Wildlife carrying capacities in relation to human settlement

S.K. ELTRINGHAM

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Human encroachment into wildlife areas, which has increased almost exponentially over the past few decades, has usually resulted in the elimination of the larger species, particularly the large mammals. This is not an inevitable consequence and this paper considers the extent to which man and wildlife can coexist. There is a linear inverse relationship between human and elephant densities and the reasons for this are discussed with particular reference to Uganda. Such a relationship does not necessarily hold for all species and the outcome of increasing human pressure on wildlife habitats varies with a variety of factors including the species concerned, the rainfall, vegetation, soil and, above all, the attitudes of the people towards wildlife. Wild animals are more likely to be tolerated if they do no harm to human activities or if the harm they do is outweighed by the benefits to be obtained from their exploitation. In many parts of Africa utilisation is likely to be the best hope for the conservation of wildlife. Some examples are given of situations in which worthwhile carrying capacities of wildlife can be maintained in the presence of human activities.

Key words: wildlife, carrying capacity, settlement, elephant, Uganda, conservation.

S.K. Eltringham, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K.

Introduction

The national park concept involves the exclusion of people from wildlife areas apart from visitors and employees concerned with management. National parks as inviolate sanctuaries will continue to be necessary for the protection of species, such as the large predators, whose habits are incompatible with human activities, but many species can coexist successfully with man. Human settlement will, however, affect the number of animals that can survive in an area and hence influence the carrying capacities for the species. Before proceeding further with a discussion of wildife carrying capacities it is best to consider the meaning of the concept.

Carrying capacity is a term that has been used somewhat loosely and we are indebted to Caughley (1979) for clarifying the position. It may be defined in an number of ways but in the context of large herbivorous mammals, it refers to the equilibrium between a population and its resources in a particular area and is measured, therefore, in terms of density. In an undisturbed ecosystem it is known as the ecological carrying capacity and is defined as the equilibrium point at which the rate of production of edible vegetation is equalled by the rate of consumption. If a population is reduced by man, e.g. through cropping, the equilibrium will fall to a new level, called the economic carrying capacity. According to Caughley, either equilibrium depends on three factors, each operating as a function of plant density.

These factors are: the rate at which the plant biomass increases, the rate per animal at which the plant biomass is removed by herbivory and the rate at which the herbivore increases in number. Although the concept is stated in terms of a herbivore/plant relationship, the same principles apply to one of predator and prey. Any of these rates can be changed if the animal is denied access to a resource through the operation of an extrinsic factor, such as human settlement, which usually leads to a conflict of interest between

animals and man. The result is inevitably a lowering of the ecological carrying capacity of the area for the animal but that does not preclude the species from continuing to exist satisfactorily at a stable economic carrying capacity.

Settlement may directly affect the first and third of the factors considered above and indirectly the second. It can have a profound effect on plant growth if, for example, much of the natural vegetation is replaced by crop plants and it can reduce the population growth rates of animals through direct killing. The destruction of natural vegetation is also likely to reduce the amount of food available to animals and so lower the individual intake rate. It may be expected, therefore, that human settlement will lower wildlife carrying capacities but this paper is concerned with the extent to which wildlife populations can continue to exist in the presence of human activity. The discussion is biased towards the African situation but most of the conclusions have general applicability.

Sources of human/animal conflict

There are four principal situations in which people are likely to come into conflict with animals as a result of settlement. The first is when animals become a threat to human life. Dangerous animals are not necessarily carnivores for many of the large herbivores, such as buffalo *Syncerus caffer*, elephant *Loxodonta africana* and hippopotamus *Hippopotamus amphibius*, are often more aggressive. Disease organisms and their vectors are also included in this category.

A second cause of friction is the destruction of domestic stock by wild animals. Direct killing is almost always the work of predators although the larger herbivores such as elephant or rhinoceros *Diceros bicornis* are capable of killing cattle. Loss of livestock from disease acquired from wildlife belongs in this category. In many cases the wild animals are symptomless carriers e.g. wildebeest *Connochaetes taurinus* of foot-and-mouth disease in Botswana or of brucellosis in Tanzania.

The third reason why wild animals may not be favoured by people is the direct competition for food that can arise on natural grassland between wild herbivores and domestic stock. This is sometimes more apparent than real, for ecological separation, or resource partitioning, is characteristic of of natural communities (Bell 1970; Field 1972) and only those species closely related to domestic animals might be expected to compete. Even so, Field, Harrington & Pratchett (1973) found a slight, but distinct, ecological separation between such close relatives as buffalo and cattle.

Finally, there are problems with crop-raiding herbivores. Most human crop plants are very palatable to wildlife for a number of reasons. Those grown for animal forage are particularly attractive since the wild species is often the ancestor or a near relative of the domestic breed and has similar tastes. Crops grown for human food are also favoured by wild herbivores since the seeds and fruits of cultivated plants are usually bigger than those of wild varieties and, through selective breeding, are lacking in distasteful secondary compounds. Such herbivores may be said to be in competition with man for a resource which is in short supply to the farmer but not to the animal, since it has continued access to vegetation that is useless as human food. Attempts to defend crops from raiders is a common cause of death in farming communities e.g. between 10 and 20 people a year are killed by elephants in Karnataka State in southern India (Sukumar 1986).

In considering the carrying capacity of wildlife in relation to human settlement, therefore, it is necessary to distinguish both between the type of wildlife concerned and the human land-use practice. In almost all cases, problems are likely to arise only with mammals.

Some birds of prey may take chickens or other small domestic mammals and many snakes and crocodiles can be dangerous, but on the whole, the problem wildlife species is likely to be a mammal. Such animals tend to be persecuted so that they are the ones whose carrying capacities tend to be affected by human settlement. Other species should be capable of coexisting with people although they may suffer from loss of habitat as a result of human activities.

Human settlement, therefore, usually has a depressing effect on the carrying capacity of an area for wildlife but there is no universal mathematical relationship between human densities and animal carrying capacities. Although there has been a general retreat of wildlife in the face of expanding human settlement, this need not be inevitable. It is not always the result of conscious decisions by people, who are not as antagonistic to wildlife as is sometimes supposed. Harcourt, Pennington & Weber (1986) found that in countries as diverse as Tanzania, Rwanda, Brazil and the U.S.A., there was widespread support for conservation, particularly if some benefit accrued from wildlife. There are various ways in which conserved populations may be exploited (Eltringham 1984; Caro 1986) including tourism, sport hunting, cropping and ranching (domestication). Natural vegetation also provides traditional medicines and other useful products. Some of these activities, such as national park management, require the involvement of government but others can operate at the local level and, indeed, they are the ones most likely to be successful as experience on the communal lands of Zimbabwe has shown (Martin 1986).

The taking of animals as a crop will inevitably reduce a population that is at ecological carrying capacity since such a population is incapable of generating a yield. It can also result in a reduction in species diversity since certain predators and potentially competing herbivores are likely to be eliminated. Non-consumptive utilisation, on the other hand, usually leads to increased numbers even in reserves surrounded by dense human populations. Thus, poaching of gorillas in the Parc National des Volcans in Rwanda declined when a management programme was instituted to encourage tourists to visit the gorillas. The reason was that the greatly increased revenue from tourism provided the necessary incentive and means to protect the park adequately (Harcourt 1986). The result of protection was not immediately apparent from an increase in the population size but the number of infants and immatures per female increased significantly showing that numbers were beginning to rise to a new carrying capacity.

As a result of human protection, the densities of large mammals in most rangeland parks are higher than those outside and may even exceed the ecological carrying capacity for a time. Normally, density dependent factors soon bring numbers back down again but they may not act quickly enough in the case of the slow-breeding megaherbivores, whose destructive feeding habits may cause the carrying capacity to fall quicker than the population's ability to adapt to it. The result is extensive, and possibly irreversible, habitat damage.

Land-use practice and wildlife carrying capacities

This discussion has shown that the carrying capacity of an area for wildlife depends on the use to which the area is put. Hence it is necessary to identify the limits within which the animals can be tolerated. This can best be done by considering each land-use practice in turn.

1. *National Park or Similarly Protected Area*

As no human settlement is allowed in such protected areas, the natural carrying capa-

cities ought to be achieved for all wildlife. In practice, of course, there is some human settlement, even if transient, in many of the reserves. In addition to tourists there are park managers living in the park and often other people, such as hotel staff and research biologists. It is possible that the presence of tourists can lower the carrying capacity of the park for some species e.g. nesting ostriches *Struthio camelus* and shoebill stork *Balaeniceps rex* have been known to desert their nests because of over-enthusiastic bird-watching (*pers. obs.*). On the other hand, the carrying capacity may be increased locally by the provision of waterholes or supplementary feeding around the lodges. Grazers are also attracted to the closely mown lawns because of the greater nutritive quality of regenerating grass and by the lights of the lodge, which give some protection from being surprised by predators. Hence even fully protected reserves are not immune from having their carrying capacities manipulated by man.

There is also risk from human settlement outside the park. This often restricts the home ranges of wildlife or interferes with their migrations but more active disturbance comes from illegal encroachment. Poachers obviously cause the greatest problems but collectors of firewood and others wandering through the parks may cause animals to desert their territories. The carrying capacities of a park, therefore, are likely to be reduced in direct proportion to the density of settlement on its borders.

The degree of risk from this cause has been analysed by Kurji (1976) for the national parks of Tanzania. He took 23 demographic variables likely to influence human population size such as percentages of children, mean household size, female fecundity and immigration trends, and subjected them to principal component analysis. His results showed that, in terms of likely future pressure from human settlement, the parks could be divided into two broad divisions, one in the north and the other in the south, with the northern parks being much more at risk than the southern. The approach is illuminating but on its own, does not provide a human density figure at which the carrying capacities of the parks for wildlife begin to be seriously affected.

2. *Hunting Reserve*

Areas are set aside in many African countries for sport hunting but usually for no other human activity. The wildlife populations of such reserves should be near ecological carrying capacity, since the hunting does not remove a significant proportion of the stock, but in practice, they are subjected to poaching pressures of varying degrees. Although the poachers are not settlers, many of them come from surrounding regions. This is not necessarily true of ivory or rhino horn poaching, which is usually controlled by people living hundreds or even thousands of miles away. The presence of sport hunters acts as a deterrent to poaching and so helps to maintain the carrying capacity of the area.

3. *Forest*

Not much is known about the effects on carrying capacity of human settlement in forests although it is known that the exploitation of forests for timber can have a destructive effect on wildlife. This need not be catastrophic, however, for some primate and bird species can survive even intensive logging, albeit at a lower density (Johns 1985). Our ignorance of the consequencies of settlement in forests is partly due to the fact that until recently there has been little of it, except for indigenous people such as pygmies, who are effectively part of the natural ecosystem. Most other people in forests are there as temporary visitors rather than as settlers.

The situation is beginning to change as more roads are driven through forests and settlers come to live beside them. The effects of such

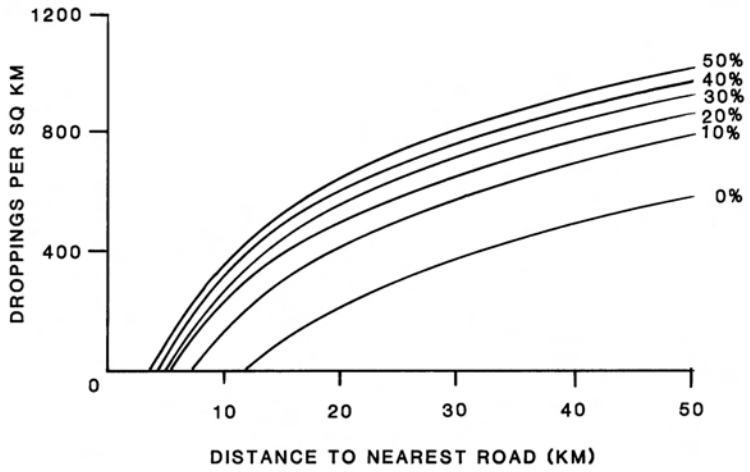

Fig. 1. The density of elephant droppings in the rain forests of Gabon in relation to the distance from the nearest road. The percentage figures on the right refer to the proportion of secondary vegetation in the forest (Barnes *et al. in press*).

settlement on the distribution of elephants in Gabon has been studied by Barnes, Barnes, Alers & Blom (*in press*). They estimated the densities of forest elephants from droppings counts and assessed the distribution in relation to two factors, distance from the nearest human habitation and the percentage of secondary growth in the vegetation. Secondary forest is more attractive to elephants than primary forest because the reduced plant defences of pioneering vegetation make it more palatable (Merz 1981).

Barnes *et al.* showed that very few droppings were present either near villages or roads and that the stratum of low density extended for about 7 km from a road (Fig. 1). This is not a reflection of differences in the distribution of vegetation types since the percentage of secondary forest near a road was not significantly different from what it was deeper in the forest. Fig. 1 also shows the the effect of increasing proportions of secondary vegetation in the forest. The attraction of this vegetation caused the elephants to venture nearer to the road in direct proportion to its abundance. At the time of the survey there was very little poaching in the forest so it seems that the animals were not driven away from regions of human settlement but simply avoided them. A multiple regression showed that the amount of secondary forest and the distance from the nearest human habitation accounted for 81% of the variation in droppings density in the case of villages and 85% in the case of roads. The regression equations for distance and droppings density for villages and roads are:

Villages:
$Y_d = 926 \log_n X_v - 2161$ ($r = 0.82$; $P < 0.0001$)
Roads:
$Y_d = 514 \log_n X_r - 1080$ ($r = 0.83$; $P < 0.001$)

where Y_d = number of droppings per km^2,
X_v = distance in km from nearest village and
X_r = distance in km from nearest road.

Since the amount of secondary forest reflects past human activity, these results show that man has been a factor in determining the

distribution of forest elephants for many years.

4. *Unprotected Areas*

These represent most of the land area in Africa and are where one might expect conflict between animals and people to be most obvious. The two often compete and consequently, the wildlife is unlikely to reach ecological carrying capacities in many areas, but the question is whether or not the animals can achieve a stable carrying capacity and if so, whether it is possible to calculate it. The answer to the first question is almost certainly yes but it is unlikely that the second can be answered with any degree of precision.

The level at which the carrying capacity is reached by a large mammal species is largely a matter of human choice, which is usually determined from an economic perspective e.g. a species that has some economic potential is more likely to be tolerated than one that is a pest or is of neutral value. The value attached to a species may change over the years. Thus in recent decades, elephants have been lucratively exploited for their tusks as well as for meat and skin but in precolonial times, ivory was not particularly valuable and in parts of Uganda, for instance, tusks were used for fencing cattle (Baker 1866).

The human/wildlife conflict can best be understood from a consideration of the situation in the days before the European or Arab penetration of Africa, taking as an example, the history of the elephant in Uganda, which has been examined by Malpas (1978). In the nineteenth century, the evidence from early explorers suggest that the elephant population in Uganda was very large (Lugard 1893) and that it dominated the agriculturalists to the extent that the latter could exist only in large, well-defended villages. Any farmer attempting to cultivate in remoter regions would very soon lose his crops to marauding elephants. The people have hunted the elephants for millennia for fossil finds elsewhere of skeletal remains associated with wooden spears date back some 250 000 years (Kortlandt 1976). The elephant was hunted primarily for meat and as a single animal could supply a whole village for several weeks, not many were taken.

This balance between a large, extensive elephant population and a sparse, concentrated human one was disturbed by the incursion of Arab traders and European explorers into Uganda. This had several very significant effects on the balance between elephants and people, the first favouring the elephant through the introduction of human and animal diseases. These included a disastrous outbreak of rinderpest, which affected the whole of Africa at the end of the nineteenth century and which killed most of the cattle and many wildlife species but, significantly, not elephant. An immediate outcome amongst pastoralists was famine and the people, weakened by hunger, had little resistance to introduced diseases, particularly smallpox but also including chickenpox, measles, poliomyelitis, influenza and whooping cough. An outbreak of the jigger flea throughout East Africa was a further bane. This west African pest burrows into the skin and produces abscesses but it is of little consequence to people familiar with it for it can be easily removed before much harm is caused. To a naive population, however, it is a serious scourge leading to blood poisoning and death.

As a result of these several calamities organised society tended to break down, with much intertribal fighting and disruption of settled communities throughout East Africa towards the end of the nineteenth century. As if this were not enough, an epidemic of sleeping sickness broke out in Uganda and reached a peak around 1910-1912. Traditionally, the disease was controlled through the cultural and land apportionment systems that had evolved amongst the people (Ford 1971) but with the breakdown of the settled order, wide-

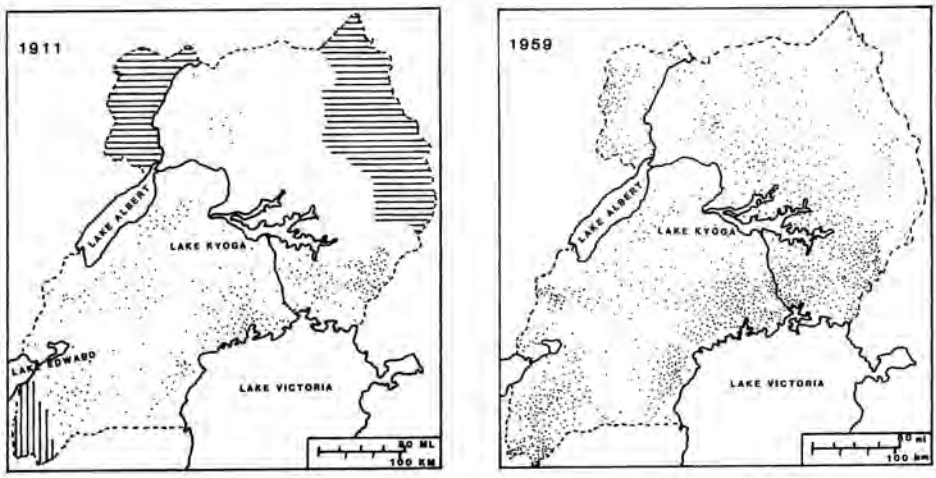

Fig.. 2. Distribution and density of the human population of Uganda in (a) 1911 and (b) 1959. Each dot represents 5 000 people. The comparison should be confined to the southern part of the country (south of Lake Kyoga) as the distributions in some northern districts were not mapped in 1911. The horizontally hatched areas were not under Ugandan administration in 1911. The vertically hatched area is the New Territory, which contained 100 000 people in 1911. (After Langlands 1971.)

spread mortality occurred and compelled the authorities to evacuate the population. In the absence of people and with a reduction in potential wildlife competitors, the elephants expanded to fill the gaps and by about the time of the first World War, the traditional situation of a dominant elephant population had become restablished but now with the people virtually under seige.

This situation did not last for long, however, for other consequencies stemmed from the influx of foreigners into East Africa. In the first place, the Arab traders had placed a cash value on ivory, which provided an incentive for hunting elephants, and in the second, the colonial powers had introduced firearms, which tilted the elephant/people balance very much in favour of man, who was now able to dominate the elephants (Swynnerton 1923). Elephant control was instigated so that it was possible for small settlements to spread into previously elephant-dominated regions. Other factors speeded up this expansion. These included a change from subsistence agriculture to cash-crop production, which requires large areas of land, the introduction of bush-clearance schemes, the widespread eradication of the tsetse fly and a decline in intertribal warfare imposed by the colonial authorities. The human population, therefore, was released from the restriction dictated by elephants and, as a result of improved medical and veterinary care, was able to expand in numbers as well as in space (Fig. 2). This led to an increase in elephant/man confrontations giving the erroneous impression that elephant numbers were rising at a time when they were almost certainly declining drastically.

The situation in Uganda was probably not very different from that elsewhere in East Africa or in Africa as a whole. Parker & Graham (1989) attribute this to the competitive exclusion principle but it is more a case of man and elephants being incompatible, with elephants disappearing once human den-

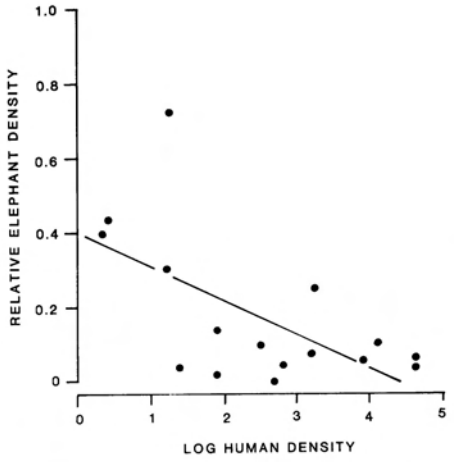

Fig. 3. The relationship between human and elephant densities on fertile soils in agticultural areas of Kenya. The slope predicts the extinction of elephants at a human density of 82,5 persons per km^2 (Parker & Graham 1989)..

sities rise above a certain level. Parker & Graham showed a significant inverse relationship between human and elephant densities in Kenya and Zimbabwe. The point at which the regression line cuts the x axis provides an estimate of the human density beyond which elephants cannot survive. For the fertile soils of the Kenyan agricultural regions the value is 82.5 people per square kilometre (Fig. 3). The regression equation is $y = -0.925x + 0.4093$ ($r = -0.82$, $P < 0.001$). For the more barren soils of Zimbabwe, the tolerable density figure is much lower at 18.9 persons per square kilometre (Fig. 4) with a regression of $y = -0.268x + 0.787$ ($r = -0.99$, $P < 0.001$).

According to Parker (1984) the ecological requirements of agricultural man and elephants were not originally coincidental since peak elephant density occurs between 1400 and 1800 mm annual rainfall whereas peak human densities lie between 1000 and 1400 mm. The increasing human population, however, has tended to shift the peak human densities up the rainfall gradient into the elephant's range. Where this has happened, there has been a decline in elephants, which has been in inverse linear relationship to human increase until elephants have fallen to 5% of their original numbers. After this, the linear relation breaks down, probably because by then most of the elephants are within protected national parks or forests.

The inverse relationship between human and animal densities would almost certainly be found to apply to most large mammal species in Africa but this need not be inevitable. It is necessary to distinguish between those species whose presence is inimical to human interests and those which could coexist with man. The division is not absolute for it depends on the form of land-use concerned. Thus pure agriculture, particularly on small holdings, cannot tolerate any large mammals, even those that do not feed on the crops because of the damage caused by their trampell-

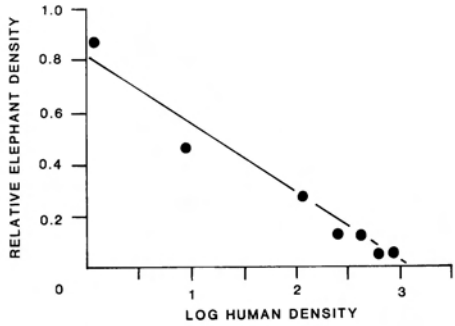

Fig. 4. The relationship between human and elephant densities on infertile soils in Zimbabwe. The slope predicts the extinction of elephants at a human density of 18,9 persons per km^2. The difference from the figure for Kenya is assumed to be due to edaphic factors (Parker & Graham 1989).

ing. Conflict is most likely where agriculture extends up to the boundaries of national parks, as often happens. If a more compatible form of land-use cannot be found the only solution is to protect the crops with electric fencing or some other barrier.

Pastoralism or ranching causes lesser problems, as is demonstrated by the prosperity of such pastoral tribes as the Masai in the rich wildlife plains of East Africa, but the presence of cattle will reduce the overall carrying capacity for the wildlife or, put in a more anthropocentric way, wildlife will reduce the carrying capacity for cattle. This will not be true of all species but only of those whose ecologies are similar to those of livestock, such as buffalo. Any management reduction of bush cover to increase grazing area, however, will lower the carrying capacity for browsers.

The exploitation of wildlife by ranchers may well increase the ecological carrying capacity expecially where restocking has been practised, as in South Africa. Many regions that had been depleted of their wildlife are now highly productive in terms of game meat (Skinner 1989). Human settlement or, rather, a change in land use by settled people, has therefore had a beneficial effect on wildlife carrying capacities.

Whether or not wildlife will be able to coexist with ranched livestock, therefore, depends on management policies. If wildlife is desired, the required densities must be stated and the numbers of domestic stock adjusted accordingly. Examples of species which do little harm on ranches include such predominantly browsers as giraffe *Giraffa camelopardalis*, gazelles *Gazella* spp, eland *Taurotragus oryx* and bushbuck *Tragelaphus scriptus*. Although a grazer, the zebra *Equus burchelli* tends to feed on grass of a different species or growth stage than do cattle and is unlikely to compete with livestock to any extent. The black rhinoceros *Diceros bicornis* would be acceptable ecologically although its legendary irascible temper might cause problems. Ecological separation ensures that many grazers can coexist with cattle and experience has shown that a mixed cattle/game ranch is more productive than one carrying only one or the other (Mentis 1977). Cattle, or any other domestic animal, should be regarded as simply another species to be slotted into the ecosystem. Calculation of the correct carrying capacities for the various species is not easy but sufficient knowledge of feeding habits exist for rough estimates, at least, to be made and subsequently adjusted in the light of experience.

Although browsing large mammals are of little concern on rangelands, they are certainly a problem in forest plantations and their presence there cannot be tolerated. Natural forests are not so affected by the presence of browsers except for elephants, which can damage commercially valuable trees. Most forest managers try to eliminate them, usually without success (Laws, Parker & Johnstone 1975). Small browsers such as dikdik *Madoqua* sp. and steenbok *Raphicerus campestris* pose little or no threat to forestry although they can be a nuisance in gardens. Their numbers rarely reach the full potential of the carrying capacity, however, due to the loss of habitat that usually results from human settlement. A few wildlife species which do not interfere with agricultural or forestry practices are nevertheless unacceptable because of their danger to man or domestic animals. These include most of the large carnivores, although their danger is often exaggerated, the black rhinoceros and some reptiles such as crocodiles and poisonous snakes. For them, the carrying capacity in settled areas must be zero and their future lies in national parks from which human residents are excluded. Where people do live in the vicinity of national parks, as in the fishing villages within the Queen Elizabeth National Park in Uganda, it is surprising how habituated dangerous animals can become towards people

who do them no harm. Thus women from Katwe village can be seen on most days washing clothes within a few metres of hippos in Lake Edward.

The carrying capacities for small mammalian carnivores ought not to be affected by settlement and may even be enhanced through the extra food resources provided by the rodents and other pests attracted to stored produce. Nevertheless, small predators are often killed whenever possible, usually on the grounds that they take small domestic animals, but it has proved impossible to eliminate them entirely.

Conclusions

The history of interaction between man and wildlife in Africa has been one of continuous reduction in animal carrying capacities in the face of human expansion, as it has been in other parts of the world. The human population in Africa is rising faster than those in most other continents so one might expect wildlife numbers to diminish further but this need not be inevitable. There are many species whose ways are not inimical to human interests and which can live alongside people provided they are tolerated. They are more likely to be if some benefit stems from their presence. This has been clearly demonstrated in Zimbabwe, where the CAMPFIRE (Communal Area Plan for Indigenous Resources) project for the utilization of wildlife is proving to be highly effective in conserving the wildlife while providing income for local people (Martin 1986). So attractive is the project that one community has voluntarily withdrawn from a substantial area of land in order that wild animals can expand into it. The reason that CAMPFIRE is succeeding whereas so many similar projects have failed is due to the fact that the operating company is owned and managed by the people themselves and not by an official body on their behalf. If similar arrangements are made elsewhere in Africa, the future of the large mammals should be secure. This will require a different approach to conservation, with wildlife being conserved alongside people, although there will continue to be a need for the traditional type of national park to protect those species that do not easily coexist with man.

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