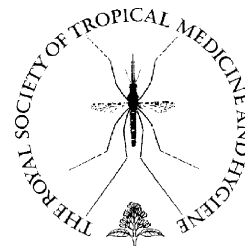




available at www.sciencedirect.com



journal homepage: www.elsevierhealth.com/journals/trst



Density-dependent host choice by disease vectors: epidemiological implications of the ideal free distribution

María-Gloria Basáñez^{a,*}, Karina Razali^{b,1}, Alfons Renz^c, David Kelly^{d,2}

^a Department of Infectious Disease Epidemiology, Faculty of Medicine (St Mary's Campus), Imperial College London, Norfolk Place, London W2 1PG, UK

^b Former Wellcome Trust Centre for the Epidemiology of Infectious Disease, University of Oxford, South Parks Road, Oxford OX1 3PS, UK

^c Universität Tübingen, Institut für Tierphysiologie, AG Parasitologie, Friedhofstrasse 73, D-72074 Tübingen, Germany

^d Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK

Received 27 January 2006; received in revised form 23 August 2006; accepted 25 August 2006

Available online 16 November 2006

KEYWORDS

Human blood index;
Density dependence;
Vector-borne
diseases;
Onchocerciasis;
Simulium damnosum
s.l.;
Ideal free distribution

Summary The proportion of vector blood meals taken on humans (the human blood index, h) appears as a squared term in classical expressions of the basic reproduction ratio (R_0) for vector-borne infections. Consequently, R_0 varies non-linearly with h . Estimates of h , however, constitute mere snapshots of a parameter that is predicted, from evolutionary theory, to vary with vector and host abundance. We test this prediction using a population dynamics model of river blindness assuming that, before initiation of vector control or chemotherapy, recorded measures of vector density and human infection accurately represent endemic equilibrium. We obtain values of h that satisfy the condition that the effective reproduction ratio (R_e) must equal 1 at equilibrium. Values of h thus obtained decrease with vector density, decrease with the vector:human ratio and make R_0 respond non-linearly rather than increase linearly with vector density. We conclude that if vectors are less able to obtain human blood meals as their density increases, antivectorial measures may not lead to proportional reductions in R_0 until very low vector levels are achieved. Density dependence in the contact rate of infectious diseases transmitted by insects may be an important non-linear process with implications for their epidemiology and control.

© 2006 Royal Society of Tropical Medicine and Hygiene. Published by Elsevier Ltd. All rights reserved.

* Corresponding author. Tel.: +44 207 594 3295; fax: +44 207 402 3927.

E-mail address: m.basanez@imperial.ac.uk (M.-G. Basáñez).

¹ Present address: National Centre in HIV Epidemiology and Clinical Research, University of New South Wales, Level 2, 376 Victoria Street, Sydney, NSW 2010, Australia.

² Present address: OXITEC Limited, 71 Milton Park, Oxford OX14 4RX, UK.

1. Introduction

Transmission models that successfully predict infection prevalence and intensity in host populations are important tools for predicting the impact on transmission dynamics of ecological change as well as for understanding the causes of control failure. The realised or effective (as opposed to innate) vector feeding preference for the host species affected by the pathogen in question (in this paper the human host) is a critical component of models of vector-borne diseases, and in particular of those transmitted by dipteran insects (Randolph, 1998). The proportion of blood meals taken on humans, denoted here by parameter h (Basáñez et al., 2002), is one of the constituents of the per vector biting rate on humans and is also known as the human blood index (Garrett-Jones, 1964).

The basic reproduction ratio (R_0) is the average number of secondary cases arising, during the infectious period, from an infectious case introduced into a wholly susceptible population (Anderson and May, 1991). In such composite measures of pathogen transmission success for vector-borne diseases, the proportion of blood meals taken on humans appears as a squared term, since vectors must bite at least twice to acquire the pathogen and transmit it after completion of the extrinsic incubation period. This signifies that R_0 varies non-linearly with vector host choice. At present, effective host preference is treated in most existing disease transmission models as a fixed proportion of vectors feeding on humans (Bailey, 1982), and as a result R_0 is linearly related to measures of vector density such as the annual biting rate (ABR) (Basáñez and Boussinesq, 1999; Dietz, 1982).

The ABR consists of the product of the vector:human ratio (V/H), the number of bites per unit time per vector and the human blood index h (Dye, 1992), and is usually measured as a compound single parameter by collecting host-seeking vectors coming to feed on human attractants (Duke, 1968; Dye, 1986). Estimations of h are usually based on snapshot samples ignoring its possible temporal and spatial variation. In reality, vectors are probably flexibly anthropophagic or zoophagic, with the human blood index h varying between 0 and 1 depending on intrinsic vector-specific propensities to feed on particular host species. Also, the human blood index will depend on the relative abundance of preferred and maintenance hosts, overall vector abundance, defensive host behaviour and other determinants of density-dependent feeding success (Kelly and Thompson, 2000). It is well known, for instance, that certain species of *Culex* mosquitoes shift host preference seasonally between large mammals, birds and humans, with important consequences to the epidemiology of the viruses they transmit (Apperson et al., 2004).

At its simplest, effective host preference will vary with the relative abundance of non-human and human hosts, and R_0 will exhibit only weak non-linear responses as a result of the squared term (Killeen et al., 2001). However, effective host preference may also vary with the ratio of vectors to hosts (Gurtler et al., 1997). This is predicted to be a strongly non-linear relationship, and R_0 must also vary non-linearly with vector abundance in addition to varying with the ratio of host abundances (Kelly and Thompson, 2000). The question is, therefore, of applied interest. Control strategies that seek to reduce vector abundance will have very different

impacts on disease transmission depending on the shape of the relationship between R_0 and the vector:host ratio. The same applies to control through zooprophylactic manipulation of the abundance of alternative hosts (Bruce-Chwatt, 1985; Sota and Mogi, 1989).

Underlying interpretations both of the proximate mechanisms and of epidemiological implications of host choice is the evolutionary theory of optimal foraging, as there must be intense selection pressures on haematophagous insects to feed on those hosts that are more amenable to being bitten. Given the importance of obtaining complete blood meals for lifetime reproductive success, blood-sucking insects would have evolved strategies to minimise their encounters with defensive hosts. However, a point will be reached where the evolved host choice strategy results in a distribution of vectors among hosts such that the effective per fly feeding success is the same upon all possible hosts, i.e. there will be an optimised distribution of vector densities among hosts for which (density-dependent) host defensive behaviour will be the same. Any novel host-seeking strategy that might lead an individual fly to 'move' hosts would cause a decrease in that particular fly's feeding success and could not, therefore, invade (Kelly, 2001). This distribution, known as the 'ideal free distribution' (IFD), is thus an evolutionary stable strategy (Fretwell and Lucas, 1970; Sutherland, 1983, 1996). It is 'ideal' because it assumes perfect knowledge (evolved or learnt) of the quality as a blood resource of all available hosts, and 'free' because it also assumes that there are no travelling costs associated with host-seeking (Sutherland, 1983).

In this paper, and as a case study, we modify a previously described mathematical model for the population biology of *Onchocerca volvulus* (the causative filarial parasite of river blindness) in West African savannah settings (Basáñez and Boussinesq, 1999) to derive theoretical estimates of the proportion of vector blood meals of human origin that would be compatible with observed measures of vector and parasite density in (pre-control) endemic villages of Cameroon, Burkina Faso and Côte d'Ivoire. By assuming that recorded *O. volvulus* microfilarial loads in human skin (our measure of parasite density) correspond to true endemic equilibrium values (before the initiation of antivectorial or antiparasitic measures), and by using an expression for the effective reproduction ratio (R_e) of the parasite (i.e. in the presence of density dependence), we calculate a village-specific proportion of vector blood meals taken on humans, extending preliminary work by Razali et al. (2002). We explore the effects of heterogeneity in host choice by vectors on the R_0 values estimated for this infection and discuss the epidemiological implications of our findings in terms of the IFD of vectors among hosts.

2. Models and methods

2.1. The basic and effective reproduction ratios

For dioecious (separate sexes) helminth parasites, the basic reproduction number R_0 refers not to the number of secondary cases arising from a primary case, but to the number of mature female worms produced, on average, by a female worm during her reproductive lifespan in the absence of

Download English Version:

<https://daneshyari.com/en/article/3421015>

Download Persian Version:

<https://daneshyari.com/article/3421015>

[Daneshyari.com](https://daneshyari.com)