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WHAT IT TAKES TO BE A RESERVOIR HOST

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Abstract. The majority of parasitic infections of man are of zoonotic origin. In a conceptual framework for the incrimination of mammalian reservoir hosts, these are defined as being essential to the maintenance of parasite suprapopulations. A series of guidelines are given for the accumulation of the relevant information. It is proposed that mammal ecologists can contribute significantly to the understanding of medically important zoonoses.

Key words: zoonoses, reservoirs, epidemiology.

INTRODUCTION

Zoonoses, diseases transmitted between man and other animals are of great public health importance, so have been the subjects of much investigation. Many such infections are highly pathogenic and, while most occur only sporadically, some are responsible for important epidemics. Zoonoses with wild animal reservoir hosts often occur focally, obeying Pavlovsky's rules of «natural nidality» (PAVLOVSKY, undated). Controlling the transmission of such zoonoses may depend on the description of the natural reservoir, and on a deep understanding of the ecology of the reservoir host(s). This article is intended to contribute to a conceptual framework for the study of eukaryote zoonoses by describing general features and providing definitions and guidelines for the incrimination of reservoir hosts. Microbial zoonoses are not included; while these obey similar rules, the study of prokaryotes requires a set of different methods.

A CONCEPTUAL FRAMEWORK

Zoonoses

At the latest count (Unpublished result based largely on BEAVER *et al*., 1984 and COOMBS & CROMPTON, 1991) some 374 species of eukaryote have been recorded as natural parasites of *Homo sapiens* L., 1758. Among these, no fewer than 299 are thought to be purely zoonotic. That is, their suprapopulations are never dependent on *H. sapiens* for their long term survival; human infection is derived directly or indirectly from another species of vertebrate. A further 31 forms are partially zoonotic, being maintained by *H. sapiens* as well as other hosts. Only 44 species are regarded as being entirely dependent on man. This last number is likely to fall with increasing information, while the other two are likely to increase.

Most zoonoses are derived from natural mammalian hosts. Fig. 1 illustrates the mammalian orders and the numbers of zoonotic parasitic infections maintained in each one. Relative to the number of species in the order, the Carnivora and ungulates are the most important sources of human infection, but the Rodentia are also very important. For a considerable number of presumably zoonotic infections, the reservoir host is unknown

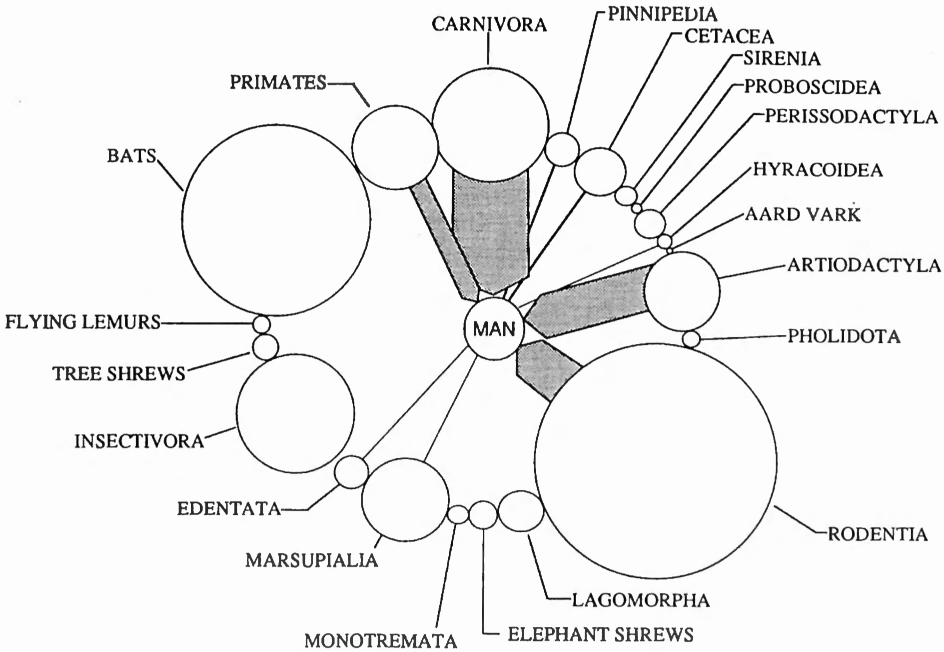

Fig. 1. – Mammalian reservoir hosts for zoonotic endoparasites. The area of each circle is proportional to the number of species in the order; the width of each arrow is proportional to the number of zoonotic endoparasitic infections harboured by the species of the order.

The concept of zoonosis is strictly anthropocentric so, in itself, has no general scientific relevance. However, the economic importance of zoonoses has led to much research on them and they may be used as paradigms illustrating many general parasitological principles. Thus, a reservoir host of a zoonotic infection is a maintenance host of a parasite which also infects another host species, and the structure of reservoir systems can readily be generalised to describe parasite - host systems in general.

Reservoir Systems

A reservoir of infection is best defined as an ecological system in which the infectious agent survives indefinitely. Where a vertebrate host or group of hosts is essential to such a system, these are termed the reservoir host(s).

For relatively specialised parasites such as *Leishmania aethiopica* the reservoir system may comprise one or a few reservoir hosts (the hyraxes *Procavia* spp. and *Heterohyrax* brucei [Gray, 1868]) For generalist parasites such as *Toxoplasma gondii* or *Trichinella spiralis* (Owen, 1835), the system may include numerous reservoir hosts in any one place, and these may vary geographically. It is important to distinguish between hosts which are essential to the system and those which are merely incidental. That is, those which form part of an ecological source and those which are merely ecological sinks.

To be an essential component of a reservoir system, the vertebrate host must at least be susceptible to infection and the agent must reach its transmission stage. The other features of reservoir hosts are less easy to define or measure, and depend on long term quantitative interpretation. At all stages the whole reservoir system must be considered and it is only when the system has been described at least semi-quantitatively that a final assessment can be made. The question is particularly intractable with generalist parasites for which any one host species may be insufficient to ensure long term persistence of a suprapopulation.

In order to satisfy the requirements of a reservoir host, an infected individual must, on average, be responsible for the subsequent infection of at least one other individual. As shown schematically in Fig. 2 it is hypothetically possible for the reservoir system to include more than one reservoir host species. In the example given, based on *T. gondii*, the reservoir system includes the cat as definitive host and various rodents and birds as intermediate hosts. Suppose the average infected cat infects one each of *Apodemus, Arvicola, Mus, Rattus* and *Passer*; then each of these in turn infects 0.25 cats, so a total of 1.25 cats are subsequently infected and the cycle can continue. However, no single intermediate host species is either essential or sufficient to maintain the system. In this example any four of the five intermediate hosts are required: all must be termed reservoir hosts. Extending this hypothetical example, each infected individual of *Rattus* spec. has a small

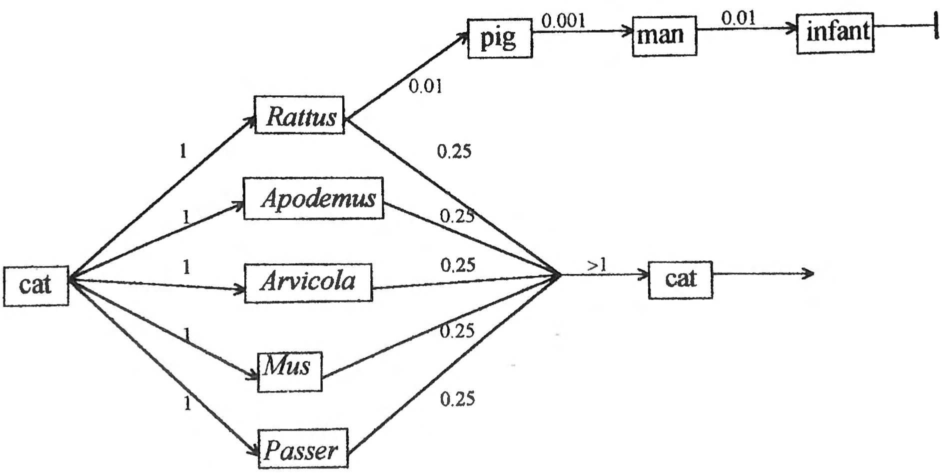

Fig. 2. – Hypothetical scheme for a complex reservoir system in which more than one reservoir host is required. Based on the life cycle of *Toxoplasma gondii*, but figures are for illustration only. See text for explanation.

probability of infecting a pig which, in turn, has a small possibility of infecting a human. The pig is most unlikely to infect a cat or, in any other way, to contribute to the maintenance of the system, so is not a reservoir host. From the anthropocentric point of view, the pig is an important source of human infection. Such a host, which causes humans to be exposed to infection, but plays no part in the maintenance of the reservoir system is termed a liaison host (GARNHAM , 1971).

Incrimination of Reservoir Hosts

The ideal goal in describing a zoonotic disease would be to enter all the numbers on a diagram resembling Fig. 2. However, there is probably no zoonosis whose ecology is sufficiently well known to measure all the parameters required to formally construct such a comprehensive mathematical model. Fortunately however, quantitative information on parts of the system is frequently sufficient that 'intuitive' interpretation may be quite convincing. Further, at this level of complexity (where accuracy risks becoming divorced from precision) it is doubtful that any biomathematical model could be more reliable than informed 'intuition'. It must be emphasised that the fact that comprehensive mathematical models are of limited value in no way denies the essential value of quantitative data, or of models of small parts of systems.

In practice, the measurement of various parameters is possible which are sufficient to incriminate most reservoir hosts with reasonable certainty. This can be illustrated by the various zoonotic species of *Leishmania*, which show a wide variety of patterns within a homogeneous group of parasites. The roles of mammals in the maintenance of Leishmaniasis systems has been reviewed by ASHFORD (1996).

Selection of field study site

This usually depends on the location of cases of human infection, preferably foci in which many cases occur. Travel histories are vital; it is important to visit homes and carefully interview subjects. Age and occupation risk factors may be strong indicators of specific transmission sites; infection in infants frequently indicates peridomestic transmission, so is especially valuable. This information can usually be gathered from existing records and informal open questionnaire, without resort to formal epidemiological investigation. Epidemics in which humans are temporary sources of human infection may be very misleading. In southern Sudan epidemics of *L. donovani* occur over a wide area but these seem to be anthroponotic; there appear to be residual foci of zoonotic infection in sparsely inhabited areas, whose structure remains to be described, which cannot readily be located during epidemics. Strong parallels exist in this respect with plague.

Collection and incrimination of candidate reservoir hosts

The importance of accurate identification of the vertebrate host cannot be overemphasised. Candidates may be chosen according to *prima facie* evidence. A maintenance host for one *Leishmania* species is likely to be a good host for others; it is likely to constitute a large proportion of the mammalian biomass, at least in restricted areas, so is either abundant or gregarious. Alternatively there may be a specific association between a sandfly vector and vertebrate host which increases the chances of transmission. This has been found for sloths *Choloepus* and *Bradypus* spp, which maintain *L. panamensis* and *L. guyanensis*. Experimental infection may be very misleading; many workers have found great difficulty in infecting natural hosts with cultured *Leishmania* parasites. If the season and age group of maximum prevalence can be predicted, the number of animals needed to be examined in order to exclude a candidate is unlikely to exceed 100.

Detection of parasite

Here again taxonomy and identification present real difficulties. Workers in central Asia misjudged the risk of zoonotic *L. major* infection for many years before it was discovered that they were dealing with two species of parasite, *L. major*, which infects humans and *L. turanica* which does not. The results of a massive effort by the American Navy in southern Sudan in the 1960s are uncertain today owing to doubt about the identity of the parasites they isolated from *Arvicanthis niloticus* (Desmarest, 1822). Biochemical methods of classification and identification have contributed greatly in recent years. Wherever possible parasites must be isolated in culture for detailed identification. It is important to establish that the parasite reaches a stage in which it can be transmitted.

Estimation of parasite population parameters

The most important parameters are prevalence, incidence and duration of infection. Incidence, which is the most expensive parameter to measure, can be estimated as prevalence / duration, but care must be taken to allow for seasonal effects. The most valuable practical measure for most host - parasite combinations is the relation between host age and prevalence of active or past infection. The use of eye lens weight as a measure of the age of rodents has proven to be of immense value in our own (unpublished) study of *L. major* in *Psammomys obesus* Crezschmar, 1828 in North Africa.

Estimation of host population parameters

The main population factors favouring a reservoir role are high density, and longevity sufficient to provide a habitat for the parasite during any non-transmission season. Many of the normal topics of mammal ecology studies, such as nutrition, are of limited interest in medical mammalogy. Some parameters can only be measured with longitudinal study of a population by removal. This can conveniently be combined with parasitological study as described above. Mobility and longevity can, however, best be measured by mark-capture-recapture methods without removing the animals, which is incompatible with parasitology. Indirect methods such as serology may overcome this problem, but are only valid when the structure of a focus has been qualitatively described.

Effect of parasite on host

The old idea that a 'well adapted' parasite does not harm its host is clearly not a valid generalisation: many parasites depend on the death of their host for transmission, and certainly accelerate this death. Nevertheless, it is generally difficult to demonstrate serious effects of common parasites on individual mammalian hosts. Any effect on natural host populations is even more difficult to demonstrate. *Leishmania* species in their natural hosts may infect the skin or viscera; infections last for the life of the host, but are not known to cause significant pathology, nor to reduce ecological fitness. Cutaneous infections are frequently undetectable visually. It is only the domestic dog, which must be a secondary reservoir host of *L. infantum*, and man, as a presumed secondary maintenance host of *L. donovani*, which suffer serious disease.

The measurement of effects of parasites on natural host populations requires extended longitudinal study, and such effects have rarely been demonstrated. Reservoir hosts are, by definition, maintenance hosts so infection is likely to be either too infrequent or too benign to have any regulating effect on populations. An acutely pathogenic parasite is likely to be in an unusual host species.

CONCLUSION

The identification of reservoir hosts is an essential component of programmes for the control of zoonoses. Only with a thorough understanding of the basic ecology of the host will efficient control be possible and, with parasitic zoonoses, there have been very few comprehensive ecological studies aimed at the reduction of transmission to man. Mammalogists have tended to measure parameters relevant to basic ecology or crop protection, without reference to zoonotic parasites. Parasitologists have tended to examine large numbers of hosts haphazardly, without reference to their population structure. Carefully designed studies of the interaction between host and parasite populations are called for. These are expensive and, meanwhile, mammalogists should be more aware of parasitology, and parasitologists should be more meticulous in the gathering of data concerning the hosts they are studying. Microbial zoonoses such as rabies and plague are much more thoroughly understood in this respect, and interaction between the relevant experts would be highly productive, initially to develop a consistent terminology for the subject of zoonoses as a whole.

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