Supplement to *Koedoe* 1984: 11-20

THE KALAHARI ECOSYSTEM

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Abstract – Our present knowledge of the functional processes within the Kalahari ecosystem is insufficient to provide a total understanding of the system. In this paper the uniqueness of the Kalahari ecosystem is discussed, with special emphasis on its faunal and floristic components as well as the remarkable micro-ecosystems which are encountered.

Introduction

The term Kalahari was derived from a black tribe, the Kgalagadi, who used to inhabit this area. The word as we know it today was probably used for the first time by Dr. Andrew Smith in 1834.

The Kalahari stretches from the Orange River to tropical Africa and is described as the largest continuous sand area in the world. The concept of the Kalahari is confused by the fact that Passarge (1904) and Wellington (1958) included the well-watered Okavango Delta and the Makgadigadi internal drainage system in a description of the Middle Kalahari. Others interpret the Kalahari as an arid sandy area with no surface water. The latter interpretation suits me better, and I do not construe the Okavango Delta as part of the Kalahari *sensu stricto*.

It is irrelevant whether the Kalahari is accepted as a desert or semi-desert. It is of importance, though, to acknowledge that it forms part of the South West Arid biome. Two other such areas occur in Africa, namely the Somali Arid and Sudan Arid.

In recent years a gradual shift of emphasis has taken place in the study of ecosystems. It has moved away from the mere description of the structural components to the study of energy flow, nutrient cycles, productivity and other functional aspects. We have a reasonable knowledge of the structure of the Kalahari ecosystem, because there is a fair amount of data available on the landscape, the geology and geological history, the soils, the climate, the vegetation and animals, but we do not know enough about the functional relationships as yet. Consequently, we do not have a total understanding of the Kalahari ecosystem and therefore it is difficult to obtain a holistic view of the situation.

I have chosen the easy way of surveying the ecosystem, namely by discussing a few ecological phenomena which give the Kalahari its particular identity thereby accentuating its uniqueness and difference. There are a number of facets which distinguish the Kalahari from other biomes, and I will take a closer look at the

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wonder of the Kalahari ecosystem, the distinctive character of its vegetation and animals and the influence of man on this ecosystem.

Vegetation

In an arid ecosystem food, water and shelter are the most important resources competed for. As far as the vegetation is concerned, I am going to refer briefly to a) plants as a source of food and water and b) the role of trees in the Kalahari.

The Kalahari vegetation is not a typical desert vegetation and the large number of ephemerals which occur is a special characteristic. These are annuals distinguished by a short life cycle. As soon as it rains during the growing season, the seed immediately germinates and the life cycle is completed in an unbelievably short span of time. It is an important source of food for all species of game and has a great influence on the migratory patterns of the larger species.

The annuals in some parts of the South West Arid are of the most beautiful examples of South Africa's wealth of flowers, and there could hardly be any other place in the world where so many plant species occur which can be used as a source of water by man and animal.

The best-known of these is the tsama (*Citrullus lanatus*), which is the most important source of food and water in the Kalahari. I regard it as the wonderplant of the Kalahari, because it is utilised by many animal species and it is the only source of water for the Bushmen over long periods of time. The latter also use it as a source of food, either raw or cooked.

Apart from the tsama, there are also the different types of wild cucumbers, as well as the large number of survival plants in the form of bulbs and tubers and other growths which occur subterrestrially. Unfortunately I do not have a list of all the underground growths utilised by animals, but if one regards all the fresh diggings by gemsbok and other species of game, porcupines and other rodents, encountered in the Kalahari every morning, one realises what great food potential lies beneath the surface of the soil. It is of immeasurable value to survival in an arid ecosystem in particular.

Trees play an important part in providing food and shelter for a variety of animals in all biomes, but in arid areas where it is dry and hot, the tree plays an even greater role than in other ecosystems. Where there are trees, there is life.

A tree offers shelter and nesting for birds; it is the permanent home of the tree rat *Thallomys paedulcus* and certain reptile species; it provides shade against the searing heat for antelopes and other animals; it is the lair of the lion and leopard and many other smaller mammals; the pods of the camel thorn and other *Acacia* species are important sources of food, while the animals eating it play an important role in the distribution and germination of the seed. Life in the Kalahari to a large extent revolves around two trees, namely the camel thorn *Acacia erioloba* and the shepherd's tree *Boscia albitrunca*.

The trees of the Kalahari also play an important role in the lives of insects and other invertebrates, although indirectly at times. A good example is the sand tampan *Ornithodornus savignyi* which is characteristic of the Kalahari sandveld and depends on game for food, on sandy soil and shadow provided by a tree. Any of these three components can have a limiting influence on its distribution.

It will suffice to say that the survival mechanisms of mammals are of the most dynamic aspects of the Kalahari ecosystem. Other aspects of mammal ecology which I would like to mention, are energy relationships, one of the fundamental concepts in modern ecology which is of great importance in an arid area.

Just as a water balance is of importance, there also exists an energy balance which means that the energy which enters an ecosystem, must be equal to or exceed the energy consumed. This phenomenon places serious restrictions on individual animals as well as populations. The energy available for herbivores, and thus also for carnivores, is supplied by the primary producer, namely plants, and the amount of energy produced is determined by the soil, vegetation, sunshine, rainfall and temperature of the environment. Should any of these factors display large fluctuations from year to year, the amount of energy that enters an ecosystem will vary accordingly. The changeability in the influx of energy indeed poses one of the biggest problems for the fauna in an arid area such as the Kalahari.

Not much is known about the energy relationships of the mammals of Africa, and even less is known about the mammals of the arid areas.

According to a tentative model of energy flow in the Serengeti ecosystem, mammals utilise about 15% of the total amount of annual primary production. The rest of the primary production is removed by invertebrates and fire.

Neither is much known about the predator-prey energy relationships. In the Serengeti it was determined that about 30 000 kg/dry weight of food per year is necessary to maintain one cheetah, which represents a relationship of cheetah : prey : vegetation of 1 : 55 : 512.

The maintenance of predators in an ecosystem is very expensive in terms of energy. According to Delaney & Happold (1979) the relationship between the cheetah and its prey is representative of all carnivores, but it seems as if this statement is not applicable to the Kalahari lion *Panthera leo vernayi*. I cannot comment about other carnivores. Compared to the cheetah : prey mass relationship of 1 : 55, that for the Kalahari lion is 1 : 18. I do not know the food intake of the lion's prey animals, so the energy pyramid cannot be completed.

However, I do know that a lion utilises relatively less energy than a cheetah to maintain itself in its ecosystem, and it is also possible that the predators which occur in an arid ecosystem eat less than those in other ecosystems.

This strengthens the hypothesis that the number of lion and other predators is restricted by their own food resources and that predation plays a small part in the regulation of prey population numbers.

Micro-ecosystems within the Kalahari

Since it is beyond my comprehensive faculty to totally grasp the larger Kalahari ecosystem with all its biotic populations and abiotic components, I prefer to look (perforce by isolation) at smaller ecosystems which exist within the larger ecosystem instead.

What are the requirements for a system to be regarded as a smaller ecosystem? As far as I am concerned, an entity can be regarded as an ecosystem as long as all the main components are present and cooperate in obtaining some or other form

of stability, even only for a short while. A temporary pool of water is a classical example of a short-lived ecosystem and examples occur in the Kalahari on an irregular basis. However, allow me to refer to four smaller ecosystems which function on a permanent basis and have been in existence for millennia and which have just as much functional stability as the larger Kalahari ecosystem.

One of the few thorough studies on aspects of the ecosystem in the Kalahari, is the work of Parris (1976) on the Kalahari pan ecosystem in which the interaction of biotic and abiotic components is described. The interactive role played by vegetation, animals, soil, water and wind in creating and maintaining the pans which play such an important role in the lives of the animals, may be of greater importance than that of water itself. In this study most of the basic components of an ecosystem are present and it is a beautiful example of a micro-ecosystem.

Another remarkable example of a small ecosystem which contains all the components of a large ecosystem, is the nest of the social weaver. This bird mainly nests in camel thorn trees, though other trees and telephone posts are also used. The shelter provided by the nest reduces the effect of the daily temperature fluctuations and is a good example of a microclimate in an environment characterised by extreme temperatures and unfavourable moisture conditions. It is rainproof and provides shade in summer, insulation against the cold in winter, while a relatively constant degree of moisture is maintained inside the nest. The effect of such a favourable microclimate enables the birds to breed at any time of the year. Reproduction seems to be independent of the photo period, but can probably be triggered by rainfall which will ensure a substantial source of food for the young birds.

Unluckily for the birds this nest also provides shelter for a number of other animals. Some of these are harmless, such as lizards and certain smaller bird species. The giant eagle owl *Bubo lacteus*, and to a lesser degree the martial eagle *Polemaetus bellicosus*, use the roof of the nest as a platform for their own nests. The pygmy falcon *Poliohierax semitorquatus* sometimes nests inside a social weaver nest. It is known that they will eat some of the eggs and young birds, but they do not seem to be a serious threat. The only real predator who shares the nest of the social weaver, is the Cape cobra *Naja nivea*, which can wipe out a whole colony of young birds. These birds have a better chance of survival by breeding during winter when the snakes are inactive.

I have already mentioned that I regard the tsama as the wonderplant of the Kalahari. Maybe the shepherd's tree should have this honour, but let us call this tree the wondertree of the Kalahari. The role played by this tree cannot be overestimated. No wonder Palgrave (1977) called it "the tree of life". Bothma (1982a, 1982b) wrote two interesting articles on the shepherd's tree in which he illustrated what an important source of food and shelter it provides for different species of animals and how this tree with its overhanging branches creates an ideal microhabitat for the larger predators and their young. Not only does it create ideal shelter, but the temperature of the sand under the tree can be up to 21 °C lower than that of the sand in the open which may have a temperature of 70 °C.

Over the years I have noted the types of tree under which the Kalahari lion rests up during the day, and in 90% of the 150 observations lion used shepherd's trees for this purpose. I have never found young lion cubs in the Kalahari under any other tree than a shepherd's tree.

This plant provides shelter for large species of game and small mammals alike. Innumerable insects hide in the dense branches. In the cool sand beneath the tree the sand tampan occurs, while the giant millipede and many other invertebrates, lizards and geckos occur on the surface of the soil. The social weaver nests in this tree, and it provides food and shelter or a place to nest for many other bird species. With the interaction of so many biotic and abiotic components this is a good example of a micro-ecosystem.

The fourth micro-system I would like to mention is the one which occurs below the soil and which has probably reached its maximal development in the Kalahari with its extensive sand cover. An outstanding characteristic of the Kalahari is the occurrence of thousands, probably millions, of holes and tunnels in the sand and out of which an unbelievable variety of animal species appear at day or night to carry out their activities.

It may be far-fetched to state that these underground inhabitants are functionally related, yet they form a distinctive community with its own microclimate, to a great extent attached by an underground habitat, sometimes by the same food web, or maybe only by their daily contact.

While the shepherd's tree is the rendezvous point above the ground for many animal species, the ant-bear hole fulfils this role under ground. The following mammals use ant-bear holes for shelter, escape and breeding purposes: leopard *Panthera pardus*, spotted hyaena *Crocuta crocuta*, brown hyaena *Hyaena brunnea*, Cape wild cat *Felis lybica*, aardwolf *Proteles cristatus*, black-backed jackal *Canis mesomelas*, various smaller predators and the porcupine *Hystrix africaeaustralis*. Smithers (1971) mentioned that the python *Python sebae* lays its eggs in ant-bear holes, and it can be accepted that other snakes such as the Cape cobra, and most probably lizards will also make use of these holes. The Ant-eating Chat *Myrmecocichla formicivora* sometimes makes its nest in the roof of an ant-bear hole.

Thus the ant-bear *Orycteropus afer* plays an important role in the ecology of this ecosystem, because it provides a home with favourable temperature and moisture conditions to a large variety of animal species. Since the inhabitants of ant-bear holes usually only make use of it on a temporary basis as escape or shelter or for breeding purposes, it is difficult to describe it as a functional unit. But when a hyaena gives birth to her young and raises them there, maybe for several generations, there may be a functional stability for a period of time during which the soil, certain physical factors, one or more animal species and the surrounding vegetation play a part.

The smaller holes and tunnel systems which are characteristic of the Kalahari and which have been described *inter alia* by De Graaff & Nel (1965) are utilised on a much more permanent basis (De Graaff & Nel *op. cit.*). They identified six plant species used for nesting purposes in the tunnel system of the Karoo rat *Parotomys brantsii*; the associated fauna consisted of a lizard, four types of scorpion and various types of beetle, which all lived in harmony with the Karoo rat in a very favourable microclimate as far as moisture and temperature are concerned.

Nel (1967) found seed of the devil's thorn *Tribulus terrestris*, the mesquite tree *Prosopis* sp. and various grass species in the tunnel system of the short-tailed gerbil *Desmodillus auricularis*. The associated fauna consisted of three types of lizard, two scorpions, and a large number of millipedes.

Another type of community occurs in the tunnels of the ground squirrel *Xerus inauris*. These rodents live in colonies, and the yellow mongoose *Cynictis penicillata*, the suricate *Suricata suricatta* and possibly also smaller rodents cohabit with it. According to Smithers (1971) the yellow mongoose may sometimes prey on the young of the ground squirrel.

I think the underground vegetation and animal life of the Kalahari are its most important distinguishing characteristics.

Man in the Kalahari ecosystem

A well-known ecologist, Robert Smith (1974), said the following regarding the basic concepts of an ecosystem: "The ecosystem has historical aspects; the present is related to the past, and the future is related to the present." In order to see an ecosystem in perspective, one may not ignore its history.

It is not always realised that the Kalahari of today is not necessarily the Kalahari which existed a thousand years ago. Even as recent as 1850 permanent water occurred at many places in the Kalahari. This water disappeared, however, and caused great changes in the game populations.

Animals which are dependent on water, such as buffalo *Syncerus caffer*, zebra *Equus burchelli*, elephant *Loxodonta africana* and rhinoceros *Diceros bicornis*, disappeared while other species such as the gemsbok *Oryx gazella*, eland *Taurotragus oryx*, red hartebeest *Alcelaphus buselaphus caama*, springbok *Antidorcas marsupialis* and probably also the blue wildebeest *Connochaetes taurinus*, flourished.

If we go back further, to the Middle Stone Age 20 000 to 100 000 years ago, we find that giant zebra *Equus capensis*, giant buffalo *Pelorovis antiquus*, dwarf springbok *Antidorcas bondi*, and possibly also giant hartebeest, occurred in the Kalahari. The presence of the zebra and buffalo indicates that the climate must have been cooler and moister than at present.

The veil is also slowly being lifted from the history of man. Artefacts dating from the Earlier Stone Age more than 100 000 years ago, are being found along the riverbeds in the Kalahari.

One gets a clear picture of man and his activities in the Later Stone Age (20 000 BC to the 20th century AD). The people of this period were the San Bushmen and their ancestors. The terms San and Bushmen are used rather loosely in the following paragraphs.

The Bushmen are the oldest Kalahari dwellers and played an important role in the Kalahari ecosystem. However, they also lived in a wide variety of environments apart from the Kalahari — the Karoo, the Bushveld, the Lowveld, the Highveld, and even the Drakensberg. The physical characteristics which distinguish the Bushman, such as a childlike appearance, a small posture and steatopygia, are not desert adaptions. Neither anatomy nor physiology, but his cultural adaptability, has enabled him to inhabit such a wide variety of environments.

The San plays a dual part in his ecosystem: he is a hunter and gatherer of veldfood. He hunts a wide variety of animals: insects, snakes, tortoises, birds, rodents (mice, springhares and porcupines), predators such as various types of jackal and even cheetah, and all types of available game from steenbok to eland and giraffe. The

San does not waste any food, and therefore he kills only as much as he needs. His method of hunting (with bow and arrow) and by using traps, does not really disturb the game. He has very little impact on the environment.

One of the most remarkable aspects of the San's life in a hunter-gatherer economy, is his dependence on veldfood and his territorial behaviour. Veldfood means more to them than meat and more than half of his diet consists thereof. Tsama, the gemsbok cucumber *Acanthosicyos naudinianus*, wild cucumber *Cucumis hookeri*, in fact everything eaten by wild animals, appears on the San's menu, and the tsama in particular is indispensable as a source of food and water.

According to Campbell (1976) some Bushman diets consist of more than 90% of vegetable matter. More than 200 types of edible plants, which are utilised by them in some form or another, occur in the Okavango. The variety will be much smaller in the dry, waterless Kalahari and Silberbauer (1965) mentioned 34 plant species utilised by these people in this area, but the actual number is probably much higher.

Robert Ardrey (1967) said in his well-known book *"The Territorial Imperative"*: "Man is as much a territorial animal as is a mocking bird singing in the clear Californian night." Just as many animals have a territorium where they hunt and live and which they defend against other animals of their kind, each San group has its own area outside which they will not hunt or gather food. Their way of living reminds one of the hyaenas of the Ngorongoro Crater where the floor of the crater is divided into a number of territoria. A hyaena will never hunt outside its territorium, and if it is pursuing an antelope, it will not follow its prey beyond the imaginary borders of the territorium. Such an action could result in a fight. According to Ardrey a Bushman will not follow even a wounded animal into another group's territorium. As a result the San is a nature conservationist. They work sparingly with veldfood and game in their own territorium and will never scare away the game from their area.

From about 200 BC Black stockfarmers moved into the Kalahari from the northeast and north of Botswana, and they had a serious influence on the habitat. Their hunting methods also differed from those of the Bushmen. While the San used bow and arrow and traps, the Blacks organised large hunts and were armed with kierie, assegai and axes. They even used dogs.

It is not certain when the first White farmers settled in the Kalahari, but their farming activities, such as fences, water installations, changing the habitat, hunting with rifles and the use of poison, had a great impact on this area. Man's influence had a wide impact. The fences which were erected to control foot and mouth disease and other illnesses, in many instances cut right across the traditional migration routes of the wildebeest, zebra and maybe other animals too. This had a destructive influence on the blue wildebeest in particular.

According to Silberbauer (1965) a game census executed in 1964 indicated that fresh carcasses counted along one of the fences in Botswana represented one-tenth of the remaining animals. In an article published on 23 May 1983 Mr. Stanley Johnson, Conservative Member of Parliament in England and Vice-President of the EEC's committee on environment and public health, said, among other things, the following about the fences in Botswana: "Unseen and unheard, a disaster is threat-

ening the herds of animals which inhabit one of Africa's last great natural reserves. I have just been in Botswana and seen the dangers facing the wildebeest, hartebeest, elephant, buffalo and zebra roaming the Kalahari.

In its simplest terms, the problem is fences.

The most notorious barrier built before independence — the Kuke fence which has shut off wildlife from its watering places in the Okavango Delta and along the Boteti River — has resulted in the death, directly or indirectly, of hundreds or thousands of animals. More than a quarter of a million of wild animals die in the country as a whole each year because of the fences."

Conclusion

There are few areas in the world which contain so many exciting components as the Kalahari ecosystem: the historical and alas diminishing migratory movements of its animals, its remarkable sand-dunes, its survival problems, its underground plant food, its underground animal community, its remarkable micro-ecosystems, its primitive territorial man; apparently unattached components, but then I remember the words of Leopold (1966): "The land is one organism. Its parts, like our own parts, compete with each other and co-operate with each other." This is how we must regard the Kalahari: one ecosystem, one giant organism, the parts of which compete with each other but also live together in harmony.

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