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Ecological mechanisms that promote arbovirus survival: a mathematical model of Ross River virus transmission

K. Glass*

National Centre for Epidemiology and Population Health, The Australian National University, Canberra, ACT 0200, Australia

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Summary Many assessments of host and vector competence for arboviruses focus on level and length of infectivity and ignore ecological mechanisms that contribute to virus survival. In this paper, mathematical models are used to compare local survival mechanisms for a range of scenarios, using Ross River virus as a case study. Ross River virus is an Australian arbovirus with many mosquito vectors and reservoir hosts. The mechanisms for maintaining long-term transmission of the virus vary between salt and freshwater mosquito vectors, and according to the availability of susceptible hosts. The models demonstrate that overwintering of virus in adult freshwater mosquitoes requires a large host population, while overwintering of virus in infected eggs of saltwater mosquitoes is an effective survival strategy when filial infection rates are high. The virus survives longer when both salt and freshwater mosquito species are included in the model than when only one mosquito species is present. When the marsupial host is replaced by a host with higher birth rate and shorter infectious period, the virus survived longer under all models. This suggests that birth rate can be a key factor when assessing the competence of reservoir hosts to maintain virus transmission.

1. Introduction

A rapidly changing world presents many opportunities for pathogens to spread into new areas (Dobson and Foufopoulos, 2001; Gubler, 2002; Heymann et al., 2001). The dangers of proliferation are heightened by population growth (Gubler, 1996), increasing human mobility (Lanciotti et al., 1999), changes in species biodiversity (Ostfeld and Keesing, 2000), and changes in weather patterns and climate (Hales et al., 2002). Zoonotic pathogens are likely to be particularly sensitive to such changes (Taylor et al., 2001), and often human disease follows from disruptions to local ecosystems

* Tel.: +61 2 6125 2468; fax: +61 2 6125 0740.
E-mail address: kathryn.glass@anu.edu.au.

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(Cook et al., 2004). When attempting to predict the effects of ecological changes on pathogen dispersal, it is important to consider the mechanisms that contribute to survival of the pathogen.

Ross River virus is a mosquito-borne virus (an arbovirus), which causes around 5000 human notifications each year in Australia (Russell and Dwyer, 2000). The main symptoms are joint pain and swelling, although other symptoms can include rash, fatigue, fever and muscle pain (Mylonas et al., 2002). Patients without other conditions usually recover within 3 to 6 months (Harley et al., 2002; Mylonas et al., 2002).

Many species have been identified as possible reservoir hosts for Ross River virus, and a number of mosquito species are capable of transmitting the virus. This leads to a diverse range of local transmission cycles (Russell, 1998; Weinstein, 1997), with various mechanisms contributing to virus survival. Lindsay et al. (1993) listed five mechanisms that have been suggested to explain the survival of Australian arboviruses: (1) year-round transmission of virus in tropical regions of Australia; (2) overwintering in long-lived adults of certain mosquito species; (3) reintroduction from endemic foci via migrating vertebrates; (4) movement of the virus by movement of viraemic humans or livestock; and (5) vertical transmission of the virus in certain mosquito species, with persistence of the virus in desiccation-resistant eggs.

Owing to its wide distribution in Australia, the mechanisms driving survival of Ross River virus may vary between regions. Mechanisms three and four both rely on movement of hosts between regions, and assist virus survival at a broad scale. This paper considers a range of possible regional scenarios, and looks at the mechanisms that enhance survival at the local level. Although these local survival mechanisms have been documented for Ross River virus, the rate at which they occur in populations of mosquitoes is less well known. This reflects the difficulty in finding infected mosquitoes: about one in every 1000 trapped mosquitoes is infected with the virus (Harley et al., 2000). In this context, mathematical models can be highly valuable in identifying the consequences of the ecological interactions for virus survival (Fine and LeDuc, 1978). Previous modelling work on Australian arboviruses described the transmission of virus over periods of less than 1 year (Choi et al., 2002; Kay et al., 1987). In this paper, I describe a series of compartmental transmission models (Anderson and May, 1991) that allow birth and death of the host, and discuss the behaviour of these models over a number of years.

2. Materials and methods

2.1. Enzootic transmission cycle

Ross River virus has a range of potential hosts and vectors. Antibody prevalence surveys have shown that many species may be infected with the virus, and experimental studies assessing the level and duration of viraemia have been conducted on around 30 vertebrates. On the basis of this experimental evidence, marsupials are generally considered to be the main reservoir host for the virus (Kay and Aaskov, 1989). Ross River virus has been isolated from over 30 mosquito species (Harley et al., 2001), but it is believed that the main species are the freshwater breeding mosquito *Culex annulirostris*, and two saltwater breeding mosquitoes, *Aedes vigilax* and *A. camptorynchus* (Russell, 1994).

The vectors modelled in this paper are *A. vigilax* and *C. annulirostris*. After a female mosquito ingests an infected blood meal, there is an extrinsic incubation period of 5 to 10 days before virus is released in the saliva (Woodruff et al., 2001). Given that the percentage of mosquitoes surviving a given day is generally low (estimates for *C. annulirostris* range from 55 to 90% while the species is actively feeding and breeding [Kay et al., 1981]), the majority of infected mosquitoes die before becoming infectious to new hosts. The main differences between the life cycles of *A. vigilax* and *C. annulirostris* lie in the choice of egg-laying locations and the overwintering mechanisms. *Culex annulirostris* lays its eggs on the surface of the water, and these hatch within a few days (Kay et al., 1981). When temperatures drop below a threshold of about 18 °C, *C. annulirostris* becomes inactive, and overwinters in the adult stage (McDonald et al., 1980). In contrast, *A. vigilax* lays desiccation-resistant eggs that hatch only after a flooding event, and the species overwinters in the egg stage (Kay et al., 1981). These life cycles lead to different survival mechanisms for the virus when transmission is interrupted by cold weather. When transmission involves *C. annulirostris* as the dominant vector, the virus must overwinter in inactive adults of the species. When transmission involves *A. vigilax*, the virus must survive in the eggs. In order for this last to be possible, the adult females of the species must transmit the virus to their eggs. This has been observed for *A. vigilax* both in the laboratory (Kay, 1982), and in the field (Lindsay et al., 1993).

2.2. Models

As the main aim of the work is to consider factors that promote survival of Ross River virus, a