1990. Vertebrate Pest Management, a Training Manual, Joe E. Brooks, Ejaz Ahmad, Iftikhar Hussain, Shahid Munir and A. Aziz Khan, editors, pgs. 9-16.

PRINCIPLES OF ECOLOGY AS THEY RELATE TO VERTEBRATE PEST MANAGEMENT

By Joe E. Brooks

A. General Nature of Environmental Responses

1. General Concept of the Ecosystem

The *ecosystem* is the basic functional unit of ecology. The ecosystem includes the non-living or *abiotic* environmental substances and gradients, such as water, carbon dioxide, calcium, oxygen, carbonates, phosphorous, temperature, moisture, winds and sunlight, and the *biotic* components - plants, animals, insects and microbes. These all interact in a fundamentally energy- dependent fashion. The abiotic physico-chemical environment and the biotic assemblage of plants, animals and microbes comprise an ecological system, or ecosystem. The ecosystem acts as a whole and all its parts are interconnected.

2. Concepts of Habitat and Ecological Niche

Ecologists use the term *habitat* to mean the place where an animal lives, and the term *ecological niche* to mean the role that the organism plays in the ecosystem. For example, lesser bandicoot rats would occupy the agroecosystem habitat of irrigated wheat, rice and sugarcane fields in the central Punjab in Pakistan. This is the rats' "address", so to speak. In these fields it is an herbivore mainly, eating the stems and grains of the several crops and it is in turn eaten by jackals, hawks, and owls. Its ecological niche is its "profession" or the part it plays in the ecosystem, in this case an herbivore, a primary consumer, serving as supplementary food for several carnivorous (meat-eating) animals.

B. Energy in Ecological Systems

1. Energy Flow in the Ecosystem

The biotic and abiotic parts of the ecosystem are linked by a constant exchange of materials - nutrient cycles - driven by energy from the sun. The basic pattern of energy and material flow in the ecosystem is shown in Fig. 1. Plants manufacture organic compounds, utilizing energy obtained from sunlight and nutrients from soil and water. The plants use these compounds as a source of building materials for their tissues and as a source of energy for their maintenance functions. To release stored chemical energy, plants break apart organic compounds into their original inorganic constituents - carbon dioxide, water, nitrates, phosphates, etc., - thus completing the nutrient cycle.

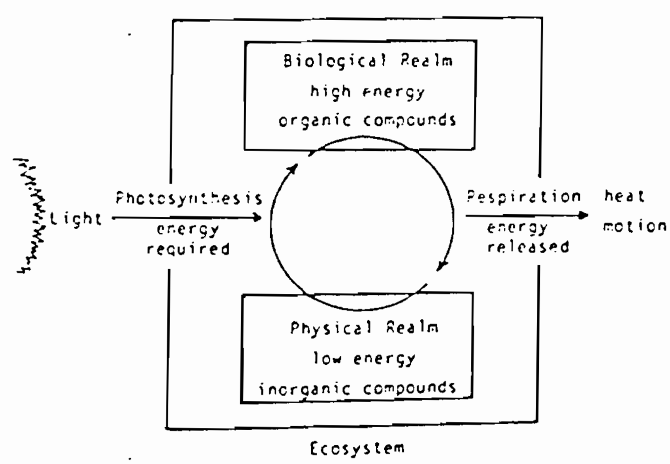

Fig. 1. Schematic diagram of the flow of energy through the ecosystem and the cycling of chemical nutrients within the system.

2. The Food Chain and Trophic Structure

Plants make their own "food" from raw materials, and are known as *autotrophs*, literally self-nourishers. Animals obtain their energy in ready-made food by eating plants or other animals; therefore they are referred to as *heterotrophs*, meaning nourished from others. The specialization of living forms as food-producers and food-consumers creates an energetic structure, called the *trophic structure*, in biological communities, through which energy flows in nutrients cycles. The food chain from grass -> grasshopper -> sparrow -> snake -> hawk depicts the path of organic materials and the energy and nutrient minerals they contain (Fig. 2). Each link in the food chain, each trophic level in the community, dissipates most of the food energy it consumes as heat, motion and sometimes, light (luminescent organisms). None of these energy forms is useful to other organisms. Hence, with each step in the food chain, the total amount of usable energy that passes through to the next higher trophic level becomes smaller.

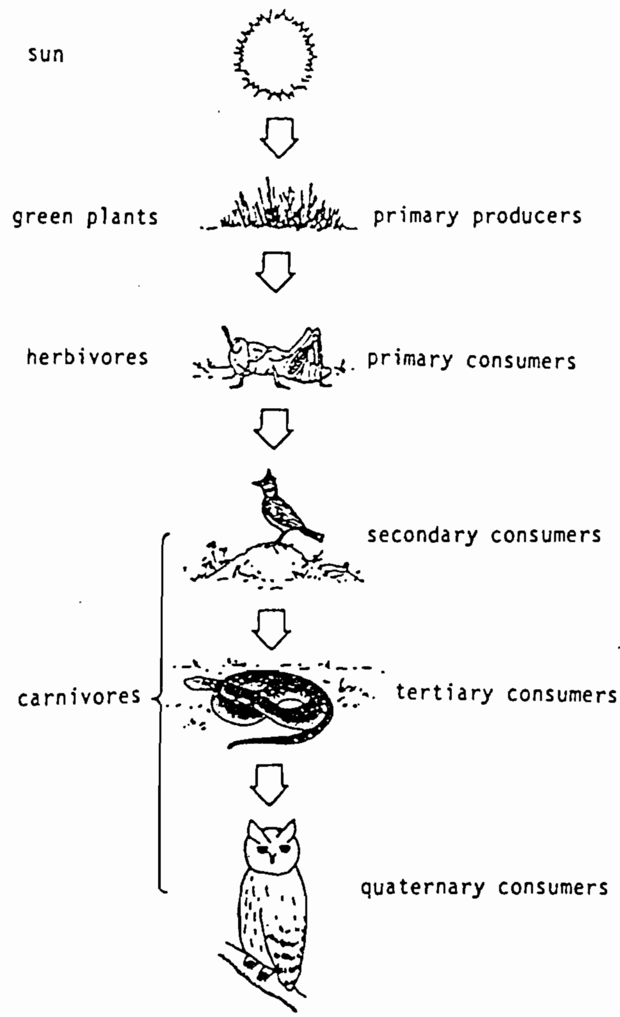

Fig. 2. A simplified terrestrial food chain showing the sequence of trophic levels.

3. Ecological Pyramids

If each trophic level in the community is represented by a block whose size corresponds to the productivity of the trophic level, and then the blocks are stacked on top of each other with the primary producers at the bottom, an *ecological pyramid* is obtained (Fig. 3). The structure of the pyramid will vary from community to community depending upon the ecological efficiency of the trophic levels. They illustrate the sharp decrease in the availability of energy at progressively higher trophic levels.

In vertebrate pest management we are concerned with where the pest species fit into the ecosystem, the role they play and the interactions they exert upon other members of the ecosystem. We are concerned that the vertebrate pest management methods we use have the *least impact* upon the ecosystem.

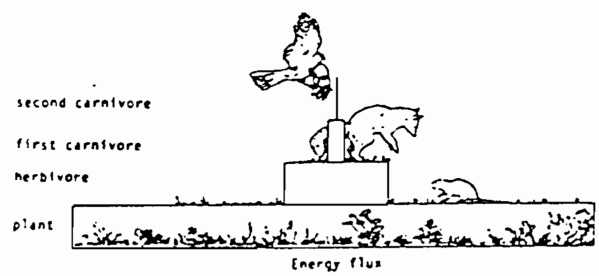

Fig. 3. Ecological pyramid based upon the net productivity of each trophic level in the ecosystem.

4. Concept of Productivity and Other Characteristics of Ecosystems

We have seen that ecosystems have a structure and the components perform functions which are essential to maintain the integrity of the system. There are 4 other characteristics of ecosystems that require brief mention: *productivity, maturity, stability*, and *species diversity*. To illustrate:

Compare a wheat field with a forest (Table 1). The field has very few species of plants and animals, the forest has many. The biomass (B) of the wheat field is small as compared to that of the forest. If, however, we compare the amount of energy fixed (productivity = P) in relationship to the biomass we find this ratio (P/B) is much higher in the wheat field than it is in the forest. Much of this production, of course, is harvested by man in the field, while that in the forest passes through many hundreds of species. If the field is abandoned, the wheat species soon becomes extinct and is replaced by various weeds and grasses. If the area is not burned, shrubs and trees soon invade and the area eventually reverts to forest. The field, then, is highly unstable and immature, while the forest is mature and relatively stable. The forest tends to moderate the extremes in the physical environment and provides conditions suitable for a much greater diversity of animal species than does the wheat field, where temperature and moisture may fluctuate markedly over the course of a day.

Table 1. Comparison of an agroecosystem (wheat field) with a natural ecosystem (mature forest).

Characteristics	Agroecosystem (Wheat field)	Natural Ecosystem (Mature Forest)
Number of species of plants & animals	Few	Many
Biomass	Small	Large
Productivity	High (production harvested by man & removed)	Low (production passes through many hundreds of species)
Stability	Highly unstable (wide fluctuations in animal density)	Very stable (fluctuations in animal density very little)
Maturity	Immature	Mature

Animals of immature systems may show wide fluctuations in density. There are fewer biotic controls where species diversity is low and the physical environment is less stable. The average population density for a wheat field species will be greater than that of its forest counterpart.

C. Limiting Factors in Ecological Systems

1. Concept of Limiting Factors

One of the main problems in ecology is to understand the distribution and abundance of plants and animals. We know that many plants and animals occur only in limited areas or may be abundant one year and few the next. Even in a wheat field, the distribution and abundance of the plants may vary from one part of the field to another. Explaining these differences requires an understanding of limiting factors and tolerance levels.

Any factor that slows the rate of metabolism or potential growth in an ecosystem is said to be a *limiting factor*. Years ago the idea of a limiting factor in plants was that it depended upon whatever essential element was in short supply - thus the formulation of Liebig's *Law of the Minimum*, meaning that the essential material available in amounts most closely approaching the critical minimum would tend to be limiting. This idea was extended by Shelford 70 years later to the *Law of Tolerance*, which states that the abundance or distribution of an organism can be controlled by factors exceeding the maximum or minimum levels of tolerance for that organism. This focuses upon the ecologic requirements of plants and animals in terms of climatic, topographic and biologic factors. In some instances one or more factors might be critical or might work in combination. These factors could be divided into physical, biological, and ecological factors.

2. Physical Factors

The most obvious physical factors that can limit an organism are temperature and moisture. Other physical and chemical limiting factors are light and the nutrients and chemicals present in the soil and water. Organisms have two options in dealing with temperature conditions in their habitat. They can simply put up with the temperature as it is, or they can escape from it by some form of evolutionary adaptation. Every organism has an upper and lower lethal temperature, but these vary widely from animal to animal. Consider how a burrowing rat like *B. bengalensis* copes with extremely hot dry days in a wheat field. The hot temperature at the soil surface is moderated, first of all, by the plant stand and the shade it provides. Soil is also an excellent insulator, and at a depth of 50 cm below the soil surface, the bandicoots' burrow would register temperatures only of 25 to 26°C when the outside air temperature reaches around 38 to 45°C. Furthermore, the bandicoot closes the burrow openings before dawn and effectively seals in burrow moisture and keeps out hot, dry air. The bandicoot is nocturnal and emerges to feed only after dark, thus minimizing its exposure to the daytime heat. It avoids the need for surface water by feeding upon vegetation of high water content or by utilizing the dew that collects on plants after dark.

3. Ecological Indicators

Despite the wide range in adaptation, certain plant or animal species may serve as a useful indication of environmental conditions. The rarer species make the best indicators. For example, the decline in abundance of certain rarer range grasses that are sensitive to grazing will indicate the approach of overgrazing before it becomes apparent in the grassland as a whole. The rarer, sensitive species thus act as *ecological indicators* of the effect of limiting factors.

D. Population Ecology

We now take up the more purely biological aspects of ecology, that is, the interaction of organisms with organisms in the maintenance of community structure and function. So far we have focused mainly on the role of the great physical and chemical forces in the ecosystem. What we have not yet considered are the principles dealing with interactions within and between populations, i.e., population ecology.

1. Population Characteristics

Populations are fundamental units in ecology; they are major components of communities and ecosystems. A population is a collective group of a particular kind in the community. In practice, a population is simply all of the organisms of the same species found occupying a given space, e.g., house mice in a grain warehouse or bandicoot rats in ricefields. A population has a number of characteristics unique to itself: density, natality or birth rate, mortality or death rate, age distribution, and growth rate, to name a few that we will examine.

Density: It is population size in relation to a unit of space. As density increases in a population, crowding begins, interactions between individuals become more frequent, resources become scarce and disease epidemics and death may follow.

Birth Rate (Natality): Birth rate at which new individuals are added to the population by reproduction. For most small mammals it is virtually impossible to determine the birth rate directly because we can't conduct a complete census of all animals. For birds, it may be possible to do so because all nests in a given area could be visited and the number of newly hatched young could be counted. For small mammals, therefore we usually rely on estimates made from a small portion of the population, such as trapped animals. The number of embryos in pregnant females is frequently used to estimate the birth rate but other data, such as how often females have litters and the age structure of the population, need to be determined.

Death Rate (Mortality): Death rate at which individuals are lost by death. Mortality is usually measured by starting with a group of animals of the same age, say 100 rats, and finding how long it will take for half the group to die. The rate will depend upon what age one starts with the group, since mortality rates will vary with age. Starting with juvenile animals just out of the nest, the rate could be fairly high, say 5 to 6 weeks. If the animals were adults of 3 to 4 months, the rate might be another 2 to 3 months before half died. Mortality rates are difficult to measure in the field and good studies are few.

Dispersal: Dispersal is the rate at which individuals immigrate into the population or emigrate out of the population. Population changes frequently result from large-scale movements of animals, especially young animals, into or out of an area. These movements may take place seasonally, as after a peak breeding effort or may result from weather extremes or harvesting of crops over a wide area.

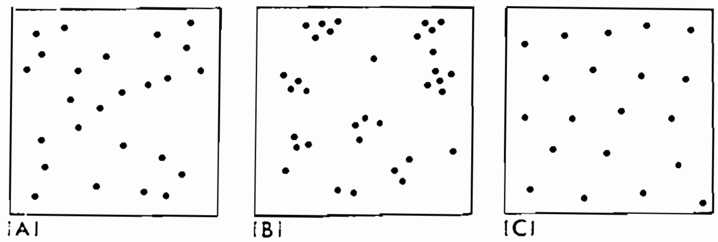

Fig. 4. Dispersion patterns of populations. A: Random. B: Clumped. C: Uniform.

Dispersion: It is the way in which individuals are distributed in space, generally in three broad patterns: 1) random distribution, 2) uniform distribution, and 3) clumped distribution (the most common in nature) (Fig. 4).

Age Distribution: It is the proportion of individuals of different ages in the population. It is important to know if the population contains a good proportion of young breeding males and females or if it is headed towards senescence, a predominance of older animals. The former indicates an increasing population while the latter would indicate one in decline.

2. Population Growth Patterns

Natural populations of animals are changing constantly. The amplitude of some numerical changes may not be detectable by casual observation or the population may reach plague proportions and then decrease catastrophically. Changes in populations can be described easily. The rate of population growth is the net result of natality, mortality and dispersal. But description and measurement are two entirely different things. Each factor contributing to population change is complex and involves interrelationships with the others. The main features can be outlined in theory.

Mainly we want to answer two things: what are the environmental factors that influence the abundance of a species in various habitats and seasons and how fast can a population increase? Is there an optional time of year for carrying out control operations? What consideration should be given to uncultivated, waste or marginal areas? At what level of reinfestation should control operations again be done? If a population is reduced by 90%, how long will it take to recover? Answers to these questions require a knowledge of population theory and an understanding of local conditions.

The growth patterns of many animal populations follow one of two general patterns: logistic or irruptive (Fig. 5A & B). There are many variations of each. Both types of population growth have a similar pattern of slow initial growth followed by a period of rapid geometric or exponential increase. In the upper stages, however, the growth curves differ markedly. Irruptive population curves are limited by sudden, often catastrophic mortality. Logistic curves achieve a gradual leveling off to a more stable asymptote. Neither pattern of population growth can be considered a law of population growth.

In general, irruptive growth patterns are found in many insect and vertebrate populations in unstable environments. They are also characteristic of disease epidemics. Logistic growth patterns are common in organisms with simple life histories, particularly in stable environments.

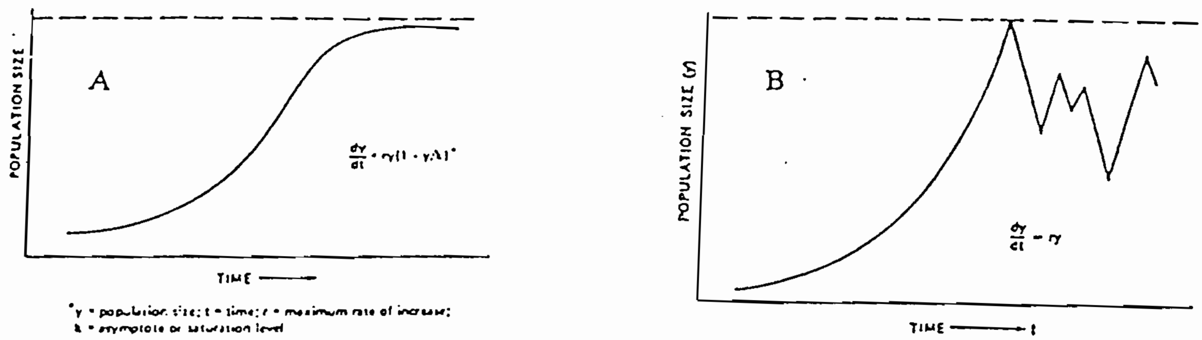

Fig. 5. Population growth pattern typical of A) logistic growth B) irruptive growth.

3. Species Interaction at Populations Level

a) Types of Interaction

At our present level of understanding, we need some framework for managing agro-ecosystems and the pest species living within. It is not realistic to consider a pest population as though it lived in a void of other species. Interactions with species other than those that provide the food base are to be expected and knowledge of these is basic to understand the total system and how it affects the target species. We will discuss only interspecific competition, predation and parasitism.

b) Interspecific Competition

Interspecific competition occurs when two or more species require a common resource that is in limited supply. It is assumed that either closely related or ecologically similar species will compete most intensively because their requirements are most similar. We have a principle that two species cannot occupy the same niche indefinitely: one will eventually exclude the other.

The main evidence for competition in the field comes from occasional observations where one species has replaced another (Norway rat vs. roof rat in Europe and USA and bandicoot rat vs. roof rat in India, Bangladesh and Burma). The mechanisms of competition are poorly understood and it is seldom possible to identify the resource which is presumably limited. Species do exist together in many cases, however - what patterns do we see? In wheat fields in Pakistan are found bandicoot rats, short-tailed mole rats and house mice. One pattern that seems evident for coexisting-species is to differ in body size; for example 20 g for house mice, 125 g for mole rats and 250 + g for bandicoot rats.

c) Predation

A predator is an animal that kills another animal for food. Since predation is a direct cause of mortality, its possible effects on population dynamics should be considered. The effect of predation on vertebrate populations is one of the most controversial topics in ecology. The problems of assessing the consequence of predation (primarily by carnivores, raptors, and snakes) on mammal populations are that they have their own density- limiting mechanisms and it is difficult to separate the effects of predation on the population from these inherent density-limiting factors.

One viewpoint about predation is that in certain circumstances predators may control a mammal population which has a high degree of vulnerability (e.g. lack of cover) and the predator populations have an alternative food supply. Otherwise, the predators would destroy their own food supply. Another, more general viewpoint, is that predators mainly take surplus animals that would soon die anyhow and if predation does reduce a prey population, the prey compensate by higher levels of breeding and increased survival of young animals. Opinions vary widely so attempting generalizations about predation are rather fruitless. As an example, past attempts to control rats by introducing the mongoose to islands in the Caribbean and to Hawaii have had no obvious success and have produced undesirable side-effects.

d) Parasites and Disease

The term parasite covers a wide variety of relationships whereby one organism lives at the expense of another, contributing no obvious benefit to the relationship and being potentially harmful to the host. Ectoparasites, such as fleas, lice, ticks and mites seldom debilitate the host unless they transmit a possibly lethal disease. More restricted use of the term parasite is applied to those organisms obliged to spend some part of their life cycle in intimate contact with the tissues of the host.

Parasites of mammals, by the above definition, could be viruses, bacteria, fungi, protozoans, helminths and insects. Of real concern is the real or potential pathogenicity of the parasite, since it is evident that in most cases the survival of the parasite and its progeny depends upon the continued survival of its host. With few exceptions, a parasite that kills its host also kills itself.

The use of pathogens to control pest mammals is an old idea. In practice, virtually nothing exists that the host does not eventually adapt to. Myxomatosis introduced into rabbit populations in Australia is the most spectacular example of biological control in mammals. About 20 years after it was introduced, the rabbit population in Australia had largely recovered, however. Possibilities for biological control of pest mammals with pathogens remain largely hypothetical. No good organism has been found, for example, in rat control, that the rat populations do not adapt to in a short time. Meanwhile, the hazards of the organism producing disease in humans, pets and livestock preclude the use of such techniques.

E. Applied Ecology

Applied ecology is the use of ecological tools and knowledge to most effectively and efficiently manage ecosystems for the maximum benefit of most organisms. Ideally, this would mean that mans' activities would have the least impact possible upon natural ecosystems. Unfortunately or not, mans' impact on natural ecosystems has been enormous and generally to the detriment of most organisms that originally lived there. The agricultural ecosystem, or simply agroecosystem, that man creates out of natural systems, is a finely-tuned, greatly simplified and highly unstable system.

1. Agroecosystem

a) Monoculture

The most productive and, in some ways, easiest agroecosystem for man to manage is the monocultural system, where one crop variety is grown over a vast area. This is one of the most unstable of all agroecosystems, however. Pests, plant diseases, effects of weather extremes, all can operate to effectively cause an almost total crop failure in times of adversity.

b) Crop Diversity

Ideally, the agroecosystem should consist of diversity and intermixture in crop types, and a large spread in planting dates to create a more stable system, less susceptible to catastrophic failure. Luckily, this is what we see in the diversified agriculture in the irrigated areas of the Punjab and Sind Provinces, less so in the barani (rainfed) areas of Punjab and NWFP. However, crop diversity can bring with it a curse as well as a blessing. By having several varieties of food crops in the fields, rodents, wild boar and pest birds are given a variety of crop types of which to attack in season, to hide in, etc. and then move on to the next crop type as the growing season advances.

2. Vertebrate Damage Control

It is essentially impossible to attempt to eradicate vertebrate pests from crop growing areas. There are too many marginal habitats, waste areas, and "reservoir habitats" in which they will survive even if rigorously eliminated from crop fields. Attempts at total eradication are not economically feasible; the first 90% of population reduction may be relatively easy and inexpensive while the last 10% would cost a fortune to achieve, if possible.

The key to vertebrate damage control in agroecosystems is to intervene as little as possible and still be able to reduce crop damage. This may mean reducing the pest populations in the crops just prior to the damage period. It may mean repelling the pest species only during the short period that the crops are vulnerable to attack. It might be as simple as exclusion measures to keep pests out of field crop situations, such as low fencing to keep desert hares from chickpea plots or electric fencing to keep wild boar out of maize fields. It might mean the simultaneous planting of one variety of field crop or advancing the date of sowing so as to avoid migratory bird populations. Other alternative methods in suppressing field populations of mammal pests involve habitat modification, e.g., removal of weed patches and scrub areas. This will create less suitable conditions for the survival of the pest species during periods when the fields are fallow.

3. Rodents and Human Diseases

Diseases and infections naturally transmitted between vertebrate animals and man are called zoonoses. Many are known to occur in rodents although not all seriously affect human health. Some diseases carried by rodents, such as brucellosis, are hardly ever transmitted to man. In contrast, the effects of a disease like plague can be devastating to the human populations and the role of rats in its transmission is extremely important.

Under natural conditions, the infections disease organisms, the host (rats) and the vector (fleas, ticks or mites) exist together as part of the ecosystem. The three kinds of organisms have a set of ecological requirements such as climatic, edaphic and vegetation conditions, and live together in a balanced relationship. The infection in rats and other rodents is often maintained permanently only in restricted areas (foci) and these are often in situations uninhabited by man so that disease transmission does not take place. Infection only occurs when man moves into these areas. For example, this could occur due to changing land use, e.g., forest clearance, agricultural development or urbanization. This brings man into a closer, more permanent association with the disease focus. Sometimes modification of the habitat can create a more beneficial environment for the host.

Plague transmission in South Africa illustrates well the above mentioned example. Man there has inadvertently created suitable habitats for the multimammate mouse (*Praomys*) in his farm buildings. *Praomys* is not the primary host of plague in this area. The main reservoir is the highveld gerbil, *Tatera brantsi*, with transmission of plague through its flea, *Xenopsylla philoxera*. This gerbil has little or no contact with man. However, when an outbreak of plague occurs, many gerbils die and *Praomys* move into the empty burrows. Because this species has a wider ecological range than the gerbil, its range extends into human habitations. Plague then spreads through this species populations and into close association with man. Spread is often accelerated through the house rat (*Rattus*) population with which the multimammate mouse comes into contact. Part of this description has been oversimplified but it illustrates the ecological complexity of the transmission route.