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Game Cropping and Wildlife Conservation in Kenya: A Dynamic Simulation Model with Adaptive Control

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ABSTRACT

We use a dynamic stochastic simulation model of forage, herbivores, predators and domestic livestock in the Machakos District of Kenya to address policies related to the multiple use of rangeland resources. The particular policy examined is that of switching from a traditional system, where commercial ranchers do not harvest wildlife herbivores, to one where ranchers are provided economic incentives to adopt multiple-use management of the range resource. Simulations using an adaptive controller indicate that the effects of the policy change on wildlife populations depend on the conditions of the ecosystem and, importantly, on ranchers' attitudes to risk. When forage is abundant, and game and livestock do not compete for food, the policy change leads to reduced wildlife populations, especially of the relatively more valuable species. This indicates that game cropping may not be more compatible with nature conservation than standard pastoralist practices. However, in periods of drought when competition for forage occurs, the policy change may dampen the decline in game populations, as risk-averse ranchers may decide to sell more cattle and harvest wildlife instead. Game cropping reduces wildlife populations, but increases their stability.

INTRODUCTION

Wildlife conservation is the responsibility of the Kenya Wildlife Service (KWS), a government corporation attached to the Ministry of Tourism and Wildlife that is mandated for this role by the Wildlife Conservation and Management Act (1989). The goals of the Act are: to conserve the natural environments of Kenya, and its fauna and flora, for the benefit of present and future generations and as a world heritage; to use the wildlife resources of Kenya sustainably for the nation's economic development and for the benefit of the people living in wildlife areas; and to protect people and property from injury or damage by wildlife (KWS 1990). A lack of clear economic incentives has hampered efforts by the KWS to conserve wildlife on privately-owned rangelands. In the past, private land owners had exhibited a high degree of tolerance to conservation efforts, despite their having to bear the costs of wildlife protection—competition for forage and water, predation of livestock by carnivores (or costs to prevent predation), transmission of diseases to livestock by game animals and destruction of private property by game animals (KWS 1990). Potentially this policy was unsustainable as a preservation policy because private land owners cannot continue to subsidise national and international conservation efforts. Therefore, the KWS introduced policies that compensate owners for damages or permit private land owners to utilise game animals found on their land.

The purpose of this study is to develop a simulation model for examining alternative institutional arrangements and economic incentives for accomplishing the task of allocating range resources in a way that achieves the conservation goals of the Wildlife Conservation and Management Act, and leads to sustainable development of the local economy. We developed a dynamic stochastic simulation model with adaptive management of herbivores, predators and domestic livestock in the Machakos District of Kenya and used it to address policies related to the multiple use of rangeland resources. The purpose of the model was to provide insights into range economics and economic institutions; it was not intended to describe the range-herbivore ecology in all its richness and diversity. The results from the model do indicate, however, that dynamic analytical tools can be suitably applied to gain insights into multiple-use resource allocation and policy analysis problems that face wildlife conservationists and range managers.

With the dynamic stochastic simulation model, the implications of a switch from a traditional pastoral regime to game cropping are analysed. It has been argued in the economics literature that switching to game cropping might contribute to both wildlife conservation and alleviation of poverty and hunger (MacNab, 1993; Sommerlatte & Hopcraft, 1992). According to our dynamic adaptive-management model in which, for instance, non-use benefits and potential revenues from safari-tourism are disregarded, this claim is not necessarily correct.

We proceed in the next section by considering in greater detail the components of the system to be modeled. We use existing data to develop a simulation model of the interactions among plant and animal species. The adaptive controller used in the model is also described. Then the model is used to explore the effects of different policies on wildlife populations and a ranch's economic returns. The conclusions ensue.

METHODS

Range management is concerned with the synthesis and use of information relating to the structure and function of the rangeland ecosystem, to provide information concerning what is physically and biologically possible (technical feasibility), and the application of economics to ranch management decisions where the ranch is viewed as a business. In addition to profit, the objectives of ranch management (ranching operations) are to achieve an equilibrium between animal numbers, on the one hand, and ranch forage and water resources, on the other, coupled with maintenance or improvement of range condition (Pratt & Gwynne, 1977). To achieve these objectives, ranch managers use the technical tools of range management and development, namely, grazing management, improvement of range vegetation (range forage) and techniques of water development.

In the context of the management of private commercial ranches, the KWS's new wildlife conservation policy, which involves economic exploitation of wildlife on privately-owned ranches, translates into a multiple-use approach to resource allocation between wildlife and livestock, which inevitably gives rise to the conflicts mentioned above. Fortunately, these conflicts are not serious enough to rule out the compatibility of livestock production and wildlife conservation, as has been demonstrated by pastoralists who have historically operated their livestock in coexistence with wildlife (International Livestock Centre for Africa, 1978). Thus, combining wildlife conservation and livestock production enterprises is technically possible and a pragmatic way of attaining wildlife conservation on privately-owned rangelands; in fact, at compatible population levels, grazing both livestock and game animals may actually increase the rangeland carrying capacity (International Livestock Centre for Africa, 1978). The multiple-use approach to commercial ranching in Kenya implies production and management of:

(1) the vegetation forage resource base;
(2) wildlife; and
(3) livestock.

The current study focuses on a 73 000-ha area in Machakos district, Kenya, that is comprised of twelve ranches looking to adopt game cropping alongside livestock operations. This region has a mean annual rainfall of 510 mm. Typical vegetation is wooded or tree grassland savanna, dominated by *Themeda-Acacia or Themeda-Balanites* wooded grassland (Sommerlatte & Hopcraft, 1992). This vegetation type occupies basement and volcanic soils and, under grumosolic soils of impeded drainage, *Acacia drepanolobium* wooded grassland vegetation type dominates. The district has a wide variety of plains game, with the key species being Thompson's gazelle (*Gazelle thomsoni*), Grant's gazelle (*Gazelle granti*), Coke's hartebeest or kongoni (*Alcelaphus buselaphus*), wildebeest (*Connochaetes taurinus*), giraffe (*Giraffa camelopardalis*) and impala (*Aepyceros melampus*), all of which are grazers except the latter two (Sommerlatte & Hopcraft, 1992). The main livestock species are beef cattle, sheep and goats, although some ranches have concentrated solely on cattle.

The carrying capacity of the range is fairly high, with less than 4 ha required to sustain one livestock unit. Controlled burning is an integral management practice to prevent encroachment of woody species, and to enable some of the smaller and more palatable grasses to persist in competition with the taller species which tend to become rank and unpalatable as they mature (Pratt & Gwynne, 1977). We assume a level of range management that keeps the balance among the various grass species, and between grasses and woody species, relatively constant in the face of grazing pressure (especially by cattle) and drought, the combination of which tends to increase wood plants (browse) and less palatable grass species (Cook & Stubbendieck, 1986). This assumption is mainly one of convenience because then the interactions between plants and herbivores do not need to be completely modelled. Existing ecological models of interactions across different trophic levels are still far from perfect.

Trees and shrub provide browse and shelter to wild animals, but individual tree and shrub species vary in their productivity and in their value to different animal species. There are a number of techniques for determining browse biomass (Cook & Stubbendieck, 1986) but a pragmatic way of quantifying biomass is to use total canopy biomass per unit area as a proxy for the browse biomass state variable. Grass forage is the other component of vegetation forage resources and the main diet for the grazing herbivores. The major grass species in the area of focus is *Themeda triadra*, also called red oat grass, which is a tufted perennial with a height range of 50–150 cm (Pratt & Gwynne, 1977). Herbage biomass is defined as the weight of total aerial parts of herbs (or non-woody plants including grass), individually and collectively, and is one of the most important characteristics of range vegetation and possibly the best single measure of growth; it is adopted in this study as a suitable proxy for grass forage biomass. Techniques for determining herbage biomass include direct methods, such as clipping, and indirect methods, such as using precipitation as an index for herbage production (Cook & Stubbendieck, 1986).

Letting F_{it} be the total biomass at time t (i = browse, herbage), inter-seasonal change in F_i is stipulated to be a function of new growth net of decay, or the intrinsic growth rate g_i, and of the biomass itself, subject to a maximum sustainable herbage biomass carrying capacity K_i, which is a function of the environment and site productivity potential. Both herbage and browse plant species grow in interspersion with each other on the same area of land, with some interactive competition. Moreover, both forage resources are affected by the herbivores H_m ($m = 1,..,n$) which are discussed below. Herbivores impact the intrinsic growth rate of forage and reduce the biomass carry-over from one year to the next. The forage relations can be depicted as a modified logistic growth function:

$$F_{i,t+1} - F_{it} = \left(g_i - \sum_{m=1}^{n} \alpha_{im} H_{mt}\right) F_{it} \left(1 - \frac{F_{it} + \beta_j F_{jt}}{K_i}\right) - \sum_{m=1}^{n} \omega_{im} H_{mt} \qquad (1)$$

In this equation $\alpha_{i\,m}$ is a parameter capturing the effect that herbivore m has on the growth rate of F_i; β_j is the herbage-browse plant species competition coefficient; $\omega_{i\,m}$ is the consumption rate of forage species i by herbivore m; and i and j ($i \neq j$) denote the forage species, canopy browse and herbage.

In (eqn 1), we subtract from the intrinsic growth rate a term that reflects the impact of the herbivores. While grazing lowers the intrinsic growth rate of the 'decreasers' ($\alpha_{im} > 0$), it might have a positive effect on the growth rate of some other species ($\alpha_{im} < 0$) (see Dyksterhuis, 1949). The overall effect will vary by species of herbivore, but we would expect that, in general, it would be negative. An increase in the biomass of j will reduce the biomass of i available in the next period. The 'biomass competition term', $\beta_j F_{jt}$, thus acts as a brake on next year's population, just as a larger population of the species in question does in the logistics growth equation. In this model, however, range management (e.g. burning) is assumed to maintain a constant canopy ratio and constant proportion among herb species, so that $\beta_j = 0$. Finally, we subtract from the forage equation the amount of forage eaten by the herbivores.

GAME ANIMALS, PREDATORS AND LIVESTOCK

Since the dominant component of vegetation is grass, the majority of game animal species in this area are grazers. The key species are Thompson's gazelle (Th), Grant's gazelle (Gr), kongoni (Ko), and wildebeest (Wb); giraffe (Gi), a principal browser, and impala (Im), a mixed feeder, are also found in this area. From a sample of seven stomach contents, food partition in impala was found to be 56% grass and 44% browse (Talbot & Talbot, 1961). In addition, there are resident predators, the major ones being cheetah (*Acinonyx jubatus*), hyena (*Crocuta crocuta*), jackal (*Canis spp.*), and, occasionally, predators such as lions (*Panthera leo*) and wild dog (*Lycaon pictus*) (Sommerlatte & Hopcraft, 1992). Jackals are chiefly predators of small mammals and insects, and are not relevant for the current study, while lions are irregular to the area and are also not explicitly modeled. The foci of predation are only hyena (Hy) and cheetah (Ch). The dominant prey species for hyenas are wildebeest and kongoni while, for cheetah, they are impalas, G. gazelles, T. gazelles and kongoni (Moss, 1982).

The general equations describing the population dynamics for the herbivores are as follows:

$$H_{i,t+1} - H_{it} = \left(g_i - \sum_{k=1}^{s} b_{ik} Y_{kt} + \sum_{r=1}^{q} c_{ir} F_{rt}\right) H_{it} \left(1 - \frac{H_{it} + \sum_{j=1}^{n} \alpha_{ij} H_{jt}}{K_i}\right) - \sum_{k=1}^{s} d_{ik} Y_{kt} \qquad (2)$$

where H_i refers to herbivore species i (of which there are n); g_i is the intrinsic growth rate for species i; K_i is the carrying capacity of the ecosystem for species i in the absence of any other species; H_j refers to herbivore species j that competes with i for forage ($i \neq j$); and parameters a_{ij} (>0) are bionomic competition factors, such that $\sum_j a_{ij} H_j$ is the cumulative effect that the presence of other herbivores has on next period's population of species i.

A herbivore species' intrinsic growth rate is modified by the negative effect of predation and the positive effect of increased forage. Y_k refers to the kth predator species of which there are s ($=2$), while b_{ik} (>0) ($i \neq k$) are predation parameters, such that $\sum_k b_{ik} Y_k$ is the cumulative effect of predator abundance (or lack thereof) on the growth rate of herbivore i. F_r refers to forage species r, of which there are two (r = browse, grass); most herbivores consume either browse or grass, except impala which is a mixed feeder. Parameters c_{ir} (>0) ($i \neq r$) are forage parameters which, together with forage availability, describe the effect of forage on the growth rate of herbivore i.

The final term in (eqn 2) represents the number of animals taken by predators, with d_{ik} (>0) being the predation parameter or the amount of prey i that is taken by predator k.

Likewise, the population dynamics of the predators depend on their intrinsic growth rates and the availability of prey. The general functional form is:

$$Y_{i,t+1} - Y_{it} = \left(g_i + \sum_{k=1}^{n} \delta_{ik} H_{kt} \right) Y_{it} \left(1 - \frac{Y_{it} + \theta_{ij} Y_{jt}}{K_i} \right) \qquad (3)$$

where g_i refers to the intrinsic growth rate of predator i and K_i is the carrying capacity for predator i. The intrinsic growth rate is positively affected by the availability of herbivores, with parameter δ_{ik} (>0) determining the effect of herbivore k on the growth of predator i. The ultimate population of one predator species is determined by the numbers of the other predator and their interaction parameter θ_{ij} (>0) (i,j = cheetah, hyena).

Unless commercial utilisation of game animals is permitted, livestock production is the sole economic base for commercial ranches. There are three main livestock species (beef cattle, mutton sheep and meat goats), but ranches generally produce either cattle only, or cattle in combination with sheep and/or goats. The focus in this study is on a cattle operation only. The beef cattle (Ca) enterprise is concerned with the production of slaughter stock, although milk production in excess of that required by calves is a by-product of beef production and of secondary commercial importance. (Also important, but less so in commercial ranching enterprises, are draft power from cattle and reclamation of some of the meat of animals that have died.) Calving tends to be continuous but there are identifiable peaks coinciding with the rainy season; with good management, a calving rate of up to 90% is attainable, while one below 70% is indicative of poor management (Pratt & Gwynne, 1977).

Theoretically, the population dynamics for cattle are similar to those of the herbivores as represented in equation (eqn 2). Cattle compete with herbivores for grass forage and occasionally consume browse: in some cases, there is complementarity between wildlife grazing and cattle. The essential difference, however, lies with management. Cattle are regularly culled and management results in high calving rates and low mortality rates; for example, cattle are usually corralled at night. Logically, there is a limit to the number of cattle that can occupy the range, even in the absence of other herbivores, with wild herbivores generally serving to reduce the forage available to the cattle.

MODELING INTERACTIONS AMONG ANIMAL AND PLANT SPECIES

For the study region, there is little direct information about the interactions among the various wildlife and domestic animal species (herbivores and predators), and within the herbivory. Also lacking is quantitative knowledge about the dynamics of the various animal populations and plant species. These shortcomings are severe impediments for validating any simulation model for this region. Therefore, the initial task is to develop the required interactions and dynamics. The means for accomplishing this task is through a computer simulation model that relies on existing data from other areas on various individual components of the ecosystem—forage, herbivores and predators—and intimate first-hand knowledge of the range ecosystem in the study region. The population dynamics for forage are modeled as in equation (1), but the wildlife population dynamics are modeled using information on births and mortality, forage requirements by herbivores and kills by predators, although the basic interactions described in equations (2) and (3) remain. The model is stochastic because calving and mortality rates are randomly determined, with feedback constraints to prevent populations from rising or falling indefinitely [as in (eqn 2) and (eqn 3)]. The model is of a representative 8 100-hectare cattle ranch.

In the analysis, we rely on a range ecosystem that has a 20% canopy (80% grass, 20% browse) as a result of management, one domestic livestock species (cattle), six wildlife herbivores (giraffe, impala, G. gazelle, T. gazelle, kongoni and wildebeest) and two predators (cheetah and hyena). The interactions among species are illustrated in Fig. 1, which also serves as the

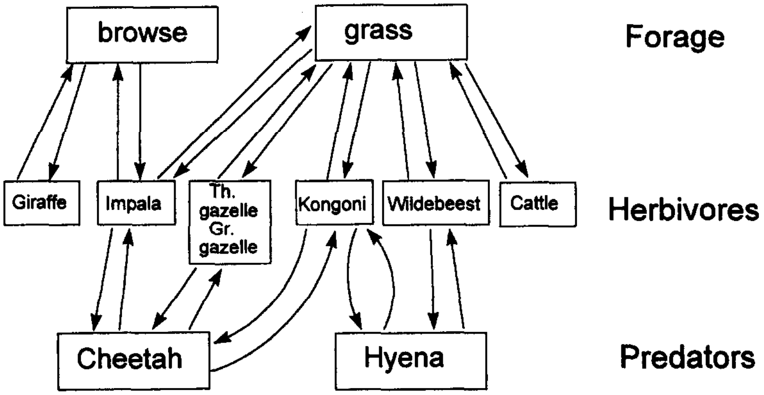

Fig. 1. The herbivory ecosystem consists of forage, herbivores and predators. The arrows indicate the links with an upward arrow indicating that the species feeds on the species to which the arrow is drawn, while a downward arrow indicates the feedback that density/availability of the species has on the growth of the feeder.

framework for the simulation model described below. First, each of the components of the ecosystem is considered followed by a more detailed description of the simulation model.

Data on browse and forage are available from a Zimbabwian study that investigated production of biomass in the absence of foraging (Kelly & Walker, 1976). The current study region is slightly drier than the area in Zimbabwe upon which the data are based, and for that reason the estimated carrying capacities for browse and grass were reduced by 10%. Further, range management is assumed to keep canopy cover at 20%, so that browse and grass forage growth are independent. With these adjustments and using the logistic functional form, data from Kelly and Walker (1976) were used to estimate the browse (B) and grass (G) biomass equations. From non-linear least squares estimation, the parameter of the growth rate was statistically significant at the 1% level. Adjusting the carrying capacities as described above, the browse and grass biomass equations on a per hectare basis are:

$$B_{t+1} - B_t = 0.\cdot 2427\, B_t(1 - B_t/6\,000)$$

$$G_{t+1} - G_t = 1.\cdot 1791\, G_t(1 - G_t/25\,000)$$

where the respective carrying capacities equal 6000 and 25 000 kg of dry matter per ha. Maximum sustained yield stocks of browse and grass are 3000 and 12 500 kg, respectively, while maximum sustained yields for forage outputs are 364 kg/ha and 7370 kg/ha for browse and grass.

The carrying capacity of the range depends, among other things, on climate conditions. In periods of drought, less browse and herbs will be available. Arbitrarily, we assume that a severe drought can be represented by a fallback in biomass of 90%. The effect of policy change on wildlife populations will be simulated under both conditions. In our simulation model, drought occurs randomly, with its effect lasting up to three periods.

Cross-section data are available for seven species of herbivores for Kenya's Kajiado district (Grunblatt, Said & Mutira, 1989), which is adjacent to the study area. Population estimates and standard deviations for the six wildlife species and cattle are provided in columns (1) and (2) of Table 1. (No information is available on the variance-covariance matrix of animal populations.) The data are based on 54 flown transects covering an area of 1156·31 square kilometers (km^2), and extended to the entire Kajiado district's 21 851·59 km^2. Sampling took place between 12 March and 26 March 1987. Assuming that species are evenly distributed across the landscape, the expected number of each species that might be found on the 8100 ha ranch are provided in column (3) of Table 1. Lacking better data for the study region, we use these figures for validation purposes in the next section.

Mortality rates for each of the herbivore species are provided in Table 2, while calving rates are found in Table 3 (Moss, 1975). While calving for most species occurs only at the adult stage, calving does occur in the 2–3 year old age category for kongoni and wildebeest, but at only half the rate of adults. Mortality rates are only available for adults and for birth to adult, so extrapolation was used to determine mortality in other age categories. In addition to calving and mortality rates, the assumed standard deviations of these rates are provided in Tables 2 and 3. The standard deviations are used in the simulation model described below. Finally, animal weights by age category are provided in Table 3.

Using data on mortality rates and food consumption (including wastage) for the Serengeti ecosystem in Tanzania (Moss, 1982; Houston, 1979), and estimates of food availability on the ranch, it is possible to estimate the numbers of hyena and cheetah that one might expect to find on the ranch. On average, female hyenas produce a litter of two cubs every 18 months (cubbing rate of 133% per year); infant mortality (to adulthood) is 60%, while that of adults is 7%. Adult hyenas average 57 kilograms (kg) and consume 1095 kg of prey per annum, consisting primarily of non-adult wildebeest and kongoni. Female cheetah produce two offspring per year, infant mortality is 43% and adult mortality is 5.5%. Adult cheetah weigh about 54·5 kg and consume 3650 kg of prey (of which more than 12% is wasted).

Calculations based on Leslie matrices (described below) enable us to determine the numbers of herbivores in each of the age categories (Tables 2 and 3). Along with data on animal weights (Table 2), it is possible to determine the total meat available to the two predators. For the total area of the ranch, we estimate initial predator populations of 0·4 cheetah and 1·9 hyena for the prey populations and animal weights from Tables 1 and 2.

TABLE 1

Herbivore Survey Population Estimates and Simulated Population Estimate: Kajiado District, Kenya

Species	*(1) Population estimate*	*(2) Population s.d.*	*(3) Ranch (census) population*	*(4) Simulated ranch population*	*(5) Simulated as % of census population*
Cattle	475 769	39 981	1800	2500	138·9
Giraffe	5 820	805	21	15	71·4
Thompson's gazelle	8 712	3105	32	20	62·5
Grant's gazelle	19 502	2290	72	50	69·4
Kongoni	2230	687	8	8	100·0
Impala	10 375	2277	38	25	78·1
Wildebeest	22 791	6574	84	80	95·2

Source: Cols 1 and 2, Grunblatt, Said & Mutira (1989); Cols 3–5, by calculation.

ECOLOGICAL SIMULATION MODEL

Stochastic simulation is used to model the interactions among plant species, herbivores and predators over time. An outline of the simulation model is found in Figs 1 and 2. Giraffe consume only browse and are assumed to have no predators. Impala consume browse (44%) and grass (56%). All other wildlife species and cattle are grazers. Mortality rates for cattle are low as a result of management (e.g. cattle are placed in pens at night).

The population dynamics are modeled using Leslie matrices (Leslie, 1945, 1948; Pollard, 1966; Usher, 1972; Mendelssohn, 1976), as opposed to the logistics equations (2) and (3), because estimates of the parameters (especially for the interactive terms) in these equations are unavailable due to lack of data. Except for functional form and stochasticity, however, (eqn 2) and

TABLE 2
Mortality Rates and Body Weights by Age for Herbivores and Predators

Species	*Item*	*Age category*						
		0–1	*1–2*	*2–3*	*3–4*	*4–5*	*5–6*	*Adult*
Giraffe	mortality	0·350	0·250	0·220	0·180	0·150	0·12	0·070
	s.d.	0·075	0·075	0·050	0·050	0·050	0·05	0·025
	weight (kg)	124	238	352	466	580	694	750
Thompson's gazelle	mortality	0·600	0·330	—	—	—	—	0·150
	s.d.	0·075	0·050	—	—	—	—	0·045
	weight (kg)	4	18	—	—	—	—	23
Grant's gazelle	mortality	0·500	0·300	—	—	—	—	0·150
	s.d.	0·075	0·050	—	—	—	—	0·045
	weight (kg)	10	47	—	—	—	—	62
Kongoni	mortality	0·750	0·550	0·250	—	—	—	0·090
	s.d.	0·075	0·075	0·050	—	—	—	0·025
	weight (kg)	31	83	138	—	—	—	166
Impala	mortality	0·600	0·190	—	—	—	—	0·120
	s.d.	0·075	0·050	—	—	—	—	0·025
	weight (kg)	10	38	—	—	—	—	50
Wildebeest	mortality	0·650	0·450	0·200	—	—	—	0·150
	s.d.	0·075	0·075	0·050	—	—	—	0·025
	weight (kg)	31	93	155	—	—	—	185
Cattle	mortality	0·050	0·042	0·034	—	—	—	0·030
	s.d.	0·015	0·015	0·010	—	—	—	0·010
	weight (kg)	73	171	269	—	—	—	185
Cheetah	mortality	0·196	0·196	—	—	—	—	0·055
	s.d.	0·075	0·075	—	—	—	—	0·015
	weight (kg)	—	20	—	—	—	—	55
Hyena	mortality	0·265	0·265	—	—	—	—	0·070
	s.d.	0·005	0·005	—	—	—	—	0·045
	weight (kg)	—	22	—	—	—	—	57

Source: Arnold & Sanchez-Orozco (1989); Moss (1982); Houston (1979); Kenya Rangeland Ecological Monitoring Unit (1979); Bertram (1979); Pratt & Gwynne (1977).

TABLE 3
Birth Rates for Herbivores and Predators

Species	*Birth rate*[a]	*Calving rate (s.d.)*
Giraffe	0·60	0·05
Thompson's gazelle	1·50	0·05
Grant's gazelle	1·05	0·05
Kongoni	0·90	0·05
Impala	0·95	0·05
Wildebeest	0·90	0·05
Cattle	0·80	0·015
Cheetah	2·00	0·05
Hyena	1·33	0·05

Source: Arnold and Sanchez-Orozco (1989); Moss (1982); Bertram (1979); Pratt and Gwynne (1977).

[a] Calving rates are for females. For both Kongoni and Wildebeest, the calving rate is 45% for females in the 2–3 year age category and 90% for adults. Only the latter is reported in the table. The s.d. of the calving rate is the same for both adult females and females in the 2–3 year category.

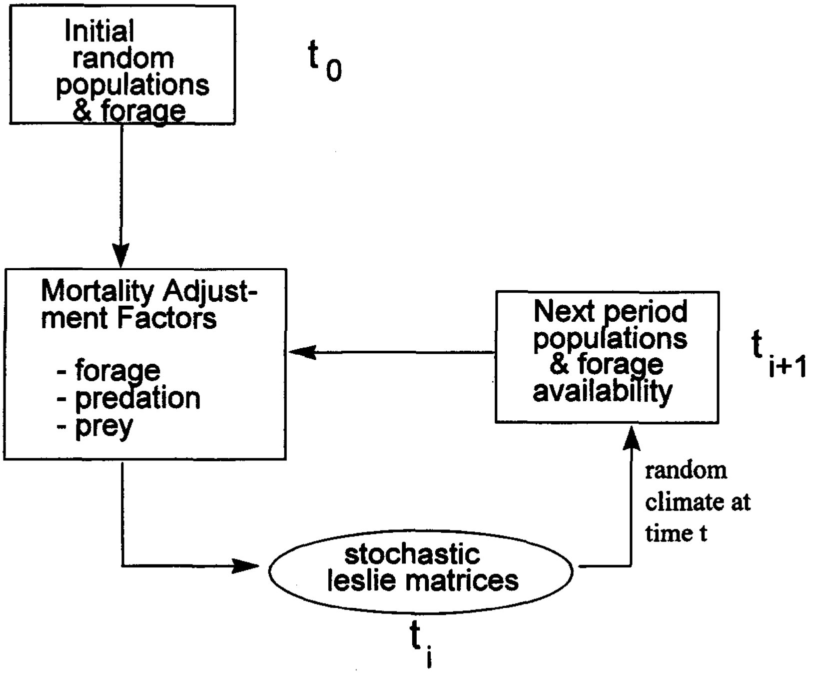

Fig. 2. Herbivore–Predation Dynamics. Initial forage availability and age-distributed wildlife populations are determined and then used to calculate the mortality adjustment factors that, in turn, determine the actual elements of the Leslie matrices. The Leslie matrices move the wildlife populations at a given time *t* to the next period, while consumption by herbivores and random climate determine next period's forage availability. The process then repeats.

(eqn 3) are still indicative of how the system is modeled. For each wildlife species, a Leslie matrix transforms the age-distribution of animals from one year to the next. New births are determined as the number of adults (or near-adults in the case of kongoni and wildebeest) multiplied by the calving rate divided by two (since only females bear offspring). The number of animals in the second age category is determined by the number of offspring in the previous year adjusted for mortality. Likewise, the numbers at year $t+1$ in the third, fourth and other age categories before adulthood are determined by the number at year t in the preceding age category adjusted for mortality. Finally, the number of adults at year $t+1$ is given by the number of adults at year t plus the number at year t in the age category preceding adulthood, both adjusted for mortality (Table 2).

As reported, mortality rates already assume some predation, including by other predators. For example, although giraffes are not explicitly preyed upon in the model, they are clearly subject to predation. Further, there are predators other than hyena and cheetah, and these also prey on species (and sizes) other than those indicated. However, these forms of predation are already considered in the values of the unadjusted mortality rates. The current model only considers deviations in the mortality rates.

Likewise, it is assumed that herbivores have access to 'normal' levels of plant nutrients, and predators to an adequate population of prey. However, if there are too many herbivores, there will eventually be a reduction in the amount of forage available to all of the animals and, as well, there is likely to be a greater population of cheetah and hyena. Both these factors will serve to reduce the number of herbivores and thereby increase plant biomass and reduce the numbers of predators. These feedback effects are all made through adjustments in the mortality rates of the herbivores and predators. That is, since mortality rates include 'normal' conditions of herbivore competition and predation, increased numbers of herbivores and/or predators will increase mortality rates and eventually reduce herbivore population levels; reductions in the populations of herbivores of the pre-adult age categories will lead to a reduction in the numbers of predators. The response of the plant species is given by the estimated browse and grass equations, minus the forage consumed by the animals of the herbivory. This adjustment is accomplished by multiplying the numbers of animals in each age category of each species by their respective weights and by 9·125 (2·5% of body weight consumed per day for 365 days), and then summing the appropriate totals, keeping in mind that giraffe consume only browse and impala consume 44% browse and the remainder grass.

Herbivore mortality rates were adjusted for higher and lower levels of forage availability by multiplying by an adjusted ratio of consumption to forage availability. The ratio is adjusted so that it has a value of 1 when consumption is one-half or less of available biomass, a value of 2 when consumption equals available biomass, and an exponential function when consumption exceeds available biomass. This is referred to as the *forage factor*. The effect of increased predation on mortality rates is taken into account by multiplying the mortality rate by the ratio of predators at time *t* to the normal number of predators (1·9 hyena and 0·4 cheetah)—this is the *predation factor*. A limiting mortality rate of 95% for all age categories was arbitrarily chosen to prevent a species from becoming extinct during the simulations. Extinction on the ranch cannot occur in isolation because eventually wild animals from elsewhere will migrate to the vacated niche.

The mortality adjustment factor of predators is determined as the ratio of the available amount of food in the base year to the weight of the food available in the current year. Thus, if herbivore populations (except cattle and giraffe) increase above the original level, the adjustment factor is less than 1·0 and mortality of predators falls. If populations are smaller, the adjustment factor increases the predator mortality rate. This adjustment factor is referred to as the *prey factor*.

The simulation model is depicted in Fig. 2 and begins by randomly choosing starting wildlife herbivore populations using the means and standard deviations in columns (1) and (2) of Table 2 and assuming independently distributed, normal distributions for each species. The initial starting values are then adjusted to fit the 8100 ha ranch. For cattle the starting population is set at 2000 head, which is the current herd size for an average ranch located in Machakos district. Initial populations of hyena and cheetah are assumed to be 1·9 and 0·4 animals, respectively. (Since animals are not confined to the ranch but move about in a region with similar characteristics, a fraction of an animal simply refers to the proportion of the year that an animal can be expected on the ranch.) Population is distributed over the age categories by dividing by the number of age categories above one year (animals younger than 1 year were assumed not to be visible during the survey), while the population in the first age category is determined as a random function of the calving rate. Initial browse and grass biomass are assumed to be at a level that produces enough biomass for the animals on the range. Using the average ranch populations indicated in column 3 of Table 1 and average animal weights (Table 4), and recalling that canopy is maintained at 20% by prescribed burning, the stock of browse would be 5938 kg/ha, while that of grass 24 543 kg/ha.

The next time period's browse and grass biomass are determined from the estimated logistic equations (in the absence of interaction), minus that consumed by the herbivores (as described above); the forage mortality adjustments (forage factors) are also calculated. The predation factors are initially 1·0, as is the prey factor that adjusts the mortality of the predators. In the

Leslie matrices, mortality rates are randomly chosen in each period from univariate normal distributions with means and standard deviations as reported in Table 2 and Table 3, and then adjusted by the forage, predation and prey factors, as applicable. Each vector of age-animal numbers is post-multiplied by its Leslie matrix to obtain the following period's distribution of animals across age categories. The forage requirements and mortality adjustment factors are calculated and the process repeats until the simulation is halted. In the current analysis, 90 time periods are simulated.

As indicated above, validation of a simulation model generally requires a comparison of model output with real-world, usually historical, data. Given that such data are unavailable, we approach validation in two ways. First, we compare the steady-state simulated populations (column 4 of Table 1) with the expected ranch population based on census data (column 3). Simulated population as a proportion of the census population is provided in column 5 of Table 1; it indicates that the model tends to (slightly) under-estimate actual populations—the model simulates actual output fairly well, except for the two gazelle species, which seem to be under-represented in the model. Discrepancies between the census and simulated populations are the result of the randomly chosen starting population values (average population levels vary considerably under different model runs), the model's structure (including the actual parameters used) and the different ecology for the simulated study region compared to that of the regions from which the data were taken.

A second approach to validating the model consists of examining whether the deterministic version of the model results in wildlife populations that are stable over time. If populations are stable, then the model can be used to investigate the effects of natural and human disturbances (e.g. droughts, harvests, movements away from average rates of growth, birth or predation, etc.).

TABLE 4

Net Prices Per Animal, Effort and Production Parameter Values, Machakos District, Kenya

Species	*(1) Mean weight (kg)*	*(2) Net price (KS)*	*(3) Time per animal (min.)*	*(4) Effort*	*(5) Production parameter (ϕ)*
Thompson's. gazelle	17	66	127·75[a]	1	0·0309
Grant's gazelle	48	192	148·60	2·362	0·0059
Wildebeest	141	564	218·53	6·951	0·0017
Kongoni	128	512	208·76	6·295	0·0192
Impala	3	145	133·50[a]	1·377	0·0189
Giraffe	582	2328	550·16	28·721	0·0016
Cattle	255	798	—	0	—

[a] These are actual times; computed times are 124·93 min for Thompson's gazelle and 139·75 min for impala.

The population of a particular wildlife species is stable in this model if, in the absence of disturbance, it stays at some constant level over time (not deviating from that level except perhaps by very small amounts). If only the starting populations are chosen randomly, but growth rates are non-random, the current model traces out a stable system with unchanging populations—population levels of each of the species remain the same over the 90–year time horizon in this model. Again we conclude that the model is not invalidated by this approach. In the stochastic model developed next, stability may imply something different (e.g. the ability of animal populations to recover after disturbances and shocks).

SIMULATION OF WILDLIFE HARVEST AND CATTLE PRODUCTION: ECONOMICS AND ADAPTIVE CONTROL

One approach to the study of policy implementation is to develop an optimal control model and assume a steady state solution (Conrad & Clark, 1987). The objective would be to maximise the discounted net returns from the sale of cattle and harvest of wildlife, subject to the system dynamics given by equations (1–3). Policy options could be modeled as restrictions on harvests or as penalties/subsidies on decisions, such as cattle sold or harvests of wildlife. However, as noted earlier, there is too little information to estimate the parameters of the logistic equations (1–3). This may not be a drawback since our focus is on predicting the effect of a policy change, rather than optimising in a normative sense; indeed, adaptive control as opposed to optimal control may be more consistent with actual behaviour in the stochastic framework modeled here. Therefore, to include the economics of wildlife management, an adaptive controller or economic simulation model is attached to the ecological model as an integrated component, but one that is only triggered if one wishes to examine the impacts on the system of permitting ranchers to harvest wildlife. The economics component has the same time step as the ecological model and is described below.

The wildlife production parameters (ϕ) relate harvest levels to effort and wildlife population. A semi-log linear functional form (so that elasticities of harvest with respect to effort and population equal to 1·0) is used:

$$h_{it} = \phi_i E_{it} X_{it}, \tag{4}$$

where h_{it} is the harvest of species i at time t, ϕ_i is the production parameter for species i, E_{it} is labour effort (valued in Kenyan shilling) devoted to the harvest of species i at time t, and X_{it} is the population of species i at time t. In each period, the harvest of each of the species needs to be subtracted in the overall model to determine the next period's stock.

Modeling effort devoted to game cropping under conditions of imperfect information necessarily involves some arbitrary assumptions. We assume that effort is a multiplicative function of the price of game (per species) and the size of the current population relative to the five-year moving average population size: if game cropping is not allowed (such that the price of wildlife is set at zero) or wildlife populations are falling, no exploitation takes place. The latter assumption implies that the model is biased towards sustainable exploitation, and does not necessarily aim to maximise net present value of land use.

For cattle, the enterprise operates as follows. Standard management principles are that, every year, the enterprise sells 85% of the cattle at age three as live animals, with 15% retained as replacement stock. However, the possibility of future benefits of game cropping may persuade the rancher to sell a greater share of the cattle stock, thereby reducing competition for forage between game and cattle. The adaptive rule used here is that the rancher decides to sell the standard proportion, plus a possible extra quantity. The rancher will only sell extra cattle if the expected utility of doing so is greater than the expected utility of the standard practice. Expected utility is a function of expected revenues and the stability of expected revenues (as measured by variance of revenues). Under stochastic climate and other factors affecting the herbivory, a trade-off exists between expected revenues and stability. Game cropping can increase expected revenues and/or contribute to stabilising revenue. The trade-off is modeled as follows. Based on personal preferences with respect to risk, the rancher will choose a threshold for allowable competition for forage between cattle and game. The stronger the preference for stable revenues (i.e. the greater the rancher's risk aversion), the lower will be this threshold. If actual competition exceeds this threshold because of a drought, say, the rancher will sell an extra number of cattle to facilitate future wildlife harvesting and avoid the risk of a sudden fodder shortage if climate conditions turn unfavourable. This extra quantity is determined by a multiplicative rule, with a competition index and the price ratio of game meat and beef as arguments. The more intense competition for food between cattle and game, or the higher the price ratio (the average price of game divided by the price of beef), the more cattle are sold. This implies that if the actual rate of competition is lower than the threshold, or if the price ratio equals zero (as under past policy), the rancher resorts to standard practice, aiming at maintaining his cattle stock at approximately 2000 head. We discuss the implications of risk attitude in the next section.

The gross price of live animals offered for sale and of game meat sales is the price offered at the ranch gate. This price is gross because it includes various annual ranch operating costs which include annual depreciation on capital investments in ranch buildings, fencing, vehicles, roads, water development and long-term range improvements; direct cash expenses on livestock feeds, livestock disease control and marketing expenses; and imputed interest on all cash costs. Apart from depreciation on water development, which is jointly shared by game animals and livestock, and depreciation on wildlife slaughter facilities which is specific to game animals, all other expenses are allocated to livestock. These costs are divided by annual sale weight (kg) of game and livestock, respectively, to arrive at cost per kg. The cost per kg is then netted out of the gross sale price to yield net sale price per kg, P. Hunting and game meat processing labour is categorised as effort, E, expended in harvesting game animal resources in 'worker day equivalents' and priced at w, with w determined as the wage for hunting, slaughtering and preparing a Thompson's gazelle carcass. Annual net revenue for the ranching system is as follows:

$$\begin{aligned} NR = {} & P_{Gi}h_{Gi} + P_{Th}h_{Th} + P_{Gr}h_{Gr} + P_{Im}h_{Im} + P_{Wb}h_{Wb} + P_{Ko}h_{Ko} \\ & - W(E_{Gi} + E_{Th} + E_{Gr} + E_{Im} + E_{Wb} + E_{Ko}) + P_{Ca}S_{Ca} \end{aligned} \tag{5}$$

where the subscripts on prices refer to the species, h refers to harvest, E to effort, S_{Ca} to sales of cattle and w is the wage rate (see below).

Data on effort or labour required to harvest and prepare meat from wild animals are derived from cropping studies done at Kekopey ranch, Kenya (Arnold & Sanchez-Orozco, 1989). It is assumed that harvest times are the same for most game species of interest. Variation in labour requirements applies to carcass processing time, which averages 15·25 and 21 minutes for Thompson's gazelle and impala, respectively. Processing time is, therefore, a convenient basis for defining effort. Thompson gazelle, being the smallest animal, has a processing time of 15·25 minutes, and is adopted as the reference point for the effort index E. In this respect, one impala requires 1·377 (=21÷15·25) units of effort. The wage rate for one unit of effort, defined as the time required to hunt, kill and prepare a Thompson's gazelle carcass, is computed to be 30·90 Kenya shillings (KS). If hunting effort is assumed to be the same for all species, the effort required for other species varies according to processing time only.

For the other game animals, effort requirements (i.e. processing times) are inferred on the basis of their weight as follows. The average processing time per kg of gazelle is 0·923 minutes, while that for impala is 0·580 minutes (Arnold & Sanchez-Orozco, 1989). The average time is 0·752 minutes per kg. The processing times for the other game animals are calculated by multiplying their respective average weight by 0·752. Total time per animal is obtained by adding to this time the common hunting time (112·5 minutes). The effort index is obtained by dividing these times by that of the Thompson's gazelle. Finally, the production parameters ϕ_i adjust harvests to take into account relative abundance or scarcity of game, and the difficulty of stalking one species vs another. The production parameters (col. 5, Table 4) are calculated by solving equation (4) for ϕ_i using actual harvest data at the Kekopey ranch (Arnold & Sanchez-Orozco, 1989), the estimated ranch populations (col. 3, Table 1), and our values for effort (col. 4, Table 4). For convenience, the production parameters are assumed constant in our model.

The net prices per animal were computed from net income data (essentially returns to land) provided by Arnold and Sanchez-Orozco (1989). They are provided in column 2 of Table 4. The net prices for game animals exclude effort.

The simulation program is written in Gauss and is available from the authors upon request.

BIOECONOMICS: DYNAMIC SIMULATION RESULTS

In this section, the simulation model is used to investigate the effects of allowing ranchers to harvest wildlife for their own purposes. The same random number seed is employed to ensure that the data are comparable from one simulation to the next. In Fig. 3 we present the 'base case' for the herbivore species considered. This is the scenario without game cropping and without periods of drought. Although wildlife populations fluctuate due to stochastic regeneration, they are stable; the same is true for predator populations. The stochastic system without drought is stable in the sense that the populations do not deviate far (and long) from their long-run median value.

In Fig. 4 and 5, stochastic drought periods of three years' duration are simulated. Droughts begin in years 5, 18, 43, 53, 65 and 71. The impact of droughts on herbivore populations is not equally severe. Especially in year 71, when populations of wildebeest, Thompson gazelle and Grant's gazelle are high, drought causes a dramatic decline in herbivore populations because forage production is low. Figs 4 and 5 indicate game populations with and without game cropping for a risk-averse rancher.

The implications of game cropping are as follows. Depending on the attitude towards risk, the rancher may respond by selling some cattle stock (Fig. 6). Then, the species composition of the wildlife ecosystem changes as the relatively more valuable species are exploited more intensely. Due to reduced competition for food with cattle and other game, the populations of less valuable species may increase. Alternatively, the rancher can also decide to increase his revenues without bothering about stability, and consider game cropping a sort of bonus. On the basis of these considerations, it is not clear that game cropping would contribute to nature conservation.

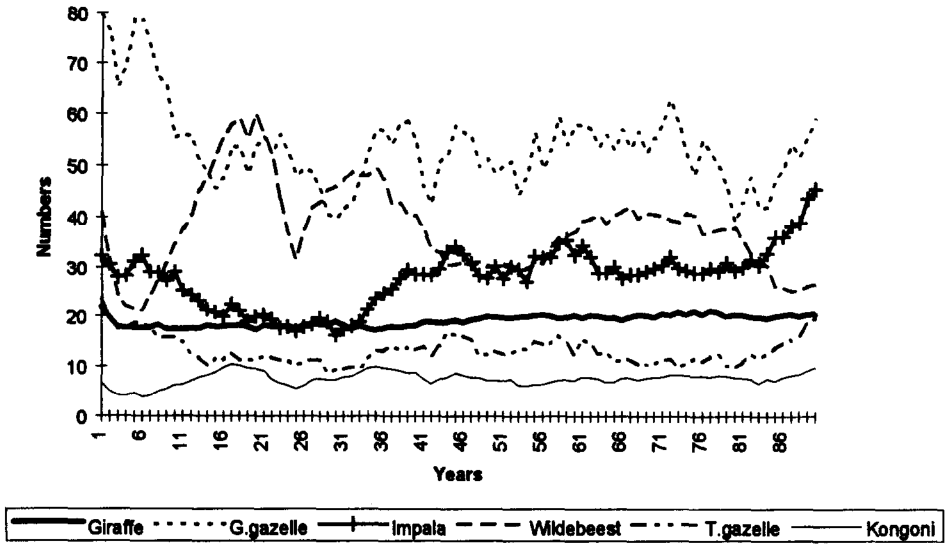

Fig. 3. In the absence of drought and game cropping, the stochastic herbivore populations are as indicated in the diagram. With the possible exception of impala, there appears to be no discernible trend over the 90-year time horizon; animal populations fluctuate randomly about a central tendency, perhaps best illustrated for the case of giraffe

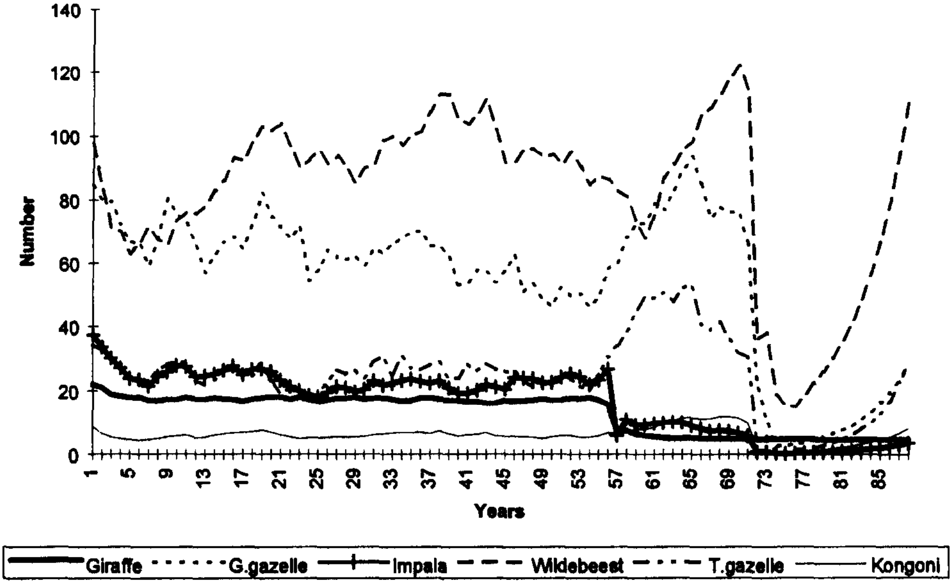

Fig. 4. By comparing this figure with Fig. 3, it is possible to see the effects of drought on stochastically-generated herbivore populations. Droughts of 3-year duration begin in years 5, 18, 43, 53, 65 and 71, with consumption of forage exceeding availability particularly after the fourth and sixth droughts.

The potential benefit of game cropping for nature conservation is clear for the rancher who favours stability—who is risk averse (see Fig. 5). In this case, the decline in herbivore populations (and consequently of predators) is much less dramatic with game cropping. The reason is that competition for food is less pressing which, in turn, is due to the reduction in the ranch's cattle herd, as indicated in Fig. 6 (where the drought plus game cropping scenario is for a risk-averse rancher). This result suggests that the benefits of game cropping may be those of stabilizing herbivore populations and (game plus cattle) revenues. Here, stability is interpreted as a (relatively) small deviation from the long-run trend in the no-drought scenario (compare Figs 4 and 5 to Fig. 3).

For less risk-averse ranchers, however, this stabilising effect does not materialise. This leaves the less desirable, selective harvesting of herbivores

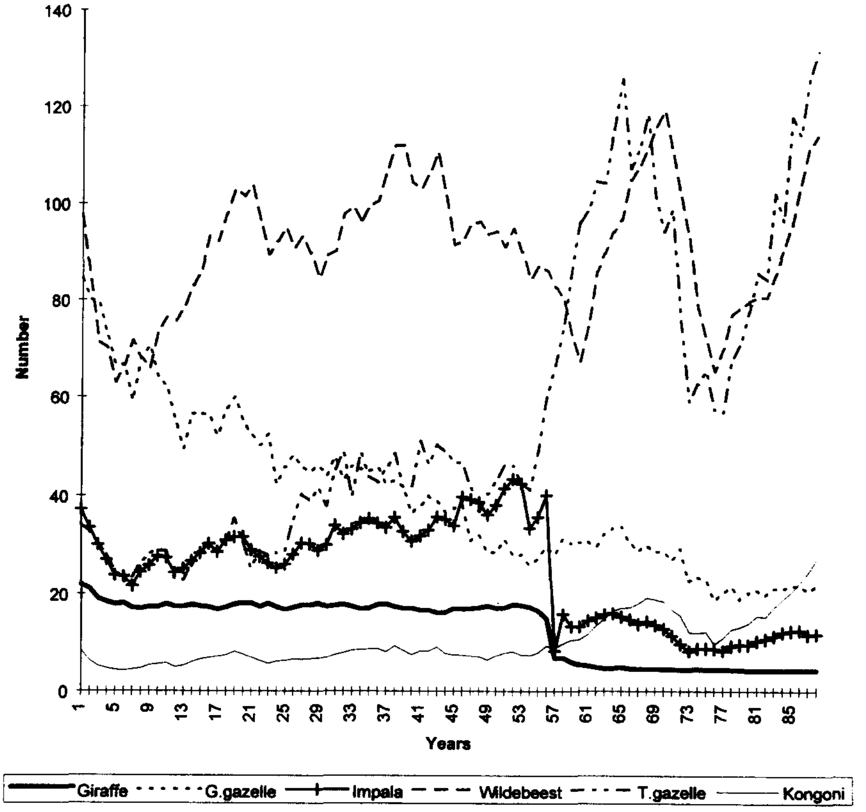

Fig. 5. By permitting game cropping, the effects of droughts on stochastically-generated wildlife populations is mitigated to some extent. Ranchers keep less cattle (Fig. 6) so that more forage is available for wildlife during periods of drought. Only in the case of the fourth drought does consumption of forage exceed forage availability to such an extent that wildlife populations are significantly reduced.

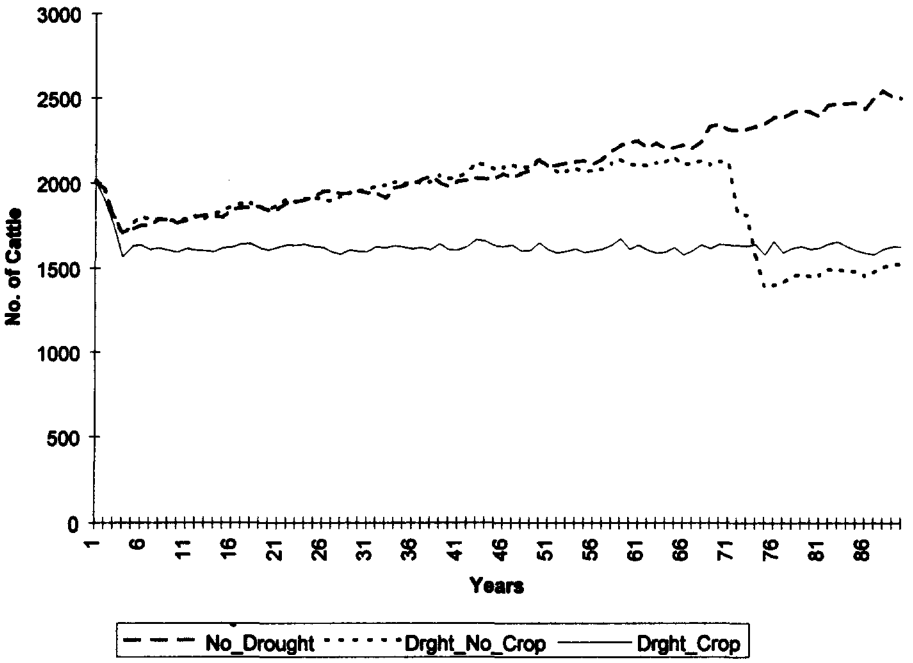

Fig. 6. With game cropping, ranchers adjust domestic livestock numbers so that they are below those that would be kept when no game cropping is permitted. In the absence of game cropping but random climate, ranchers face uncertain returns as evidenced by the sudden decline in cattle numbers in the case of drought due to lack of forage.

as the only impact on the ecosystem. The simulation model indicates that expected revenues from not reducing the cattle herd always exceed the revenues from cutting back the herd size in favour of wildlife game. The penalty for maximising revenues under stochastic climate conditions is widely fluctuating revenues. Whether ranchers are sufficiently risk-averse and susceptible to pricing incentives to make game cropping beneficial for nature conservation is an empirical matter that is the subject of future research. If contributing to nature conservation is an important goal of the proposed policy shift, we conclude that the possible success of this shift will be largely determined by preferences and attitudes of ranchers. Careful investigation of these matters is therefore proposed.

CONCLUSIONS

The Kenyan government has abandoned its reliance on the 'good will' of ranchers for maintaining wildlife populations on private lands. Instead, it is now permitting ranchers to harvest wildlife and to sell the meat for profit.

The ranchers may decide to consider the benefits from game cropping a mere bonus that increases their (fluctuating) profits. Then, some wildlife populations will be subject to hunting and the ecosystem will change. However, ranchers may also decide to opt for more stable revenues. If ranchers are risk averse and susceptible to economic incentives, the policy will have the following effects.

First, the relative importance of different populations in the ecosystem will change as the more valuable game species are subject to more intensive hunting effort. Harvesting wildlife also provides an incentive for ranchers to cull their domestic herds so that competition for forage between cattle and game is reduced but, again, less valuable game species may expand their numbers. In times of abundant forage, these effects will result in an ecosystem that substantially differs from the original one, which is probably undesirable if nature conservation is the objective of the new policy. However, in times of drought, an additional effect of game cropping is apparent: if positive prices for game can induce the rancher to reduce his cattle herd, forage required to support the total number of animals falls, and cattle and game populations are less vulnerable to drought shocks. We conclude that the main potential benefit from game cropping is that of reducing the fluctuations in, or stabilising of, wildlife and livestock populations.

Based on the simulation model developed in this study, it is difficult to draw firm conclusions about the desirability of the new policy. Depending on ranchers' behaviour and attitudes to risk, introducing economic incentives may stabilise wildlife populations, or it may provide additional support for the conclusion reached by MacNab (1993): "In view of the limited evidence to support it in its original form, the hypothesis that game cropping would conserve wildlife and their habitats whilst providing a food source to the local people must be rejected, except, possibly, in some arid and semiarid lands" (p. 2288). Clearly, imposing economic incentives whether welcomed or not on a traditional commercial ranching system may not always lead to an ecologically and economically preferred outcome.

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