The ecology of *Praomys (Mastomys) natalensis* in southern Africa

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The only non-human host of Lassa virus so far identified is the multimammate mouse, Praomys (Mastomys) natalensis, *but its precise role in the natural Lassa fever cycle remains to be determined. This species is also an important link in the plague cycle in southern Africa and is one of the commonest rodents of Africa. It is a prolific breeder and can be kept and bred easily in captivity. It is thus an excellent laboratory animal, although it needs to be handled with care because it is aggressive towards man and bites readily. The current status of knowledge of its taxonomy, ecology, distribution, and role as a disease vector is reviewed, but attention is drawn to the possibly disastrous consequences of attempting to eradicate a vector species before the natural cycle of the disease and the ecology of the vector are fully understood.*

INTRODUCTION

During 1972 Lassa virus was isolated for the first time from a non-human source, the pooled heart, lung, spleen, and kidney of each of 10 *Praomys (Mastomys) natalensis* collected in Eastern Province, Sierra Leone (1). To date, no other natural non-human host has been identified. It is unknown what role *Praomys (Mastomys) natalensis* plays in the natural Lassa fever cycle. Is it the primary reservoir host? Does it act as a transmission bridge between an as yet unidentified reservoir host and man? Does it play a role in the transmission of the virus to man and, if so, how? Or is it merely a concomitant victim of the Lassa virus?

Praomys (Mastomys) natalensis, an important link in the southern African plague cycle and a highly useful experimental laboratory animal, has been intensively investigated from the points of view of its taxonomy, ecology, distribution and disease vector status by numerous workers.

A brief review is given of the current state of knowledge of this rodent, mainly within the southern African context.

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TAXONOMY

The taxonomic confusion of the African members of the family Muridae is the result of past studies that were carried out on an uncoordinated regional basis without interregional reference. It was only in recent decades that mammologists began to attempt a classification on a Pan-African basis, as a result of which it became clear that similar murids had been classified into widely differing categories by various workers. Davis (2) made considerable progress by recognizing the problem and attempting to streamline the classification of the African murids. He divided the subfamily Murinae into two broad groups on the basis of their alveolar-molar root formula (AMF): the *Rattus*-type and the *Mus*-type. Davis did not consider *Mastomys* to be a genus in its own right. Accordingly, he proposed grouping *Mastomys* (as a subgenus) together with the subgenera *Hylomyscus* and *Myomyscus* into a single genus *Praomys* (within the *Mus*-type subgroup of the subfamily Murinae). This generic classification was based on various taxonomic criteria, such as the division of the hook of the squamosal, the smoothness of the interorbital regions, and the uniform molar root pattern.

Rosevear (3), on the other hand, prefers to follow Matthey who, on the basis of chromosome studies,

considered *Mastomys* to deserve a taxonomic position as a genus. In this paper, I shall follow the example of other workers and refer to the multimammate mouse as *Praomys* (*Mastomys*) *natalensis* (A. Smith, 1834).

DISTRIBUTION

Praomys (*Mastomys*) *natalensis* is prevalent in the southern and northern savanna biotic zones (4) and is one of the most widely distributed and abundant rodents in Africa (5). It is commonly found in bush, scrub, and cultivated lands, but is completely absent only from very arid regions, such as the Namib and Kalahari deserts, and from rocky outcrops. Fig. 1 illustrates the distribution of *Praomys* (*Mastomys*) *natalensis* on the continent of Africa.

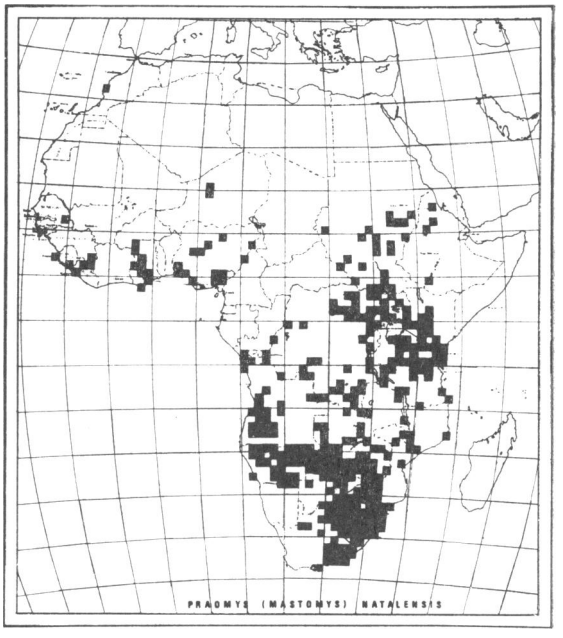

Fig. 1. Distribution of *Praomys (Mastomys) natalensis* in Africa. (Compiled from data published by Davis, 4, 22; Smithers, 12; and Rosevear, 3).

DESCRIPTION

Praomys (*Mastomys*) *natalensis* is of small to moderate size, ±10–15 cm in body length with a tail of approximately the same size (Fig. 2). The colour of the pelage varies considerably with the age of the animal and has also been noted to vary according to the terrain in which specimens are caught. The colour on the dorsal side may be grey to greyish-brown, brown or reddish buff, but it is lighter on the ventral side. A unique feature, not only for rodents, but probably for all mammals (the pig coming closest) is the large number of mammae in the female (6). These number from 8 to 12 pairs, which are continuously distributed from the pectoral to the inguinal region.

HABITS AND ECOLOGY

Praomys (*Mastomys*) *natalensis* may be regarded as a semidomestic rodent in most of Africa where it is found in close association with human habitation. Indeed, it has been suggested that its present distribution is possibly dependent on having followed early human population movements (4). Hanney (7) regards this murid as an indicator of past human settlement. The animal is nocturnal in habit and, although omnivorous and having cannibalistic tendencies, it is mainly granivorous, living on seeds of wild grasses, corn, millet, maize, and rice (8). When food is scarce it will travel several miles in search of nourishment. It is responsible for considerable damage to man's food supply inside sheds and houses, and has also been observed to cut down stalks in rice fields in Liberia (3).

In areas where true domestic rodent species, e.g., *Rattus rattus*, are present, *Praomys* (*Mastomys*) *natalensis* tends to give way (3, 5, 9). This illustrates the peaceful nature of this rodent towards members of its own and other rodent species. Rarely does it fight, which probably indicates that its territorial instinct is very weak (10). This feature is further illustrated by the fact that *Mastomys* is reluctant to make its own burrows, although it is capable of doing so in soft or cracked soil. By preference it will use burrows of other rodents, in southern Africa especially those of the gerbils *Tatera brantsi* and *Tatera leucogaster*. The occupation of such burrows is usually for nesting purposes. Shelter and refuge, on the other hand, are taken in or under anything available, whether natural or man-made, for example, outhouses, pole fences, plants, heaps of firewood, sheaves of grass, litter, refuse, sheets of corrugated iron, chicken runs, old tyres, or rubble. The multimammate mouse can climb and may be found in lofts. It is also a good floater and swimmer.

These characteristics, i.e., its easy adaptability to the different environments provided by man and wild rodents respectively, are to a great extent responsible for its success as a species. To this may

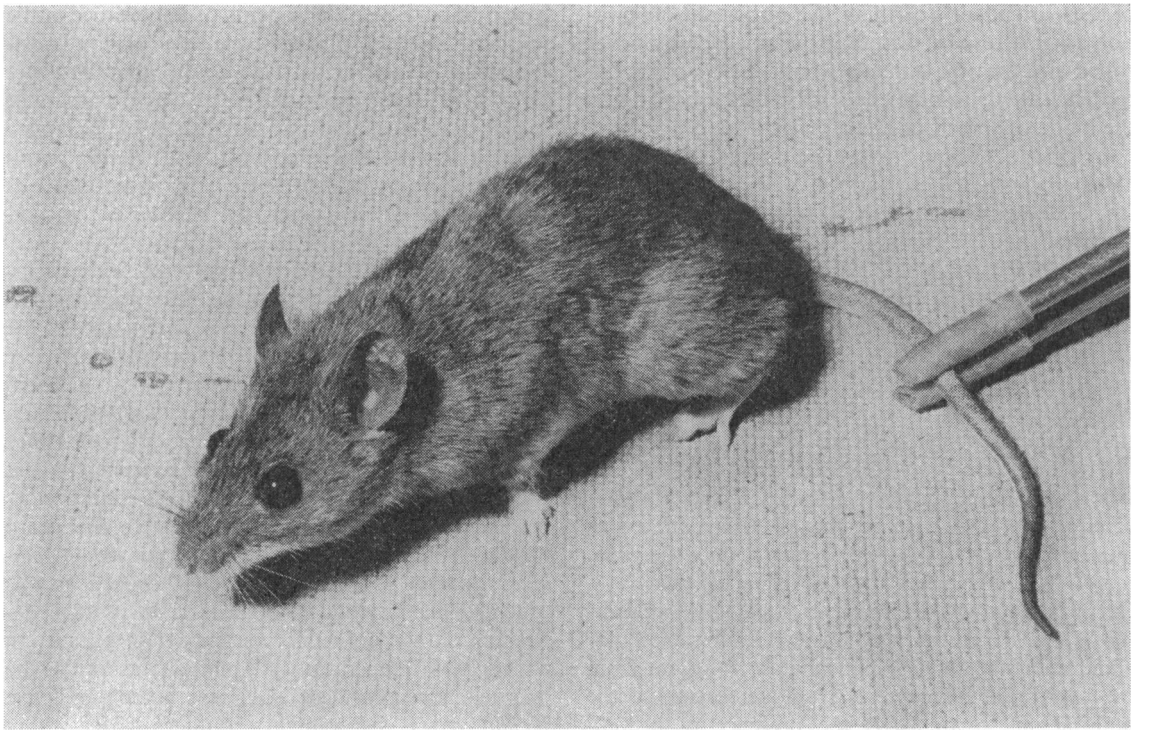

Fig. 2. *Praomys (Mastomys) natalensis.* Urination when disturbed is characteristic of the species.

be added the outstandingly prolific reproductive capacity of *Praomys* (*Mastomys*) *natalensis*. A mean litter size of 6.6–8.5 young has been established experimentally by some workers (8, 11). This is considerably more than the mean litter size of several other species of rodent tested under laboratory conditions. Clearly, the large number of mammae in the female makes it eminently suitable for raising large numbers of offspring. In addition, breeding starts at a relatively early age and the interval between litters is short.

Breeding is especially favoured by the availability of an abundant food supply. While breeding tends to take place throughout the year, a marked increase occurs during the latter part of the rainy season when ripening of grass and other seeds takes place (6, 7, 12, 13). It was also noted by Smithers (12) that the number of gravid females collected during field studies in Botswana was very low during the last 2 years of a 4-year drought period which affected the whole of southern Africa during 1962-1965. Following the end of the drought a massive rodent population explosion took place, as noted by Smithers and myself. In Sierra Leone, too, it was noted by Brambell & Davis (6) that whereas pregnant females of *Mastomys erythroleucus* could be found virtually throughout the year, a seasonal change in the rate of reproduction did occur in that breeding was most active during the latter part of the rainy season.

Praomys (*Mastomys*) *natalensis* is a clean animal, both as concerns its own body and with regard to its nest. Veenstra (10) noted that in captive animals cleanliness was of a higher standard in mated pairs than in animals that were caged without the other sex. Refuse is pushed out of the nest and droppings are rarely found in burrows occupied by this rodent. Although *Praomys* (*Mastomys*) *natalensis* is inoffensive and lives in peaceful coexistence with its own and other rodent species, it shows a certain amount of aggression towards man. It is a relatively difficult animal to handle in the laboratory because of its tendency to bite. Veenstra (10) showed that it can, however, be tamed by regular handling, but the tame state is easily lost when the animals are neglected for a few days. Two of his animals were tamed to the extent that they would regularly crawl into a pocket

of their attendant's clothing. An important observation in this respect was that the pocket was never soiled and that the animals would always come out to defaecate or urinate. This may have a bearing on the mode of spread of Lassa fever.

In 1953, a " dilute ", red-eyed mutant of *Praomys* (*Mastomys*) *natalensis* appeared in the breeding stock at The South African Institute for Medical Research and this is notably tamer than the wild type (14).

The wild type is very sensitive to stressful situations and Veenstra's observation of a female dying when a dog sniffed at her cage was repeated by myself in Lesotho when an apparently healthy, newly captured specimen died suddenly as an Alsatian dog approached the trap.

The interest in *Praomys* (*Mastomys*) *natalensis* as a laboratory animal in South Africa originated in 1939 in efforts to find an experimental animal that was more uniformly susceptible to plague than the white mice and guinea-pigs then in use (14). Davis & Oettlé (14) found that *Praomys* (*Mastomys*) *natalensis* is able to concentrate ^{131}I in the submandibular gland and that alkaline phosphatase is absent from the neutrophil leucocytes. A unique feature of the multimammate mouse is the presence of a well-developed prostate gland in the female, as first observed by Brambell & Davis (6). It was Oettlé who discovered by chance in 1953 the high rate of spontaneous adenocarcinoma of the glandular stomach that develops in this species (15).

Praomys (*Mastomys*) *natalensis* is used in our routine plague diagnostic work as well as in experimental work, such as plague vaccine trials, virulence studies, etc.

In spite of the disadvantage of aggression towards man, this rodent has many advantages over others as a laboratory animal, not the least of which is the ease with which it breeds in captivity and the large number of young that it produces. Davis (11) showed that the mean number of young born per day is 0.12 per female, which was greater even than that of a strain of white mouse investigated at the same time.

Clearly, an animal like *Praomys* (*Mastomys*) *natalensis*, which readily commutes between man's environment and that of wild rodents (in South Africa the gerbil *Tatera*), is in a good position to transmit disease from one to the other. Bubonic plague provides an example *par excellence*. The ease with which plague (and potentially other diseases) is transmitted is undoubtedly aided by the fact that the fleas that parasitize the rodents of importance in the southern African plague cycle are of low host-specificity. Thus, Davis (16) found that *Praomys* (*Mastomys*) *natalensis* is parasitized by a mixture of fleas that are normally associated with *Tatera brantsi* (*Xenopsylla philoxera* chiefly) and *Rattus rattus* (mainly *Xenopsylla brasiliensis*), in addition to its own fleas, of which *Dinopsyllus ellobius* is the commonest species.

The importance of the arthropod vector in the occurrence and distribution of zoonoses must not be underestimated. For example, whereas *Tatera* species (*T. brantsi* and to a lesser extent *T. leucogaster*) comprise the principal wild plague reservoir animals in southern Africa, the distribution of the gerbil extends well beyond the limits of the plague enzootic foci. It has been shown very clearly that plague endemicity here is determined by the combination of *Tatera* and its flea *X. philoxera*. In those areas where the gerbil *Tatera* is parasitized by other fleas but not *X. philoxera*, plague has not been known to occur in this rodent. The distribution of fleas is in its turn dependent on numerous factors, important ones being atmospheric temperature and humidity as well as the microclimates prevalent in rodent burrow systems. *X. philoxera* is distributed in southern Africa within the 600-mm isohyet of annual rainfall.

Some workers have reported that fleas tend to abandon rodents when they are unduly disturbed by handling or trapping (17) and it is quite conceivable that this may occur during hostilities, economic development programmes, large-scale bush fires, or floods. This behaviour by fleas may facilitate the spread of zoonoses.

Pulex irritans has been found on *Praomys* (*Mastomys*) *natalensis* (18). In the case of plague, if *human* ectoparasites are involved in the transmission pathways there is a more marked familial character to the outbreak than when these do not play a role (19). Table 1 shows the large variety of ectoparasites that have been found on *Praomys* (*Mastomys*) *natalensis*, many of which are known disease vectors. Some of these may be of potential importance in the Lassa fever cycle.

In the ecology of *Praomys* (*Mastomys*) *natalensis* it is also important to consider it's role in the food chain of other living organisms. Children and adults commonly hunt and catch small rodents, which are then roasted, often incompletely, and eaten. Almost invariably, *Praomys* (*Mastomys*) *natalensis* urinates when frightened and contaminates the hands of the person handling it. In view of the known persistence

Table 1. Ectoparasites found on *Praomys (Mastomys) natalensis* (A. Smith, 1834) [a]

Family	Genus and species
Calliphoridae	*Cordylobia anthropophaga* (Blanchard)
Pulicidae	*Echidnophaga gallinacea* (Westwood)
	Pulex irritans Linnaeus
	Ctenocephalides connatus (Jordan)
	Ctenocephalides felis (Bouché)
	Procaviopsylla creusae (Rothschild)
	Xenopsylla bantorum Jordan
	Xenopsylla cheopis (Bothschild)
	Xenopsylla frayi De Meillon
	Xenopsylla hipponax De Meillon
	Xenopsylla nubica (Rothschild)
	Xenopsylla philoxera Hopkins
	Xenopsylla phyllomae De Meillon
	Xenopsylla piriei Ingram
	Xenopsylla versuta Jordan
	Xenopsylla bechuanae De Meillon
	Xenopsylla brasiliensis (Baker)
	Xenopsylla morgandaviesi Hubbard
	Xenopsylla scopulifer (Rothschild)
	Xenopsylla syngenis Jordan
	Xenopsylla cryptonella De Meillon & Hardy
Pygiopsyllidae	*Stivalius alienus* Smit
	Stivalius torvus (Rothschild)
Xiphiopsyllidae	*Xiphiopsylla levis* Smit
Hystrichopsyllidae	*Ctenophthalmus acanthurus* Jordan & Rothschild
	Ctenophthalmus evidens Jordan
	Ctenophthalmus ansorgei Rothschild
	Ctenophthalmus calceatus Waterston
	Ctenophthalmus eumeces Jordan & Rothschild
	Ctenophthalmus gilliesi Hubbard
	Ctenophthalmus eximius Jordan & Rothschild
	Ctenophthalmus phyris Jordan
	Dinopsyllus apistus Jordan & Rothschild
	Dinopsyllus dirus Smit
	Dinopsyllus ellobius (Rothschild)
	Dinopsyllus grypurus Jordan & Rothschild
	Dinopsyllus longifrons Jordan & Rothschild
	Dinopsyllus lypusus Jordan & Rothschild
	Dinopsyllus pringlei Hubbard
	Dinopsyllus wansoni Berteaux
	Listropsylla agrippinae (Rothschild)
	Listropsylla chelura Rothschild
	Listropsylla dolosa Rothschild
	Listropsylla dorippae (Rothschild)
	Listropsylla fouriei De Meillon
	Listropsylla prominens Jordan
Leptopsyllidae	*Leptopsylla aethiopica* (Rothschild)
	Leptopsylla segnis (Schönherr)
Ceratophyllidae	*Nosopsyllus fasciatus* (Bosc)
	Nosopsyllus incisus (Jordan & Rothschild)
Chimaeropsyllidae	*Hypsophthalmus campestris* Jordan & Rothschild
	Epirimia aganippes (Rothschild)
	Chiastopsylla rossi (Waterston)
	Chiastopsylla godfreyi Waterston
Hoplopleuridae	*Hoplopleura captiosa* Johnson
	Hoplopleura intermedia Kellog & Ferris
	Polyplax waterstoni Bedford
Argasidae	*Ornithodoros zumpti* Heisch & Guggisberg
Ixodidae	*Ixodes* sp.
	Ixodes auriculaelongae Arthur
	Ixodes elongatus Bedford
	Ixodes nairobiensis Nuttall
	Haemaphysalis leachii Audouin
	Rhipicephalus appendiculatus Neumann
	Rhipicephalus oculatus Neumann
	Rhipicephalus pravus Dönitz
	Rhipicephalus sanguineus Latreille
	Rhipicephalus simus Koch
	Rhipicephalus tricuspis Dönitz
Laelaptidae	*Laelaps giganteus* Berlese
	Laelaps lamborni Hirst
	Laelaps muricola Trägardh
	Laelaps tillae Taufflieb
	Laelaps transvaalensis Zumpt
	Laelaps vansomereni Hirst
	Haemolaelaps glasgowi (Ewing)
	Haemolaelaps labuschagnei Zumpt & Patterson
	Haemolaelaps murinus Berlese
	Haemolaelaps taterae Zumpt & Patterson
	Androlaelaps marshalli Berlese
	Androlaelaps theseus Zumpt
Ereynetidae	*Speleognathopsis bakeri* Fain
Psorergatidae	*Psorergates oettlei* Till
Trombiculidae	*Trombicula m. mastomyia* Radford
	Trombicula sicei André
	Trombicula youhensis Abonnenc & Taufflieb
	Leptotrombidium legaci (André)
	Schongastia r. radfordi Jadin & Verc.-Grandjean
	Ascoschongastia benuensis Taufflieb & Mouchet
	Schoutedenichia benuensis (Taufflieb & Mouchet
	Schoutedenichia brachiospissi Verc.-Grandjean
	Schoutedenichia cordiformis Verc.-Grandjean
	Schoutedenichia p. panai Verc.-Grandjean
	Schoutedenichia panai luberoensis Verc.-Grandjean
	Schoutedenichia pilosa Verc.-Grandjean
	Schoutedenichia pirloti (Jadin & Verc.-Grandjean)
	Gahrliepia hypoderma (Verc.-Grandjean)
	Gahrliepia traubi Audy & Verc.-Grandjean
Listrophoridae	*Listrophoroides africanus* Radford
	Listrophoroides mastomys Radford
	Myocoptes musculinus (Koch)
Sarcoptidae	*Notoedres alepis* (Railliet & Lucet)

[a] Compiled from data published by E. Haeselbarth et al. (18) and J. R. Audy et al. (21), and from records kindly supplied by the Department of Entomology of The South African Institute for Medical Research, Johannesburg.

of the Lassa virus in urine, this tendency may play a role in the transmission of the disease to man.

During rodent die-offs—in southern Africa commonly due to plague epizootics—*Cynictis penicillata*, the yellow mongoose, which normally lives on insect material, becomes a scavenger of dead rodents. The appearance of rodent hair instead of insect chitin in its droppings is used as a criterion of abormal rodent mortality. Owls and other birds that eat small mammals must also be considered potential vectors of diseases associated with their prey.

In conclusion, a word of warning must be sounded against the eradication of a particular disease reservoir species. In South Africa a small, well-defined, and isolated plague focus exists in the Port Elizabeth-Uitenhage area. The primary reservoir host here consisted of the relatively resistant (LD_{50} 500-1000 *Y. pestis*) rodent *Desmodillus auricularis*, together with its flea, *Xenopsylla piriei*. An intensive eradication campaign had succeeded in almost totally eliminating this rodent when a renewed plague outbreak occurred. It was found that the Karoo bush rat, *Otomys unisulcatus* had become abundant and had taken over the role of perpetuating plague, as evidenced by a high seropositivity rate during the few years preceding the outbreak (20). In the attempted control of diseases such as Lassa fever, the natural cycle of which is as yet virtually unknown, the eradication of a species that plays a definite but undefined role may be disastrous.

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RÉSUMÉ

L'ÉCOLOGIE DE *PRAOMYS (MASTOMYS) NATALENSIS* EN AFRIQUE MÉRIDIONALE

La classification des Muridés africains a longtemps laissé à désirer par manque de coordination des études régionales. Il a été proposé de considérer *Mastomys* comme un sous-genre du genre *Praomys*. Mais d'autres chercheurs, se fondant sur des études chromosomiques, ont estimé que *Mastomys* méritait d'être classé comme genre.

Praomys (Mastomys) natalensis est un des rongeurs les plus abondants et les plus largement répartis en Afrique, où on le trouve couramment dans la brousse et les terres cultivées. Il s'agit d'un rongeur semi-domestique qui vit en étroite association avec l'habitat humain, mais aussi avec d'autres espèces sauvages, telles que *Tarera*, dont il utilise les terriers, principalement pour y nicher. *Praomys (Mastomys) natalensis* ne se montre agressif ni à l'égard de ses congénères ni envers d'autres espèces de rongeurs et, en cas de compétition avec des rongeurs totalement domestiques, comme *Rattus rattus*, il cède généralement la place.

En revanche, il est très agressif à l'égard de l'homme qu'il mord volontiers, mais on arrive néanmoins à l'apprivoiser en faisant preuve de patience. Les mutants de laboratoire et les souches consanguines sont beaucoup plus dociles que le type sauvage.

Praomys (Mastomys) natalensis est une animal prolifique. Ses portées, très rapprochées, comptent en moyenne de 6,6 à 8,5 petits; la reproduction a lieu tout au long de l'année, avec un maximum à la fin de la saison des pluies. Les huit à douze paires de mamelles de la femelle lui permettent d'allaiter des portées nombreuses. Ces rongeurs sont propres, tant pour eux-mêmes que pour leur nid. Malgré leur tendance à mordre, ils représentent d'excellents animaux de laboratoire, car ils s'élèvent et se reproduisent facilement en captivité.

Comme *Praomys (Mastomys) natalensis* est en contact à la fois avec l'environnement humain et avec les rongeurs sauvages, il est naturellement un bon agent de transmission des maladies, et cela d'autant plus que les puces qu'il héberge ont une faible spécificité parasitaire et se retrouvent chez plusieurs rongeurs. Le vecteur arthropode joue certainement un rôle aussi important que l'hôte réservoir dans le maintien et la transmission des maladies, et notamment de la peste. Or les programmes de développement économique et les diverses catastrophes telles que guerres, inondations ou incendies de brousse, outre qu'ils favorisent la dispersion des rongeurs sauvages parasités, amènent aussi les puces à abandonner leur hôte, ce qui est un facteur de propagation de l'infection.

Il faut insister sur la nécessité de peser soigneusement les conséquences possibles de l'éradication d'une espèce de rongeurs sauvages avant d'entreprendre toute action de ce genre, car une éradication précipitée pourrait provoquer le transfert d'une infection enzootique, comme la fièvre de lassa, à d'autres espèces, et accroître ainsi le risque de transmission à l'homme.

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DISCUSSION

ARATA: In sampling rodent populations for determination of disease prevalence it is important to understand their age structure. Rodent populations that at one point in time may comprise 70% or 80% of adult animals, may contain only 25–30% a few months later. Rates of infection (by isolation) or indication of prevalence (by serology) cannot be compared between populations (i.e., in space) or within populations (i.e., in time) unless the age structure is known.

ISAÄCSON: A couple of weeks ago we were trapping *Mastomys* in Rhodesia, in relation to the Marburg fever outbreak, and fully 95% of *Mastomys* captured were young: 2–3 weeks old. There had been a plague die-off there with a subsequent rodent population explosion that is still continuing. Obviously, if we looked for antibodies in this group of animals, we would get a completely false impression. I fully support Dr Arata's comment that it is absolutely essential to obtain a representative population sample.

K. JOHNSON: I agree with both the previous speakers, but for completely different reasons. I think they both failed to appreciate that in the case of *Mastomys* and Lassa

fever, the way we are really going to study the ecology is not by serological studies but by looking for the virus. That does not mean that it is not important to know the age structure of the population; it may turn out that one will be more likely to isolate Lassa virus from a population such as you just described, rather than one that is " more representative " and has more older animals in it. Dr Coetzee suggested that *Mastomys* ought to be considered one very complex species, even though it might have anywhere from 32 to 38 chromosomes. That seems to me to be a large potential difference genetically, and I would like to know whether or not the chromosomal number shows any geographical distribution, or whether the distribution appears to be merely random. It is fair to ask at the moment, I think, why Lassa fever does not occur in southern Africa.

COETZEE: I think the reason why we stick to the one name and regard it as a complex species is lack of information. Most of the karyological work was done on one or two specimens only, not on populations.