

Wildlife *v* Sheep and Cattle in Africa

By Leslie Brown

Giraffes eat gall-bearing acacias which domestic animals never do; elephants will eat some shrubs which, in the same conditions, even goats will not touch. In Africa wildlife is an efficient user of the poorer land, whereas nearly all grazing land is badly managed by man. It does not benefit man to destroy the wildlife in order to spread his inefficient methods over yet more land. The author—agriculturist and well-known naturalist and conservationist—pleads for sound land management based upon research which would allow a place for the wildlife as an efficient user of certain land and a valuable resource.

THE main problems in African grazing areas* arise from competition between man and his domestic animals on the one side and wildlife on the other. Problems affecting wildlife alone are much less serious. Hardly any of the natural grazing areas of Africa have been seriously and extensively damaged by even large populations of wild ungulates, whereas there are scarcely any areas densely inhabited by man and his domestic stock that have not been seriously and extensively damaged. Even in such areas as the European-owned ranches of Kenya, where many of the farmers are as skilled in practical range management practices as any in the world, there is often evidence of slow but steady deterioration of pasture quality, or of bush encroachment which requires remedial measures to maintain yield. Where wild animals damage the herbage, even in cases of relatively widespread damage, the causes can often be traced to competition with man. For instance, in the Murchison Falls, Queen Elizabeth, and Tsavo National Parks in East Africa, where a very large population of elephants has converted the *Terminalia* woodland or *Commiphora* thornbush to open plains covered with grass, this is largely, or at least partly, the result of human pressures on the elephants outside the reserves, either because of illegal hunting or through reduction of their range by cultivation.

The damage pastoral tribes do to the environment through their domestic stock is almost universal, and differs from place to place only in the degree of severity. I know of no area inhabited by pastoral tribes that can be described as undamaged, or, in range management parlance, in excellent condition, except where the human population is so sparse that damage is negligible.

This is one of the most crucial problems both in Africa and in other parts of the world. But this damage does not always come about through

*Grazing areas are defined in this paper as those parts of Africa where grass is a dominant or co-dominant form of vegetation, eaten by a population of wild or domestic animals, or both. Such areas can include both inhabited and uninhabited regions, and also woodland communities where grass forms a major portion of the ground vegetation. Forest and bare desert are excluded, though even very severe desert environments will support grazing animals as long as there is some grass.

This paper was presented at the ITC (International Institute for Aerial Survey and Earth Sciences)—Unesco Seminar on Integrated Surveys of Natural Grazing Areas, Delft, 1967.

mere fecklessness, or a desire to maintain large herds for purely prestige reasons. In many areas it springs from the fact that the only reliably obtainable item of daily diet for camel or cattle people is milk. It is therefore inevitable that the proportion of female stock desired in the family holding will be very high (in Kenya 60 per cent or over), and that this high ratio inevitably leads, in a good year, to a rapid increase in stock. In the bad years that inevitably follow, the stock damage the environment more severely than can be readily repaired in a good year (in the absence of any of the sound range management practices). Moreover in the last 50 years this natural process has been aggravated by veterinary disease control. The result today is that many areas inhabited by pastoral tribes present the well-known picture of over-grazing, erosion, bush encroachment, human misery and want. No such overgrazing situation has ever been known to arise over wide areas populated by wild animals alone. It is possible to find local patches of overgrazed ground, as for instance near a favoured watering point, or again, on the territorial display grounds of the Uganda kob. But as a rule predators, disease, drought, and other factors maintain the population of wild animals in equilibrium with their environment, with relatively minor fluctuations. The occasional patches of overgrazed ground are the exception rather than the rule, whereas in those areas inhabited by human beings and their domestic stock overgrazed and eroded ground is what one expects.

The grasslands of Africa, though of many different types, can be divided into three main groups:

1. Those with a rainfall of over 35–40 ins per annum, where it is possible to improve the natural grazing conditions by ploughing and reseeded; 'tame pasture' or agricultural land.
2. Those with a rainfall of 35–15 ins per annum where improvement in the productivity of the natural herbage can only be brought about by management; rangeland in fact. This category must be broadened to include those grasslands with rainfall of over 35–40 ins, which, because of shallow soil, steep slopes, or other factors should not be cultivated, or will not economically justify cultivation and re-seeding.
3. The very dry areas of the continent, desert or semi-desert, with annual rainfall of 15 ins or less, usually poorly distributed, where the normal range management practices, such as fencing or development of additional water supplies, cannot economically be justified by the potential productivity of the land.

The rainfall limits ascribed to these three main categories are somewhat arbitrary, but it would be a brave man who thought he would make much money by reseeded pastures with an annual rainfall of less than 35 ins or who would lay on expensive piped water to vast tracts of semi-desert – at least at present-day costs. The natural forms of usage for each of these three main categories are respectively (1) settled agriculture dependent on crops but with animals included in the system; (2) ranching, perhaps with some limited cropping in favoured patches of land, e.g. in valleys; (3) nomadism, whether by domestic or wild animals. In these very dry areas indeed, nomadism is probably the only sound method of making

use of irregularly distributed ephemeral herbage, and attempts to settle nomads at fixed points may well result in serious damage to an environment that cannot stand continuous usage by stock.

The severity of the conflict and the problems that may arise with wildlife vary in each of these several categories of land. In the first category, much of the land will in any case be covered with forest or heavy woodland, and may not be classed as grazing land at all. It will also be accepted by most wildlife conservationists that, in the present human population situation (which is certainly unlikely to improve in the immediately foreseeable future), it is necessary to recognise that most of such high-potential agricultural land will be needed for human settlement, and that this may well be a far more productive use for it than would the maintenance of the natural habitat unspoiled. It can be shown, for instance, that the better parts of Kikuyuland in Kenya, and similar ecological types on other African mountains, can be made to carry 250–300,000 lbs. liveweight of man and his domestic stock per square mile, a far greater biomass than could ever have been carried in the form of the wild animals originally inhabiting such areas. To carry this biomass it will often be necessary to destroy the original forest vegetation and substitute for it cropland and planted pastures, a process which may result in a slow creeping degeneration of soil fertility. In a prosperous agriculture, however, the ill effects of such processes can usually be ameliorated or corrected by appropriate practices, though this is certainly not so easy in the tropics as in temperate climes.

In these high-rainfall areas wild animals will probably eventually be confined to forests, or to such national parks as may be set aside for them; there is little possibility of man being able to live with numbers of them among farm land. What wildlife conservationists are entitled to resent – and it should equally be resisted by agriculturists – is the all too frequent destructive misuse of such high-potential areas by shifting cultivation, cultivation of steep slopes without soil control, and so on, leading to overspill of the human population into less favourable rainfall areas. This inefficient utilisation of the high-potential areas has been the reason for many good wildlife areas in East Africa being invaded since the war.

However, not all such high-rainfall areas are best used for agriculture. There are some where agriculture ought to be discouraged and does not pay. A good example, on a large scale, is the huge belt of *Brachystegia-Julbernardia* woodland covering much of the southern African tropics. The rainfall here is from 35–50 ins falling in intense tropical storms during six months of the year, and corresponding in its effect during that time to a more regular rainfall of 70–100 ins per year. The soils are often poor, sandy, and seriously leached of nutrients, and settled permanent agriculture can only be maintained by high capital inputs of fertilisers, while on a primitive scale crops can only be successfully grown for a year or two by, for example the destructive *Chitemene* cultivation of Zambia, where a large area of woodland has to be felled and burned in rotation over a long period of years to maintain a family's subsistence. In such an area one is entitled to wonder whether it would not be better to adopt

some other more productive form of land use, including that through wild animals, which becomes even more attractive in those parts of the *Brachystegia* woodland heavily infected by tsetse fly. Fraser Darling and others have advocated that in such conditions it is best to stop the present haphazard usage by shifting cultivation, settle the human population on better areas of land (often available but unoccupied) with more intensive practices, and utilise the poorer land in some other way. This solution, however, does not often commend itself to a pure agriculturist, who may feel a challenge to 'do something with all that *Brachystegia*', a type of reaction that can lead to either a major technical breakthrough or a costly failure such as the groundnuts scheme.

The Natural Grazing Areas

It is in the second category, the lower rainfall areas where improvement can only be achieved by management, that the problem of conflict between man with his domestic stock and wild animals becomes most evident. These are the true natural grazing areas of Africa, where grass is the dominant surface herbage. The problem is, who shall eat it; cattle and sheep or wild animals? Few ranchers, having taken trouble to fence their land and lay on piped water supplies, look kindly on large populations of wild animals, especially hartebeest, zebra, wildebeest, or buffalo, that manifestly eat the grass that cows could eat. Among pastoral tribes today there is increasing pressure to reduce or control the wild animals with which they once lived in peace. Whether it is sound, or good for the pasture, to reduce or eliminate the wild animals is beside the point. The pastoral tribes usually exist already, and short of moving them or settling them elsewhere (increasingly difficult in these days) the problem of competition between them and wild animals on the same land will remain.

What the wildlife conservationist is entitled to claim is that if wild animals, which may be a very valuable resource at present under-utilised, are to be reduced or eliminated, the area affected should thereafter be soundly managed for maximum productivity by its human occupants. Generally this is not the case; indeed, the reverse is usually true. All too often, when an area which formerly held a large population of wild animals is developed as a grazing area for cattle and sheep, deterioration, sometimes catastrophic in its rapidity, sets in, and in the long run little useful purpose has been served by eliminating wild animals and substituting human usage.

It is of course true that not all wild animals need to be eliminated in areas designated mainly for human usage. Certain types, notably large browsers such as giraffe and elephant, may perform a function complementary to that of domestic stock, feeding upon vegetation which stock do not eat. The ant-gall acacia *Acacia drepanolobium* for instance, a major bush menace in many parts of Africa on poorly drained soils, is incessantly pruned by giraffes though hardly touched by domestic stock, because of the ants. And in the Tsavo Park, on one occasion, elephants apparently feeding in grassland were found on closer approach to be selecting small *Indigofera* and *Tephrosia* shrubs, which in similar

ecological conditions are not touched by domestic stock, not even goats.

There are ranchers who maintain quite large populations of wild animals on their ranches, and others who maintain that they cannot make money without killing all the wild life. Yet others, especially in South Africa, are now again building up herds of wildlife on their ranches as a paying proposition. Usually, however, a rancher who supports a population of wildlife on his land does so because he likes to see them rather than because he understands their habits and realises that some species may benefit his enterprise; even if giraffe eat ant-gall acacias they also kick down fences. The fact is that managing a population of cattle, sheep, and less often goats is a sufficiently difficult art in itself without having to think whether eland or impala help to keep down some invading bush which may become a menace. Nomad pastoralists, while often good naturalists, apparently do not think along such lines at all. If they tolerate wild animals in their midst it is from indifference rather than any knowledge of the good or harm they may do in maintaining a balance of desirable or undesirable components of the herbage. Once such people cease to be indifferent wild animals in their area are likely to fade away, whether protected or not.

There are also the problems of disease, on which I am not qualified to expatiate, but it is undeniable that uncontrollable wildlife movements may cause the spread, for example, of foot and mouth disease, and so cause losses through the need to maintain quarantine. Such highly-transmissible diseases can, however, be spread through the medium of wildlife which is impossible to eliminate, and the destruction of all large and spectacular wild animals might not completely stop the spread of disease. Opinions among capable ranchers again differ on this point. Usually, when the necessary disease precautions, such as dipping and regular inoculations, have been taken, keeping a population of eland, impala and giraffe on a ranch will have little ill effect. It is the jackal and the white-tailed mongoose that spread rabies rather than the lion and the leopard.

Disease and Tsetse

Again, this is to a large extent a question of the standard of management. In an overgrazed area where cattle will, in any case, die in large numbers in a drought year, it is pointless to blame wildlife for the spread of foot and mouth. In the Kajiado district of Masailand in the late fifties, disease control without elementary range management practices, such as the control of stock movement and numbers, led to a population of cattle and sheep far in excess of the land's carrying capacity in a bad year. In the 1960–61 drought and floods the cattle population fell from around 700,000 to 220,000, losses comparable with the worst rinderpest epizootics. In such management conditions it is entirely pointless to suggest that wildlife should be eliminated because it may be a reservoir for disease or parasites, and the wildlife conservationist is quite entitled to resent and resist such a suggestion. Given sound management, however, which may often involve the maintenance of some wildlife in grazing lands, the wildlife conservationist would be almost bound to agree to regular control of wildlife numbers on the principle that half a loaf is better than no bread.

One category in this middle rainfall group (poor agricultural but good grazing land) that deserves special mention is that which is infested with tsetse fly. Usually savanna or woodland rather than open grassland, this is often invaded by scattered cultivators or honey hunters even when the tsetse challenge is sufficient to exclude domestic stock. There are vast areas of this type of savanna in Africa, and very serious consideration ought always to be given to the likelihood that in such areas wildlife will prove to be a more reliable and economic form of meat resource than domestic stock. I vividly remember, twenty years ago in the savannas of northern Nigeria, the appalling quality of the local beef and occasional goat by comparison with the wildlife which was my staple meat resource (and also that of most of the local inhabitants).

Where the choice lies between clearing a tsetse area for domestic stock or leaving it for an abundant wildlife population the issue should be judged on economic grounds. Tsetse clearance is never cheap and may be very costly. Figures of 40–100 shillings per acre, or £1200–£3000 per square mile can be quoted for *initial* clearing in Kenya. Once cleared, the area must then be managed in such a way that the bush, and with it the tsetse, does not return, which always involves some unwelcome control over people entering the area, and usually involves considerable recurrent expenditure.

In a long experience of several African countries I have never seen an area cleared from tsetse bush in which subsequent management was such as to keep the tsetse away permanently. Too often the result has been another patch of country devastated at large cost. I know of one area in Kenya which has been 'cleared' at least three times since 1950, at enormous expense in relation to its actual potential, and is still not managed in such a manner that the menace will not return. There are no sound grounds for clearing tsetse areas to make room for human beings who cannot or will not manage it properly thereafter; it merely magnifies the problem at the public expense. The land's potential under sound management ought to be the only criterion in assessing the need for tsetse clearing and wildlife elimination in such areas. In this category of land, with rainfall of 15–35 ins, the carrying capacity will vary, under natural pasture conditions, from one SU (stock unit) to 5/30 acres, perhaps even more. Knowing the price of beef or mutton it is possible to assess within narrow limits the potential productivity of land under domestic stock. In many parts of Africa land with a carrying capacity of one SU to 5 acres will produce a *gross* return of 20 shillings per acre at best, and land with a carrying capacity of one SU to 10 acres a return of 8 shillings per acre. Quite clearly this is not very valuable land in economic terms. When to the ordinary overhead costs of a ranch (at least £2–£3 per acre) is added an additional £2–£5 for initial tsetse clearing, the proposal becomes economically unattractive. In many cases it is better to spend available funds on some more productive enterprise and leave the tsetse bush and its wildlife alone.

Until the last decade or so this argument was more difficult to advance as it was generally held that the only economic value of wildlife was through

sport hunting by a privileged few or tourism mainly centres on national parks. However, there is now much evidence to show that a population of wild animals, properly utilised, can produce as much or more meat per acre as can a population of domestic stock. A number of organised schemes to harvest wild animals for sale as meat have been devised, but the amount of meat harvested and sold from such schemes is small compared with the amount harvested irregularly by native hunters in many parts of Africa, without of course any thought at all for sustained yield. In very large areas of tsetse-infested savanna and forest wild animals are likely to be a more reliable and cheaper form of meat protein for a protein-starved populace than domestic stock. One could argue that to the usual costs of tsetse clearing and ranch development in such areas ought to be added the cost of the loss of the existing resource, which might very well amount to as much per acre per annum as would the production after development.

Unfortunately many such areas of tsetse-infested savanna have already been invaded by scattered haphazard patches of cultivation, which, from the point of view of wildlife, sterilise as much as a hundred times their own area. This unsound land use should be discouraged, especially as it often occurs in areas so dry that crop failures are frequent. Many areas in Africa which, 20 or 30 years ago, were well stocked with wild animals, now produce an unreliable subsistence for a handful of families and nothing else at all, but they do not justify the cost of full economic development for more intensive usage.

When one surveys the whole field of human usage for grazing in areas of moderate to poor rainfall, tsetse-infested or not, one is struck by the general prevalence of poor land use, the frequent occurrence of erosion problems, and, where the human population is too dense for the environment, the likelihood of recurrent food shortages or famines which are costly in terms of relief and administration. There are cases where this situation is more or less unavoidable, where the people have been living in such areas for generations and have increased (thanks to modern medicine) to the point where the environment is overstrained. But at least such situations should not be repeated as public policy and at the public expense, as is all too often the result when tsetse areas are cleared and made available without adequate control over the subsequent usage.

In our third category, the areas with very low rainfall, nomadism is the normal way of life, both for man and his stock and for wild animals. Typically, the wild animals that inhabit such areas are adapted to go without water for long periods, while man subsists on the products of camels and goats rather than cattle and sheep, though there are areas where sheep are also very important. It ought to be perfectly obvious that wild animals that are desert-adapted and able to go without water for weeks, possibly months, can make better use of such areas than can herds of domestic stock that have to be regularly watered. Competition between man and wild animals may be less obvious than in areas of better grazing, for it often happens that wild animals are able to inhabit areas too far from available water supplies to be regularly reached by human beings and their stock. But where some 'unnatural' factor, such as a large river

flowing through a desert permits the survival of more domestic animals than the desert itself would support, human utilisation of the desert within many miles of the river is often excessive, and competition with wildlife may be severe. An example of this is in the Danakil Desert of northern Ethiopia, where most of the ground within 30 miles of the permanent Awash River is grossly overgrazed, and the few remaining wild asses have been obliged to become mountain animals, for only there can they escape competition from domestic stock.

In desert and semi-desert areas inhabited by nomadic tribes it is even more obvious that the environment is easily damaged, and that habitation by humans and their stock leads to widespread damage to the already scanty vegetation. One has only to visit an area out of reach of regular watering points to be surprised by the relative luxuriance of the vegetative cover, which is probably associated with lower mean soil temperatures and some amelioration of the generally torrid conditions. In such areas, where they do not compete with man, there may be gazelles, oryx, and other species which are not regarded as any problem.

Habitat Destruction

Besides these problems of competition between man, domestic stock and wild animals there are, of course, problems of a technical and more academic nature affecting wild animals alone. There are still areas of the continent, principally in national parks, where large herds of wild animals roam more or less unmolested and where they do not compete with any domestic stock or other human usage at all. It is in these areas that most of the recent study of the grazing behaviour of wild animals has been undertaken, especially at such places as the Serengeti Research Unit in Tanzania. The problems that have attracted attention concern generally the results of competition for food, for instance between elephants and rhinoceros for browse plants in Kenya's Tsavo Park. Such problems are not only the result of human pressures outside the areas concerned; generally speaking they arise among animals that are too big to be regularly controlled by large carnivora such as lions. Lions undoubtedly kill hippopotamus sometimes, rhinoceros rarely, and even elephants very rarely, but in general the populations of these very large and powerful animals must be controlled by other factors than predation.

In several areas where elephants have increased very greatly in numbers, such as the Murchison and Tsavo Parks, Luangwa Valley, and even parts of the Kruger Park, the problem is one of habitat destruction. There can be no question of doubt but that in Tsavo, Murchison and Luangwa, the elephants have destroyed large tracts of woody vegetation, which tends to be replaced by perennial or semi-perennial grassland. In the Murchison Falls Park the elephants have been increasingly confined by cultivation to the park but not in Tsavo. They could perfectly well go into dense *Commiphora* woodland south of the Mombasa-Nairobi railway line, but generally they do not do so, for they are liable to be killed, either legally or illegally, in that area. At times it seems that the elephant is too intelligent for its own good.

The destruction of woody vegetation means a reduction of habitat formerly available for such species as giraffe and lesser kudu in Tsavo, while that for grazing animals such as oryx, common zebra, buffalo and gazelles is increased. The rainfall and soil being what they are, perennial grass plains inevitably replace the *Commiphora* woodland. A very rich and varied population of birds associated with *Commiphora* woodland disappears, and is replaced by another associated with perennial grasslands that is poorer both in number and in variety of species. What happens to insects no one knows, though doubtless entomologists could make an intelligent guess. In some cases, as in Murchison Park, this destruction appears to be irreversible. Here, even if all the elephants were exterminated, the fierce fires that sweep annually through the tall grassland would effectively prevent regeneration of tree species. In a drier area, such as Tsavo, where a three-year-old *Commiphora* seedling may pass unscathed in a light fire, this may not be so.

The 'elephant problem' has so far generated more heat and emotion than any other, the conflict being between the obvious necessity for some kind of management and the revulsion aroused by the idea of first protecting a large number of elephants and then killing them because they eat too much. However, funds have at last been allocated to tackle the problem effectively and research should provide the guide-lines for management.

When it comes to the smaller ungulates, from buffalo and giraffe to gazelles and dikdik, two problems appear paramount, at least in areas outside national parks where some conscious effort may be made to utilise wildlife as a valuable resource: what is the maximum sustained yield that can be realised from a mixed population of wild ungulates; and how is it to be harvested and sold? I think it could be accepted that while there is evidence to show that in certain areas wild animals can produce as much or more meat per acre as domestic stock, nowhere in Africa have wild animals been managed with the same attention to details as a skilled rancher would practise in regard to his herds. This is partly because research on food habits and other fundamental aspects of wild animal behaviour is far from complete, though the strides made in the last decade are extremely striking. It is certainly essential to know whether wild animals, given effective and good management as opposed to being merely cropped at intervals, can produce not only more, but perhaps much more protein per acre than can domestic stock, with less damage to the environment as a whole.

The harvesting of wild animals for food is nowadays regarded as one of the principal justifications for maintaining large numbers of wild animals outside national parks or special reserves. Some animals which it is considered desirable to conserve, such as gorillas or crocodiles, do not lend themselves to this approach, but it applies to the majority of wild herbivores and it can be specially important in tsetse-infested areas. The difficulty is how to do it economically and how to distribute and sell the products in possible consuming areas.

The solution of all these problems, whether of competition between man and wild animals, or of conserving or harvesting wild animals and





Plate 2 AND SOME GO DOWN . .

Plate 3
AND THE GERENUKS
GO HALF-WAY

These three photographs,
plates 1-3, by
Norman Myers illustrate
how wildlife in Africa
uses all levels of the
vegetation. Giraffes more
often browse the higher
branches than graze;
elephants do both; the
gerenuk is specially adapted
for reaching the lower
browse levels.





Plate 4
ELEPHANT DAMAGE. These dead and dying trees in Murchison Falls National Park in Uganda show what can happen when elephants get out of balance with their habitat. *Richard Fitter*

their habitat, in the end resolves itself into sound land management based upon the results of investigation and research. It is generally true to say that land, including almost all grazing land in Africa, is badly managed by human beings. For any area that is well managed to produce high yields on a sustained basis one will see a thousand times that area exploited haphazardly and producing at a fifth of its potential or less. The problem of conflict between man and wild animals has been intensified especially in the last 30 years, by the expansion of the human population, which has not generally been accompanied by an intensification of land use practices – rather the reverse. It can be solved by a rational approach and intelligent land use. But it will not serve mankind to destroy the remaining populations of wild animals by expanding the present generally inefficient systems of land use. In that way he destroys a resource which may be of very great value to him and which may well, in certain areas, be a superior resource to the domestic stock that was all introduced to the continent within comparatively recent historical times.

Should the Elephants be Killed?

ELEPHANT populations appear to be out of balance throughout Africa. So far attention has focused mainly on the situation in Uganda's Murchison Falls and Kenya's Tsavo national parks, where elephant damage has been spectacular, but the Kruger park in South Africa also has the problem. In Tsavo and Murchison a build-up in the elephant herds, which are hemmed in by human settlement, agriculture and forestry and unable to emigrate as was once their natural safeguard, has led to destruction of trees and a great increase in the grassland areas. This, coupled with opening up by roads, has resulted in more and severer fires. For the elephants this means a lack of shade and browse, the latter particularly important in the dry season, for without browse they have to rely for food on the grasses just at the time when these are least nutritious, and the elephants then suffer from nutritional deficiencies. These in turn probably cause the lowered fertility of the herds revealed in the longer calving intervals and delayed sexual maturity. These factors, coupled with increased calf mortality (38 per cent in the south bank population in Murchison Falls) – which is probably the result of heat stress following the lack of shade and lowered nutrition – are leading to a population crash which in Murchison is well under way and in the Tsavo probably in the early stages.

These are the conclusions of Dr R. M. Laws, who has studied both populations intensively, and I. S. C. Parker, published in a paper *Recent Studies on Elephant Populations in East Africa*.^{*} The authors suggest that the self-regulatory mechanisms of the elephants for reducing their numbers – longer calving intervals, delayed sexual maturity, increased calf mortality – may have been adequate in the past when coupled with migration to other areas, but today, with the elephants hemmed in by cultivation, they are not sufficient to bring population stability, and the

^{*}Symposium of the Zoological Society of London 1968, No 21.