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Seasonal population dynamics and behaviour of insects in models of vector-borne pathogens

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Behaviour; models; population dynamics; seasonality; vector-borne disease

Introduction

The seasonal dynamics of insect populations and insect behaviour clearly affect the transmission cycles of vector-borne pathogens. However, their treatment in models of these pathogens varies greatly, from assumptions of no seasonality and little behavioural response, to detailed seasonal patterns and specific behaviour patterns.

Models are powerful tools that allow the integration of the complex biology of parasites, hosts and vectors to understand and analyse transmission cycles. Any vector-borne pathogen will have a minimum of three species involved (pathogen, host and vector) and, frequently, has more when multiple hosts, vectors or strains of parasite are involved. A theoretical approach is valuable regardless of the available data. When few data are available for a particular system, modelling studies are invaluable in considering alternative theories on the transmission cycle and focusing attention on aspects of the cycle (e.g. outbreaks, invasions, number of cases) that most affect the outcome of interest. With well-studied systems, models can be constructed to consider very specific questions, make predictions or investigate control strategies. However, it is worth noting that frequently, even in relatively well-studied systems, insufficient data are available to adequately estimate all parameters, and some form of sensitivity analysis is required.

Model approaches form a continuum from purely analytical to simulation-based studies. Frequently, these approaches are combined when investigating a particular system. An analytical model may benefit from simulation of the time course of an outbreak. Conversely, simulation models may benefit from reduction down to analytic principles to understand the underpinnings of model behaviour. A variety of approaches to a single system is often valuable, as each have strengths and weaknesses. Consideration of different aspects of the cycle can vary from simple functions designed to capture the essential points, but not reflect the details of a particular system, to use of detailed historical data on weather and the insect response. The choice depends not only on the particular system, but also on the questions asked and the data available.

The basic reproduction number, R_0 , has been widely used to assess the transmission and persistence of parasites and pathogens (for examples, see Anderson & May, 1991). R_0 is

defined as the average number of secondary cases produced by one primary case, in a population of susceptible hosts. As such, it encapsulates the transmission process, and exhibits threshold behaviour. By definition, it is clear that if $R_0 > 1$, the parasite can persist or invade in a population; if $R_0 < 1$, the parasite cannot invade or persist. Some of the studies discussed here use R_0 as the basis for considering the impact of seasonality in vector populations or vector behaviour on the transmission potential.

This study focuses on the incorporation of insect behaviour and population seasonality in models of vector-borne pathogens. As such, it is not meant as a comprehensive review, but uses specific studies to illustrate particular points. Only models that explicitly consider the effect of seasonality or behaviour are included. Following the traditional approach in medical and veterinary entomology, ticks are considered as honorary insects, and several studies of ticks and tick-borne pathogens are included. Most of the studies concern transmission of pathogens, but some models of insect behaviour alone are considered. Figure 1 indicates the major areas where insect behaviour and population seasonality will impact transmission cycles, and the examples of each used in the present study.

Seasonality

Climate obviously affects insects and ticks, and will affect transmission cycles of pathogens vectored by these arthropods. However, the precise nature of these effects depends on the specifics of the system, climate and variation in climate. Models may consider between-year changes or yearly variation, and may be restricted to simplified annual cycles or include detailed historical weather patterns. Climate and season will also affect the vertebrate hosts, and the interaction between the populations may be important (Fig. 1).

Seasonal population dynamics of the vector may be incorporated in models either descriptively or mechanistically. With descriptive, or forced, seasonality, the seasonal pattern of the insect population is described based on field data, but is not generated based on weather or climate. This could be as simple as a sinusoid function for insect abundance, parameterized for a particular location. For more complex seasonal abundance patterns, other distributions (e.g. normal, lognormal, gamma) can be fitted to data and assumed to occur at a particular time of year. This method is valuable when the seasonal variation in an insect population is known, but the data necessary for mechanistic models of the population dynamics are not available. By contrast, a mechanistic approach starts with weather or climate data, either long-term averages or detailed yearly data. Functions are derived that relate insect population growth parameters (e.g. fecundity, development, mortality) to climatic variables. The insect population is then output from the model or submodel and can be used for transmission models or submodels. These approaches can be mixed, approximating the climate with a simple mathematical function (e.g. a sinusoid curve for temperature), and the insect population dynamics related to this function (e.g. temperature-dependent reproduction and mortality rates). These mixed models are generally more appropriately considered as forced rather than mechanistic, because the resulting insect population pattern is often a simplification of natural patterns.

Lord *et al.* (1996) used such a forced pattern in a model of African horse sickness. African horse sickness is a disease of equines, caused by a virus transmitted by *Culicoides* biting midges. It is endemic to southern Africa, and has caused severe epidemics when introduced outside the endemic area. The seasonal variation in *Culicoides* abundance was forced, based on a sinusoid temperature curve and temperature-dependent recruitment and mortality rates. The authors considered the impact of the seasonal temperature variation, and resulting *Culicoides* population variation, on R_0 , and the chance of establishment of the virus after introduction at different times of year. By definition, R_0 is an instantaneous parameter and

cannot account for fluctuating parameters. Using matrix methodology, an index P was derived based on the eigenvalue. This index was shown to have threshold behaviour similar to R_0 , such that the virus can invade or persist if $P > 1$ and not otherwise. Thus, R_0 in a varying environment can be estimated by P , such that:

$$P = R_0 [1 + \mu \delta \Psi]$$

where:

$$\Psi = \frac{\int_0^T y(t) \sin(\theta t) dt}{\int_0^T y(t) dt}$$

Here, R_0 is the instantaneous R_0 at the moment of virus introduction, μ is the mortality rate of the vector, δ is the amplitude of the seasonal fluctuation in the vector population, and ψ is a complex integral relating to the phasing of the vector population $[\sin(\theta t)]$ and the infective host population $[y(t)]$. When the two populations are in-phase, ψ is positive and P is increased relative to the instantaneous R_0 . When the two populations are not in phase, ψ is negative and P decreases relative to the instantaneous R_0 . Thus, seasonality can either increase or decrease the potential invasion of a virus, depending on the exact timing of the vector population and factors that influence infection in hosts.

Randolph and colleagues have investigated the influence of seasonality and climate change on tick-borne encephalitis virus (TBEv) in Europe (Randolph, 2000, 2001; Randolph & Rogers, 2000; Randolph *et al.*, 2000). Based on logistic regression of the presence/absence of the virus and satellite-measured climate variables, a predictive map of TBEv was derived. The predicted risk was in good correspondence with recorded foci (Randolph, 2000). Further examination of the most predictive variables indicated that higher than average rates of autumnal cooling were associated with the presence of TBEv. Comparisons of tick seasonal activity patterns showed that sites with synchronous larval and nymphal activity were more likely to be TBEv-positive (Randolph *et al.*, 2000), which accords well with known transmission between ticks feeding simultaneously on a host. The authors hypothesized that faster autumnal cooling alters diapause patterns and results in more synchronous spring activity, enhancing TBEv transmission. The regression model was then used to consider the impact of climate change (Randolph & Rogers, 2000) and indicated that the TBEv cycle is fragile and may be disrupted by climate change. These studies demonstrate neat linkages between field studies of distribution and biology, models incorporating climate and seasonality, and the use of these models for predictions about future effects of climate.

Numerous models have been developed for many different tick and mosquito species that depend on detailed historical weather files (e.g. Mount *et al.*, 1991; Focks & Haile, 1993a,b; Hernández *et al.*, 2000; Weidhaas & Focks, 2000). Only one such model and a few of the subsequent studies using the model will be discussed here. Focks and colleagues developed the CimSim (container-inhabiting mosquito simulation; Focks & Haile, 1993a,b) and DenSim (dengue simulation; Focks *et al.*, 1995) models to investigate *Aedes aegypti* with respect to dengue transmission. The models require detailed information on weather, container types and water cycling in each location. *Aedes aegypti* is well characterized, and there was a wealth of data available on the biology of this mosquito. Historical temperature and rainfall data from different geographical areas were used in the model, which could generate different seasonal abundance patterns of mosquitoes, but the effect of mosquito

seasonal patterns *per se* on dengue transmission was not considered. The model has also been used to consider the threshold abundances of mosquitoes required for dengue transmission, control strategies, and the impact of climate change. Maguire *et al.* (1999) used the model to consider control strategies for *Ae. aegypti* in Australia, concluding that reducing breeding sites is more effective than spraying. Patz *et al.* (1998) used the model to consider the impact of various climate change scenarios in different locations on dengue transmission. The model results indicated that transmission is expected to increase under most climate change predictions, but the seasonal pattern is not expected to change in most locations.

Another example of seasonality in models is provided by Lord & Day (2001). A model of St Louis encephalitis (SLE) virus in south Florida was developed. This is a zoonotic virus, with transmission primarily between birds and mosquitoes, and the major vector in south Florida is considered to be the mosquito *Culex nigripalpus*. Transmission intensity varies from year to year, and human cases are observed typically only in years with high transmission in the bird population. The seasonal abundance pattern of the mosquito also varies from year to year, and it was anticipated that the variation in transmission would be largely explained by the variation in mosquito population seasonal abundance. The model was developed with descriptive seasonality in the mosquito population, and the parameters controlling the mosquito abundance pattern (e.g. relative abundance at different times of year, size and timing of peaks in abundance) were included in a sensitivity analysis. However, none of these parameters influenced the likelihood of an epizootic. Seasonal reproduction in the wild bird population was added, as the variation in hosts available and their age could affect the transmission dynamics. A trend was observed for epizootics to occur when the peak in bird reproduction was later in the year and the major peak of mosquito abundance was earlier. The population peaks could not overlap, but it appeared that epizootics are more likely when the peaks are closer together. The structure of the model did not allow formal testing of this interaction, but it demonstrated that interactions between parameters may be important. Further work with the model aims to investigate this in more detail.

Recently, there have been several studies examining aspects of seasonality in vector-borne pathogens. Wonham *et al.* (2004) considered the effect of a simple seasonal pattern of mosquito abundance on West Nile virus dynamics in northern America, where the mosquito population can be represented as a step function (i.e. high during July and August and low otherwise). Using an analytical approach, the model demonstrated that the critical mosquito population size required for invasion of West Nile virus is higher in the seasonal case than with a constant population. It would be of interest to examine this further, and determine not only the average population sizes required for invasion, but also how this varies seasonally. The likelihood of establishment of a pathogen introduced just before the mosquito season is expected to be greater than if the introduction is at the end of the season. Considering this in the analytical framework would be valuable. A more detailed consideration of seasonality in a dengue model (Bartley *et al.*, 2002) included monthly variation in recruitment to the mosquito population, mortality rate, biting rate and duration of the latent period. In this model, different combinations of seasonal rates resulted in different seasonal patterns of dengue infection, and provided the best fits to data from different geographical locations. This work demonstrates a major issue in the ecology of vector-borne pathogens; different factors may be the most important under different conditions. Many combinations may have to be considered to develop an understanding of the variation in the system.

Shaman and colleagues developed hydrology models to model land surface wetness, which will directly affect the availability of larval habitat for some mosquito species (Shaman *et al.*, 2002a,b, 2004). Although the models do not directly include pathogen transmission, statistical associations between the hydrological model output and mosquito abundance or

SLE transmission have been examined. In Florida, SLE transmission to sentinel chickens was associated with earlier drought (16–25 week lag) (Shaman *et al.*, 2002b). In New Jersey, modelled local wetness, lagged by 10 days, and *Aedes vexans* abundance were correlated, although this varied between years and sites (Shaman *et al.*, 2002a).

Behaviour

Vector behaviour has many effects on transmission of vector-borne pathogens, and only a few will be discussed here (Fig. 1). The most notable impact of vector behaviour occurs during vector–host contact, which is the result of the vector searching, locating a host and feeding. This is influenced by elements of vector biology such as host preference (choice of one host over another), distribution of vectors between hosts and dispersal (independent or on-host). However, vector behaviour does not occur in a vacuum, host behaviour also plays important roles. Modifications of host behaviour resulting from seasonal changes or vector density can be particularly important. Another consideration is individual variation in vector behaviour. Often, vectors are considered only at the population level, with model parameters reflecting averages. However, variation in vector behaviour may be important and should be considered when possible, as should potential effects of infection with a pathogen on behaviour.

Incorporation of vector behaviour can greatly increase the complexity of models. Often, the data necessary for development of these models are not available. However, including vector behaviour in models to consider the potential consequences on pathogen transmission can be valuable. To successfully develop and interpret models including behaviour, model assumptions must be made explicit, particularly when extrapolating from minimal data, different species or locations.

The ideal free distribution has received much attention in the ecological literature (e.g. Sutherland, 1983; Tregenza, 1995; Weber, 1998; Stephens & Stevens, 2001). This distribution is derived from the principle that foraging animals should act to maximize their resource accumulation. The distribution is 'ideal', in that animals will go to the patch where they can maximize their intake, and 'free', in that they can enter any patch without restriction. Kelly & Thompson (2000) have applied this to biting flies, considering the effect on R_0 of biting flies distributed according to the ideal free distribution, rather than homogeneously between hosts as is generally assumed. This model assumed there were density-dependent effects on feeding success, such as would occur if hosts become more or less sensitive to flies as the density increases. This is interpreted as interference between flies in the ideal free distribution. They showed that R_0 is sensitive to this assumption, and can be over or under estimated depending on the values assumed for interference between flies. It was also shown that the sensitivity in R_0 is dependent on the relative host availability and assumptions about the differential sensitivity of different host types to biting flies.

In a separate study, Kelly *et al.* (1996) used field data to consider whether the sandfly *Lutzomyia longipalpus* was distributed between hosts as predicted by the ideal free distribution. In their study, the hosts were chickens in different coops. Therefore, the theory could be tested at two levels: between coops (high travel costs) and between birds within coops (low travel costs). Flies were trapped over-night in each coop and inspected for fresh bloodmeals. Regression analysis was used to determine those factors that were significant in the proportion of flies caught with a bloodmeal. If the flies distribute according to the ideal free distribution, the regression coefficient for number of hosts in a coop (a measure of quality) should be equal but opposite in sign to the coefficient for fly density (a measure of interference between flies). Their data showed intermediate values, midway between that

predicted for a homogeneous distribution and the ideal free distribution. Extrapolating these results to within-coop, between host dynamics, the authors theorized that female fly density on individual hosts is a function of male fly density, rather than female fly feeding behaviour. Males choose particular hosts for use as lekking sites, and the females follow this distribution. This study illustrates that simply considering feeding behaviour may be insufficient; reproductive behaviour of vectors may also be important in host contact.

A model has been developed for the sheep blow fly, *Lucilia sericata*, and the incidence of sheep strike in Britain (Fenton *et al.*, 1999; Wall *et al.*, 2000). Sheep strike is a myiasis; the blow fly larvae themselves are parasitic on the sheep. As such, it is not a vector-borne disease, but the model neatly illustrates the effect aggregation may have on transmission. The prevalence of sheep strike reflects the oviposition pressure on individual sheep, and can be considered as a measure of vector-host contact. In a conventional vector-borne pathogen, this contact is via biting, and aggregated biting will affect transmission of pathogens. If particular hosts receive many more bites than others then transmission will be focused on those individuals. For blow flies, Fenton *et al.* (1999) considered fly oviposition to be aggregated on sheep based on fleece soiling, which affects fly attraction. Fleece soiling, in turn, was the result of a complex interaction of helminths (which cause diarrhoea), length of fleece (dependent on husbandry and shearing cycles) and season (primarily variation in humidity). The model demonstrated that high levels of aggregation of fly oviposition decreased the prevalence of sheep strike (Fig. 2). This was particularly noticeable at high fly densities. It is important to note two different measures of aggregation between vectors and hosts: prevalence (e.g. the proportion of hosts that receive at least one contact, either bite or oviposition) and the average number of contacts (bites or ovipositions) per host. The importance of these two measures of contact in pathogen transmission will depend on whether the pathogen of interest replicates in the host (such as a virus) and whether superinfection is relevant to disease status. Aggregation may differentially impact transmission cycles and disease, depending on the particulars. As shown by this model, aggregation can decrease incidence of disease (Fig. 2) (Fenton *et al.*, 1999).

Aggregation is likely to be important in many systems, including ticks and tick-borne pathogens. *Boophilus* cattle ticks can severely impact a cattle industry, both in their direct effect on the hosts and in the transmission of pathogens such as babesiosis and theileriosis. As a result, these ticks have been extensively studied and modelled (Smith, 1983; Sutherst & Maywald, 1985; Mount *et al.*, 1991; Floyd *et al.*, 1995; Beugnet *et al.*, 1998; Hernández *et al.*, 2000; Lodos *et al.*, 2000; Sutherst *et al.*, 2000). In one study, Beugnet *et al.* (1998) considered the persistence of tick populations in New Caledonia. The population of ticks in an individual pasture, without immigration, was simulated using a matrix model. *Boophilus* ticks are one-host ticks; only larvae search for hosts and individuals remain on the same host until females drop off to lay eggs. The eigenvalue of the matrix, λ_1 , was shown to have the same properties as R_0 ; if $\lambda_1 > 1$ the parasite population can invade and persist. The model showed that persistence of the population is sensitive to the survival rate of free living larvae and the encounter rate between larvae and cattle. These encounter rates are determined by both vector and host behaviour. For example, larvae are aggregated because females lay eggs in large batches and larvae do not move far. Cattle avoid large aggregations of larvae (Sutherst *et al.*, 1986), further influencing the encounter rate. Integrated control strategies combining impacts on survival (e.g. pesticide treatment) with those affecting the encounter rate (decreasing stock density or pasture rotation) were suggested to be the most effective.

Host choice is a major factor in transmission of vector-borne pathogens. Vectors with restricted host ranges will not persist in areas where their preferred hosts are not found, but can be highly efficient in transmitting pathogens between these hosts where they do occur. Vectors with broad host ranges can establish in many areas and develop high populations.

However, vertebrate hosts often vary in their response to the parasite, and multiple-host models of vector-borne pathogens have long shown the impact of more or less competent hosts (e.g. Rogers, 1988; Sota & Mogi, 1989; Lord *et al.*, 1996). Two models that explicitly consider host choice by the vector and the consequences on the transmission of a pathogen will be used to illustrate the impact of host choice.

Lord & Day (2001) also considered host choice in the simulation model of SLE virus discussed earlier. In this case, the question of interest concerns surveillance for the virus. Many counties in Florida monitor transmission of arboviruses using sentinel chickens. These birds are placed in the field, allowed to be bitten by mosquitoes, and tested regularly for viral antibodies. However, there is little information available on how host choice by mosquitoes could affect the interpretation of these data. In this model, two host types were considered: sentinel chickens and wild birds. Simple host preference behaviour was simulated using three levels: no preference, $2 \times$ preference for chickens and $2 \times$ preference for wild birds. There was little impact on overall transmission rates because there were relatively few chickens compared with the number of wild birds. However, the pattern of prevalence over the season varied between the two host types (Fig. 3). After virus infection, prevalence increased faster in the preferred host than the alternate host. With no preference, the surveillance system tracks the infection levels in the wild birds exactly. If chickens are preferred, the surveillance system will provide an advance warning of high levels of transmission. However, if wild birds are preferred over chickens, the surveillance system will lag behind the transmission levels in wild birds. A simple experiment (Lord & Day, 2000) indicated that *Culex nigripalpus* preferentially bites chickens over quail, but this needs to be considered in more detail and under conditions that are more reflective of the surveillance system.

Cohen & Gürtler (2001) developed a model for Chagas disease including three host types. This model reflects the situation in many rural areas of Argentina, where humans and domestic animals live in close proximity and seasonally modify their sleeping habits. In the spring, chickens, dogs and humans all sleep indoors; in the summer, most individuals of all three species sleep outdoors and the chickens typically roost in trees. The vector, a triatomid bug, prefers to feed on chickens, whereas the parasite (*Trypanosoma cruzi*) can infect dogs and humans but not chickens. In this system, host behaviour influences vector feeding because chickens are more available during the spring. Field data indicate that the prevalence of infection in bugs was influenced by the number of bugs feeding on dogs and chickens, and this was reproduced by the model (Fig. 4). They concluded that infected dogs are a high risk factor for human trypanosomiasis. The presence of infected dogs strongly increased the prevalence of infection in humans and bugs, with highest prevalence when two infected dogs were present. Chickens primarily influenced the size of the bug population, particularly in the summer. The seasonal changes in host behaviour, reducing contact between the hosts and bugs, strongly affected transmission. The results of this model will be valuable in developing public education programmes to reduce disease.

Another model of triatomid bug populations included seasonal variation in insect biology, vector–host interaction in behaviour and host quality (Castañera *et al.*, 2003). Host defensive behaviour was assumed to vary with both the stage and density of biting insects, and bug feeding behaviour depended on both host defensive behaviour and temperature. Population size was most sensitive to the degree of seasonal change in development rates, host defensive behaviour and female fecundity. Clearly, interaction between hosts and vectors, as well as between behavioural aspects and seasonality, can have strong effects on insect populations.

This intricate system, with multiple hosts, multiple biting stages of vectors, seasonal variations in behaviour and other aspects of host and bug biology, and differences in host competence for trypanosomes, demonstrates the value of models for understanding the details of vector biology and pathogen transmission cycles.

The importance of individual variation in behaviour was demonstrated by a model of *Ixodes ricinus* (Van Es *et al.*, 1999). Individual behaviour in *Ixodes ricinus* ticks was examined, quantifying the proportion of time individual adults spent questing (searching for hosts) in field enclosures. Different models were then fit to these data, showing that the distribution of time spent questing was skewed and a log-logistic model was the best fit. Although the impact on disease transmission was not considered, it is clear that more active ticks may find hosts faster, but will die sooner if they do not find hosts. In tick-transmitted pathogens, both of these factors can influence the persistence of a pathogen.

The influence of mosquito behaviour and preferences for resting or feeding indoors on malaria transmission is well known (Molineaux *et al.*, 1979; Zimmerman, 1992; Takken & Knols, 1999; Roberts *et al.*, 2000). Roberts *et al.* (2000) attempted to quantify the probabilities of *Anopheles* moving, resting or feeding indoors and outdoors with a series of experiments in Brazil on *Anopheles darlingi*. The data obtained, along with other data on various *Anopheles* species, were used in a probabilistic model to assess the impact of dichlorodiphenyltrichlorethane (DDT) repellency after in-house sprays. It was concluded that the major influence of DDT was in reducing movement of mosquitoes indoors, and that the repellent and irritant effects on behaviour can explain data showing reduced bites after spraying. Despite some difficulties in estimating various probabilities, and a lack of sensitivity analysis, this study demonstrates the usefulness of behavioural analysis and experiments.

Dispersal (movement) of vectors is a crucial factor in vector population dynamics and pathogen transmission. The level of dispersal will affect which hosts are contacted, which habitats contain infective vectors, and the variation in risk of infection in space. Dispersal may be by the vectors themselves, for mating, oviposition or host location. For some vectors, dispersal may also occur when in association with a host. This is particularly important for vectors that remain in association with the host for prolonged periods, such as ticks, fleas or lice. Van Buskirk & Ostfeld (1998) considered the impact of dispersal by hosts for the *Ixodes scapularis*–Lyme disease (*Borrelia burgdorferi*) system in the north-eastern U.S.A. In this area, rodents are important hosts for juvenile ticks, whereas deer are dominant hosts for adults. Rodents are competent for the spirochete, and are a major source of infection for ticks. Deer are not infective to ticks and, accordingly, are not a source of infection for the tick population, but are important in maintaining tick populations. The density and prevalence of infection in nymphal ticks is considered to be the greatest risk factor for human infection in this part of the U.S.A.

The model considered two habitats and dispersal between them based on their suitability (carrying capacity) for juvenile and adult hosts. Host dispersal, and thus movement of the attached ticks, increased tick abundance and prevalence of infection in the less suitable habitat (Fig. 5). This occurs at relatively low levels of dispersal. Levels of infection in ticks increase to over 40% in the less suitable habitat with only 10% of juvenile hosts dispersing. Movement of deer had less impact, but could still result in increased prevalence of infection with moderate movement (Fig. 5). Although the authors did not explicitly consider distance, it is worth noting that movement between habitats, which would be considered true dispersal by rodents, may comprise simple foraging behaviour by deer. The model was extended to a four-habitat structure and compared with field data, demonstrating that asymmetric dispersal could reproduce patterns observed in the field. It would be of interest to expand the model to

consider more than one host type for juvenile ticks because these host species vary in their competence for the spirochete, suitability as hosts for ticks, and dispersal behaviour.

Summary

It is clear that the seasonal population dynamics and behaviour of insects and other vectors should be considered in models of vector-borne pathogens. Further data are required to model these adequately, particularly for the behavioural ecology of vectors. These models would then be more valuable for exploring the transmission cycles and development of control strategies. However, it is important to recognize that it is impossible to do everything at once, and all components of vector and host biology cannot and should not be included in every model. Models with many parameters, all of which have high variability, are difficult to analyse. However, it is important to be explicit in model assumptions and, when excluding vector seasonality or behaviour from the model, ensure that it is intentional and not simply by omission.

There is a long-standing tradition of incorporating aspects of models from other disciplines into models of vector-borne pathogens, and this is useful when including behaviour, seasonality and other complex interactions in these models. Spatial structure, dispersal and foraging behaviour have been studied extensively in parasitoids (e.g. Wilson & Hassell, 1997; Hassell, 2000; Olson *et al.*, 2000). Demographic stochasticity, variable time periods, seasonal structures and individual behaviour have been considered in the epidemiology of directly transmitted pathogens (e.g. Earn *et al.*, 1998; Keeling & Grenfell, 1998, 2000; Grenfell *et al.*, 2001; Lloyd, 2001). Models of ecological systems increasingly incorporate stochastic effects, spatial structure, community structure and dispersal (e.g. Sklar & Costanza, 1990; Ives *et al.*, 1999; South, 1999; Bjørnstad & Grenfell, 2001; King & Schaffer, 2001; Wiegand *et al.*, 2001; Keeling *et al.*, 2002). There are exciting opportunities for considering these ecological factors in vector-borne diseases and exploring the impact on pathogen transmission. The research discussed here provides examples of how some of these aspects can be incorporated into models of vector-borne pathogens. Considering complex structures and models in other disciplines and incorporating relevant aspects into models of vector-borne pathogens will improve the understanding of transmission.

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Fig. 1.

Schematic showing some influences of insect seasonal population dynamics and behaviour on vector-borne pathogens and the examples discussed in the present study. Heavy arrows indicate the transmission cycle of the pathogen. Some factors affecting this cycle are outlined; light arrows indicate where these factors are likely to have strong impacts. Examples discussed are listed under each factor. AHS, African horse sickness; SLE, St Louis encephalitis; TBE, tick-borne encephalitis.

Fig. 2.

The effect of simultaneously varying the aggregation (k) in fly attack and the initial number of flies at the start of the season on the seasonal incidence of myiasis as predicted by the model. Reprinted with permission (Fenton *et al.*, 1999).

Fig. 3. Cumulative proportion of hosts infected in two host types, with and without host preference in vector feeding. Redrawn from data in Lord & Day (2001).

Fig. 4.

(A) Prevalence of infection with *Trypanosoma cruzi* in bugs as a function of the fraction of bugs containing blood meals from dogs and cats or chickens in three rural villages in Santiago del Estero, north-west Argentina. (B) Predicted prevalence rate in bugs as a function of predicted fractions of spring feeding contacts with dogs and chickens in the model. Reprinted with permission (Cohen & Gürtler, 2001).

Fig. 5.

Impact of dispersal on equilibrium densities and infection prevalence of nymphs in an environment with four kinds of habitats having different host compositions. The habitats with the lowest densities of hosts for juvenile ticks also have hosts with the highest reservoir competence. Closed circles, Habitat A (20 hosts/ha for juveniles, 5 hosts/ha for adults). Open circles, Habitat B (5 hosts/ha for juveniles, 5 hosts/ha for adults). Each point represents the results of a single simulation. Reprinted with permission (Van Buskirk & Ostfeld, 1998).