining the value of an environmental easement, leaving it to the courts to perhaps set the precedence. Less adversarial systems and a standardized appraisal process should be developed to determine the value of environmental easements (Farrier, 1995). To date, an environmental easement has not been implemented through EMCA. In addition to proposing legislative change to provide for voluntary environmental easements, the African Wildlife Foundation is working with partners to bring a consensual environmental easement to the court to process through EMCA with the aim of setting a positive precedent for voluntary easements.

Community land presents a challenge to the use of environmental easements because rights of use over land among the communities that live on the land are governed by customary law, which is unregistered. This is expected to change as the Constitution provides that the national land commission would advise the national government on a comprehensive program for the registration of title in land throughout Kenya. The laws relating to governance of community land are also to be reviewed and rationalized, and an important outcome of this process would be provision for a process to define and quantify the nature of customary rights of use over land to enhance the security of tenure and enable the use of property-rights-based conservation mechanisms, especially easements and leases.

LEASES

A lease provides an opportunity to obtain possession of a parcel of land for a given duration for specific uses. This mechanism is very common in land transactions and can be used for purposes of conserving land. For example, an appropriate entity may purchase a 99 year lease on a property and manage it for conservation purposes. Another variation is leasing specified rights on a property. Many safari and tourism companies lease land for tourism use, tented camps, and wildlife watching. The African Wildlife Foundation is using leases, for example, to conserve wildlife dispersal areas outside Amboseli National Park in southern Kenya, leasing land from landowners for habitat conservation. Through a lease, AWF is paying approximately 210 landowners to manage their land sustainably and not block wildlife movement with development, fencing, and farming. This program has protected approximately 12,500 acres of strategic wildlife habitat and is expanding by incorporating more adjacent landowners. This is another example that documents the need for tools such as leases because fragmentation by development, fencing, and agriculture is legally permissible in this area under Kenya law and landowners would choose alternative income-generating land uses that may not be compatible with wildlife. The challenge is finding a long-term funding source to sustain lease programs.

LACK OF INCENTIVES FOR WILDLIFE CONSERVATION ON PRIVATE LAND

Kenya landowners generally use land for purposes that are profitable, and land use that does not provide favorable returns is likely to be shunned. Landowners are required to absorb costs of keeping wildlife outside protected areas, and those not directly investing in ecotourism see little or no return from wildlife. In fact, many landowners face direct economic challenges from wildlife, for example, elephants raiding crops or predators killing livestock. Yet much of the wildlife in protected areas would not survive without seasonal access to adjoining private and community lands. A key challenge for wildlife conservation is therefore to find ways of making wildlife a profitable land use. One way to ensure that landowners benefit from wildlife is by compensating them for conservation of their land through conservation leases or environmental easements, such as the examples provided in the Amboseli region and in Kitengela.

One of the greatest challenges facing wildlife in Kenya today is the shift in land use from grazing to cultivation. The government's policy has promoted agricultural production through, for example, support for irrigation, financing for land subdivision and titling to establish farms, and subsidized loans to support cultivation of specific crops. Cultivation then becomes more profitable than keeping wildlife or cattle. In addition, there is significant international investment and focus on food security and large-scale agricultural development in Africa. This investment puts added pressure on land in Africa and further encourages governments to promote agricultural development without proper land use planning.

At the same time, many group ranches are going through a process of subdivision into small, fenced units, which severely fragments the landscape and impedes wildlife movement. As a result, livestock production has become limited, with less room to roam. Many pastoralists have turned to cultivation, which further fragments the landscape, increases human-wildlife conflict, makes traditional pastoralism unsustainable, and leads to habitat degradation.

Measures should be taken to encourage the government to prevent subdivision of rangelands below economically viable size to ensure that the rangelands continue to support livestock and wildlife and to provide tax incentives for landowners to establish wildlife-based tourism. Private land tools, such as conservation leases, can provide an added benefit to landowners and prevent conversion of open land to cultivated units. The greatest challenge herein is finding the funds to support conservation leases as donor funds cannot be relied upon in the long term. In some areas, tourism may directly support leases; however, this is not a viable option everywhere. Creative benefit-sharing mechanisms from existing protected areas and tourism facilities must be explored. Payment for ecosystem services is another potential source of revenue to support conservation leases.

KENYA LAND CONSERVATION TRUST

Many state institutions in Kenya have a mandate to conserve aspects of the environment; however, existing institutional frameworks for these agencies do not permit them to effectively conserve wildlife resources outside protected areas, especially through the use of property-rights-based mechanisms. This is because they have a limited mandate to conserve wildlife outside protected areas, especially on private land. Therefore, effective use of mechanisms based on property rights for conservation of wildlife habitat in Kenya requires an enabling institutional framework that until recently has been lacking. Recognizing the need for a national organization that can pilot environmental easements, leases, and land acquisition and serve as a countrywide organization, the African Wildlife Foundation helped cofound the Kenya Land Conservation Trust (KLCT) in 2005 (Box 1).

The KLCT provides an institutional framework to support the development and use of property-rights-based mechanisms such as environmental easements and land purchase for habitat conservation. It aims to work in collaboration with landowners and partners to conserve wildlife habitat in areas such as the Ewaso ecosystem and to test and advance the use of legal and economic mechanisms for habitat conservation. The KLCT can serve as the institutional holder of environmental easements and promote the advancement of private land tools.

AFRICAN WILDLIFE FOUNDATION

The African Wildlife Foundation (AWF) was founded in 1961 and works together with the people of Africa to ensure the wildlife and wildlands of Africa will endure

BOX 1.
The Kenya Land Conservation Trust.

Objectives

The Kenya Land Conservation Trust was established in 2005 as a private charitable trust, incorporated under the Trustees (Perpetual Succession) Act (Laws of Kenya, 2009). The main objective of the trust is to ensure the viable function and integrity of natural habitat on land outside protected areas and the wildlife populations that they support while taking into account the social and economic interests of landowners and communities. The trust, in partnership with landowners and other stakeholders, will do this by (1) providing landowners with an opportunity to use land conservation options, including land acquisition, environmental easements, and leases for land conservation, and (2) supporting the formulation of policies relevant to biodiversity conservation in Kenya.

The Board of Trustees

The management of the trust is currently vested in the Board of Trustees. The founding trustees are representatives of African Wildlife Foundation, Kenya Wildlife Service, and the Ministry of Lands and Housing. One of the board seats is allocated to a member of the National Land Owner Forum. This is a fully Kenyan board.

Scope of the trust

The trust is focused on biodiversity conservation outside protected areas in Kenya. It will address aspects of conservation including wildlife migratory routes, dispersal areas, forest areas, and wetlands. With the support of the African Wildlife Foundation, the trust has undertaken a process of site selection and prioritization to determine the landscapes it will target for conservation intervention in Kenya. Overall, it is important that the trust will seek to engage with and respond to the landowners and stakeholders in designing and implementing habitat conservation mechanisms.

forever. AWF's land protection program had primarily focused on supporting protected areas and helping communities protect their land through management and land use plans and zoning. To successfully achieve its conservation goals, AWF recognized that in addition to its existing conservation tools and land conservation programs, it must put more emphasis on direct conservation measures on lands outside protected areas and to do so, it must utilize new conservation approaches.

The African Wildlife Foundation is working to identify strategic conservation priorities in the Ewaso ecosystem and throughout Kenya. AWF uses a scientific approach to identify its conservation targets, considering a suite of indicator species, access to water and other natural resources, wildlife movement patterns, connectivity, threat, and natural communities. Once a property is identified, AWF carefully evaluates the appropriate tool needed to conserve the parcel. AWF firmly believes that the advancement of conservation tools, as discussed in this paper, will help itself and other conservation organizations to achieve conservation success throughout Kenya. AWF has used a variety of these tools; it has purchased land, leased land, and is currently working with partners to secure land with an environmental easement through EMCA.

To advance the development of private land conservation tools, AWF convened a team of attorneys and conservation practitioners to explore environmental easements in Kenya, review existing statutes to determine how and if voluntary easements can be implemented under existing legislation or propose new legislation and amendments, and develop valuation methodologies for environmental easements and conservation leases. The results of this working committee were published by AWF (Watson et al., 2010).

CONCLUSION

Kenya's wildlife is severely threatened by habitat fragmentation, loss of habitat, land use change, barriers to movement, and human population pressure. The current institutional frameworks for wildlife conservation have failed to effectively conserve wildlife resources outside protected areas in Kenya and provide landowners with an incentive to manage their land for wildlife. Most of Kenya's wildlife is dependent upon habitat outside of protected areas. This is especially true for the Ewaso ecosystem, where wildlife thrives largely on privately and communally owned land. To adequately address the conservation challenge in Kenya, a wide diversity of tools must be developed, enhanced, and utilized. Kenya's environmental statutes alone will not safeguard the country's wildlife and landscapes. Tools such as leases, acquisition, and environmental easements play a vital role in conserving Kenya's wildlife habitat.

Kenya's property rights regime provides substantial opportunities to use various mechanisms such as environmental leases to conserve wildlife habitat outside protected areas by restricting land use to activities that are compatible to conservation of wildlife habitat as well as providing an opportunity to purchase critical parcels of land. These mechanisms not only protect important habitats but also provide landowners with the compensation they need to effectively manage their land for wildlife and ecological integrity. Environmental leases are already being used successfully, and this model can be replicated throughout Kenya. However, creative and collaborative funding mechanisms must be developed to support the large-scale conservation that is necessary to sustain Kenya's wildlife and habitat.

The Environmental Management and Co-ordination Act provides an opportunity to use environmental easements, and this instrument has the potential to be used to conserve wildlife habitat on private land without the burden or cost of purchase. An amendment to EMCA and/or other environmental legislation in Kenya to provide for voluntary easements would help catalyze the use of this tool and significantly enhance conservation in the Ewaso ecosystem and throughout Kenya.

Kenya boasts unique landscapes and wildlife; however, with only approximately 7.5% of the country formally protected, additional tools and strategies must be adopted to conserve additional lands. The use of environmental easements, leases, and land acquisition will complement Kenya's existing conservation framework and tools to ensure the long-term sustainability of its wildlife and wildlands.

NOTES

1. Reference to the Constitution of Kenya refers to the 2010 constitution adopted and enacted through a national referendum on August 4, 2010. This replaced the 1963 Constitution of Kenya.

2. Land use control measures must be applied with caution as excessive land use regulations may be seen to amount to compulsory acquisition of the land and may be challenged on a constitutional basis as taking. In the United States, for example, land use regulations may be challenged on the grounds that they are so restrictive that the state has as good as acquired the land and may be declared unconstitutional, as was the case in *Morris City Land Improv. Co. v. Parsippany-Troy,* 40 N.L. 539, 193 A.2d 233.242 (1963) and *Lucas v. South Carolina Coastal Council,* 112 S. Ct., 22 ELR (1992).

REFERENCES

Farrier, D. 1995. Conservation Biodiversity on Private Land: Incentives for Management or Compensation for Lost Expectations? *The Harvard Environmental Law Journal,* 19 19(2):304–305.

Gaunt, J., and P. Morgan. 1997. *Gale on Easements*. London: Sweet and Maxwell.

Laws of Kenya. 1908. Land Titles Act. Chapter 282. Nairobi.

———. 1915. Government Lands Act. Chapter 280. Nairobi.

———. 1920. Registration of Titles Act. Chapter 281. Nairobi.

———. 1939. Trust Land Act. Chapter 288. Nairobi.

———. 1963a. Agriculture Act. Chapter 318. Nairobi.

———. 1963b. Registered Land Act. Chapter 300. Nairobi.

———. 1967. Land Control Act. Chapter 302. Nairobi.

———. 1968a. Land Acquisition Act. Chapter 295. Nairobi.

———. 1968b. Land Adjudication Act. Chapter 284. Nairobi.

———. 1968c. Land (Group Representatives) Act. Chapter 287. Nairobi.

———. 1970. Trust Land Act. Chapter 288. Revised edition. Nairobi.

———. 1976. Wildlife (Conservation and Management) Act. Chapter 376. Nairobi.

———. 1986. State Corporation Act. Chapter 446. Nairobi.

———. 1999. Environmental Management and Co-ordination Act. Number 8. Nairobi.

———. 2002. Water Act. Chapter 372. Nairobi.

———. 2005. Forests Act. Number 7. Nairobi.

———. 2009. Trustees (Perpetual Succession) Act. Chapter 164. Nairobi.

———. 2010. Constitution of Kenya. Nairobi.

Watson, R., K. H. Fitzgerald, and N. Gitahi. 2010. Expanding Options for Habitat Conservation Outside Protected Areas in Kenya: The Use of Environmental Easements. *African Wildlife Foundation Technical Papers*, 2.

Western, D., and M. Wright, eds. 1994. *Natural Connections: Perspectives in Community Based Conservation*. Washington, D.C: Island Press.

Landscape-Scale Conservation Planning of the Ewaso Nyiro: A Model for Land Use Planning in Kenya?

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ABSTRACT. The unique wildlife of the Ewaso Nyiro and valuable services that the ecosystem provides for humans (e.g., clean water and productive grasslands) cannot be conserved by working solely on traditional conservation strongholds such as the national reserves and private ranches of central Laikipia. To reach objectives for conserving wildlife, stakeholders must work to preserve wildlife habitat and corridors in the surrounding human-dominated landscape—a daunting task considering the complexity of working at large spatial scales (e.g., many landowners, competing land uses) and limited conservation resources available. Systematic, landscape-scale conservation planning helps stakeholders set meaningful and transparent objectives, identify where to work to meet those objectives, and prioritize areas for immediate investment. We describe results and implications of an initial landscape-scale planning exercise for the Ewaso Nyiro that culminated in a workshop in January 2006. Forty participants selected nine focal features, set quantitative objectives for four of them (elephants, Grevy's zebra, lions, wild dogs), and set spatial conservation priorities for the entire landscape on the basis of complementary needs of critical species. The modest objectives for these species (e.g., maintaining a population of 300 wild dogs) cannot be met by conservation focused solely on traditional strongholds. The exercise indicated that nearly 84% of the landscape needs conservation investment, and it identified three near-term priorities: (1) maintain current investments in conservation strongholds, (2) increase investment to secure the narrow corridor between Samburu and Laikipia Districts, and (3) increase investment to secure portions of Samburu District, including the Matthews Range. The results we describe represent the initiation of a land use planning process that, if continued, can help meet both biodiversity and livelihood development objectives. We recommend this process be carried forward in the Ewaso Nyiro and then in similar ecosystems in Kenya and eastern Africa.

INTRODUCTION

From previous chapters in this book, it seems clear that in the Ewaso Nyiro ecosystem, conservation goals cannot be achieved by focusing solely on the few parcels of land that are currently under conservation-friendly land uses and management. To improve chances of conserving wildlife in the Ewaso ecosystem and more generally throughout much of Kenya, we believe that stakeholders need to adopt a systematic approach to prioritizing conservation investments at the landscape level.

A *landscape-scale* framework for planning conservation is needed for two main reasons. First, many valued species cannot be effectively conserved on the few increasingly isolated patches of lands on which biodiversity conservation is the primary land use objective (Gardner et al., 2007). This is particularly true for species that require extremely large areas and access to many different habitats to persist, i.e., many of the large herbivores and carnivores common in Kenya. Landscape-scale approaches to conservation aim to explicitly address the needs of these area-demanding species and to ensure their long-term persistence (Nicholson et al., 2006; Rouget et al., 2006; Salomon et al., 2006).

A second reason that a landscape-scale framework is needed is that many critical ecological processes (e.g., migration and gene flow) and ecosystem services (e.g., production of clean water) also cannot be effectively conserved by working solely with landowners whose property covers only a small percentage of the landscape (Poiani et al., 2000; Chan et al., 2006; Salomon et al., 2006; Rouget et al., 2006). These processes and services are often critical for both biodiversity elements (species and ecological communities) and people. Landscape-scale planning approaches help to determine the spatial scope of activities that are needed both to meet the needs of species and to maintain ecological processes and ecosystem services important for people.

A systematic approach to planning (Margules and Pressey, 2000; Groves et al., 2002), with clearly defined steps and procedures, is also useful because it instills transparency into the process. This is particularly valuable in places where governance is weak, contested, incomplete, or has been abdicated by the state. The systematic approach aims to define a clear and transparent process for arriving at conservation priorities—a process that allows for broad stakeholder participation. Systematic conservation planning also immerses people, often for the first time, in a process focused on biodiversity rather than economic development. It also allows a wide range of stakeholders to bring to bear their distinct and often underappreciated knowledge of the ecology of a landscape. Most importantly, the systematic approach tries to instill transparent, objective, and effective criteria into a process for prioritizing conservation actions and areas (Margules and Pressey, 2000). It is almost always the case in conservation that we cannot conserve, in the immediate sense, everything we need to, and prioritization is needed. Objective and rigorous criteria help ensure that our resources are directed most efficiently.

Systematic, landscape-scale conservation planning now has a history of nearly two decades. It began when conservationists first recognized that existing protected areas were necessary but not sufficient to preserve biodiversity effectively (Rodrigues and Gaston, 2001; Brooks et al., 2006). Many hundreds of projects at various spatial scales (e.g., Younge and Fowkes, 2003) around the world now use systematic procedures for conservation planning (Sarkar et al., 2006). More recently, several international conservation organizations have created planning approaches designed particularly for the landscape scale and firmly rooted in a systematic framework (Sanderson et al., 2002; Conservation International, 2004; Henson et al., 2009; Pressey and Bottrill, 2009).

We present here the results and implications of a systematic, landscape-scale conservation planning exercise for the Ewaso ecosystem. The exercise was conducted over a six-month period that ended in a five-day workshop in 2005–2006. The approach we initiated is novel in that it was designed to skirt some of the weaknesses of existing approaches, which often demand more time and resources than are available. The methods and its novelties are described in detail in Didier et al. (2009) and in the workshop proceedings (King and Malleret-King, 2006) and are presented here only briefly.

Our objectives are to first present the results of the exercise for a larger audience not present at the workshop, including local stakeholders from the Ewaso region and the wider conservation and development community in Kenya. Second, we discuss briefly the implications of the exercise for the particular species considered and for conservation in the Ewaso Nyiro in general. Third, we discuss what we could not achieve during our time- and resource-limited project and how we think the process should be carried forward in the future.

METHODS

The group proceeded through the basic steps of systematic conservation planning as outlined in Box 1 (full description of methods can be found in King and Malleret-King, 2006, and Didier et al., 2009). Nine focal biodiversity features (in this case all "features" were species) were identified whose conservation requirements not only were considered to be complementary to each other but also, when added together, would, if met, cover the conservation needs of most other features in the landscape. We did not complete these planning steps exhaustively for all species, rather, for a subset of four species (elephant, Grevy's zebra, lion, and wild dog), aiming to produce useful products for making near-term decisions and to create a framework for proceeding with conservation priority setting in future. We proceeded in two phases. First, a six-month preparation phase by a small organizational committee and a group of ecologists who were each familiar with the landscape and particular biodiversity features produced draft plans for the four species. We completed all the planning steps for four of nine focal species, although conservation objectives (step 3; see Box 1) were considered preliminary and were not explicitly incorporated into the subsequent steps. The exercise was largely centered on the creation of five component maps for each species that were used to guide decisions about which areas were a priority for immediate conservation investment. For these maps, each 5 × 5 km grid square was classified as to (1) its current importance for supporting the population of the focal species, (2) the potential for recovering the population of the species, (3) the potential for future decreases in the population as a result of human activities, (4) the cost of conservation action, and (5) confidence in the information provided. The maps were then used as guides to make species-specific and cross-species maps of conservation priorities.

BOX 1. The steps of systematic, landscape-scale conservation planning.

The steps to systematic conservation planning at any scale (global, national, etc.) are fairly similar, are well accepted among organizations involved in conservation, and have been thoroughly described elsewhere. Our description is adapted from those of Margules and Pressey (2000), Groves et al. (2002), Groves (2003), and Sarkar et al. (2006). Further detail is also provided in the proceedings of our workshop (King and Malleret-King, 2006) and by Didier et al. (2009).

1. Define the context, compile critical information, and set overarching goals/vision. Basic information on the extent of the landscape, ecology, human influences/threats in the landscape, and stakeholders need to be summarized, and broad goals need to be set. Spatial information should be compiled on the current biodiversity value of areas throughout the planning region (i.e., presence or abundance of focal conservation targets), the vulnerability of biodiversity to future loss, the potential for recovery of biodiversity value (if locally relevant), and costs of conservation.

2. Define a set of focal biodiversity features. Because it nearly impossible to plan conservation around all the possible elements of biodiversity (species, habitats, and ecosystem functions and services), it is necessary to select a suite of focal features on which to plan conservation efforts. The number and type will depend on the context (e.g., availability of data, complexity of environment).

3. Set quantitative objectives for each focal conservation feature. It is important to set quantitative objectives for conservation feature (i.e., how much do you want?), so that the spatial extent of conservation actions necessary to meet these objectives can be considered and progress toward the objectives can be measured.

4. Assess the effectiveness of existing conservation activities/areas. This step should first involve assessing whether current activities and the extent of areas where activities are occurring are sufficient for meeting quantitative objectives for all focal features. If targets are currently at quantitative objectives across the landscape, are current activities and areas sufficient to maintain features at or above quantitative objectives (i.e., prevent future losses)? If features are currently below objectives, are current activities and areas sufficient to increase focal features to quantitative objectives?

5. Summarize the benefits and costs of continuing current activities/areas and starting new ones in order to meet or maintain quantitative objectives of conservation features. This step involves creating summary maps and indices highlighting where investment may be wise. It may include benefit:cost ratios, irreplaceability scores, or other results of reserve design algorithms (e.g., from Marxan, C-plan, etc.).

6. Negotiate a map of conservation priorities. Physically score planning units in terms of priority for investment, considering all information in previous maps, possible mistakes, and all relevant information not in the maps (e.g., political constraints, opportunities, etc.). May also include evaluating trade-offs, both among conservation features and between biodiversity features and human development objectives (e.g., increasing livestock numbers). Decision-support software can help (Marxan, C-plan, Vista).

RESULTS

VISION FOR BIODIVERSITY CONSERVATION

Workshop participants agreed on a simple, consensus vision statement for biodiversity conservation in the region: "To conserve the native biodiversity and integrity of the Ewaso Nyiro landscape."

FOCAL BIODIVERSITY FEATURES

Participants discussed and then selected a subset of the biodiversity within the Ewaso landscape that would help focus conservation planning efforts. The focal suite comprised nine biodiversity features (Table 1). Elephants, Grevy's zebra, lions, wild dogs, and reticulated giraffe (*Giraffa camelopardalis*) were selected because they represented major habitats or threats to biodiversity (see King and Malleret-King, 2006). Jackson's hartebeest (*Alcelaphus buselaphus*) was added because it was viewed by participants as being unique to the Ewaso Nyiro and participants felt its conservation could not be guaranteed by focusing attention on the other features. The suite also included what participants felt were the two most important vegetation communities: the acacia-grassland mosaic, which covers most of the landscape, and dry upland/montane forests (Matthews Range, Kirisia Hills, and Mukogodo Forest in particular). Finally, the suite of focal features included one ecological system/service, the hydrological system, because maintaining water flow and water quality in the landscape was seen as central to both conservation of biodiversity and livelihoods. As a whole, participants agreed that the suite of features would act as a good surrogate for protecting the other native biodiversity of the region and that if these features were successfully conserved, most if not all of the other native biodiversity in the landscape would also be conserved. It was agreed that the steps of conservation planning would include only four species because of available time and resources.

QUANTITATIVE OBJECTIVES FOR BIODIVERSITY FEATURES

Workshop participants produced preliminary estimates of (1) the current population size across the landscape for each of the four species, (2) a range around that estimate, and (3) a preliminary conservation objective (Table 1). Estimates represent "best information" and were based on consensus among a subset of participants working on each particular species. In some cases, estimates were based partially on empirical data collected from parts of the landscape and extrapolated to remaining areas for which empirical data did not exist. Quantitative objectives for all four species represented an increase from the current population estimate, although the objective for Grevy's zebra represented a nearly 165% increase, whereas for the three other species the objectives represented only 10%–25% increases. Although the objective for elephants represented an overall increase in the population, participants produced a more specific objective to

TABLE 1. The suite of focal biodiversity features selected by participants at the Ewaso Nyiro Landscape Conservation Planning Workshop (January 2006) and quantitative conservation objectives for these features. Subsequent to selecting these features, participants concentrated on only the top four, although the other features should be considered in future exercises. The quantitative conservation objective represents the total population that participants would like to see across the landscape in 10 years to be considered successful. Information was not compiled during this exercise for the following features: Jackson's hartebeest (*Alcelaphus buselaphus*), reticulated giraffe (*Giraffa camelopardalis reticulate*), acacia-grassland mosaic, dry upland/montane forest, and hydrological system.

Focal biodiversity feature	Estimate of current abundance (January 2006)	Range of estimated abundance	Quantitative conservation objective[a]
African elephant (*Loxodonta africana*)	8,000 animals	7,000–9,000	10,000[b]
Grevy's zebra (*Equus grevyi*)	1,700 animals[c]	1,600–2,100	4,500[d]
Lion (*Panthera leo*)	450 animals	400–500	500
African wild dog (*Lycaon pictus*)	300 animals in 17–18 packs	250–350	20 packs[e]

[a] To reach and maintain the amounts below within 10 years.
[b] Redistributed from their current distribution to 2,000 in Laikipia District (decrease from current), 6,000 in Samburu (increase), and 2,000 in the Mount Kenya region.
[c] A recent drought may have reduced the population from the more long-term mean of approximately 1,900 animals.
[d] Representing approximately a 10% increase/yr.
[e] Extrapolating from a range of 300 animals in 17–18 packs to 20 packs gives a range for the objective of 333–353 animals.

reduce populations in Laikipia District while raising them in Samburu District.

Component Maps

Participants completed, by consensus, a set of five maps for each of the four focal species (Figures 1–3). The maps were then used as guides for setting conservation priorities. Some comparative summaries of these maps are provided in Table 2, and a description of the maps for each species is provided below.

Elephants

Of all the focal species selected, elephants are considered the most resilient to many of the threats facing biodiversity, primarily because of their relatively large population in the region, high level of protection, and ecological adaptability. Workshop participants estimated that there were approximately 7,000–9,000 elephants in the landscape, between 5,000 and 6,000 in Samburu and Laikipia and possibly 2,000 in Mount Kenya, although no firm information exists for Mount Kenya. The elephant population appears to be increasing. Elephants currently use approximately 88% of the landscape (based on the current importance map in Figure 1). They are particularly abundant in and around the commercial ranches of Laikipia, Mount Kenya, and parts of Samburu, particularly in the Matthews Range, Kirisia Forest, and the national reserves. Key corridors were highlighted as being particularly important habitat features for maintaining connectivity for the elephant population across the landscape (Figure 4).

If conservation investment is not continued and in some cases increased, there is a high potential for reductions in the elephant population, particularly in known poaching hot spots that currently support high abundances of elephants (e.g., Kirisia Forest, east of Matthews Ranges, Mukogodo Forest, and the Laikipia Nature Conservancy). Failure to continue conservation investment in these areas would likely lead to increased poaching. Potential reductions are also high in the national reserves and along the Ewaso Nyiro River. The potential for future reductions in the population is generally lower in the private ranches in Laikipia, where conservation is more established, and higher in Samburu, where conservation is more tenuous.

It is also possible to recover populations in much of the landscape through conservation investment, although there is little potential for range expansion (<1% of the planning units where recovery could occur are currently unused). Potential for recovery is particularly high in much of Samburu, especially in the north, if security is improved. Recovery potential is generally lower in the national reserves, southern Samburu along the Ewaso Nyiro River, and in much of Laikipia, where elephant numbers are currently near ecological, or at least social, carrying capacity. Recovery is not possible in approximately 25% of the elephants' current range. There is also no potential for recovery in the agricultural areas of southern Laikipia and Meru Districts.

Cost of elephant conservation is higher in the southern part of their range than in the north. This is primarily because elephant conservation in the south involves securing land that is more arable and therefore more valuable than land in the north. In addition, elephant conservation in southern Laikipia requires the mitigation of human-elephant conflict, particularly crop raiding, which could involve the construction of electrified elephant-proof fences. Cost for conservation in the Kirisia Forest is considered higher than elsewhere in Samburu since currently there is little conservation investment in this area and threats are high. Conservation for elephants in most of Samburu would involve improving security, which can be done for a relatively small investment in terms of cost per unit area, and would have an impact over a large area.

For elephants, participants were fairly or highly confident in the information they provided for nearly the entire landscape, except for in the Mount Kenya region and the northwestern and northeastern corners of the landscape (Figure 3).

Grevy's Zebra

Grevy's zebra currently use about 48% of the landscape (calculated at 5 × 5 km resolution) and number around 1,700 animals. Central Laikipia, the Laisamis area in the northeast of the landscape, Wamba to the west of the Matthews Ranges, Lewa, and the national reserves currently support relatively high abundances of Grevy's zebra. Besides maintaining high abundances, certain areas are important because they contain water holes or are grazing areas, nursery areas, or corridors. Laikipia is the southern edge of the species range; the species only recently moved into this area and Lewa (since the early 1970s), and these areas are now critical for the species. Much of the information on Grevy's zebra is based on radio-tracking data, data from community scouts, and aerial surveys.

There is a high potential for future reductions in the population of Grevy's zebra across much of their current range if investment in conservation is not continued.

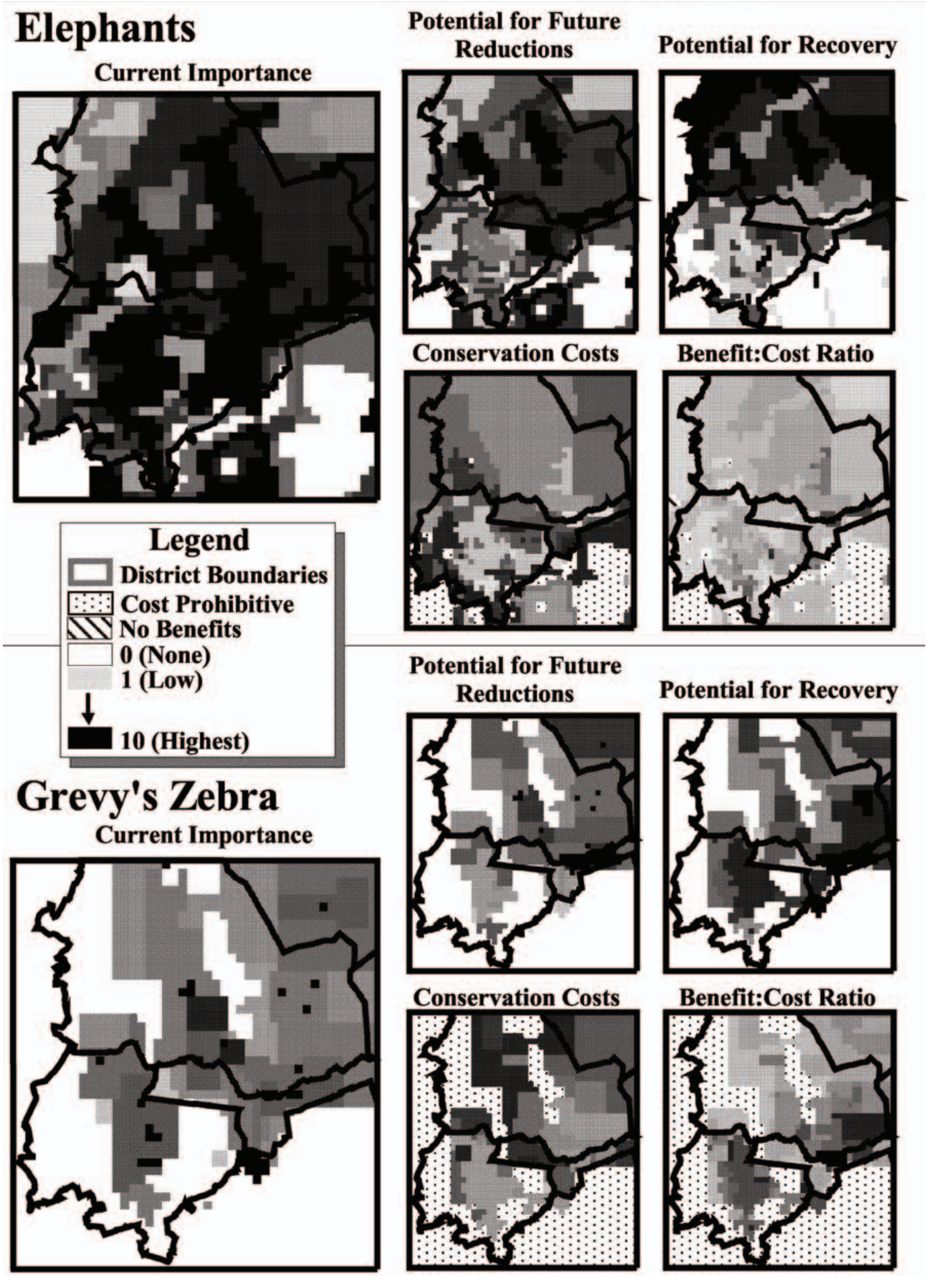

FIGURE 1. Component maps for elephants and Grevy's zebra. The maps were produced by participants at the Ewaso Landscape Planning Workshop (January 2006) and were used to help set conservation priorities.

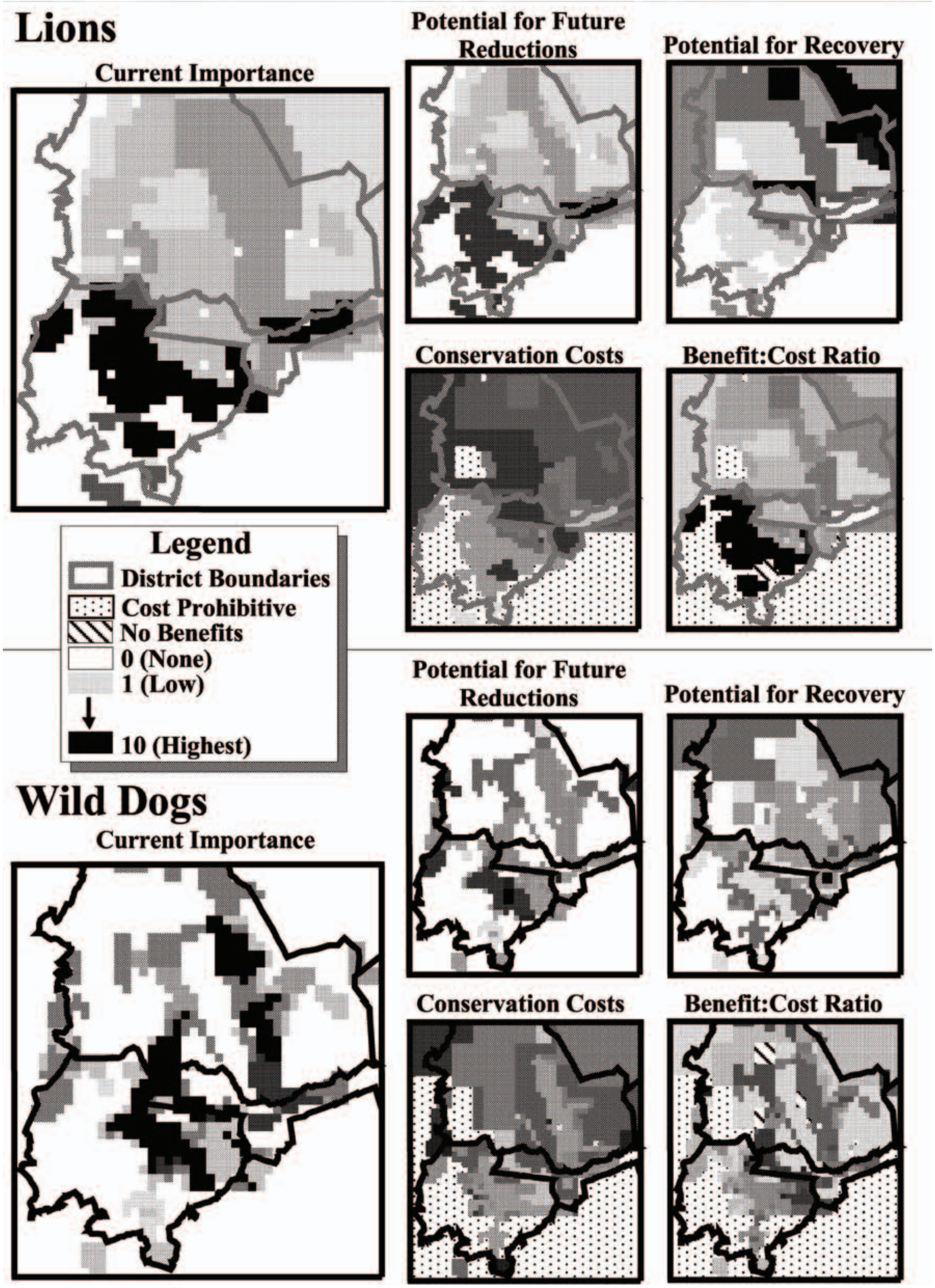

FIGURE 2. Component maps for lions and wild dogs. The maps were produced by participants at the Ewaso Landscape Planning Workshop (January 2006) and were used to help set conservation priorities.

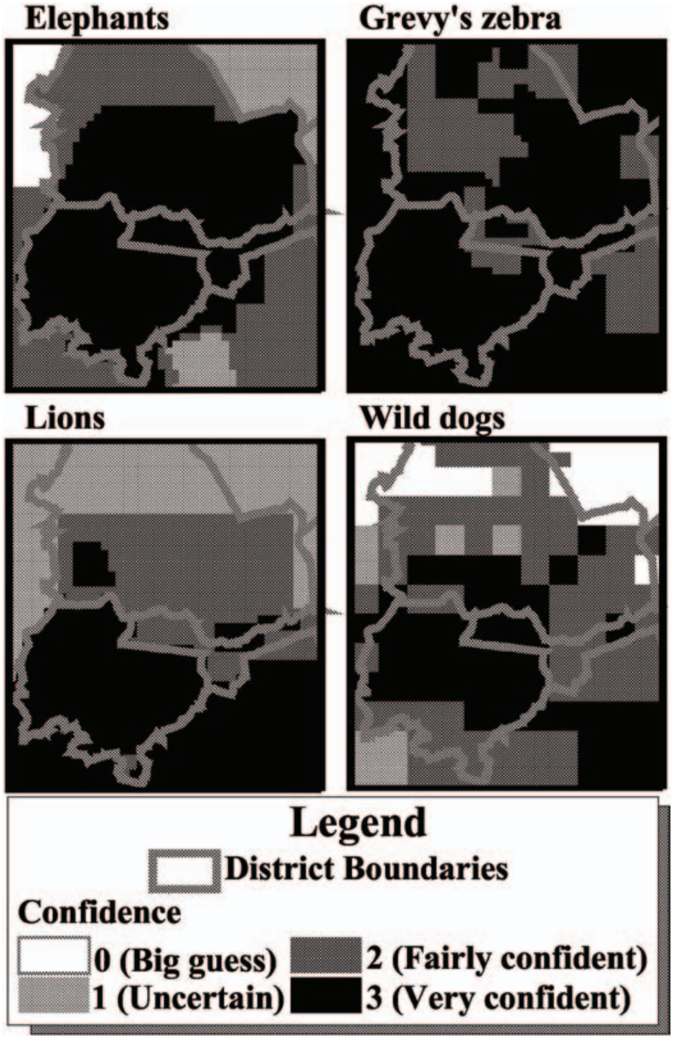

FIGURE 3. Confidence maps for the spatial data (component maps in Figures 1 and 2) for elephants, Grevy's zebra, lions, and wild dogs. The maps were produced by participants at the Ewaso Landscape Planning Workshop (January 2006).

Although the potential for reductions on the commercial ranches of Laikipia is low because landowners generally maintain wildlife-friendly land management practices, it is relatively high in community areas of Laikipia because of competition with livestock. There is high potential for loss in the national reserves, if they lose their integrity through lack of conservation investment, at key hot spots (e.g., water points), and in areas of Wamba, West Gate, and Laisamis.

It is possible to increase populations of Grevy's zebra across nearly all of its current range as all existing subpopulations are below carrying capacity. There is also some

TABLE 2. Summary of component maps for each of four biodiversity features (Figures 1 and 2). Maps were produced by participants in the Ewaso Nyiro Landscape Conservation Planning Workshop (January 2006) and were the basis for a conservation planning exercise.

	Planning units (%)		Current distribution (%)	
Focal biodiversity feature	Currently used	Potentially used[a]	Recovery not possible[b]	Future losses possible[c]
African elephant	87.6	87.8	19.6	97.7
Grevy's zebra	47.4	49.7	2.3	99.5
Lion	60.3	71.0	6.3	99.9
African wild dog	28.7	61.9	1.6	99.3

[a] If new conservation actions were taken or current ones continued.

[b] In some proportion of current range, recovery is not possible because the population is at carrying capacity.

[c] If current conservation actions were abandoned and no new ones begun.

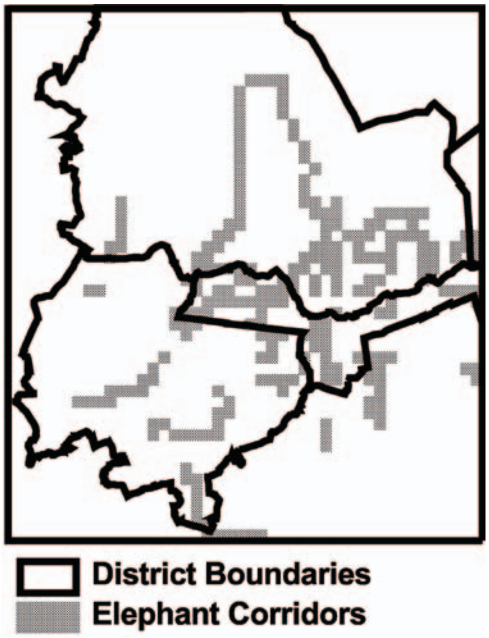

FIGURE 4. Elephant corridors. The map was produced by participants at the Ewaso Landscape Planning Workshop (January 2006) and was used to help set conservation priorities.

potential for expanding the current range to areas that are currently unused, but this is limited to ranches in Laikipia District (<3% of the landscape). Recovery is possible if conservationists can secure enough grassland habitat and safe water and limit the numbers of plains zebra and lions. The subpopulation in Laikipia is growing at only 1%–3% per year. Although the reason for the low increase is not known, it may relate to habitat quality or interspecific competition (i.e., with other herbivores) at the southern edge of their historical range. There is also a high potential for recovery in the community-managed areas of Samburu District.

In general, the cost of conservation activities aimed at Grevy's was scored lower in Laikipia and Lewa Conservancy, where there has already been substantial investment in direct conservation and conservation education with communities and where relationships have been built with local people. Cost is moderate in the national reserves and neighboring communities (West Gate, Kalama, and Wamba, where work is ongoing), and costs are highest farther north and in the Kipsing area of Isiolo.

Through most of the landscape, participants indicated high confidence in the information they provided, based on the large amount of research (radio tracking, surveys, and community monitoring) that has been performed.

Lions

Approximately 450 lions currently use around 60% of the landscape (calculated at 5 × 5 km resolution). Abundance is highest on commercial ranches of Laikipia and the national reserves of Samburu, Buffalo Springs, and Shaba. Agricultural areas cannot support lions. Other areas that support subpopulations include the Matthews Range and Kirisia Forest. The buffer areas around the national reserves are important dispersal areas for lions. There are lions throughout the pastoralist areas but in low numbers, therefore those areas are not as important for the landscape population.

In general, the areas with the highest potential reductions in the future are those where lions are currently most abundant. The highest potential for loss is on the commercial ranches in Laikipia and the national reserves and surrounding areas, where in the absence of conservation efforts, lions would likely be persecuted. In most of Samburu, threats are intense, although the current abundance of lions is low, and therefore, the potential future reductions are also low.

Potential for recovery is low in the commercial ranches of Laikipia, where lions are nearer carrying capacity, and in pastoralist areas. Potential for recovery is higher where there are few people and where habitat is suitable, including northeast Samburu and the northern Matthews Range, assuming that conservation and incentives can improve the attitudes of local people toward lions. Lions could potentially expand out from their current range to an additional 11% of the landscape, primarily in the northwestern extreme of the landscape, although participants indicated that they were uncertain about the current status of lions in this region and the possibility of recovery.

Cost for conserving lions is primarily influenced by attitudes toward conservation. Areas where communities have some conservation awareness were given lower cost than those with no exposure to or history of conservation. Costs were also low in areas where lion numbers are highest, even though lion populations in these areas will be artificially suppressed (e.g., Lewa, Solio, and Ol Pejeta).

Participants indicated that they had high confidence in their conclusion that lions would continue to persist in Laikipia and southern Samburu, and especially within the national reserves. Participants indicated that their confidence was based on the intensive research that has been performed in these places. Confidence was somewhat lower in the northern parts of the landscape, where information is based on local knowledge.

Wild Dogs

Wild dogs current use approximately 29% of the landscape and currently number around 300 animals in 17–18 packs. Core areas that support higher abundances and have resident animals are the commercial ranches in central Laikipia and the group ranches on the edge of the Laikipia escarpment. The area of Isiolo District between Laikipia and Buffalo Springs/Shaba, although it may not support resident animals, is important for maintaining connectivity between these two subpopulations. Dogs move through northern Laikipia in the Kirimun area to the east of the Kirisia Hills and the Seiya Lugga. Another very important area is the Matthews Range, where there are several wild dog packs. Local knowledge suggests there are some packs in central Samburu and a pack newly established in Shaba National Reserve.

Potential for reductions in the wild dog population is generally high where animals are resident and threats exist. Reductions could be high in the Suguta valley if more land on the Loroki Plateau is used for wheat, which would, in turn, force pastoralists to move more of their livestock into the Suguta valley. Areas where there is high potential for loss also include areas where a high level of conflict exists between human populations and wild dogs and where wild prey risk being depleted.

The wild dog population across the landscape is in a recovery phase after becoming locally extinct, at least in Laikipia. With conservation action, dogs could potentially double the size of their range to nearly 60% of the landscape (based on 5 × 5 km resolution). Hilly areas have the highest potential for recovery as wild dogs tend to prefer that habitat. Potential recovery is lower where current abundances are high, as these are likely to be already at carrying capacity. Large areas of the landscape are not suitable for wild dogs and, therefore, have no potential for recovery.

There are no areas where the cost of conservation actions aimed at wild dogs is zero, primarily because there is a major disease risk to wild dogs (primarily from domestic dogs), which has the potential to wipe out the entire population. The cost of conservation is lowest in community areas of Laikipia, on the Laikipia escarpment, and in the Matthews Range, where there is little conflict, prey species are abundant (dik-dik), wild dogs are currently doing well, and the only cost is due to disease risk. Areas where costs are high are either insecure, from the standpoint of operating a conservation project, or have depleted prey. The cost was considered prohibitive in agricultural areas where conservation would require conversion of habitat. Participants indicated that they had high confidence about the information they provided in Laikipia, where animals are radio collared, but that confidence was lower in other areas.

Spatially Explicit Conservation Priorities

After completing the five component maps for each of the four focal species, a map reflecting the benefit to cost ratio for conservation action was calculated (Figures 1, 2). Conservation benefits were calculated by weighting then adding the maps of potential recovery and maps of potential reductions. In other words, benefits from conservation in any location include either helping to recover populations or preventing future reductions. For each species, participants assigned relative weights to these two maps (i.e., how important is prevention relative to recovery). For each species, the weights (prevention:recovery) were as follows: elephant, 1:1; Grevy's zebra, 2:3; lions, 2:1; and wild dogs, 5:1.

The benefit:cost maps, in combination with the five component maps, were then used by participants as guides for producing maps of conservation priorities for each species (Figure 5, Table 3). Finally, an integrated map of conservation priorities across all four conservation targets was created (Figure 6).

Species-Specific Priorities: Elephants

For elephants, the strong conservation investment currently being put into the ranches and conservancies of Laikipia, Buffalo Springs, Samburu and Shaba National Reserves, Mount Kenya National Park, and a few group ranches and conservancies (Namunyak) in Samburu should be maintained, as these are elephant strongholds. Additional investment over the next decade should be aimed at securing strong subpopulations that are vulnerable to decline, bolstering subpopulations in some places, and securing corridors. Areas where subpopulations are currently strong but increased investment is needed to maintain them include the following:

1. Laikipia Nature Conservancy requires improved community outreach and development of community-owned conservancies and associated tourism among the neighboring communities, particularly the Pokot, to the west and north of the property. Investment is also required to improve security and upgrade elephant-proof electrified fences.
2. Mount Kenya Forest Reserve requires the mitigation of human-elephant conflict on smallholder land surrounding the forest and the establishment of corridors to the Laikipia Plateau to maintain connectivity between subpopulations.
3. Rumuruti Forest is the highest conflict area in the landscape. Unless the Marmanet and Ol Arabel forests, located west of the Rumuruti Forest, can be secured and rehabilitated, there is no future for elephants in this area, and efforts should instead focus on removing them to the large-scale ranching matrix in central Laikipia.

High-priority areas where populations could be bolstered with increased investment include the following:

1. In north Laikipia and Samburu, investment aimed at the Kirisia Forest, Mukogodo Forest, the Matthews Range, and the Sera Conservancy should attempt to reduce poaching and increase security.
2. In Lekurruki and the Livestock Marketing Division in Isiolo, activities should aim to maintain an area of low livestock densities and reduce insecurity (i.e., poaching).

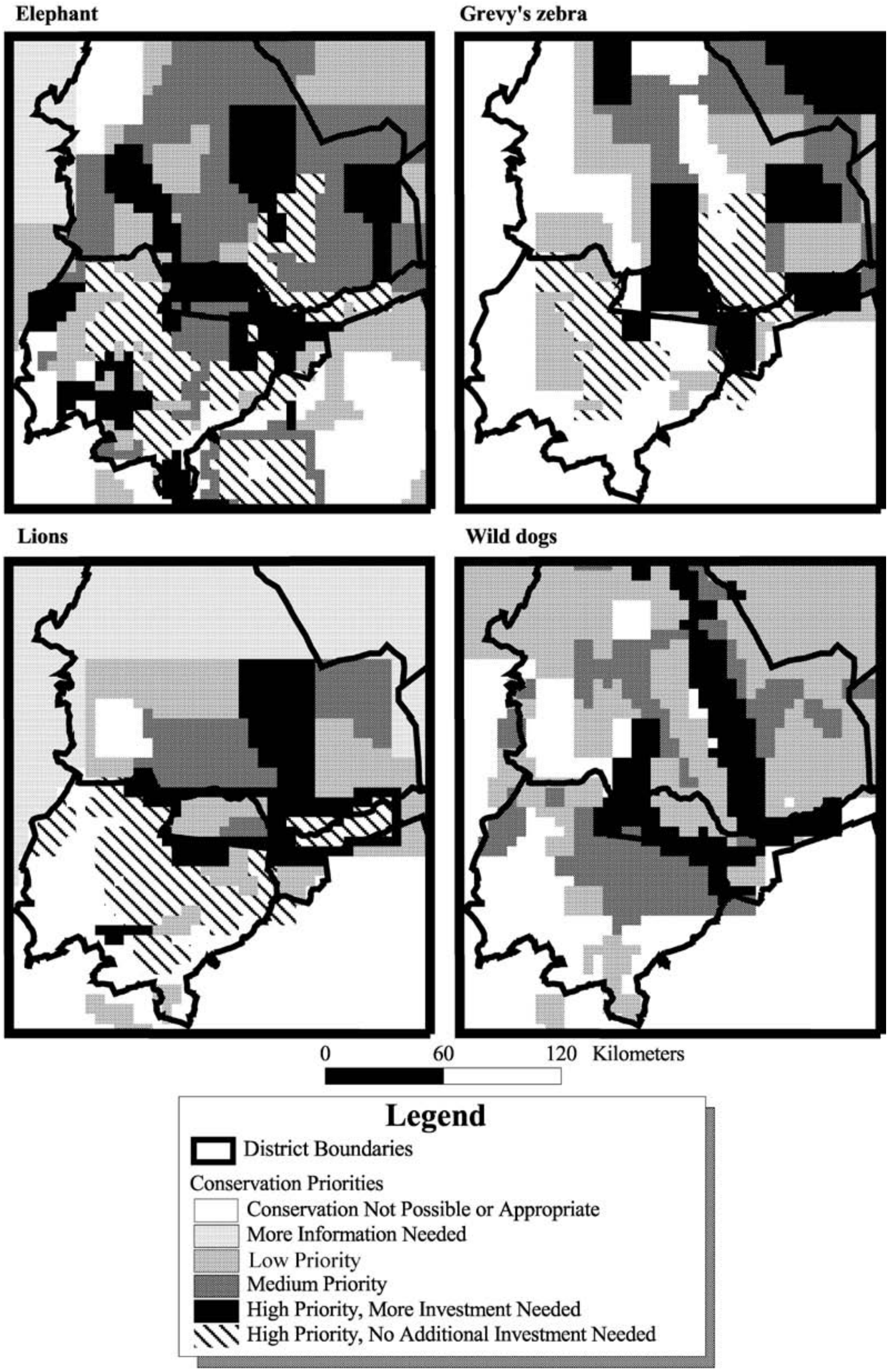

FIGURE 5. Conservation priorities for individual species as described by participants at the Ewaso Landscape Planning Workshop (January 2006).

TABLE 3. Summary of the feature-specific priority maps for each of four biodiversity features. Maps were produced by participants in the Ewaso Nyiro Landscape Conservation Planning Workshop (January 2006).

Focal biodiversity feature	Planning units needing conservation investment (%)	Range needing increased investment[a] (%)	High-priority units needing increased investment (%)
African elephant	80.1	83.4	54.8
Grevy's zebra	47.3	80.2	59.5
Lion	69.5	84.9	48.6
African wild dog	60.1	100	100

[a] Range here is defined as any of the 5 × 5 km planning units needing conservation of some kind (continued investment at current level or increased). This column reflects the percentage of those units that need increased investment (low, medium, or high priority or for more information).

Several critical corridors need to be maintained through increased investment, particularly those linking Mount Kenya to Laikipia and several through Isiolo, which link Laikipia and Samburu.

Species-Specific Priorities: Grevy's Zebra

For Grevy's zebra, current levels of conservation investment are sufficient in some areas, including the commercial ranches of Laikipia, Lewa, Il Ngwesi, Namunyak, West Gate, and Kalama and the reserves of Samburu and Buffalo Springs. These levels need to be maintained to ensure continued success.

High-priority areas needing additional investment include areas that are important for grazing, watering, and reproduction. Securing these areas is considered essential for both recovering the species and preventing any future declines. Specific areas that are a high priority for increased investment include Shaba National Reserve and the Livestock Marketing Division and Kipsing areas of Isiolo. These latter two areas are important for retaining the migration link between the Laikipia and the northern subpopulations of Grevy's zebra. They are also important for recovery or recolonization, as they were good habitat in the past. Additional high-priority areas around Laisamis, Serolivi, and the northernmost subpopulation near Baragoi are areas that were historically the core of the species range and where there is high potential for recovery.

Conservation is not possible in areas that are outside the historical range of the species, unsuitable habitat (e.g., mountains and forest), and agricultural land.

Species-Specific Priorities: Lions

For lions, current levels of conservation investment are sufficient in the commercial ranches of Laikipia and the national reserves and should continue in these areas. Additional investment is critically needed in the community areas of Laikipia (e.g., Naibunga), through the Kipsing and Livestock Marketing Division area of Isiolo (particularly along luggas, which lions favor as habitat), and in a buffer zone around the reserves (to allow for safe dispersal of lions out of the reserves). There also needs to be more investment in education and awareness in these community areas to maintain connectivity for lions in the landscape. The Matthews Range is also a high priority for increased investment, as this is potentially important habitat that could support more lions and has low human population density. Additional investment is also strongly needed in the area north of Ol Pejeta to create a link to the rest of Laikipia. Areas where there are many people and high densities of livestock are considered to be areas where either priority is low or conservation is not possible. The level of knowledge on lions in much of the north of the landscape was considered insufficient to make a decision on priorities. More research is needed in that area as there may be potential for recovering lions.

In general, educational efforts aimed at community residents are needed to explain the rationale for and practice of predator conservation. People are receptive to the idea when presented in terms meaningful to their own lives, but it is not always easy to convince them that they can benefit from wildlife, especially predators on their livestock. Development of tourism in the communities, with

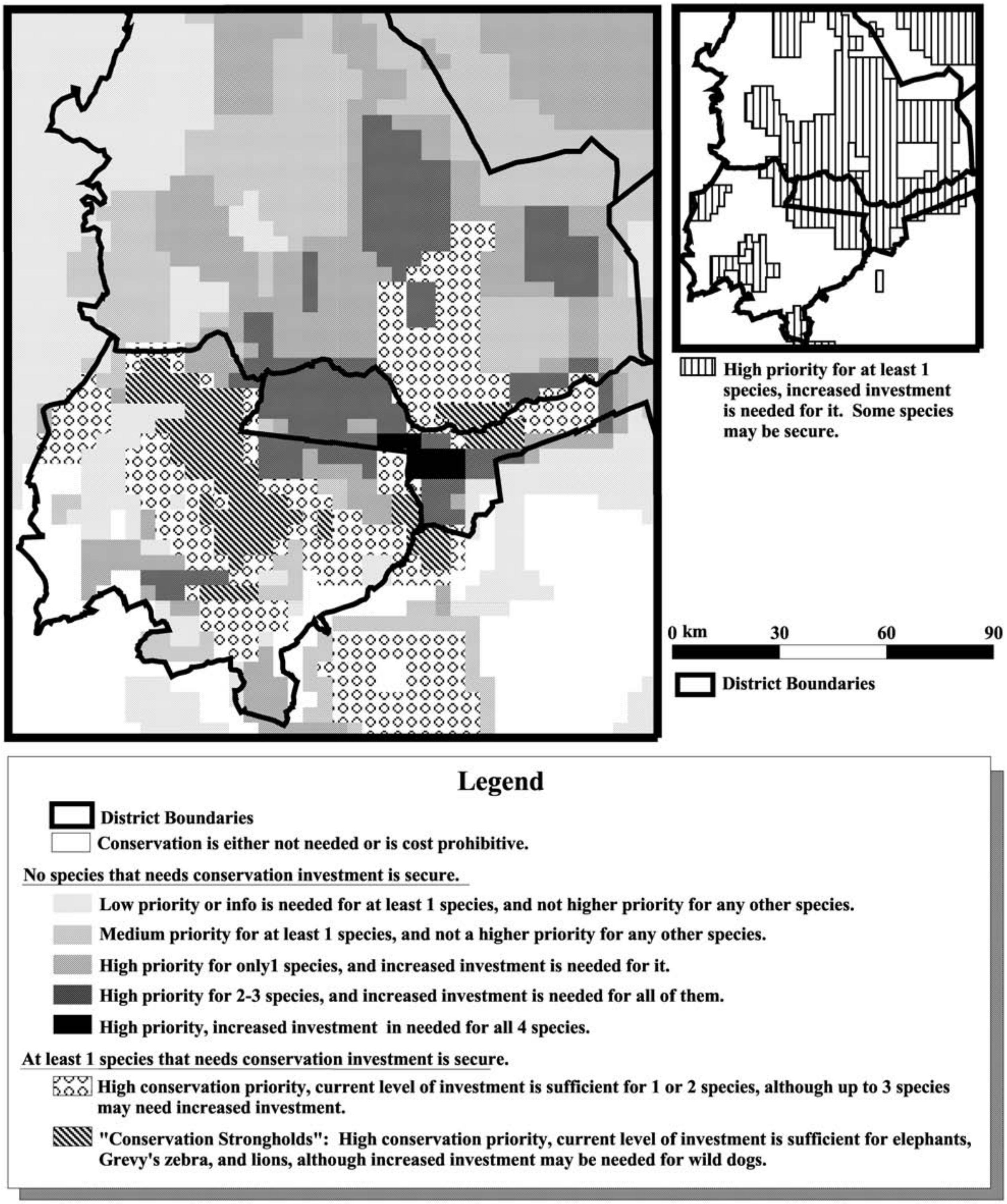

FIGURE 6. Conservation priorities across four species. The map was produced by combining priority maps for individual species and creating useful categories and is a product of the Ewaso Landscape Planning Workshop (January 2006).

transparent and equable distribution of profits, would provide some incentive for people to tolerate carnivores. Trophy hunting would have great potential in northern Laikipia, especially given the good numbers of leopard and great kudu.

Species-Specific Priorities: Wild Dogs

For wild dogs, investment in conservation is insufficient across the entire landscape. Risk of infectious diseases is a major threat to wild dogs, with highest risk in community areas. The priority for conservation is to secure the known populations of wild dogs. Community areas along the Laikipia escarpment (e.g., Naibunga Conservancy) and into Isiolo District (with linkages through Isiolo into Samburu) are important habitat for wild dogs and a high priority for conservation needing additional investment. The Seiya Lugga, Matthews Range, and Ndotos Range are also high conservation priorities needing additional investment. The commercial ranches of Laikipia are considered medium priority. Some additional areas are considered medium priority and are important for providing connectivity. Southern Laikipia and Meru Districts are not considered suitable habitat for wild dogs and are unlikely to ever become a part of the wild dog range. Therefore, conservation is not possible in those areas.

Cross-Species Priorities

Overall, participants indicated that if current levels of conservation investment are maintained, only about 3.6% of the landscape is secure (i.e., does not need additional investment) for all four species. Approximately 4.6% of the landscape is secure for three or four species but often needs additional investment for wild dogs (diagonally hatched areas shown in Figure 6). These areas are the most secure areas in the landscape and include the commercial ranches and conservancies of central Laikipia, Lewa Wildlife Conservancy, a small area in Samburu around West Gate and Wamba, and Samburu and Buffalo Springs National Reserves. For the remainder of the paper, we will refer to these areas as the "conservation strongholds."

An additional 13.4% of the planning units are "partially" secure, meaning that levels of investment are sufficient for one or two species that require it but up to three species may need increased investment (areas with small circles in Figure 6). An excellent example of this type of area is Shaba National Reserve, which is secure for elephants and lions but is a high priority for increased investment for Grevy's zebra and wild dogs.

The analysis concluded that fully 84% of the landscape needs continued or additional conservation investment at low to high priority. Almost half (45%) of the landscape was given high-priority status for continued or additional conservation investment for at least one species. About one-third of the landscape was given a high-priority status for at least one species and was identified as needing increased investment (Figure 6, small map). Specifically, this land includes all of the national reserves and land west; Solio; Laikipia ranches, Naibunga Conservancy, and parts of southwestern Laikipia; elephant corridors between Ngare Ndare Forest to Mount Kenya and Solio to Mount Kenya; much of Samburu, including the Kirisia Forest and the Matthews Range; Sera; and the northeastern part of the landscape in Marsabit District.

About 1% of the landscape is at high priority for additional investment for all four species, and about 4% is at high priority for at least three species. Increased investment in these high-priority locations would benefit not only all or most of these species but also, by association, much of the biodiversity of the region. The majority of planning units in this category are located in either the "peninsula" of Isiolo District between Laikipia and Samburu Districts or the Matthews Range in Samburu.

DISCUSSION

IMPLICATIONS FOR CONSERVATION IN THE EWASO ECOSYSTEM

We suggest there are three important implications of this exercise for conservation practitioners working in the Ewaso ecosystem. These implications are likely to be similar for ecosystems throughout Kenya and eastern Africa.

1. *Conservation objectives in the Ewaso Nyiro cannot be achieved by focusing only on traditional strongholds of biodiversity conservation. Planning and investment strategies are needed across much of the landscape.*

The traditional strongholds of conservation in the Ewaso Nyiro include about 9,500 km^2 of land (~18% of the landscape), composed mostly of the commercial ranches and conservancies of central Laikipia, Lewa Conservancy, and two of the three national reserves (Buffalo Springs and Samburu; see the areas in Figure 6 with diagonal hatch-marks). The critical question is, can we meet our objectives for biodiversity conservation (see Table 1) by focusing conservation only on the traditional strongholds? The four species on which our exercise focused are excellent examples of why the answer is a resounding *no*.

Although it may seem possible to reach modest conservation objectives, such as reaching and maintaining a population of 10,000 elephants within 10 years, by simply trying to increase the number of animals within the traditional strongholds, this supposition is not true for two main reasons. First, for all four species, substantial portions of their populations currently reside outside of the conservation strongholds. For example, significant subpopulations of Grevy's zebra are resident in and around Laisamis in the northeast of the landscape and Wamba to the west of the Matthews Range, and lions, elephants, and wild dogs all have significant subpopulations in the Matthews Range (see the current importance maps in Figures 1 and 2). If conservation investment is not increased in those areas, these subpopulations could decrease dramatically in the next 10 years because of changing land use patterns, poaching, settlement, and disease (see the future reductions maps). These factors would make it difficult to maintain current numbers, let alone increase populations to the conservation objectives.

The second reason that it will be impossible to reach conservation goals by focusing only on strongholds is that even subpopulations within the strongholds rely on habitat in the surrounding landscape. This dependence is particularly evident for the 8,000 or so elephants currently living in the landscape. This population relies on an enormous proportion of the total area (nearly 88% of the planning units), far beyond the strongholds, including a large number of corridors connecting various subpopulations (Figure 4). A failure to increase investment in areas beyond the strongholds will likely lead to declines in the elephant population. Further, increasing the population to 10,000 animals will require that habitat outside of the strongholds is used more intensively (see the potential for recovery maps in Figures 1 and 2), especially considering that elephant subpopulations in most of the strongholds are currently at or near carrying capacity. The same is more or less true for the other species considered in our exercise: although their populations spend more time within the strongholds, they rely heavily on habitat and corridors outside of those strongholds (from 29% to 47% of the planning units in the landscape) and will need to spend more time in this habitat if populations are to increase.

In addition to the four species considered here, we suspect that conservation focused only on strongholds will be insufficient for protecting many of the other species, ecological processes (such as herbivore migrations), and ecosystem services of the Ewaso Nyiro. Gardner et al. (2007) recently demonstrated that strictly protected areas created for large mammals in Tanzania were ineffective at conserving other taxa (e.g., butterflies and birds). The same is likely true for the Ewaso Nyiro. Although we do not yet have conservation objectives or maps for the other focal biodiversity features chosen by workshop participants (Table 1), many certainly require conservation at landscape scales and beyond the current strongholds. For example, reticulated giraffe populations suffer from poaching, mostly for meat and mostly in areas outside of the conservation strongholds. Finally, the hydrological system, which provides a critical service to both the wildlife and humans living in the Ewaso Nyiro, obviously cannot be effectively conserved with activities focused within the traditional strongholds. In fact, one can make the case that although the Ewaso River itself is the most critical resource to wildlife residing in the strongholds, its flow and water quality can only be assured by effective water management and conservation upstream, in the agricultural areas and at its source in the forests of Mount Kenya, where logging inside and outside of the national park is a problem.

2. *Thus far, the systematic, landscape-scale process suggests three priorities for conservation investment, which are, in order of priority, continue conservation investments at current levels to preserve the strongholds, increase investments to prevent the loss of the Isiolo corridor, and increase investments to improve the status of biodiversity features in portions of Samburu District.*

Because there is so much land in the Ewaso Nyiro that requires some level of conservation investment (about 84% of the landscape) and it is certainly beyond current resources to work in all of that land, a process for prioritizing future investments is needed. Thus far, although the planning process has focused on only four of nine species, three clear priorities have emerged for how conservation practitioners should invest their resources in the future. Although other priorities exist on an individual species basis (e.g., Kirisia Forest is a high priority for increased investment for elephants), the priorities below represent ones where the combined energy of the conservation community can be marshaled to benefit a large range of biodiversity.

First, the planning process clearly demonstrates the importance of continuing the levels of investment currently being directed at conservation strongholds. With the possible exception of elephants, the majority of the populations of the four focal species reside within the conservation strongholds. Further, the potential for future reductions maps (Figures 1, 2) indicate that in the absence of current levels of investment by conservation practitioners, large reductions in the subpopulations residing on the strongholds would likely occur. Although the land use practices on many of the privately owned ranches and conservancies in Laikipia would probably remain wildlife friendly in absence of active conservation and research (assuming ownership did not change), the national reserves would likely lose their integrity. Continuing investment in active conservation on strongholds will ensure that subpopulations persist and, often, increase. In some cases, additional investment in the strongholds is needed in order to preserve and recover wild dogs, although these investments are often a lower priority for dogs than those needed outside of the strongholds (Il Ngewsi, Loisaba Conservancy, and the national reserves are a high priority for increased investment for wild dogs). The resources currently being invested in the strongholds should in no way be redirected toward the other priorities below.

Second, in the near future, practitioners should raise and invest resources to secure, as continued wildlife habitat, the Isiolo corridor: the peninsula of Isiolo District separating Laikipia and Samburu Districts. Increased investment is needed in several critical locations. Most important is a stretch of land in the center of the Livestock Marketing Division, along the Ewaso Nyiro River, which separates northeastern Laikipia (Il Ngwesi, Lukurruki Ranch, Mukogodo Forest, etc.) from Buffalo Springs National Reserve (Figure 6). Increased investment in this area is a high priority for all four species considered in our exercise and would certainly benefit the species by both preventing future declines of subpopulations using the region and helping to increase subpopulations. Most importantly, however, investments could help secure the area as a corridor between the strongholds of central Laikipia and the national reserves (and by extension, much of northern Samburu, including the Matthews Range).

Increased investment should also be focused on other portions of Isiolo District, including Kipsing and Ol DoNgiro, especially the northern portions of these areas bordering Samburu, which are important for three species. Similarly, the group ranches along the Laikipia escarpment bordering Isiolo (e.g., Naibunga Ranch) and Lekurruki Ranch need increased investment.

Concerns about the future of the Isiolo corridor center around (1) increased interest of local communities and government in livestock marketing and the possibility of creating an abattoir with extensive livestock holding grounds and (2) the lack of interest or perceived value by local communities in wildlife. Any development that did not consider wildlife would certainly be injurious to conservation since this vital wildlife corridor could be permanently closed. Engagement particularly with the Isiolo County Council along with the councils in Samburu and Laikipia is critical for success in the corridor, as these councils hold trust over most of the land.

Finally, increased investment should be aimed at several portions of Samburu District. In particular, Matthews Range and surrounding areas represent an important forest and thicket habitat for elephants, wild dogs, and lions (but not for Grevy's zebra, which are restricted to more open habitats). Increased investment should be aimed at securing this area as a vital "island" that would create a "source" for recovering populations across the northern half of the landscape. Other important areas for increased attention in Samburu include the following. The habitat in and around Sera Conservancy in western Samburu could help increase subpopulations of both Grevy's zebra and elephants in addition to the two carnivores. Namunyak and Kalama conservancies, although they are secure for the herbivores, need increased investment for wild dogs and lions, and they form an important link between the national reserves and the Matthews Range. Finally, the group ranches south of Kirisia Forest are also important for both wild dogs and elephants as linkages from Laikipia to the Kirisia Forest and areas east.

3. *Some conservation objectives will conflict with human livelihood objectives. Part of a comprehensive landscape-scale planning process needs to be dedicated to negotiating these conflicts so that all objectives can be met to the greatest extent possible.*

Assessment of the landscape-scale priorities for our four focal species highlighted a challenge of conservation in Ewaso Nyiro: it may be difficult to meet all conservation objectives and human livelihood development objectives on the same areas of land. For example, it will be difficult to maintain or increase livestock grazing and marketing on lands also important for meeting conservation objectives for conserving predators and large herbivores. We believe that, ultimately, conservation planning in the Ewaso landscape needs to evolve into comprehensive land use planning that incorporates both conservation and development objectives and negotiates trade-offs. Sometimes, the objectives of both may be partially met on the same lands (e.g., wildlife tourism), but often, this may not be the case, and priority may need to be given to one objective at the expense of another.

NEXT STEPS FOR SYSTEMATIC, LANDSCAPE-SCALE PLANNING IN THE EWASO NYIRO

Although this exercise proved valuable for clarifying the scope of the conservation challenge in the Ewaso Nyiro, compiling useful information, and prioritizing some areas for conservation investment, it was only partially complete. We recommend that landscape-scale planning, as we have demonstrated here, continue and, in fact, become an integral part of conservation thinking in the Ewaso Nyiro. The process should be revisited and updated over time, possibly once every two to five years, depending on the changing conservation and development context. If substantial progress toward conserving biodiversity is made (e.g., the Isiolo corridor is secured), priorities should be reevaluated. The same should happen in the case of failure. We recommend that an inclusive and collaborative group of stakeholders concerned with landscape-scale conservation and development, such as the recently formed Ewaso Conservation Group, take a leadership role in carrying the process forward. Important next steps for the planning process include the following:

1. *Review the quantitative objectives for the elephants, Grevy's zebra, lions, and wild dogs (Table 1) and incorporate these more explicitly into the spatially explicit priority setting.*

The objectives shown in Table 1 represent preliminary and short-term (over the next 10 years) conservation objectives. A more formal and rigorous process for establishing quantitative objectives would be useful, such as those described in Groves (2003), Tear et al. (2005), and Sanderson (2006). Several possible quantitative objectives should be considered (e.g., minimum viable populations, ecologically functional populations, sustainable yield objectives, historical levels, several redundant populations), as this will help stakeholders set near- and long-term objectives and consider what is truly necessary for long-term conservation success (e.g., are 20 packs of wild dogs a sufficient long-term goal?). These objectives then need to be compared on a quantitative basis with the maps produced in this exercise to guide decisions about how much land is needed to reach the objectives (e.g., could areas marked as a high priority support sufficient number of animals to reach the objectives?) (Rodrigues and Gaston, 2001; Boshoff et al., 2002). If maps can be expressed in the same units as the quantitative targets (e.g., abundance), indices that are useful for prioritizing areas can be produced, including irreplaceability and marginal benefit:cost ratios (Cawardine et al., 2006), and "optimal" networks of conservation areas that meet objectives for all focal targets can also be produced.

2. *Complete the planning steps for the remaining focal conservation features.*

Thus far, the planning process has proceeded while considering only four of nine focal conservation features. Workshop participants agreed that planning based on all nine features was necessary to ensure that other forms of biodiversity, critical ecological functions (e.g., herbivore migration), and services (e.g., production of clean water) were well protected. Therefore, the planning process (especially steps 4–6; see Box 1) should include consideration of the remaining five features (i.e., reticulated giraffe, Jackson's Hartebeest, acacia-grassland mosaic, dry upland/montane forest, and the hydrological system) and possibly examine how well these surrogates represent a wider range of taxa (Gardner et al., 2007). The process of setting quantitative targets, producing the component maps (e.g., current importance), and prioritizing actions for each feature doubtlessly would be enlightening and may significantly shift near-term priorities.

3. *Complete the planning steps for livelihood development goals and objectives and negotiate land use solutions that meet both conservation and development objectives.*

As we noted above, we do not believe a landscape-scale plan can be successfully implemented if it has not also incorporated, to some degree, objectives for human livelihood development and attempted to negotiate a network of land uses that meet both conservation and development objectives (Faith and Walker, 1996; Stewart and Possingham, 2005). If both sets of objectives are not considered in a transparent and relatively objective process, conservation priorities run the danger of being largely irrelevant in future land use decisions. Local stakeholders interested in pursuing development objectives, such as county councils and development nongovernmental organizations, need to be given at least equal time, so that they buy into the process as a whole and do not simply disregard it as an attempt to usurp their rights to the land. Development objectives should not be treated as "opportunity costs" of conservation (as in Stewart and Possingham, 2005) but, rather, as true objectives on an equal level with conservation objectives. In this way true conflicts, where conservation and development objectives are incompatible, as well as unique opportunities to meet both sets of objectives can be identified.

We recommend that first, conservation and development priorities be assessed separately, possibly in separate workshops, but using the same framework (such as the one in Box 1). The framework should ask participants to express their development objectives in quantitative and measurable terms and to consider the benefits and costs of various areas for meeting those objectives (e.g., what are the benefits and costs of increasing livestock grazing in particular areas). After independently setting priorities, development objectives and conservation objectives should be brought together, and solutions for meeting both negotiated. Producing future conservation and development scenarios (e.g., Baker et al., 2004; Hulse, 2004) may be a useful way for exploring options and their consequences. In general, land use planning processes that explicitly incorporate both conservation and development objectives are in their infancy, but the Ewaso Nyiro could easily lead in this arena.

CONCLUSIONS

In many places in eastern Africa and, indeed, the world it is becoming apparent that the traditional approach of conservation focusing on protected-area creation and management, though essential, will likely be insufficient to meet conservation goals. Many species, especially the area-demanding ones that are so common in eastern Africa, and ecosystem services simply cannot be effectively conserved on small patches of land. Conservation practitioners need to increase their effort beyond the traditional conservation strongholds to the surrounding landscape dominated by human land uses. Unfortunately, taking conservation to sufficiently large scales is often a daunting undertaking, as was demonstrated in our exercise (84% of the landscape needs conservation investment), and requires conservationists to work with a huge range of landowners and stakeholders who may not be primarily concerned with conservation. Systematic, landscape-scale conservation planning approaches help practitioners to set ecologically meaningful and transparent objectives, to define the scale at which they need to work to meet these objectives, and to define priorities that help ensure that they invest their limited resources to make the most efficient progress toward their daunting objectives. The planning approach we have demonstrated here is an important step for scaling up conservation in the Ewaso Nyiro and setting clear conservation priorities for immediate action. It has produced concrete, near-term priorities for investment (e.g., secure the Isiolo corridor) that conservation practitioners in the region can work together to meet. It has catalyzed the creation of the Ewaso Conservation Group, a partnership of organizations and local governments that is charged with carrying the planning and prioritizing process forward and implementing actions based on the process. We encourage all those interested in creating a landscape that meets the needs of people and wildlife to help the Ewaso Conservation Group carry the process forward in the Ewaso Nyiro and to other areas of Kenya, such as Tsavo or the Mara, which face similar challenges.

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REFERENCES

Baker, J. P., D. W. Hulse, S. V. Gregory, D. White, J. Van Sickle, P. A. Berger, D. Dole, and N. H. Schumaker. 2004. Alternative Futures for the Willamette River Basin, Oregon. *Ecological Applications,* 14:313–324.

Boshoff, A. F., G. I. H. Kerley, and R. M. Cowling. 2002. Estimated Spatial Requirements of the Medium- to Large-Size Mammals, According to Broad Habitat Units, in the Cape Floristic Region, South Africa. *African Journal of Range and Forage Science,* 19:29–44.

Brooks, T. M., M. I. Bakaar, T. Boucher, G. A. B. D. Fonseca, C. Hilton-Taylor, J. M. Hoekstra, T. Moritz, S. Olivieri, J. Parrish, R. L. Pressey, A. S. L. Rodrigues, W. Sechrest, A. Stattersfield, W. Strahm, and S. N. Stuart. 2006. Coverage Provided by the Global Protected-Area System: Is It Enough? *BioScience,* 54:1081–1091.

Chan, K. M. A., M. R. Shaw, D. R. Cameron, E. C. Underwood, and G. C. Daily. 2006. Conservation Planning for Ecosystem Services. *PLoS Biology,* 4:2138–2152, e379, doi:10.1371/journal.pbio.0040379.

Cawardine, J., W. A. Rochester, K. S. Richardson, K. J. Williams, R. L. Pressey, and H. P. Possingham. 2006. Conservation Planning with Irreplaceability: Does It Matter? *Biodiversity and Conservation,* 16:245–258.

Conservation International. 2004. *Conserving Earth's Living Heritage: A Proposed Framework for Designing Biodiversity Conservation Strategies*. Washington, D.C.: Conservation International.

Didier, K., D. Wilkie, I. Douglas-Hamilton, L. Frank, N. Georgiadis, M. Graham, F. Ihwagi, A. King, A. Cotterill, D. Rubenstein, and R. Woodroffe. 2009. Conservation Planning on a Budget: A Possible "Resource Light" Method for Mapping Priorities at a Landscape Scale? *Biodiversity and Conservation*, 18:1979–2000.

Faith, D. P., and P. A. Walker. 1996. Integrating Conservation and Development: Effective Trade-offs between Biodiversity and Cost in the Selection of Protected Areas, *Biodiversity and Conservation,* 5:431–446.

Gardner, T. A., T. Caro, E. B. Fitzherbert, T. Banda, and P. Lalbhai. 2007. Conservation Value of Multiple Use Areas in East Africa. *Conservation Biology*, 21, doi:10.1111/j.1523-1739.2007.00794.x.

Groves, C. R. 2003. *Drafting a Conservation Blueprint: A Practitioner's Guide to Planning for Biodiversity*. Washington, D.C.: Island Press.

Groves, C. R., D. B. Jensen, L. L. Valutis, K. H. Redford, M. L. Shaffer, J. M. Scott, J. V. Baumgartner, J. V. Higgins, M. W. Beck, and M. G. Anderson. 2002. Planning for Biodiversity Conservation: Putting Conservation Science into Practice. *Bioscience,* 52:499–512.

Henson, A., D. Williams, J. Dupain, H. Gichohi, and P. Muruthi. 2009. The Heartland Conservation Process: Enhancing Biodiversity Conservation and Livelihoods through Landscape-Scale Conservation Planning in Africa. *Oryx,* 43(4):508–519.

Hulse, D. W., A. Branscomb, and S. G. Payne. 2004. Envisioning Alternatives: Using Citizen Guidance to Map Future Land and Water Use. *Ecological Applications,* 14(2):325–341.

King, J., and D. Malleret-King, eds. 2006. *Proceedings of the Ewaso Landscape Planning Workshop*. Laikipia, Kenya: Mpala Research Centre. http://wcslivinglandscapes.com/landscapes/media/file/Final-Proceedings_SamburuLaikipia_LandscapePlanning.pdf (accessed September 2007 and available from K. Didier on request).

Margules, C. R., and R. L. Pressey. 2000. Systematic Conservation Planning. *Nature,* 405:243–253.

Nicholson, E., I. Westphal, K. Frank, R. A. Rochester, R. L. Pressey, D. B. Lindenmayer, and H. P. Possingham. 2006. A New Method for Conservation Planning for the Persistence of Multiple Species. *Ecology Letters,* 9:1049–1060.

Poiani, K. A., B. D. Richter, M. G. Anderson, and H. E. Richter. 2000. Biodiversity Conservation at Multiple Scales: Functional Sites, Landscapes, and Networks. *BioScience,* 50:133–146.

Pressey, R. L., and M. C. Bottrill. 2009. Approaches to Landscape- and Seascape-Scale Conservation Planning: Convergence, Contrasts, and Challenges. *Oryx,* 43(4):464–475.

Rodrigues, A. S. L., and K. J. Gaston. 2001. How Large Do Reserve Networks Need To Be? *Ecology Letters,* 4:602–609.

Rouget, M., R. M. Cowling, A. T. Lombard, A. T. Knight, and G. I. H. Kerley. 2006. Designing Large-Scale Conservation Corridors for Pattern and Process. *Conservation Biology,* 20:549–561.

Salomon, A. K., J. L. Ruesink, and R. E. DeWreede. 2006. Population Viability, Ecological Processes and Biodiversity: Valuing Sites for Reserve Selection. *Biological Conservation,* 128:79–82.

Sanderson, E. 2006. How Many Animals Do We Want To Save? The Many Ways of Setting Population Target Levels for Conservation. *Bioscience*, 56:911–922.

Sanderson, E. W., K. H. Redford, A. Vedder, P. B. Coppolillo, and S. E. Ward. 2002. A Conceptual Model for Conservation Planning Based on Landscape Species Requirements. *Landscape and Urban Planning,* 58:41–56.

Sarkar, S., R. L. Pressey, D. P. Faith, C. R. Margules, T. Fuller, D. M. Stoms, A. Moffett, K. A. Wilson, K. J.Williams, P. H. Williams, and S. Andelman. 2006. Biodiversity Conservation Planning Tools: Present Status and Challenges for the Future. *Annual Review of Environmental Resources,* 31:123–159.

Stewart, R. R., and H. P. Possingham. 2005. Efficiency, Costs and Trade-offs in Marine Reserve System Design. *Environmental Modeling and Assessment,* 10:203–213.

Tear, T. H., P. Kareiva, P. L. Angermeier, P. Comer, B. Czech, R. Kautz, L. Landon, D. Mehlman, K. Murphy, M. Ruckelshaus, J. M. Scott, and G. Wilhere. 2005. How Much Is Enough? The Recurrent Problem of Setting Measurable Objectives in Conservation. *BioScience,* 55:835–849.

Younge, A., and S. Fowkes. 2003. The Cape Action Plan for the Environment: Overview of an Ecoregional Planning Process. *Biological Conservation,* 112:15–28.

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