The Nidality of Zoonoses

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Summary

Many infectious diseases show a natural nidality dependent on the presence of a suitable population which can maintain the infection in the ecosystem.

Field investigations of *Leptospira interrogans* serovar *ballum* in rats showed a high prevalence of infection in ship rats (*Rattus rattus*) of low population density. Although a similar prevalence of infection was detected in high population densities of Norway rats (*R. norvegicus*), infection could not be demonstrated in populations of low density.

Studies of both domestic stock and wildlife, showed that different serovars are restricted to specific groups of animals in the ecosystem. By relating information from these field studies, with the results of experimental infection of laboratory mice with different serovars, it was possible to define a maintenance host as an animal which is capable of acting as a natural source of infection for its own species. A maintenance population was defined as a population of a species of animal which acts as a continuous reservoir of infection in a specific ecosystem.

It is suggested that the identification of such populations and individuals, is important in establishing the nidality of a disease.

Introduction

The concept of the natural nidality of disease was introduced by Audy (1958) and popularised by Pavlovsky (1966). He suggested that many infectious diseases, particularly vector borne zoonoses have strict geographical boundaries. These foci or nidi of infection are associated with the biotopes which support both the reservoir host of the pathogen and the arthropod vector the vector being responsible for both transmission in the reservoir population and to humans who entered the biotope. As stated by Schwabe et al. (1977) the biotopic community and the biotope comprise a specific ecosystem.

Zoonoses cannot be considered host specific diseases, as they affect both animals and man. Few infectious diseases, with the possible exception of some associated with viruses, are completely host-specific. However, within a particular ecosystem, or series of ecosystems, in which a disease is present, high rates of infection are often confined to only one or two species of animal. Populations of such infected animals are termed reservoir or maintenance hosts. In Europe rabies is endemic in red foxes (*Vulpes vulpes*) which comprise the major maintenance population for rabies. Infection in other animals and man is sporadic.

In many ecosystems the pathogen and maintenance hosts are confined to a specific niche. Often, due to man’s intervention, a disease may escape from its niche boundary and a new nidus of infection established. This has occurred in certain areas of New Zealand, where bovine tuberculosis has spread from cattle at the bush–pasture boundary to possums (*Trichosurus vulpecula*) in the bush.

In any disease control program, all populations which can maintain endemic infections must be under constant surveillance. The establishment of a maintenance...
population depends on both the characteristic of the total population and the intrinsic attributes of individuals comprising the population. Such maintenance populations and the individual animals comprising them, can include both domestic stock and free-living wild animals. When wild or feral animal populations maintain infection, control measures become difficult or even impossible. In New Zealand the only maintenance population for *Brucella abortus* appears to be domestic cattle. Conversely *Yersinia pseudotuberculosis* is probably maintained in a large number of wild and domesticated birds and mammals.

A three-year study of leptospirosis in domestic stock and wildlife in New Zealand indicated that each of the six endemic serovars had different maintenance populations. Both natural and synanthropic nidi of leptospirosis were clearly demonstrated and defined. From studies of naturally occurring infection and from experimental studies it was possible to define the characteristics of a maintenance host for a specific serovar and the characteristics of a population which maintains a nidus of infection. Such information is important in applying landscape epidemiological techniques to define the likely distribution of leptospirosis.

The concepts introduced in this paper relate to field studies of *ballum* infection in Norway rats (*Rattus norvegicus*) and Ship rats (*Rattus rattus*) and to experimental studies of laboratory mice (*Mus musculus*). It is believed these studies help to define a maintenance host and population and the factors affecting the nidality of a disease.

Leptospirosis is an important zoonosis in New Zealand, particularly amongst dairy farmers. The serovars most frequently associated, being *hardjo* and *pomona* (Christmas et al., 1974 and Philip, 1976).

The six serovars which have been isolated in New Zealand are *pomona* (Anon., 1951), *copenhageni* (Kirschner and Gray, 1951), *ballum* (Anon., 1967), *hardjo* (Lake, 1973), *tarassovi* (Ryan and Marshall, 1976) and *balcanica* (Marshall et al., 1976). With the possible exception of *copenhageni* and *tarassovi*, all serovars appear to be widely distributed with a high endemic prevalence in certain animal populations. *Hardjo* is maintained by cattle (Hellstrom, 1978), *pomona*, and to a lesser extent *tarassovi*, by pigs (Ryan, 1978), *balcanica* by possums (Hathaway et al., 1978) and *ballum* by a variety of small wild mammals (Brockie and Till, 1977; Hathaway, 1978). *Copenhageni* appears to have a more limited distribution and is usually associated with Norway rats (Brockie, 1977). Previous work by Hathaway (1978) has clearly demonstrated that possums are a maintenance population for *balcanica* and the infection shows a strict nidality related to the distribution of this animal.

### Field investigations of rats

(a) **General methods**

The majority of Norway rats were collected by shooting and the Ship rats by trapping. Objective estimates of the relative abundance of Norway rats on rubbish tips, were made on at least three occasions at each site, from the number shot in 1.5 hours and by the number seen in a 360° sweep of a spot light made in a 2 minute period. The relative abundance of Ship rats was estimated from trap night averages (Hathaway, 1978). The low numbers of Norway rats present in other areas, prevented the estimation of their relative abundance.

The sex and body weight of all animals were recorded. Norway rats of 150 g or more, and Ship rats of 60 g or more, were regarded as sexually mature. Cultural examination of kidneys and microscopic agglutination tests on sera were carried out as described by Hathaway (1978).
(b) Results

232 Norway rats and 52 Ship rats were collected from a variety of different biotopes. All were subjected to cultural examination and 155 (67 per cent) of Norway rats and 21 (40 per cent) of Ship rats to serological examination.

Table 1 shows the sites at which Norway and Ship rats were collected and the bacteriological prevalence of *ballum* infection. All isolates were identified as belonging to the Ballum serogroup.

Isolates were obtained from sixty-three (27 per cent) of Norway rats and seventeen (33 per cent) of Ship rats. Only five (3 per cent) of Norway rats and five (24 per cent) of Ship rats had titres to *ballum* (1:12). One Ship rat was sero-positive but culture negative. Many isolates were recovered from sero-negative rats. The range of titres was from 1:12 to 1:48 and from 1:48 to 1:192 for Norway and Ship rats respectively. The ratio of serological prevalence to bacteriological prevalence was approximately 1:10 and 1:2 respectively.

There was no significant sex difference in the prevalence of infection in either species. All Ship rats examined were considered to be sexually mature. Isolates were obtained from only two of twenty immature Norway rats examined.

Table 1 indicates considerable differences in the prevalence of infection of Norway rats from different rubbish tips (3-43 per cent). No isolates were obtained from animals from other areas where population sizes and densities were very low. These differences in prevalence of infection are highly significant (x² = 26.72 P < 0.001). The different rates of infection recorded from Ship rats from different locations were not significant (P < 0.75). Neither was there any significant correlation between relative abundance of Ship rats and prevalence of infection (P < 0.05).

Combining the assessments of the relative abundance of Norway rats on rubbish tips, a relative index of abundance to the tip with the largest population (Fielding) was calculated for each of the four major tips investigated. There was a strong correlation between the relative abundance and prevalence of infection (P < 0.01). Figure 1 shows the regression (P < 0.005) of prevalence of *ballum* infection in Norway rats on the subjective estimate of relative abundance. Thus there was an 8.2 per cent increase in prevalence for each 0.2 unit increase in relative abundance.

![Table 1: Bacteriological Prevalence of Ballum in Norway and Ship Rats](image)

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Infected Ship rats were collected from both natural and synanthropic biotopes, where population densities were low. Infected Norway rats were only found in synanthropic foci where population densities were high. It was also noted that the rubbish tips which supported the largest Norway rat population were those in which backfilling and rat burrow destruction was not regularly practised.

**Survey of interspecies relationship**

The bacteriological and serological prevalence of leptospirosis was investigated in different wild and domestic animals inhabiting an area of approximately 90 hectares of Massey University farmland. This area contained a town supply dairy herd of approximately 130 cows and a pig research unit which constantly maintained approximately 600 pigs. Wildlife examined from the area included house mice (*Mus musculus*), Ship rats, Norway rats, hedgehogs (*Erinaceus europaeus*), feral cats, possums, rabbits (*Oryctolagus cuniculus*), one stoat (*Mustela erminea*), and both grey and mallard ducks (*Anas superciliosa* and *Anas platyrhynchos*).

There was a high prevalence endemic of *hardjo* in cattle (Hellstrom and Blackmore, 1979) and an even higher prevalence of *pomona* in the pigs (Ryan, 1978), with some groups showing infection rates of 80 per cent.

In this survey most of the species of wildlife were collected by trapping and Table 2...
shows the numbers collected and the bacteriological and serological prevalence of leptospirosis.

Despite the high prevalence of infection in some groups of animal, there was no bacteriological, and very little serological, evidence to suggest cross transmission of specific serovars between different groups of animals, particularly domestic stock and wildlife.

In the ecosystem studied, cattle were the maintenance population for hardjo, pigs for pomona, mice, Ship rats and hedgehogs for ballum and possums for balcanica. Each serovar showed a definite nidality related to the distribution of the species of animal constituting the maintenance population. In this ecosystem there was an obvious overlapping of niche boundaries.

Table 2: Prevalence of Leptospirosis in Wildlife

<table>
<thead>
<tr>
<th>Species of Wildlife</th>
<th>No. examined</th>
<th>Bacteriological prevalence (%)</th>
<th>Serological prevalence (%)</th>
<th>Serovar isolated</th>
</tr>
</thead>
<tbody>
<tr>
<td>House mouse</td>
<td>58</td>
<td>16</td>
<td>9</td>
<td>ballum</td>
</tr>
<tr>
<td>Norway rat</td>
<td>13</td>
<td>0</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>Ship rat</td>
<td>11</td>
<td>36</td>
<td>38</td>
<td>ballum</td>
</tr>
<tr>
<td>Hedgehog</td>
<td>13</td>
<td>23</td>
<td>50</td>
<td>ballum</td>
</tr>
<tr>
<td>Possum</td>
<td>8</td>
<td>38</td>
<td>38</td>
<td>balcanica</td>
</tr>
<tr>
<td>Feral cat</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Stoat</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Rabbit</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Grey duck</td>
<td>29</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Mallard duck</td>
<td>29</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

Experimental investigations of leptospirosis in mice

Groups of Specific Pathogen Free (S.P.F.) mice were inoculated by the intraperitoneal route with recent isolates of ballum, balcanica, hardjo and pomona. These animals were monitored serologically, bacteriologically and clinically to assess the infective dose, pathogenic effects and duration of leptospirosis associated with different serovars. In other experiments infected animals were introduced to uninfected groups to study intraspecies transmission (Hathaway, 1978).

No clinical signs of disease were noted in any group of mice. The minimum infective dose for ballum and pomona was in the range of only 10 organisms, while for hardjo and balcanica it was in the region of 10⁷ organisms. Serological responses were weak and the geometric mean titre against ballum was only 1:29. It was higher for pomona (1:285).

Leptospirosis persisted for six months when mice were infected with either ballum or pomona. Leptospirosis in mice infected with ballum was constant and intense, while for those infected with pomona, organisms were shed less intensely and more sporadically. Leptospirosis was not detected in mice infected with hardjo or balcanica.
Natural intraspecies transmission in the laboratory mice could only be achieved with *ballum*. Infected males transmitted infection to all littermates of both sexes and the dams. Infection was also transmitted between single sex and different sex pairs of mice, but infection only occurred after the onset of sexual maturity. Maternally derived antibody was shown to be protective for up to 28 days of age, but was not after 56 days of age.

**Maintenance hosts and populations**

The original concept of a maintenance host for an infectious agent was put forward by Audy (1958) and later expanded by Roth et al. (1963). From the studies outlined in this contribution, an attempt can be made to more closely define the characteristics of both a maintenance host and a maintenance population. This differentiation is not a matter of semantics, but an important factor affecting the distribution of an infectious disease and attempts to predict the nidality of an infection by the use of landscape epidemiological techniques.

Although serovar *ballum* has been isolated from a wide variety of hosts throughout the world, it was first recorded from a mouse in Denmark (Borg-Peterson, 1944). The mouse is most commonly considered to be the maintenance host for this serovar.

From the data presented, Ship rats are clearly maintenance hosts for *ballum*. The population densities of Ship rats in their natural environment is often less than 3/ha (Daniel, 1972). From the evidence presented, endemic infection in Norway rats only occurs in synanthropic foci, when population densities were very large (many 1000/ha). Thus from knowledge of the species of rat and the population in an ecosystem, predictions can be made as to the existence of nidus of infections and potential public health risks.

Experimental transmission of *ballum* in laboratory mice showed the animals to be highly susceptible to infection, resistant to pathological effects, to develop a persistent leptospirosis and to be capable of naturally transmitting the infection to other mice in the population. Similar experimental work on the transmission of serovar *balcanica* to possums has shown similar results (Hathaway, 1978).

It is suggested that the high prevalence of *ballum* infection in low density populations of Ship rats, indicates that these animals respond in a similar manner to mice to infection with this serovar.

As a result of the studies outlined, a maintenance host has been defined as an animal which is capable of acting as a natural source of infection for its own species.

Leptospiral infection in a maintained host is characterised by the following genotypic characteristics:

(a) High susceptibility of infection (low infective dose).
(b) Low pathogenicity of serovar for the host.
(c) Long term kidney infection related to the systemic phase of infection.
(d) Natural transmission within the species.

Norway rats only constituted a maintenance population for *ballum* when the population density was high. This indicates that the animal is not a typical maintenance host for this serovar. This atypical response could be accounted for by many host and agent attributes. Two factors which could be particularly related to the creation of a maintenance population only when population densities are high, are the minimal infective dose and duration and intensity of leptospirosis. This hypothesis could be tested by experimental studies in laboratory rats (*Rattus norvigicus*). It is therefore important to appreciate the difference between a maintenance host and a maintenance population. The latter has therefore been defined as a population of a
species of animal which acts as a continuous reservoir of infection in a specific ecosystem. In such a population the agent will be transmitted naturally between individuals of the population and successive generations.

The establishment of leptospiral infection in a maintenance population is dependent on factors mainly of an environmental nature which have an effect on:

(a) Initial exposure to the agent.
(b) Population dynamics and the size and density of the species.
(c) Population behaviour.
(d) General environmental conditions and method of husbandry.
(e) Concurrent disease and physiological status of the population.
(f) Stability of the infectious agent.

Any epidemiological investigation designed to define the nidality of disease, must differentiate between, and identify, both maintenance hosts and populations. It is hoped that some of the criteria outlined in this contribution indicate the type of information required. Cross-sectional surveys of wildlife must be periodically repeated and include estimates of population density. Such information will help to differentiate between sporadic disease and endemic infection in a maintenance population.

Although this contribution has been concerned with studies of wildlife, the criteria outlined could explain the sporadic nature of *pomona* infection in New Zealand cattle. Bovines do not fulfil the criteria of a maintenance host for this serovar. A knowledge of the distribution of maintenance populations of the different serovars, defines the nidality of leptospirosis in New Zealand. This allows some assessment of the public health risks associated with this important zoonosis.

REFERENCES


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