Ecology, Social Behavior, and Conservation in Zebras

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I. Introduction

One of the central tenets of behavioral ecology is that features of the environment shape animal behavior (Krebs and Davies, 1997). The abundance and distribution of alternative food sources determines optimal patterns of diet choice just as the abundance and distribution of females affect the mating behavior of males. When food is widely scattered and travel from a central place to find it is lengthy, the loads foragers bring home are larger than if food is more abundant and search times are shorter (Giraldeau and Kramer, 1982). When demand for rare, localized, high-quality food items is high, as is the case for small-bodied ungulates such as dik-dik, duiker, and bushbuck, pairs defend territories and mate monogamously. But when large-bodied ungulates, such as impala, waterbuck, and Cape buffalo, need large quantities of food, their ability to subsist on abundant low-quality forage limits competition, allows groups to form and favors polygamous mating (Jarman, 1974). In general, the absolute patterning of key resources in relation to the actions of other individuals influences the costs and benefits of alternative actions that affect survival and fecundity. Those tactics maximizing the difference between benefits and costs, maximize reproductive success. In this way, the environment is the ultimate determinant of fitness and of which behavioral strategies are evolutionarily favored and stable.

Less appreciated is the fact that behavior shaped by the environment exerts feedbacks that shape the environment. In general, individual actions influence population and ecological dynamics as well as resource availability (Sibly and Smith, 1985). In many species, social relationships affect reproductive physiology and in turn fecundity and population growth (Dunbar, 1985), while temporal and spatial patterns of prey abundance shape feeding behavior, habitat choice, and ultimately population cycles of both predators and prey (Partridge and Green, 1985). Foraging in mixed species

assemblages can also transform landscapes in ways that influence each other's foraging behavior, nutritional state, and population processes. As large-bodied hindgut fermenting zebras consume less digestible forage, they increase the availability of more digestible forage required for foregut fermenting wildebeest. Wildebeest in turn, increases the availability of the most digestible vegetation for the small-bodied, high-quality resource-dependent Thompson's gazelle (Bell, 1971; Owen-Smith, 1988).

Given the strong link between environment and behavior, changes in the environment should lead to changes in behavior. If not, environmental change could be pathological, lowering survival and fecundity. However, if species experiencing changes are equipped with sufficient genetic and epigenetic variation, behavioral adjustments are likely. If these behaviors maintain positive net benefits, they will be favored by selection and will provide species with flexibility when facing environmental uncertainty. If conservation biologists can decipher the rules determining how environmental features shape behavior, then they could intervene and manipulate this link by changing human behavior to improve species' survival prospects, enhance ecosystem function, and improve human livelihoods in environmentally sustainable ways.

In this chapter, I will use zebras to illustrate how environments shape behavior that results in different social structures for two evolutionarily closely related species and how human-induced environmental changes are challenging zebra survival. The chapter will be divided into three parts. In the first, I will elucidate the rules by which environmental features account for differences in the sociality of two zebra species at core, as well as at higher, societal levels. In the second, I will explore the challenges facing people and zebras inhabiting the arid lands of Kenya and show how human actions are changing environments that are disrupting normal zebra behavior. In the third, I will illustrate how understanding the needs of three different classes of landholders can induce appropriate changes in their behavior that changes landscapes in ways that improve economic welfare and allow zebras to sustain themselves.

II. MATERIAL AND METHODS

A. FOCAL SPECIES

Plains (*Equus burchelli*) and Grevy's (*E. grevyi*) zebras are large-bodied grazing ungulates that inhabit grasslands of East Africa. Since 1999, both species of zebras have been studied on Lewa, Ol Pejeta, and Mpala

Conservancies, Ol Jogi, El Karama, and Segera ranches as well as a number of pastoral group ranches. All properties are located in the Laikipa and Samburu ecosystems of central Kenya.

B. Field Methods

Population densities, herd sizes, and group composition were collected by searching for herds while driving or walking predetermined survey routes. For each herd sighted, we identified all males present and recorded their status, as bachelor or stallion. We also recorded the number of adult females present in each harem and whether or not they were lactating. Stripes were used to individually identify zebras. Individuals in a herd were typically close together, relative to the distance separating them from other herds. If more than 100 m separated two groups of zebras, we considered them to be in different herds.

We used instantaneous scan sampling during one hour blocks to record the time and occurrence of grazing, drinking, walking, standing, and socializing. If the majority of herd members were grazing, measures of resource abundance and quality were recorded. Along a 25-m transect a welding rod was dropped at meter intervals. Vegetation touching the pin was keyed to species and counts were used to estimate percent cover and species diversity. Hits per pin by any plant part, leaf hits per pin, hits by green plant parts, and highest leaf hit provided estimates of biomass, quality, and height. Since many of the variables covaried, principle components analysis was used to identify independent composite variables to characterize the vegetation. Table I shows that three components explain 79% of the variation: PC1 is composed of variables depicting "quantity;" PC2 is composed of variables corresponding to "quality;" and PC3 is composed of variables corresponding to "species diversity". Bitterlict stick tree intercepts measured habitat openness and habitat visibility. The Laikipia Predator Project provided counts of lions, hyena, and leopards (L. Frank and R. Woodroffe, personal communication). Predator impact and context specific risk were combined to generate a predator intensity index $= \sum_i [$Abundance ith predator $\times$ Impact of ith predator$] \times [$Habitat visibility $\times$ Diel period score$]$. Dawn and dusk were given higher diel period scores than periods from 8:00 to 18:00 when conditions of full sun prevailed.

C. Predator Identification from Dung

Samples of lion dung were collected and air-dried. Hairs were removed and examined with a transmission light microscope to determine the size of a hair's cortex and medulla. Hairs taken from skins of various ungulates were

TABLE I

PRINCIPAL COMPONENT ANALYSIS OF VEGETATION

	Principal component loadings		
	PC 1	PC 2	PC 3
% Cover	0.42	−**0.48**	0.17
% Green	0.03	**0.80**	0.33
Species diversity	0.08	−0.20	**0.90**
Average height	**0.64**	−0.02	−0.23
Average leaf hits/pin	**0.63**	0.32	−0.02

Axis Name: "*Quantity*" "*Quality*" "*Diversity*".

79% variation explained by three components.

Five measures of vegetation gathered from 25 m. Transects were reduced to three independent axes. Based on the loadings they represent measures of "Quantity", "Quality," and "Diversity".
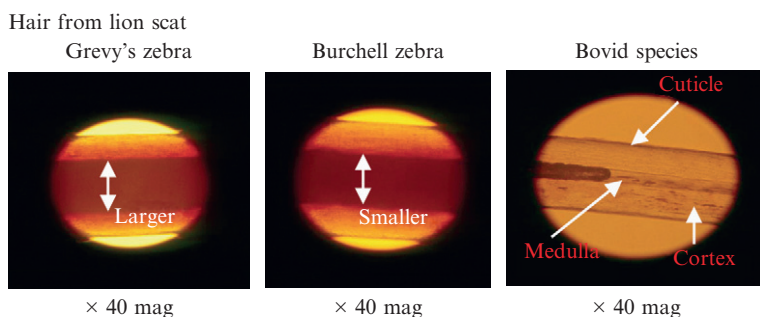
Hair from lion scat

FIG. 1. Transmission microscopic pictures of body hairs of a typical adult Grevy's zebra, plains zebra and bovid. Each hair has three parts: The outer cuticle and the internal cortex, and medula. The medulla of zebras is solid and dark whereas those bovids and other antelope are lighter brown and have breaks. The medullas of Grevy's zebras are wider relative to the cortext than those of plains zebras.

analyzed to create keys for prey species. Figure 1 shows the cross section of a Grevy's zebra hair, a plains zebra hair, and the hair of a bovid species. Discriminant function analysis was used to assign individual zebra hairs to species.

D.   PARASITE LOADS

Dung was collected from defecating zebras to insure freshness and the correct assignment of age and sex class of the defecating individual and when possible, its individual identity. Separation of eggs followed standard techniques (Ezenwa, 2002) so that counts of eggs using two-chambered McMaster slides could be converted to eggs per gram.

E. POPULATION FORECASTING

A two sex, age-structured model (Dobson and Lyles, 1989) was used to forecast yearly birth rates and population sizes of zebras. All females 4 year old or greater were assumed to be reproductive and 3-year-old females were assumed to be capable of reproducing depending upon population density (Fig. 2). Age-specific survival rates and fecundity were estimated from ''Sight–Resight'' data. These vital rates were also affected by density (see Appendix for age-structured model description).

F. ANALYSES

General Linear Models were used to determine the extent to which ecological and sociosexual variables affect social organization.

III. ECOLOGY OF ZEBRA SOCIALITY

A. ZEBRA MATING SYSTEM

Zebras exhibit two mating systems (Klingel, 1969a,b; Rubenstein 1986, 1994). In one, plains zebras live in closed membership family groups (harems), comprised of a stallion, females, and their infants and juveniles. In the other, Grevy's zebras live in open membership groups in which males and females change partners frequently. Sometimes, Grevy's zebra groups consist of only adult females, some with young and others without, while at other times females associate with a male whose territory they occupy.

Population projection model

$$
\begin{bmatrix} I \\ J \\ A \end{bmatrix}_{t+1} =
\begin{bmatrix}
0 & \alpha, Ff\,(N_t) & Ff\,(N_t) \\
Sf\,(N)_t & 0 & 0 \\
0 & Sf\,(N_t) & Sf\,(N_t)
\end{bmatrix}
\bullet
\begin{bmatrix} I \\ J \\ A \end{bmatrix}_t
$$

FIG. 2. Example of a stage-structured population projection matrix. The top row (light) depicts fecundities for each stage class. Only adults (A) reproduce with certainty, bearing F young per year. A fraction of juveniles (α) also reproduce. Both fecundity and the fraction of juveniles breeding for the first time are affected by density (f[N]) which is affected by rainfall, a proxy for environmental conditions. Infants (I) are too young to reproduce. The next two rows (gray) depict survival (S) from one class to another. Again, survival is also density dependent. Values for the variables are derived from ''Sight-Resight'' analyses of each population. The actual population projection was based on a more complete age-structured version of the model (see appendix for details).

Both mating systems are polygynous since breeding males gain mating access to a number of females by keeping other males away. In both systems, reproductively unsuccessful males form bachelor groups whose membership changes over time. For females, however, the diversity of mating options are different for the two species. Female plains zebras are monoandrous since females remain tightly bonded to one male for long periods, while Grevy's zebra females are polyandrous since they move among males during single reproductive episodes (Ginsberg and Rubenstein, 1990).

Differences in the ecological circumstances of each species account for the major social differences of the species. Plains zebras typically live in mesic habitats where food and water are close together and food is moderately abundant and evenly distributed even during dry seasons. Relatively abundant food and water supplies reduces competition between different reproductive classes of females and allows them to live together and derive material rewards from stallions. Harem polygyny intensifies male–male competition that results in sexual harassment of females by partner and strange males. Reduced harassment provides females with more time to forage and more freedom to search for, and acquire, better forage (Rubenstein, 1986, 1994). Ultimately, females in groups with quality males have higher per capita reproductive success as measured by number of young surviving to age of independence (Nuñez et al., 2009; Rubenstein, 1986). Males in these groups also achieve higher reproductive success since peaceful groups are large and last for long periods of time (Nuñez et al., 2009).

Grevy's zebras traditionally live in more xeric habitats where food and water are located far apart and where food supplies are more sparsely distributed (Rubenstein, 1986). Competition among Grevy's zebra females is thus higher than among those of plains zebras. Moreover, the larger body size of Grevy's zebras, by reducing the need for all females to drink daily, allows those without young to wander widely in search of abundant food but restricts those with young foals to remaining within half a days' travel to water. These differences become particularly pronounced as the dry season intensifies (Fig. 3) and ultimately lead to tearing the social fabric as females in different reproductive states go their separate ways. Since both classes of females are equally valuable to males, stallions are unable to associate permanently with both classes. Instead, they establish large resource territories. Dominant males place these near open watering points to attract females with young foals as well as those coming to drink every few days (Ginsberg, 1989; Sundaresan et al., 2007). Subordinate males establish territories farther from water in areas with abundant vegetation and thus gain mating access with only one class of females, those without young foals (Rubenstein, 1986, 1994).
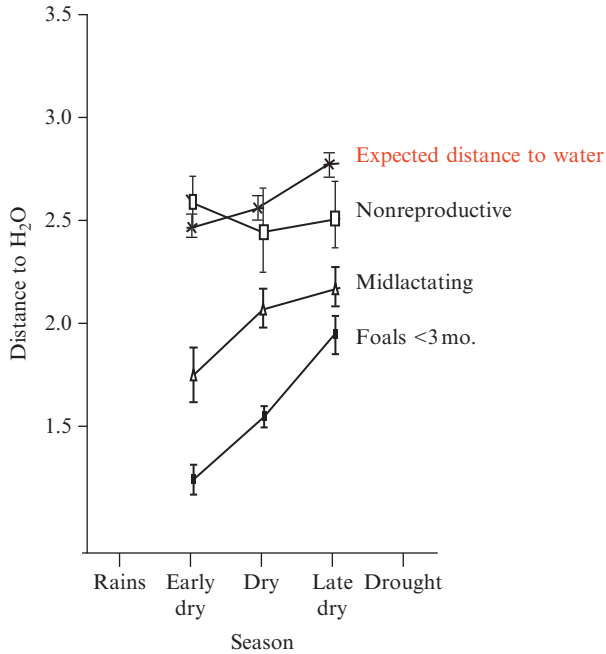
FIG. 3. Dry season impacts on availability of water. Drying increases the average distance from water for each of class of females. All remain closer to water than expected, with those with the youngest offspring (<3 months) remaining closest to water under all conditions. Expected distances were computed by randomly placing points on the landscape and measuring the distance to the nearest drinking point at each season. Since watering points dry up as the dry season progresses the expected distance increases over time. Means and standard errors are shown.

B. HIGHER ORDER SOCIAL ORGANIZATION

Unlike Grevy's zebras and horses (*E. caballus*), another equid in which females and males live in closed membership harem groups (Linklater, 1999; Rubenstein, 1986), plains zebras inhabit multilevel societies in which core social groups—harems and bachelor groups—come together to form herds. Herd size and composition change regularly as core groups fuse and fission. They can range in size from 2 to 20 groups, often containing hundreds of individuals (Rubenstein and Hack, 2004). Sometimes, family groups show preferential associations for other groups (Rubenstein, 1986).

When levels of social organization above core units form, they usually do so because these additional units provide a function that underlying units do not. In harem-dwelling gelada baboons (*Theropithecus gelada*), higher

level clans and bands help lower predation risk (Dunbar, 1986), while in hamadryas baboons (*Papio hamadryas*), these same higher units facilitate mate and resource defense (Stambach, 1978). These examples show that both top-down (predation) and bottom-up (resource availability) ecological forces can play important roles in determining the existence and function of higher forms of social structure. Yet, a third factor, sociosexual forces, also appears to be implicated in the formation of higher ordered units. In the populations of plains zebras where preferential associations exist among harems, coalitions of males are more successful in driving off incursions by bachelors than solitary harem males (Rubenstein, 1986).

In order to measure the relative importance that predation, resource, and sexual competition play in determining the size of plains zebra herds, we compared herd size on commercial ranches and conservancies that varied in vegetation abundance, quality and diversity, predator intensity, and type of legal cropping. While some ranches and conservancies did not crop zebras, those that did, cropped in different ways. Some landholders hunted only bachelor males, whereas others hunted only harem groups. When bachelors were removed, intruder, or cuckolding, pressure as measured by the ratio of bachelor males to stallions declined. When harem groups were shot, not only were females removed from the population, thus increasing sexual selection intensity, but cuckolding pressure also increased since fewer males were available to form defensive coalitions to protect mating rights.

A General Linear Model (Table II) shows that herd size is determined by both the size of the zebra population and the abundance of available vegetation in an area. Although a paucity of zebras in an area limits the size of herds that can form, large populations do not guarantee that herds

TABLE II
GENERAL LINEAR MODEL PREDICTING PLAINS ZEBRA HERD SIZE

Variable	Slope	P value
Zebra density	0.09	< **0.01**
PC 1: "Quantity"	0.18	< **0.05**
PC 2: "Quantity"	− 0.09	< 0.10
PC 3: "Diversity"	− 0.66	< 0.60
Predator index	− 0.03	< 0.15
Social factor: No. of bachelors/stallions	2.44	< **0.0001**

Six variables were included in the model, zebra density, the three vegetation principle components, the predator index, and the sociosexual bachelor to stallion ratio.

$F_{4,227} = 77.9$; $P < 0.0001$; $r^2 = 0.67$.

will be large. To some extent, vegetation abundance, not vegetation quality or diversity, enables large herds to form. But the most significant factor influencing herd size is cuckoldry pressure. Where culling is restricted to bachelors, herds are on average one harem smaller than where stallions and family groups are hunted (Rubenstein and Hack, 2004). Predation risk is often assumed to be the greatest force responsible for group living. In Laikipia, however, predation pressure appears to have little direct impact on zebra herd size, probably because the marginal gains of increasing group size beyond that of harems already containing 8–10 individuals are so small. But predation could still be having an indirect effect on herd size because zebra bachelor male groups are almost three times as large as those of feral horses whose predators have been extirpated (personal observation). Thus, the existence of large core groups of bachelors intensifies cuckolding pressure in general and this leads to an arms race among males.

Proximate factors associated with foraging rate underpin much of the decision-making associated with joining or leaving herds (Rubenstein and Hack, 2004). Males and females in solitary harems have high intake rates that only decline slightly as other harems join the herd. When bachelors attach themselves to a solitary harem, however, the stallion's defensive actions reduce his intake rate while those of his females remain high. If he is with other stallions, then sharing anticuckolding duties allows them to maintain intake rates similar to their females. Thus, reducing the risk of being "parasitized" by bachelors appears to be triggered by stallions banding together to reduce long-term debilitating reductions in foraging rate.

Active decision-making by males could mistakenly imply that females are passive actors in determining the composition of herds. Unchanged foraging success despite the coalition forming behavior of males may make females indifferent to changes in herd size. With respect to shaping herd composition, however, female preferences emerge. Herds vary in the types of harems that come together. Some herds are more homogeneous than others typically with respect to the abundance of lactating females and their foals. Personal predation risk often increases when an individual's phenotype deviates from the norm (Landeau and Terborgh, 1986). To reduce this risk plains zebras females with young foals appear to band together. As habitat visibility decreases (higher bitterlict score) and the number of lions sighted increases, the percentage of harems with foals increases. The number of stallions in the herd, the sociosexual factor that affected herd size most strongly, has no effect on the composition of herds (Table III). Apparently as predation risk increases, the composition, but not the size, of herds change.

TABLE III

GENERAL LINEAR MODEL PREDICTING THE PERCENTAGE OF HAREMS CONTAINING YOUNG FOALS
COMPRISING PLAINS ZEBRA HERDS

	Predation risk affects group composition (% young foals)		
GLM variable	Slope	F value	P value
No. of stallions	− 0.004	1.09	< 0.30
Visibility index	− 0.003	4.40	< **0.04**
No. of lions	0.005	4.21	< **0.05**

$F_{3,678} = 3.89; p < 0.01; r^2 = 0.18.$

IV. CHALLENGES FACING PEOPLE AND WILDLIFE IN KENYA

Kenya is potentially one of the richest countries in East Africa. It is endowed with fertile soils and abundant natural resources, including large wildlife populations that fuel a profitable ecotourist industry. Gross domestic production (GDP) has gone through cycles during the last 50 years. Immediately after independence (1964), GDP stood at 6.6%. During the 1970s, it averaged 5.2% dipping slightly in the 1980s to 4.1%. But during the political turmoil of the 1990s, it dropped further to a low of 2.1%. After peaceful elections, GDP rose to 6.4% by 2006. Yet, despite these encouraging national trends, the benefits of high economic growth are not equally available to many segments of the population. Pastoral herders inhabiting semiarid lands that are prone to large natural environmental fluctuations, receive few of these benefits. Average wages of herders on commercial ranches range from $1 to $2 per day. Those living on group ranches who own their own herds have limited commercial options and earn more indirectly from relatives working in towns, ecolodges, or on commercial ranches, than from their own livestock. Since large herds are important for cultural reasons and provide insurance as seed stock for rebuilding after drought-induced die offs, grazing pressure on rangelands continues to increase as human population size increases.

For wildlife populations inhabiting dry lands, human impacts are great. Throughout Africa, habitats of plains zebras are being fragmented and lost to development. Yet in central Kenya, especially in Laikipia, plains zebra numbers have been increasing over the last decade, apart from temporary declines associated with a La Nina driven drought in 2000 (Georgiadis et al., 2007). Grevy's zebra numbers, however, have been in steady decline since the mid-1970s reaching a low of about 2000 in Kenya and 2200 worldwide (Fig. 4). Although habitat loss and degradation play an important role in this decline, Kenya has set aside large tracts of the dry land as protected areas.
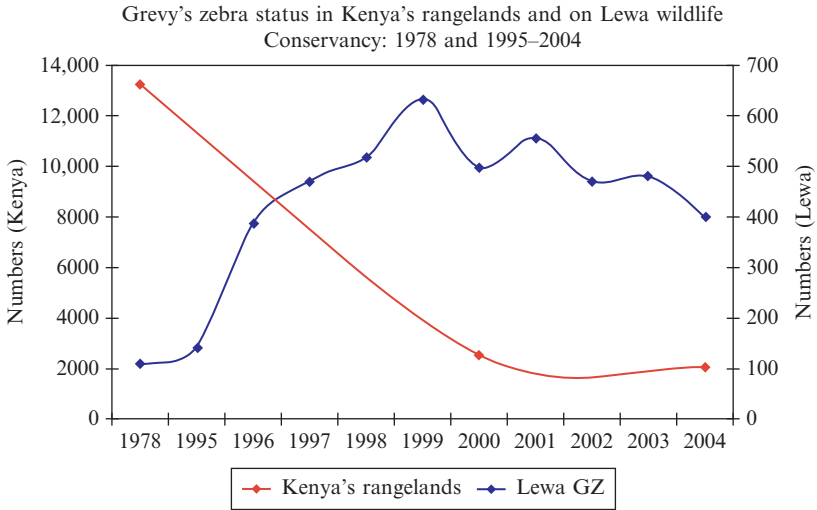
Fig. 4. Grevy's zebra numbers over 25 years throughout Kenya (grey line) and on the Lewa Conservancy (black line).

Numbers have not yet increased even on fenced conservancies where herders and their livestock have been excluded (Fig. 4). Since over 70% of Kenya's wildlife still inhabits private lands (Western et al., 2009), human activity on these shared lands is likely to be a problem. But what is the size of the human footprint and how does it compare against the impact of nature's own forces?

A. NATURALISTIC CONDITIONS

Our studies on Grevy's and plains zebras illustrate how both natural and anthropogenic forces help shape behavior and reproductive success. On conservancies, such as Lewa, where cattle have historically been excluded, zebras have been able to range independently of most human impacts. Under such conditions, we can examine how Darwin's hostile forces—competition, predation, and parasitism—affect behavior in order to establish human-free baselines. When free to choose when to drink, both species prefer to drink during mid-morning (Fig. 5). Plains and Grevy's zebras also largely share the same habitats (Fig. 6), although Grevy's zebra females without foals range farther from water than do either plains zebra females or Grevy's females without young foals (Fig. 7). When together, plains zebras significantly reduce foraging intake rate of Grevy's zebras, in
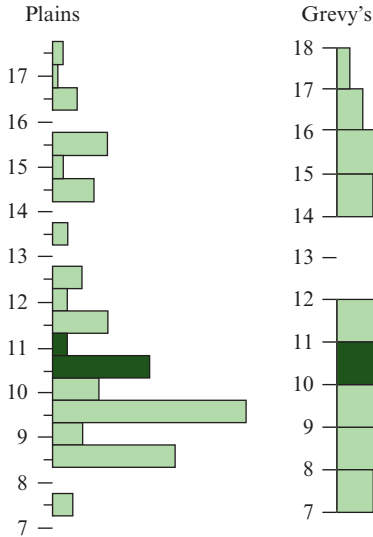
FIG. 5. Frequency distribution of arrival times at watering points for plains and Grevy's zebras on the Lewa Conservancy when livestock were absent.
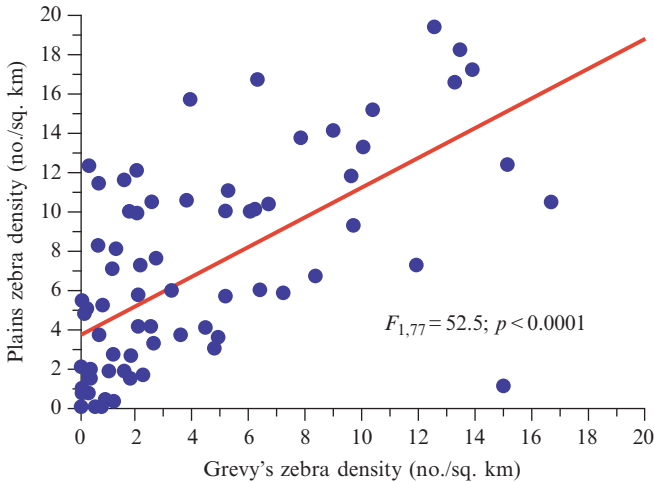

$F_{1,77} = 52.5;\ p < 0.0001$

FIG. 6. Co-occurance of Grevy's and plains zebras.

proportion to their numerical abundance. Grevy's zebras have no such effect on plains zebras (Fig. 8), thus tipping the competitive balance towards Plains zebras. Seventy years ago, no Grevy's zebras inhabited the
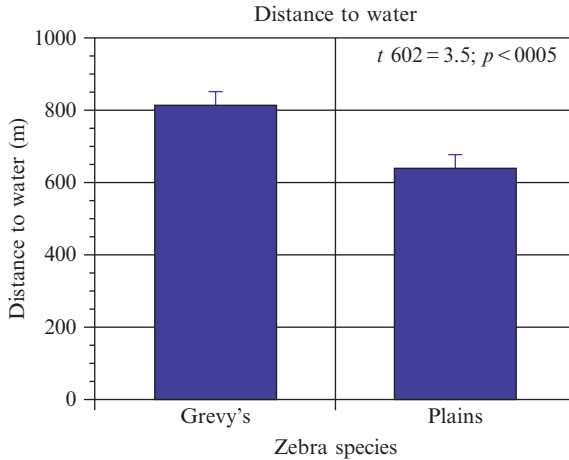
FIG. 7. Average distance from water of Grevy's and plains zebras. Standard errors shown.

Lewa Conservancy. Today 400 Grevy's live there. As Grevy's zebras move south into typical plains zebra habitat, competitive dominance by plains zebra will likely limit the ability of Grevy's zebras to sustain their populations.

Predator numbers generally increase as conditions become more hospitable. Thus, as Grevy's zebras move south into more mesic habitats, predation pressure is likely to increase. Moreover, since conservancies depend mostly on ecotourism revenues, conservancies try to sustain large populations of predators and their zebra prey. Lewa had no lions prior to 1999, but lion numbers have increased steadily since then. What is striking is that when hairs are collected from dried lion dung, those of zebras are disproportionally represented relative to other ungulates (73% contain zebra hair) and those from Grevy's zebras are slightly more abundant than those of plains zebras (55% contain Grevy's zebra hair). Since plains zebras outnumber Grevy's zebras by 4 to 1, the proportionate selectivity of lions for Grevy's zebra is highly significant ($\chi^2 = 9.25$; $p < 0.005$; $n = 50$ lion scats (Rubenstein and Njonjo, 2004).

With respect to parasite burden, Grevy's zebras are better off than plains zebras. Not only are worm egg outputs lower than in plains zebras, but absolute levels fall below the threshold of 1500 eggs/g where health is compromised (Fig. 9). Thus, of Darwin's three hostile forces, two impact Grevy's zebras more than plains zebras. Even under conditions where the direct effects of humans are eliminated, Grevy's zebras are at risk and will be challenged to maintain, let alone increase, their populations.
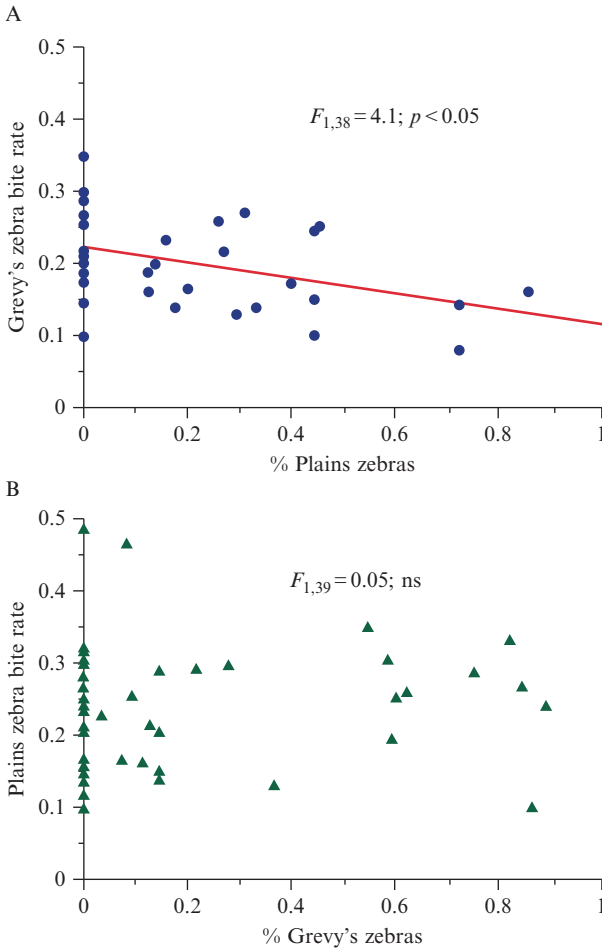
A

B

Fig. 8. Impact of local abundance of each zebra species on the vegetation clipping rate of the other. In mixed herds, as the fraction of plains zebras increases Grevy's zebra clipping rate declines significantly (A), but the reverse is not true when Grevy's zebra frequency increases in the presence of plains zebras (B).

B. ANTHROPOGENIC CIRCUMSTANCES

The fate of wildlife populations in the developed world has changed over time. Historically, development has meant transforming landscapes. Natural resources were harvested without regard for sustaining wildlife populations. Industrialization multiplied wealth increases, encouraging further habitat transformation. As wildlife disappeared, protected areas were created.
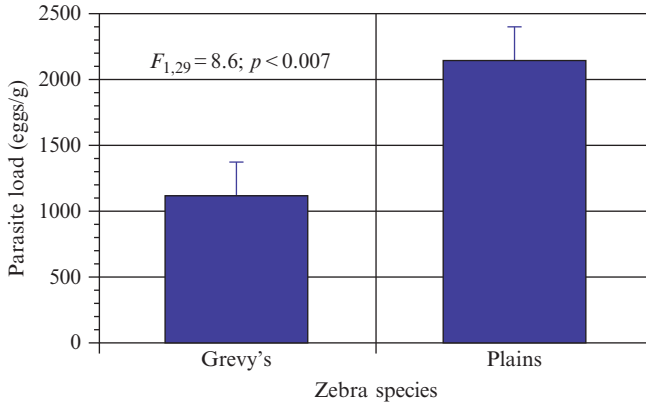
FIG. 9. Parasite load of Grevy's and plains zebras as measured by nematode 1500 eggs/g threshold of feces. Grevy's zebras excrete significantly fewer eggs than plains zebras. Grevy's zebra levels are below the 1500 eggs/g threshold for when harmful affects appear.
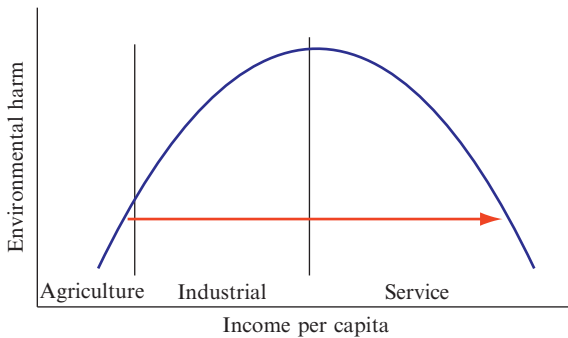

FIG. 10. Kuznet's curve depicting historical trends of increases of percapita income levels on the environment of developed nations (black line). When humans live at subsistence levels impact is low, but as resources are converted into wealth during periods of industrialization environmental degradation increases. Only at high income levels when quality of life becomes important does increasing investment in restoring ecosystems lead to reductions in damage to the environment. Since pastoral herders are still at subsistence levels can an alternative trajectory be adopted that leads to increases in income levels without inflicting significant harm to the environment (gray arrow)?

Later, as desire for improving quality of life grew, improvements in quality of life led to restoring the environment, improving ecosystem function, and conserving endangered and threatened species. An Environmental Kuznets curve (Fig. 10) depicts the "western way" of development that puts economic

Δ Environment ——→ Δ Behavior

Δ *Human behavior* ◂······ Conservation
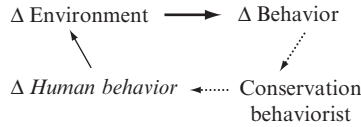   behaviorist

FIG. 11. Expansion of the central behavioral ecological tenet that features of the environment shape animal behavior. The top link (solid line) proposes that a change in the environment will lead to a change in behavior. In today's world most environmental change is anthropogenic (solid line). The dashed lines suggest an understanding of why animals have changed their behavior by a conservation minded behavioral ecologist can lead to interventions that change the behavior of humans using the landscape so that subsequent changes in their land use practices can lead to positive changes in animal behavior, and in turn, population dynamics.

expansion first and environmentalism second. In developing countries that are on the cusp of industrialization and rapid exploitation of natural resources, is there an alternative to the "western way" of development? Can development in these countries improve human livelihoods while allowing wildlife to sustain itself? The jury is still out, but our research suggests that as long as developers and conservationists understand human needs as well as the rules that link wildlife behavior to the environment, this knowledge can be used to change human behavior in ways that modify environments so that wildlife can sustain their populations (Fig. 11).

V. ACTIONS FOR SUSTAINING ZEBRAS AND HUMAN ECONOMIC DEVELOPMENT

People living with wildlife fall along an economic continuum. At one end are conservancy owners who earn income from commercial ranching, ecotourism or both and are financially moderately well off. Typically, their lands encompass 100 or more square kilometers and their management practices are generally wildlife friendly (Georgiadis et al., 2007). In the middle are private landowners with smaller holdings in the thousands of hectares. They make ends meet via a mixture of agriculture and commercial livestock husbandry, but wildlife are often viewed as a threat. At the other extreme are pastoral herders who live on communal or "group" ranches and are financially challenged. Although partially sedentarized, they herd livestock in traditional ways. Overstocking and limited ranging typically results in rangeland degradation that harms livestock, wildlife, and human welfare. Not surprisingly, pastoralists have the least tolerance for wildlife and thus offer the greatest challenge to changing human behavior in ways that benefit wildlife. Given this range of environmental perspectives and

levels of wealth, one strategy will not fit all landowners. What follows is a case-specific analysis of the types of behavioral and ecological changes that are appropriate for each type of landowner.

A. CONSERVANCIES

Trying to maintain high numbers of zebras—Grevy's or plains—and lions in order to satisfy the desires of ecotourists, is not easy. In fact, on both the Lewa and Ol Pejeta conservancies, lion densities rose to some of the highest in Laikipia by 2005. The typical density of lions on unfenced properties is approximately 6 per 100 km^2. On Lewa, lion density has reached 28 per 100 km^2 and on Ol Pejeta density has gone as high as 31 per 100 km^2.

Survival prospects for zebra populations living with such high densities of lions can be forecast using population projection models tuned with population specific survival rates and fecundities. Because zebras are identified by their stripes, "Sight-Resight" studies can be used to estimate age and sex specific vital rates. Given that lions prefer Grevy's zebras over plains zebras on Lewa, it is not surprising that average yearly adult and infant survival rates of Grevy's zebras are 0.88 and 0.27, respectively. When used in the stage-structured model, Grevy's zebra numbers decline markedly. From a peak of 450 Grevy's zebras when lions were seen for the first time on Lewa, the population is expected to decline by about 50% in 30 years (Table IV). For the rest of Laikipia where lion numbers are much lower, infant yearly survival rates are significantly higher than on Lewa (0.50), while adult survival rates are slightly lower (0.80). On unfenced lands, such as Mpala, populations hold their own, experiencing more modest declines of about 15% over 30 years (Table IV). If Mpala-like vital rates could be reproduced

TABLE IV
GREVY'S ZEBRA POPULATION PROJECTIONS

Location	Zebra species	Adult survival	Infant survival	Initial population size	Final population size (mean ± SE)
Lewa	Grevy's	0.88	0.27	450	226 ± 15
Laikipia (Mpala)	Grevy's	0.81	0.50	150	122 ± 11
Lewa	Grevy's	0.81*	0.50*	450	622 ± 12*

Survival estimates were derived from "Sight-Resight" analyses. They were included in a two sex, age-dependent stochastic population projection model incorporating density dependent parameters tuned to rainfall as described in the appendix and Dobson and Lyles (1989). Final population sizes are projections after 30 years and those with an * incorporate survival values from elsewhere and thus represent hypothetical outputs.

on Lewa given its highly productive, water rich habitats, Grevy's zebra numbers would be expected to increase by almost 60% from today's levels (Table IV). In an attempt to reproduce Laikipia-wide survival rates of Grevy's zebras on Lewa, appeals were made to the Kenya Wildlife Service to translocate lions to areas in Kenya where they are declining. Unfortunately, these were denied and as a result, Grevy's numbers continue to decline on Lewa.

On the Ol Pejeta Conservancy where plains zebras are the most abundant herbivore, impacts of lion predation are unsustainable. Although the adult survival rate is 0.76, only slightly lower than that of the majority of Laikipia, the infant survival rate is only 0.13. At these levels, the model predicts the population will be driven to extinction in 30 years. Initially Ol Pejeta Conservancy was divided into a fenced tourist area and an unfenced cattle ranch. Age structure comparisons of the two populations showed that the population living with cattle had higher percentages of infants and juveniles than the one in the tourist reserve (Fig. 12A). Thus, the population living with cattle had the best recruitment potential. When faced with these figures a new management strategy was developed and implemented. The entire conservancy is now fenced, but strategically placed gaps in the fence enabled both predators and prey to leave or enter the conservancy. In addition, the fence dividing the east and west sides of the Conservancy was removed. Almost immediately the lions redistributed themselves, and after 3 years the significant differences in the age structure of the two populations have been eliminated with the fraction of infants and juveniles increasing in the population formerly restricted to the tourist reserve (Fig. 12B). A simple change in the landscape induced a redistribution predation pressure. The combined population of zebras now experiences lower predation levels and normal anti-predator behavior has allowed it to develop a more sustainable age structure.

B. SMALL-SCALE LANDHOLDER

Private land holders often view wildlife as a nuisance since they eat crops and compete with livestock for forage. Since profits from livestock ranching are small, utilizing wildlife for profit may be one way in which ''wildlife could pay to stay''. Until recently, local wildlife forums were allowed to allocate and monitor cropping quotas set by the government. For small-scale landholders, could zebra cropping be done sustainably and generate sufficient revenue to encourage sharing rangeland with wildlife?
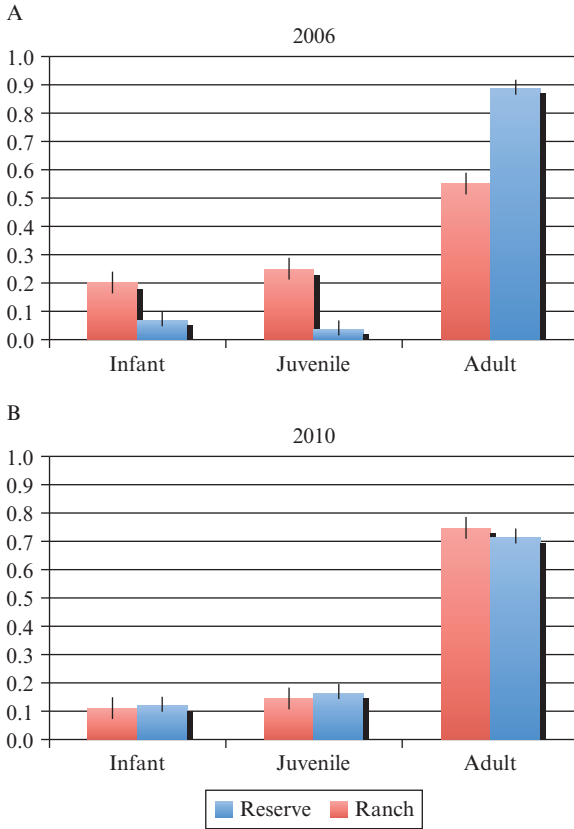
FIG. 12. Relative abundances of Infants, juveniles and adult plains zebras on the Ol Pejeta conservancy. (A) Age class abundances in 2006 when the reserve and the ranch were separated by a fence and lion densities on the reserve side were five times greater than on the ranch side. Signifiantly fewer recruits (infants and juveniles) were found on the reserve side as compared to the ranch side ($\chi^2 = 6.5; p < 0.001; N = 24$) Age class abundances in 2010 after the dividing fence was removed. Over time the two populations have become more similar ($\chi^2 = 2.3; p < 0.55; N = 215$).

Figure 13 shows the population growth trajectory of non-harvested plains zebra populations on private lands based on the survival and fecundity variables estimated from our "Sight-Resight" studies on unfenced Laikipia zebra populations. Clearly when left alone, zebras in Laikipia can take care of themselves. From an estimated population of 35,000 in 2000, numbers are predicted to increase by almost 35% over 30 years. However, if random cropping were permitted at government-sanctioned levels of 10%, the model predicts that the population would disappear
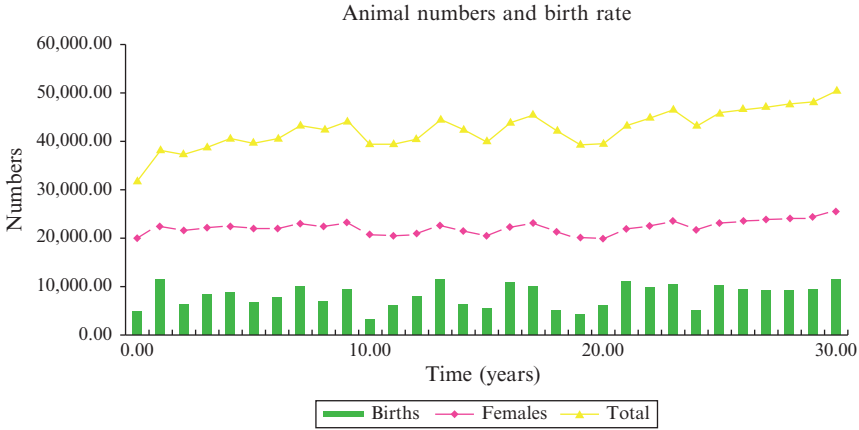
Animal numbers and birth rate

FIG. 13. Average predicted population growth trajectory of the total population as well as the number of adult females and infants for plains zebras throughout Liakipia. Survival and fecundity data were estimated from ''Sight-Resight'' data.

(Fig. 14A). If random cropping was reduced to 6% the population is predicted to stabilize at a new equilibrium around 25,000 zebras (Fig. 14B). Thus, it appears that zebras can be cropped in an ecologically sustainable fashion if its population biology is understood. But is cropping at this level economically profitable?

With 25,000 zebras inhabiting Laikipia's approximately 10,000 square kilometer, zebra density will be about 2.5 per square kilometer. If a small holding covers 2000 hectares, then approximately 50 zebras will inhabit the average small holding at any time. A 6% cropping rate would yield three zebras per year. Given that there is no market for wildlife meat in Kenya, profit comes from the sale of hides to foreign tanneries and savings on reduced meat purchases for humans and dogs. In general, a zebra is worth about $300, the same as a cow in good condition. Income from cropping three zebras per year would generate $900. This sum could cover the salary of about one worker per year if wages were between $2 and $3 per day, which is about the national average. Thus for many small holders zebra cropping at an ecologically sustainable level can provide important economic benefits.

C. PASTORAL HERDERS

Grevy's zebras living on pastoral lands potentially face many challenges. Understanding what these are and the degree to which they disrupt normal Grevy's zebra behavior is difficult for noncommunity members to ascertain.
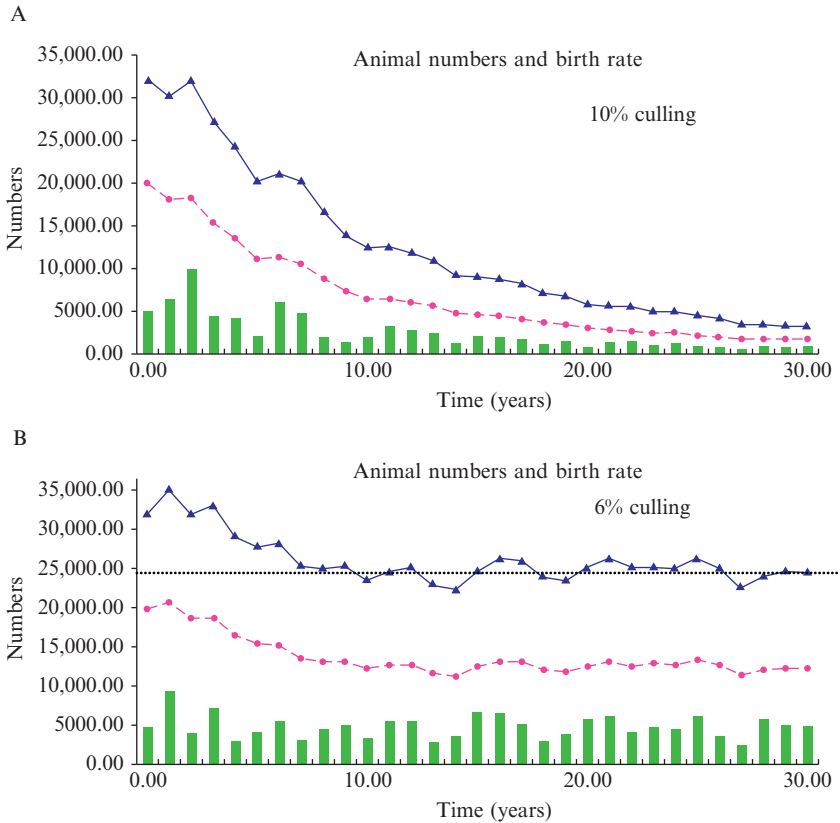
A

B

Fig. 14. Average predicted population growth trajectories of the total population of a culled plains zebra population. (A) Trajectory goes to extinction if 10% of the zebras are hunted at random. (B) Trajectory stabilizes at a new carrying capacity of 25,000 zebras if 6% of the zebras are hunted at random.

As a result, we created a Grevy's zebra scout program (Low et al., 2009). Two women and one man from eight communities were paid $3 per day to record the number of Grevy's zebras seen while engaged in normal daily activities. For men this entailed herding livestock mostly in the more open areas of the group ranch. For women this meant walking through more wooded areas when collecting firewood and water. When zebras were seen, scouts recorded their location on hand-held GPS units. They also recorded the abundance and activities (grazing, walking, or resting) of each age and sex class, in addition to the openness of the habitat, the presence or absence of water by type and the identity of other wildlife

and livestock species if they were within 100 m of the Grevy's zebras. Once I received the data, I could assess what natural and anthropogenic factors influenced the spatial and temporal location and composition of Grevy's zebra herds.

Findings that herd size decreased as the dry season intensified matched previous observations on conservancies. Moreover, when experienced field workers compared their data on conservancy zebras to scout data, the concordance was high. Thus, when scout data revealed that herd sizes increased as the day progressed (Fig. 15), when herd sizes generally remained constant on conservancies, it became clear that zebra behavior on group ranches appeared to be altered in significant ways. Discussions at community meetings revealed that pastoralists knew that their activities disrupted normal zebra activities. The pastoralists knew what the conse-quences would be—that the zebras would mill around the water hole for much of the afternoon until the last of the herds departed for home and the safety of their bomas (corrals). Men also acknowledged that in the morning their dogs broke up the large nighttime herds.

Even more interesting was the finding that no more than 30% of the sightings of Grevy's zebras cooccurred with livestock and that nonlactating females were seen least often in the presence of livestock (Fig. 16A). If we assume that livestock occupy the best grazing areas and that nonlactating females need the highest quality food to rebuild body condition after weaning, then limited access to the best grazing areas could prolong inter-birth interval for these females. Since these are the females that will provide

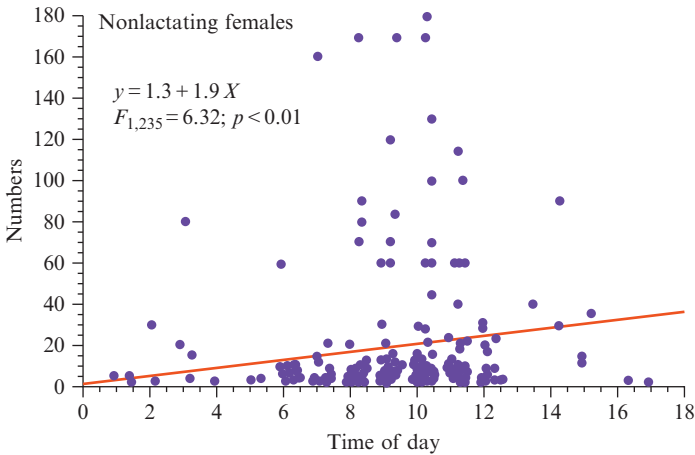

$$y = 1.3 + 1.9\,X$$
$$F_{1,235} = 6.32;\ p < 0.01$$

FIG. 15. The number of nonlactating females within herds increases as a function of time of day.
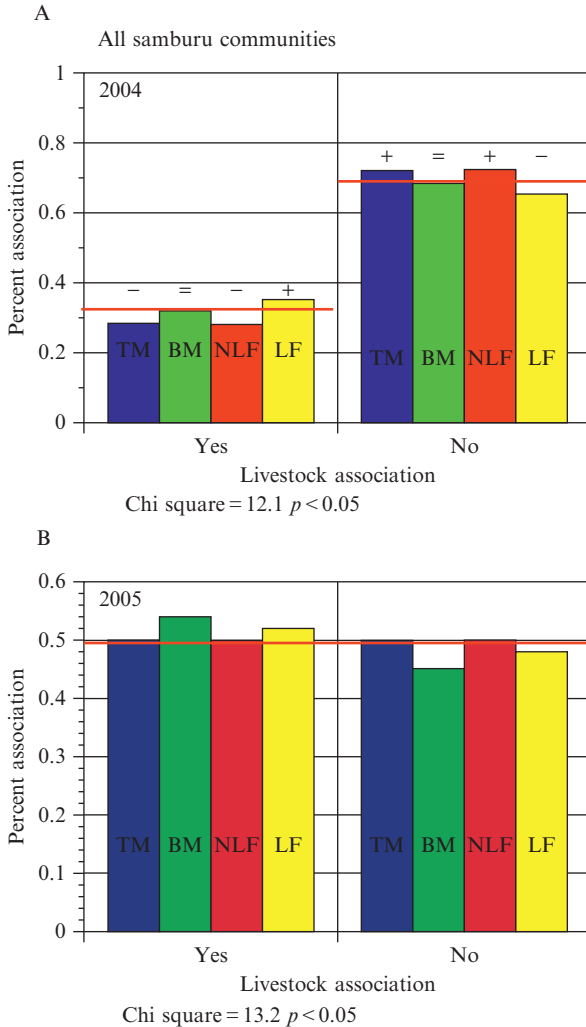
FIG. 16. Percentage of sightings of Grevy's zebras by scout patrols with livestock. (A) At the start of the scout program in 2004. (B) One year after the start of the program and meetings with the community. (TM = Territorial males; BM = Bachelor males; NLF = Non-lactating females; and LF = Lactating females).

most of the recruits to sustain the population, this inability to graze with livestock could be a serious problem. Perhaps because we presented this hypothesis to the communities, within 12 months communities no longer harassed Grevy's zebras and sightings of Grevy's zebras with livestock

increased to 50% (Fig. 16B). Since scouts work two days per week, each scout earns about $300 per year, which then often gets spread among relatives within the community. For the first time wildlife is generating significant income to communities, income that would be hard to acquire in any other way. But perhaps just as important is the empowerment that comes from gathering the data and owning the results, whether good or bad. As one scout noted ''I now understand my zebras''. It suggests that by converting individuals from being part of the problem to being part of the solution, it is possible to encourage people to modify the landscape in ways that enable wildlife to change their behavior so that survival prospects and fecundity are improved.

VI. CONCLUSIONS

Behavioral ecology has much to offer for solving conservation problems (Caro, 1998). Since features of the environment shape many facets of an individual's behavior, changes to the environment will often lead to changes in behavior. Zebra mating systems and higher levels of sociality vary depending on the distribution and abundance of key resources. Much of today's environmental change is human induced and is large enough to disrupt normal behavior of animals. If behavioral repertoires are large enough, however, then coping is possible. If not, then human intervention is needed to restructure the environment in ways that either allow normal function to reappear (Curio, 1998), or that complement the new behavioral tendencies that emerge. In zebras both interventions can be effective. Removing barriers to predator dispersal reduced predator density. Normal plains zebra antipredator responses were then able to provide a level of protection sufficient for slightly higher predator intensity in an inherently arms-race driven system. Alternatively, not banishing Grevy's zebras from good grasslands or excluding them from watering points when livestock were present allowed zebras to adjust their feeding and ranging behavior in ways that have been fine-tuned by selection to be appropriate responses to normal levels of change associated with intra- and interspecific fluctuations in population density and community composition. It is clear that if nudged in the right direction and within normal ranges of facultative environmental responses, even endangered species can cope.

The ability to modify environments in ways that foster behavioral variants that allow individuals to cope with limited degrees of change requires an understanding of what species-specific features can change and why they change in the direction they do for specific alterations in the environment. Understanding the science behind coping is only part of the solution.

Understanding what motivates people to change and for what rewards, is equally important. Zebras sharing landscapes with people and their herds have shown that different landholders have different affinities for wildlife, yet all expect some return for sustaining their presence. For people to change, they also have to be engaged and empowered. Ultimately, conservation and management actions will only be sustainable if local communities believe in the goals of the project, among which is uncovering the rules linking behavioral change with environmental change and understanding the value of the emerging knowledge so that it can be put to profitable use.

APPENDIX. ZEBRA POPULATION PROJECTION MODEL

A two sex, age-structured, stochastic model was used to examine the demography of zebra populations inhabiting the dry lands of central Kenya. It is similar in form to a two-sex Leslie matrix model, except that it is modified to allow density dependence in survival and the recruitment rate—essentially the birth-rate of young horses—of particular populations. The model divides zebra populations into two sexes, each of which contains "n" age classes: infants (0–1), yearlings (1–2), two year olds (2–3), juvenile, and subadults (3–4) and so on through adults 8 years old and older which are combined into one class (8+). I assume that equal numbers of males and females are born in any year, so the model first determines the number of infants that might be born and dives them equally between the sexes. The number of young born in any year is ultimately determined by the

interaction between population density and rainfall since rainfall influences primary production. This linkage incorporates both density-dependence and environmental stochasticity into the populations' birth and survival rates.

The model also assumes that all females three years old and older are capable of reproducing. However, the proportion of 3 year olds bearing foals is a function of the density of zebras in the population; the proportion of all females producing offspring is made a function of density and rainfall in the current year. The functions describing changes in the age of first reproduction and the inter-birth interval are those most sensitive to changes in density; a third function—female survival—is also sensitive to density, but such changes are the last to be observed and the weighting in the model is reduced.

Density dependence is captured by examining the interaction between population density and the plant resources generated by rainfall by location in any year. The density-dependent function that determines age of first reproduction, or survival, is based on a simple two-parameter model widely used in studies of exploited populations (Hassell and May, 1985). It takes the form

$$F_1(N) = \frac{1}{\left(1 + [N/K]^b\right)}$$

where b determines the steepness of the slope with which fecundity in primaparous females declines as population size exceeds K, the density at which half the females in an age class reproduce. If $b > 1$ then fecundity drops off rapidly as population size exceeds K; in contrast if $b < 1$, fecundity declines more smoothly. Since the change in the age of first reproduction is virtually instantaneous, almost like a step function, we set this parameter to 5.

Allometric relationships can be used to determine K (Calder, 1984; Peters, 1984) such that

$$K = \frac{\text{Area} \times (10^{1.685 \times \log(\text{meanrain}) - 1.095})}{\text{Body weight}}.$$

In this equation "Area" is the size of the conservancy, ranch or region in km^2, "BodyWeight" is the mass of zebras (estimated to be 250 kg. for plains zebras and 450 kg. for Grevy's zebras) and "meanrain" is average long-term annual rainfall which in Laikipia and Sambure varies by location form 400 mm to 500 mm.

A second function couples more loosely the overall fecundity of all females in a population to rainfall in any year. This function can either be set as a constant which determines the proportion of females that produce surviving

foals at any density, or the model can allow rainfall to vary as a random variable around an observed mean. In the latter case, the interaction between rainfall and population density will determine the numbers of females that produce surviving young. The function takes the following form:

$$F_2 = \frac{(\text{rainfall}/0.5 \text{ meanrain})^{b2}}{\left(1 + (\text{rainfall}/0.5 \text{ meanrain})^{b2}\right)}.$$

Here "rainfall" is the rainfall in any calendar year and "meanrain" is again the long-term average rainfall at a particular location. The parameter $b2$ determines how rapidly fecundity declines in years with poor rainfall. $B2$ is set to 5 based on studies of feral horses that allowed the population to equilibrate at around the correct density and about the rate actually observed after a perturbation changed carrying capacity.

These equations adjust survival and fecundity estimates of zebra vital rates and allows for area specific forecasting of population growth under actual or hypothetical conditions. In this way, the model is a tool for examining "what if" scenarios as environmental conditions change.

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