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The Effect of Multiple Vectors on Arbovirus Transmission

Cynthia C. Lord

Florida Medical Entomology Laboratory, University of Florida—IFAS, 200 9th Street SE, Vero Beach, Florida 32962-4699, USA

Abstract

Many mosquito-borne arboviruses have more than one competent vector. These vectors may or may not overlap in space and time, and may interact differently with vertebrate hosts. The presence of multiple vectors for a particular virus at one location over time will influence the epidemiology of the system, and could be important in the design of intervention strategies to protect particular hosts. A simulation model previously developed for West Nile and St. Louis encephalitis viruses and *Culex nigripalpus* was expanded to consider two vector species. These vectors differed in their abundance through the year, but were otherwise similar. The model was used to examine the consequences of different combinations of abundance patterns on the transmission dynamics of the virus. The abundance pattern based on *Cx. nigripalpus* dominated the system and was a key factor in generating epidemics in the wild bird population. The presence of two vectors often resulted in multiple epidemic peaks of transmission. A species which was active in the winter could enable virus persistence until another vector became active in the spring, summer, or fall. The day the virus was introduced into the system was critical in determining how many epidemic peaks were observed and when the first peak occurred. The number of epidemic peaks influenced the overall proportion of birds infected. The implications of these results for assessing the relative importance of different vector species are discussed.

Keywords

arbovirus; vector; model; West Nile virus; *Culex*

INTRODUCTION

Mosquito-borne arboviruses have a complex transmission cycle, alternating between vertebrate and invertebrate hosts. In many cases, more than one host species is capable of supporting viral replication, in either the mosquito or vertebrate host phase. The vertebrate hosts are also serving as blood meal hosts for the mosquitoes, leading to a network of associations between vertebrates, mosquitoes, and virus. Considering the transmission cycle from the perspective of community ecology is necessary to understand how different species are contributing to the cycle (Keesing et al., 2006) and how intervention strategies may affect it. Theoretical ecology has been used to consider the effect of community ecology on pathogen transmission, primarily examining the effect of multiple host species or structure within a single vertebrate species (e.g., age structure). Some examples include studies on malaria (zoophylaxis, Sota and Mogi, 1989), trypanosomiasis (Rogers, 1988), and Lyme disease (*Borrelia*; e.g., Schmidt and Ostfeld, 2001; LoGiudice et al., 2003; Brisson et al., 2008). In viruses, there have been studies on *Culicoides*-borne arboviruses (e.g., African horse sickness, Lord et al., 1996a,b; 1997) and mosquito-borne viruses (e.g., SLEv and WNV: Lord and Day, 2001a,b; age structure: Lord and Day, 2001b; Unnasch et al., 2006).

* Author to whom correspondence should be addressed. clord@ufl.edu.

These studies have shown that the presence of multiple vertebrate hosts can have strong effects on the transmission dynamics of a pathogen, and can also have effects on control strategies designed to mitigate infection in vertebrate species of particular interest.

We would expect that multiple-vector species would also have strong effects on arbovirus transmission dynamics, but there have been few theoretical studies. Glass (2005) showed that the presence of two vectors for Ross River virus (RRv) improved virus survival; in this case the two vectors are very different in their ecology and overwintering strategies. The virus persists over the winter in eggs of *Aedes vigilax* or adults of *Culex annulirostris* and the two species respond differently to climatic variation in temperatures or flooding events. Thus, the presence of both species increases the probability of long term virus survival. However, this model did not control for number of vectors (the total number of mosquitoes increased when both vectors were included) and this may have contributed to the increased survival of the virus. Bicout and Sabatier (2004) modeled the relationship between rainfall and two vectors for Rift Valley fever virus (RVFv) in Senegal, and showed that the presence of both vectors could increase transmission and change the pattern of transmission dynamics. The two vectors respond differently to rainfall and are seasonally offset. The authors concluded that the relative importance of the two vectors was dependent on their abundance and the timing of emergence. However, the abundance patterns used were derived from statistical models of rainfall-driven dynamics, and the observed effects on transmission were not partitioned into the contributions of abundance or seasonality. Theoretical studies could be used to partition out effects such as density, seasonality, or aspects of vector competence. This will increase our understanding of the role of multiple species and improve our predictive ability.

There is a great diversity among mosquito-borne viruses in their interaction with mosquito species. Some viruses are vectored by a limited set of mosquito species, which can result in areas with only a single vector of the virus. Dengue is an example, transmitted primarily by *Ae. aegypti* and *Ae. albopictus*, although other related *Aedes* may be involved in some locations (Kettle, 1990). Ross River virus (RRv) is predominantly transmitted by three vectors (*Ae. vigilax*, *Ae. normanensis*, and *Cx. annulirostris*) that differ in their habitats and ecology. Overlap between the species affects the transmission cycle and epidemiology of the virus (Glass, 2005; Jacups et al., 2008). Other viruses, such as St. Louis encephalitis virus (SLEv), are transmitted by a larger number of different species (several species of *Culex*, including *Cx. pipiens pipiens*, *Cx. pipiens quinquefasciatus*, and *Cx. nigripalpus*); however, in general there are only a few (in some cases only 1 or 2) major vector species present in any geographic area (Mitchell et al., 1980). With increased numbers of vector species comes greater potential for the species to overlap in space or time, and for multiple-vector species to be involved in outbreaks or endemic transmission. Bridge vector systems involve a primary vector transmitting the virus in zoonotic cycles by mosquitoes that rarely bite humans or domestic animals, but sympatric mosquito species, more opportunistic in their feeding habits, bridge from this cycle to vertebrate hosts of concern (which may not be infective for vectors; e.g., humans or horses and eastern equine encephalitis, Kettle, 1990). These systems can be very complex and involve genetic variation in the virus. Venezuelan equine encephalitis virus (VEEv) has a zoonotic, sylvatic cycle between *Culex (Melanoconion)* spp. and wild rodents. Genetic changes can occur in the virus, which enable a wider host range (both vertebrate and mosquito) and can result in epidemic cycles between horses and floodwater mosquitoes, such as *Ae. taeniorhynchus* (Weaver and Barrett, 2004). This increases transmission to both horses and humans and can result in epidemics of the virus. Finally, there are viruses such as West Nile virus (WNV) and RVFv, which have been found in many different species and genera of mosquitoes. For WNV, many species of mosquitoes have been found infected in the field in Florida (e.g., Hribar et al., 2003; Rutledge et al., 2003) and elsewhere in the US (CDC, 2009), and the ability of many species

to replicate, disseminate, or transmit the virus has been demonstrated in the lab (e.g., Turell et al., 2000, 2001, 2005; Sardelis et al., 2001; Goddard et al., 2002). However, this diversity makes it difficult to determine which species are most important in transmission in a particular place and time. An improved understanding of how multiple vectors can affect transmission cycles would aid in assessing the relative importance of different species and in designing intervention strategies to protect particular hosts.

Mosquito species vary greatly in their seasonality, and in one location different species may dominate the community at different times of year. Across their spatial range, species may also shift their abundance pattern in response to the changes in climate. While some species have broad tolerances for climate and are widespread (e.g., *Cx. p. pipiens*), others are restricted by cold or heat tolerance and their ability to persist through the seasons near their tolerances. This provides a complex background against which we must consider arbovirus transmission. Generally, we do not have a good understanding of the roles different mosquito species play in the overall ecology of an arbovirus. While it is frequently assumed that the most abundant vector is contributing the most to arbovirus transmission cycles, a less abundant vector which occurs at a different time of year may be a critical part of the cycle. Variations in aspects of vector competence such as host preference, survival rates, susceptibility, and transmission between species and season will affect the relative contributions to the transmission cycle.

Given the complexity of these systems, it is useful to start with one mosquito vector, and then add in aspects of multiple vectors to identify key features which affect virus introduction, transmission, and impacts on vertebrate hosts of interest. We previously developed a model for SLEv and WNv in Florida (Lord and Day, 2001a,b) with one vector; here a second vector is added to consider the effects of different seasonal patterns. The presence of a second vector at a different time of year may influence the likelihood of a successful introduction of a virus and whether there are subsequent waves of transmission activity. This study was designed to examine how parameters relating to the seasonal activity pattern of two vector populations affect the transmission pattern of an arbovirus. In addition, the results from these models will be used in ongoing studies considering how other aspects of vector biology affect transmission dynamics in a multiple vector system.

MATERIALS AND METHODS

BASIC MODEL

The model used previously to investigate SLEv and WNv in south Florida (Lord and Day, 2001a,b) was modified to include a second vector species. This is a compartmental, deterministic model, with age structure in the wild bird amplification hosts. Avian population dynamics and age structure were as previously described in model II of Lord and Day (2001a), and further details of structure and parameter estimates can be found there. Wild birds are considered as one population without species-specific variation. This simplification was used to focus attention on the effects of the mosquito populations; in reality many species of bird are involved in WNv and SLEv cycles and vary in their interactions with mosquitoes and viruses. The structure and parameter ranges were chosen (Lord and Day, 2001a,b) to reflect competent avian hosts which are year-round residents and where nestlings are more susceptible to the virus of interest. For SLEv, this would include birds such as mourning doves and common grackles, and these hosts were considered in the original parameter development. However, the bird population in the model was not meant to reflect any one species, but rather an aggregate of species that are competent for the virus and have seasonal variation in recruitment. The added complexity of age was retained to allow for interaction between seasonal mosquito activity and seasonal nesting activity. Based on the previous models, bird population parameters were chosen in ranges that were

permissive for epidemics following virus introduction. Briefly, birds of the year are recruited into the more vulnerable, virus-susceptible stage, where they remain until they are infected, mature into the less vulnerable stage, or die. For convenience, we refer to the more vulnerable stage as juveniles and the less vulnerable stage as adults, but note that these classes are defined based on host response to the virus, not reproductive maturity. Recruitment into the population is higher during the spring breeding season, but continues at a low level throughout the year. In the models, the more vulnerable age class is more susceptible to the virus, more infectious to mosquitoes, and remains viremic longer. Bird population parameters were set to generate populations that were constant from year to year and had a spring peak in recruitment.

Vector competence and population size parameters were chosen based on the previous parameter distributions to be permissive for epidemics but be close to the values defined as the center of the probability distributions. The vector population structure (susceptible, latent, infectious) was duplicated and the recruitment function structured to allow different population types (see below for details). Other than the equations necessary for the second species and to accommodate different population types, the basic structure of the model is the same as in Lord and Day, (2001a,b) and the details and equations can be found there. Table 1 shows the parameters used in the model and the values and distributions used in the sensitivity analysis. Over a two year cycle, mosquito populations are driven by specified emergence patterns and parameter values (drawn from specific distributions, see below and Table 1) and vary over time and between simulations, while bird populations were dynamic over time but the same between simulations. Virus prevalence was zero initially and one infected bird was introduced at $t = t_{crit}$. Initial conditions for mosquito populations varied between simulation runs based on the specifics of the populations. Thus, in each run the dynamics are deterministic, but simulation runs differ because they differ in the values of the parameters used to run the model.

In the past analysis, simulations were set to begin on the coldest day (Jan. 15) and were run for 365 days. Because of the diversity of mosquito populations in this study, this would not provide the same information for populations occurring at different times of the year. To accommodate this, simulations were run for 730 days. All simulations and analyses were conducted in MatLab (version R2008b).

MOSQUITO POPULATIONS

The seasonal abundance patterns used were broadly based on *Culex* species present in Florida. In central and southern Florida, mosquitoes can be active all year. There is a reduction in activity in the winter, driven by dry conditions in addition to cooler temperatures affecting development and activity. Species individually show varied activity patterns, although many have not been examined in depth. *Culex* species vary in their seasonal abundance pattern, and this can also vary by habitat and the local availability of oviposition sites. Because of its association with SLEv, *Cx. nigripalpus* is well studied; it can be found all year but has activity peaks in summer and fall which are largely driven by rainfall (see, e.g., Nayar, 1982; O'Meara and Evans, 1983; Day and Edman, 1988; Day and Curtis, 1989, 1993; O'Meara et al., 1989). *Culex. p. quinquefasciatus* varies in its seasonal pattern abundance in different aquatic habitats, but can be found all year in Florida and is generally more active in the summer (O'Meara and Evans, 1983; O'Meara et al., 1989). *Culex restuans* and *Cx. salinarius* are most often found in the winter and spring; they are less active during the extreme heat of the summer (O'Meara and Evans, 1983; O'Meara et al., 1989; Zyzak et al., 2002). The dominance of particular *Culex* species at a particular location can change rapidly in Florida and elsewhere (e.g., Rutledge et al., 2003; Kunkel et al., 2006). However, it should be noted that our methods for assessing species composition and seasonal dynamics usually depend on various types of traps; known biases in species

collection in different trap types (e.g., O'Meara et al., 1989; Vaidyanathan and Edman, 1997a,b) and host preference changes over time (e.g., Edman and Taylor, 1968) can affect the accuracy of our assessment of seasonal abundance patterns.

Four population patterns were defined, based on the recruitment of new individuals into the population, and were used to consider different patterns possible in Florida. Some of the patterns considered would not occur in more temperate areas. Other than *Cx. nigripalpus*, the patterns were not meant to reflect any particular species, but rather to investigate how the presence of mosquitoes at different times of year would affect virus introduction and epidemiology.

The seasonal abundance pattern for *Cx. nigripalpus* (N) was the same as in the previous model, consisting of baseline pulses of recruitment, an early summer peak and a late summer or fall peak. Winter (W), Summer (S), and Fall–Spring (F) patterns were defined. The W and S patterns had one population peak, while the F pattern had two population peaks, one in fall and one in spring. All possible population pairs were considered and simulation sets are noted by the pairs used, e.g., FN had a fall–spring species and *Cx. nigripalpus*, while SW had a summer and a winter species. In this model, the populations of mosquitoes were considered to be identical except for the seasonal abundance pattern, to focus attention on the consequences of mosquito activity at different times of the year. This included the total number of female mosquitoes recruited into the population yearly. The model retained the temperature curve based on Indian River County (east central Florida) and the virus development rate and mosquito mortality were linear, increasing functions of temperature, identical for the four population types. Note, however, that the combination of the time of year of the peak in recruitment and the temperature based mortality curve resulted in different actual mortality in the 4 populations. Later studies will relax these assumptions and consider species which also vary in other vector competence parameters.

The number of mosquitoes recruited into each population over the year (R_{tot}) is divided up into three phases: baseline (year round recruitment), first peak, and second peak. Only the N population has any baseline recruitment; the first peak is in spring–early summer and the second in late summer–fall. The F population has the first peak in the spring and the second in the fall. The W and S populations have only a first peak, in the winter and summer respectively. For populations with multiple peaks, proportion of the total vector recruitment in the baseline (p_{base}) and first peak ($p_{\delta 1}$) is specified; the proportion in the second peak ($p_{\delta 2}$) is the remainder [$1 - (p_{base} + p_{\delta 1})$]. The baseline is defined as a number of females (ρ_b) added to the population at intervals (iv); the two main peaks are described by normal distributions (δ_1, δ_2). The equation for recruitment of females into each population is thus

$$\rho(t) = \rho_b(t) + p_{\delta 1} R_{tot} \delta_1(t) + [1 - (p_{base} + p_{\delta 1}) R_{tot} \delta_2(t)],$$

where

$$\delta_k(t) = \frac{1}{2\pi\sigma_k} \exp\left(-\frac{1(q_k - t)^2}{2\sigma_k^2}\right); k=1, 2$$

$$\rho_b(t) = \frac{p_{base} R_{tot}}{iv}$$

For all populations except N, $p_{base} = 0$; for S and W, $p_{\delta 1} = 1$.

SENSITIVITY ANALYSIS

Since the population patterns contained different parameters, it was not possible to compare across population types within one sensitivity analysis based on distributions of parameters. In order to compare the effects of parameters both within population types and between pairs of populations, a sampling scheme was designed using elements of a Latin Hypercube scheme (LHC) and systematic variation. Briefly, LHC is a technique that allows exploration of the full parameter space with a greatly reduced number of simulation runs (Iman and Shortencarrier, 1984; Blower et al., 1991; Blower and Dowlatabadi, 1994). In a structured manner, LHC permits the determination of those parameters which explain the greatest variation in model output, relative to a given range of variation in each parameter considered. A probability distribution is chosen for each independent parameter. The corresponding cumulative probability distribution is divided into n equal intervals, where n is the number of runs desired. Within each interval, a value is chosen at random and backtransformed to the original parameter axis. Many different probability distributions can be used, depending on the information available (Iman and Shortencarrier, 1984). Here, we used triangular and uniform distributions (Table 1) to focus attention on populations separated in time, while including some probability of overlapping. The n values for each parameter then are reassorted randomly into n sets of parameters to use in the simulations. We used LHC to generate 100 samples for each of the mosquito population parameters, designated by numbers 1–100. The model was then simulated with all possible pairs of populations for each set of parameters. For each parameter set and population type, a simulation was also run with the single population doubled in size, to compare the effect of total number of mosquitoes and the distribution throughout the year. In addition to the parameters describing the populations, the parameter t_{crit} was included in the LHC sampling. This parameter defines when during the simulation the virus is introduced, by adding one infected adult bird to the population. This resulted in 1000 simulation runs, divided into 10 sets of 100 runs each by population type: SF, SW, SN, FW, FN, WN, SS, FF, WW, and NN. Each set is designated by the two populations included, e.g., SF has a summer population and a fall–spring population. The double populations (SS, FF, WW, and NN) consisted of the single population with the total number of females doubled, to provide a comparison between population pairs and single populations while controlling for the number of vectors. Between the sets, simulation runs with the same run number have the same parameter values for the populations they share, e.g., SF1, SW1 and SN1 have the same parameters for the summer population, while SF1 and FW1 have the same parameters for the fall-spring population.

ANALYSIS

To facilitate comparisons of infection across the population types, the period from t_{crit} to $(t_{crit} + 365)$ was analyzed for each simulation. This provided a fixed time period for comparison, while encompassing the times of peak abundance for each mosquito population. After virus introduction, the infection rates were tested at each time step of the simulation for virus extinction. Six state variables described infected hosts or vectors: infected juveniles, infected adults, latently infected mosquitoes of species A, B, and infectious mosquitoes of species A, B. If all of these variables were simultaneously <0.5 , the virus was deemed to have died out. If the maximum number of birds infected before the virus die-out was <2 , the simulation was designated non-epidemic. This type of arbitrary cutoff is necessary in a deterministic model, because otherwise extremely low levels of virus may persist for long periods; in the natural system there would be a high probability that the virus would go extinct. This method was tested using preliminary simulations (data not shown) and determined to adequately differentiate between simulations with extended periods of low virus presence and those which maintained sufficient infection rates for persistence.

Runs with at least one peak of infection (see below for assessment of peaks) which met the criteria for persistence were designated as epidemic.

Because of the nature of the study, with multiple mosquito population peaks, we frequently observed multiple peaks in infection in the bird population. To characterize this, we summed the two bird infection variables (all infected = juvenile + adult infected) and identified peaks (local maximal values) in the summed variable. To prevent counting peaks that were minor fluctuations during periods of low virus activity, those that were <3 birds were dropped. In addition, to avoid counting multiple peaks that were very close in time and represented small fluctuations during a period of higher virus activity, the minimum between two local peaks (in time) was tested. If the minimum was >50% of the value of the smaller peak, the smaller peak was not counted as a maximum. Identification of peaks was done using MatLab code modified from the *extrema.m* file available on the MatLab user file exchange. Each simulation was thus scored as having 0 (not epidemic) to 3 (the maximum observed in the study) peaks. The global maximum value for the summed bird infection was extracted, as was the time when this occurred, and was also analyzed. Finally, the total number of birds infected during the analysis period was determined.

This resulted in four variables: the number of epidemic peaks, total number of birds infected in the simulation, maximum (peak) infection in birds, and the day when that maximum occurred. These variables were analyzed using generalized linear modeling (MatLab function *glmfit*) on each set of runs separately, with independent variables consisting of the parameters used to run that set of simulations. All simulations were included in the regression for number of epidemic peaks (i.e., including runs with zero epidemic peaks, or not epidemic), but only runs scored as epidemic were included in the models assessing the size (total number of birds and maximum infection in birds) and timing of epidemics. The regression models assessed the contribution of each parameter to the outcomes by population pair; comparing the models and effect of parameters across population pairs provides information on how this differs based on the populations included.

RESULTS

Overall, the parameter values chosen for the fixed parameters were very permissive for epidemics (Table 2). In all sets of runs, there were many runs with epidemics and multiple peaks. This is particularly noticeable for population pairs including *Cx. nigripalpus* (N), where epidemics occurred with all parameter sets and all runs were epidemic. An example of the mosquito populations and the resulting infection dynamics in bird populations with selected pairs of mosquito populations is shown in Fig. 1. This example clearly demonstrates a result that was observed in many cases: the particular pair of mosquito populations strongly influenced the presence and number of epidemics. In this example, the number of epidemics ranged from 0 to 3, with the higher number occurring with the SN, WN, and SW pairs. Although the higher numbers of epidemics frequently occurred with population pairs generating multiple peaks of mosquito abundance (N and F), there were parameter combinations where the SW pair (both single peak populations) generated multiple epidemic peaks. In part, this is an artifact of the analysis method used, considering the period from t_{crit} to $(t_{crit} + 365)$. In some situations, changing the analysis period would have changed the number of epidemics.

The distributions shown in Table 2 show the effect of the different populations and combinations. All simulations including the N population (2 main abundance peaks and multiple small pulses through the year) had at least 1 epidemic. Doubled populations with only 1 peak (WW and SS) frequently were not epidemic, while population combinations with 2 or 3 abundance peaks (SW, FW, SF) were intermediate. It is interesting to note,

however, that 3 epidemics occurred most frequently in the SW pair, with two separate mosquito population peaks. These results show that the presence of multiple vector species in the system can increase the likelihood of virus establishment and create more complex epidemiological dynamics.

REGRESSION MODELS

The number of epidemics resulting from a particular parameter set was most consistently influenced by the time of introduction (t_{crit}) (Table 3, Fig. 2), with this variable contributing significantly to the regression model in all pairs but FW. Other variables were significant in specific pairs, but there was no consistency or pattern. The model R^2 varied from 0.12 to 0.49, indicating a substantial amount of variance left unexplained.

The models examining infection in birds (accumulated infection and peak infection) were dissimilar. The regression model for peak infection was significant only in SF and SS pairs, and few parameters were significant (data not shown). Full regression models for accumulated infection are not shown due to space limitations, but the model R^2 , p values, and significant parameters are given in Table 4. Accumulated infection was more sensitive to the direct effects of the parameters, with all regression models significant except WW (with a p value of 0.1). Not surprisingly, the number of epidemics was the most important parameter in all models (except SS, where multiple epidemics did not occur). A higher proportion of the variance was explained by these models (0.28–0.79), but there is clearly variance left unexplained. The variance left unexplained in sets of deterministic models indicates that interactions between parameters were important, but there was insufficient power to examine interactions in these regression models.

The timing of the first peak of infection was strongly dependent on the time of virus introduction (full models not shown; R^2 , p and significant parameters in Table 4), as expected from previous work with this model. The regression models were significant and t_{crit} was a significant parameter in all population pairs. Unlike the other regression models, these models explained most of the variance, with all R^2 values >0.95 .

DISCUSSION

Many mosquito-borne arboviruses can be transmitted by more than one vector species. In some systems these species rarely overlap geographically, but in others there may be a complex community of vectors interacting with a community of hosts. Which vector is most important to the overall transmission cycle or to transmission to a particular host of interest is likely to vary in space and time. However, we would like to understand this process in order to predict transmission risk to different vertebrate species and develop intervention strategies based on vector control.

Because of historic information on virus activity (Day and Stark, 1996) and our general understanding of the SLEv and WNV systems in Florida, we expected the winter population to be a minor contributor to virus transmission. While the virus tended to die out more often when only the winter population was present, the winter population did contribute to virus introduction and transmission. In some simulations, the presence of the winter population allowed the virus to establish and then have higher transmission when other mosquito populations became active. By controlling for population size (populations are often lower in winter in Florida due to dry conditions, not temperature), we removed one major factor. However, these results indicate that during wet winters or in locations where winter populations become larger than normal (under new water management strategies, for example), mosquito activity at this time of year could be important in virus establishment and transmission. This is likely to also play a role in the longer term dynamics of endemic

species; low-level transmission by vectors otherwise of little concern may allow viruses to persist between the active seasons of more dominant vectors. While we were specifically considering Florida, this has relevance to any areas where one season has reduced mosquito abundance that may be affected by specific local conditions.

The contribution by the winter species was, in part, driven by temperature dependence in survival. Although there was also temperature dependence in virus development, the longer lifespans were sufficient to allow survival through the extrinsic incubation period. The underlying parameters and functions for survival and virus development were identical in each population, but the realized values were very different for winter and summer populations. The parameter values were taken from previous studies based on *Cx. nigripalpus*, which is a long-lived mosquito (Nayar, 1982; Lord, unpublished data). The winter species may not contribute as much, and the fall–spring population may also show reduced contributions, if survival was less sensitive to temperature. Careful consideration of available data on lifespans of mosquitoes active at different times of year will be needed to adequately parameterize subsequent studies expanding on this work. However, frequently the data needed are not available, and sensitivity analysis on this and other parameters will be necessary to assess their relative importance.

It is of interest to note the dominance of the *Cx. nigripalpus* abundance pattern in this study. Simulations including this pattern always had epidemics, indicating that our previously defined “most likely” parameter values were permissive for epidemics. Parameters relating to this population were generally important in the regression models on the number of epidemics and the accumulated number of birds infected. This population was very different from the others, with at least some recruitment year-round. Clearly, this then interacted with the presence of the other species to increase the likelihood of successful virus establishment. In areas without year-round mosquito presence, the degree of temporal overlap between vectors and the fraction of the year without mosquito activity may have strong influences on the invasion or persistence of a virus.

Previously, we found significant effects of parameters on the peak infection in birds during the first epidemic peak (Lord and Day 2001a,b). In this set of simulations, there was little direct effect of the parameters and the first-order regression models were either not significant or explained a very low proportion of the variance. This is a difficulty as the number of parameters in a model increases. Obviously, the outcome variables in a deterministic model must be influenced by the input parameters. If the first-order model does not adequately explain the variance, then higher order terms must be involved. However, with the number of parameters in these models (as with many models), it is difficult to examine all possible interactions. Reducing the number of parameters considered or the number of populations and increasing the number of simulation runs will improve the potential to examine interactions, and will be addressed in future work.

Detailed studies of the seasonal patterns of potential vectors are not available for many systems and locations; the focus is generally on the species thought to be most important in transmission to the vertebrate of interest (usually humans or domestic animals). The recent introduction of WNV to the USA has generated many studies of potential vectors and provides some examples of situations where different vectors are active at different times of the year. Most notably, *Cx. restuans* is generally found in spring and early summer, while other *Culex* species are present later in the season (O’Meara and Evans, 1983; O’Meara et al., 1989; Andreadis, 2001; Ebel et al., 2005). In another study, the *Cx. pipiens/restuans* complex (not differentiated due to morphological similarity) responded differently to weather variables in western New York (USA) than another potential WNV vector, *Ae. vexans* (Trawinski and Mackay, 2008). Conversely, *Cx. pipiens* and *Cx. p. quinquefasciatus*

showed similar seasonal distributions in Tennessee (USA), although *Cx. p. quinquefasciatus* had a broader seasonal distribution and there was variation between sites (Savage et al., 2008).

Rift Valley fever virus also has many potential vectors, but the seasonal dynamics have not been well studied throughout its range. The model of prevalence discussed earlier (Bicout and Sabatier, 2004) was based on field data from two species of concern, *Ae. vexans* and *Cx. poicilipes*. These vectors have different life histories (floodwater and permanent water larval habitats, respectively) and responded differently to the onset of seasonal rainfall in Senegal. *Aedes vexans* abundance increased quickly but the increase in *Cx. poicilipes* was delayed by about 2 months. This study demonstrated that relatively small differences in seasonal distribution could affect the transmission dynamics of RVFv, and it is likely that multiple vector species affect transmission in other areas endemic for RVFv.

A similar situation may occur with VEEv, where different vectors are involved in epidemic and endemic transmission. The endemic vectors are primarily permanent water species and have relatively stable populations through the year, while the epidemic vectors are primarily floodwater species with large seasonal variation (Weaver and Barrett, 2004). Genetic changes in the virus occur that allow transmission by epidemic vectors, but the seasonal dynamics of the vector species may also play a role in the emergence of epidemics (Weaver and Barrett, 2004).

In this study, potential interactions between the mosquito species were not considered, but they are likely to play a role in the dynamics of the mosquito populations and arbovirus transmission. Interactions in the larval stage such as competition and predation have recently been studied, primarily in *Aedes*, and the outcome of these interactions depends on the particular habitat and conditions (reviewed in Juliano, 2009). Predictions of which species will be most affected, the ultimate adult population sizes, and the temporal distribution of emergence are difficult to make due to the complex interactions and effects of environment (Juliano, 2009). Competitive interactions can also affect susceptibility to arboviruses (Alto et al., 2005, 2008). However, much of this work has been done in container-inhabiting *Aedes* (Juliano, 2009, and references therein), and it is unknown how important competition is in other environments, nor the potential effect on susceptibility to arboviruses in other systems.

Mosquitoes may also compete or interfere in the adult stage, while blood feeding. Host defensive behavior increases with mosquito density for some species, and high densities can reduce feeding success (e.g., Edman et al., 1972, 1974). Density of both mosquitoes and sandflies (*Lutzomyia longipalpus*) affected the distribution of sandflies among hosts (Kelly et al., 1996), which could in turn affect the number of hosts potentially receiving infectious bites. However, interference in blood feeding may increase the number of interrupted meals, increasing the overall biting frequency and potential transmission rate. Longer-term effects of density on blood feeding success are poorly known; vertebrate hosts respond to mosquitoes immunologically and this can affect feeding success (reviewed in Billingsley et al., 2006; see also Schneider and Higgs, 2008) and arbovirus transmission (Schneider and Higgs, 2008) but the effect on mosquito populations is not well understood. Competition and interference in blood feeding is likely to affect arbovirus transmission in complex ways that are difficult to predict.

When species overlap in their seasonal distribution, there will be more opportunities for competitive interactions; the distributions used here had minimal overlap so there would be less direct interaction or competition. Indirect and longer-term interactions between mosquito species, such as increasing predator density or effects on the immunological status

of host populations, are poorly understood, but clearly could have effects on the contributions by different mosquito species to arbovirus transmission. Including these types of interactions in models of vector–host communities and examining the effects on arbovirus transmission would be of interest. However, these interactions are more likely to have an effect when considering species which overlap in their seasonal distributions, rather than those which are separated in time as was considered here. Future work will begin to examine the effect of competitive interactions on arbovirus transmission.

Here, the focus was on seasonal abundance patterns of mosquitoes. This provides a platform for further explorations of the effects of other aspects of mosquito biology, such as vector competence and survival. As with any modeling study, the structure of this model and analysis affected the outcome, but the model provided insights into what may happen under certain conditions. We considered the consequences of a virus introduction to naïve populations. This is relevant not only for exotic pathogens introduced to new areas, but for some endemic viruses. Genetic changes have been shown to occur and spread in WNV, indicating the introduction of new strains of virus to previously invaded or endemic areas (e.g., Anderson et al., 2001; Davis et al., 2005). Genetic diversity in SLEV suggests that it may die out at a very local level and be re-introduced by movement of hosts or vectors (Chandler et al., 2001). The dynamics of these viruses thus may be partly those of an endemic virus (where herd immunity can be a factor) and partly those of an exotic virus, with no previously existing immunity in the vertebrate population. Obviously, the host species complex is intimately involved in these dynamics. The dynamics in systems where the hosts are short-lived or do not mount long term immune responses to particular viruses will be more apt to behave like successive introductions of virus to a naïve population, while those with longer-lived hosts or long term immune responses will require models which incorporate the immune structure. Long term dynamics will also require a more stochastic approach rather than the criteria used in this deterministic study to prevent maintenance of virus at extremely low levels. Future model analysis to examine other aspects of vector competence may be expanded to incorporate a stochastic approach to virus persistence. In modeling studies, it is always necessary to balance simplicity with complexity; the dynamics are easier to observe and interpret in deterministic or less complex models, but this may omit important details such as stochastic virus extinction or complex interactions. In addition, the availability of empirical data to estimate parameters must be taken into account; as models become more complex, sensitivity analyses become more difficult to analyze and interpret.

This study, although restricted in focus, emphasizes the importance of considering how the activity patterns of mosquito species will affect the role they play in the overall dynamics of an arbovirus. These models have demonstrated the need for a more complete understanding of the vector community and the contributions of vectors during different seasons to the overall transmission cycle. Climate generally determines the overall seasonal activity patterns, but weather patterns can change the dynamics from year to year and spatially. Species active at times of year when overall abundance is low may allow virus introduction or persistence, but may not be detected during studies of transmission during other times of year. The introduction of an exotic vector that responds differently to climate and weather could change the transmission dynamics of a virus, even if it is not a major vector or a vector to vertebrate species of particular concern. Further data on the seasonal abundance of different species, as well as their vector competence and survival, will be required to assess the relative importance of specific vectors to transmission cycles and to the risk of transmission to particular host species.

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Fig. 1.

Example of mosquito populations and resulting transmission dynamics for selected population pairs. A. W and N populations. Parameter values for W: $q_1 = -2.95918$, $\sigma_1 = 8.381646$; N: $p_{base} = 0.067631$, $iv = 13.78$, $p_{SI} = 0.223717$, $q_1 = 157.0072$, $\sigma_1 = 2.25494$, $q_2 = 237.936$, $\sigma_2 = 9.06871$. B. S and F populations. Parameter values for S: $q_1 = 207.3976$, $\sigma_1 = 15.76943$; F: $p_{SI} = 0.38136$, $q_1 = 98.98622$, $\sigma_1 = 20.3434$, $q_2 = 270.4228$, $\sigma_2 = 15.24998$. C. Results from simulation with SN pair. Arrows mark day of virus introduction ($t_{crit} = 212$) and the endpoint of analysis (end = 577). There were three epidemic peaks identified in this simulation, marked by *. D. Results from SF pair, with 2 epidemic peaks. E: Results from SS, the doubled S population, with one epidemic peak. All other parameters for the simulations are given in Table 1.

Fig. 2. Number of epidemics observed in each simulation run for each population pair. Each run had a different value of t_{crit} which was held constant between simulations with different pairs. Double populations of each type (WW, NN, SS, FF) are in red-yellow colors; pairs including N are in shades of green for easier comparison. Within each population pair, t_{crit} had a strong effect on the number of epidemics observed.

Parameters used in models

Table 1

Description	Symbol	Distribution ^a	Population ^b	Range ^c	Center ^d
Population size of host type <i>i</i>					
Juveniles	J	C			5
Adults	A	C			371
Mortality rate of host type <i>i</i> (days ⁻¹)					
Juveniles	m_J	C			0.05
Adults	m_A	C			0.003
Recovery rate of host type <i>i</i> (days ⁻¹)					
Juveniles	r_J	C			0.22
Adults	r_A	C			0.5
Days between meals on all hosts	α	C			7
Biting rate (bites/mosquito/day)	a_i	Calc ^e			
Transmission from					
Vector to juveniles	b_J	C			0.9
Vector to adults	b_A	C			0.7
Juveniles to vector	β_J	C			0.7
Adults to vector	β_A	C			0.5
Daily vector recruitment	ρ	Calc ^e			
Yearly total recruitment of vectors per population	ρ_{max}	C			19000
Total recruitment of vectors ($= \rho_{max} * (J + A)$)	R_{tot}	Calc ^e			
Proportion of vector recruitment in baseline	p_{base}	Uni.	N	0.005–0.3	
Interval between baseline pulses	i_v	Uni.	N	3–40	
Proportion of vector recruitment in first peak	p_1	Uni.	N	0–0.25	
Proportion of vector recruitment in second peak	p_2	Tri.	F	0.25–0.75	0.5
Number of females added in baseline pulse	ρ_b	Calc ^e	N,F		
First peak of recruitment	δ_1	Calc ^e			

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Description	Symbol	Distribution ^a	Population ^b	Range ^c	Center ^d
Timing of peak 1 (days from Jan. 15)	q_1	Tri.	N	104–108	160
		Tri.	S	140–250	195
		Tri.	F	50–160	105
		Tri.	W	–40–70	15
Spread of peak 1 (variance in days)	σ_1	Uni.	N	2–10	
		Tri.	S	8–25	15
		Tri.	F	8–25	15
		Tri.	W	8–25	15
Second peak of recruitment	δ_2	Calc ^e			
Timing of peak 2 (days from Jan. 15)	q_2	Tri.	N	181–286	195
		Tri.	F	230–340	285
Spread of peak 2 (variance in days)	σ_2	Uni.	N	2–10	
		Tri.	F	8–25	15
Vector mortality rate (days ⁻¹)	μ	Calc ^e			
Slope of temperature relationship	μ_s	C			0.006
Mortality at 22.5 °C	$\mu_{22.5}$	C			0.08
Virus development rate (days ⁻¹)	γ	Calc ^e			
Slope of temperature relationship	γ_s	C			0.005
Development at 22.5 °C	$\gamma_{22.5}$	C			0.08
Bird recruitment	f	Calc ^e			
Baseline (birds/day)	f_b	C			0.3
Timing of peak (days from Jan. 15)	q_f	C			105
Spread of peak (variance in days)	σ_f	C			35
Proportional increase in breeding season (%)	f_p	C			2.6
Duration of more vulnerable period	t	C			15
Day virus is introduced (days from Jan. 15)	t_{crit}	Tri.		1–365	125

^aTri.—Triangular; Uni.—Uniform; Calc—Calculated; C—Constant.
^bMosquito population type: N—Cx. nigripalpus; F—fall-spring; S—summer; W—winter.
^cMinimum–maximum values.

^dMost probable value, used in triangular distribution only.

^eSee details of calculations and equations in Lord and Day (2001a, b).

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Table 2

Distribution of number of epidemics by population pair.

	<u>Not epidemic</u>	<u>Number of epidemics</u>		
	0	1	2	3
Population pair				
FN	0	23	77	0
FW	22	27	48	3
SF	7	18	74	1
SN	0	28	70	2
SW	24	20	46	10
WN	0	19	75	6
NN	0	25	74	1
SS	51	49	0	0
WW	73	19	8	0
FF	22	22	51	5

Table 3

Regression models for the number of epidemics in each set of simulation runs. Values indicated are for the coefficient of the parameter in the regression model. Bold indicates coefficients which were significantly different from 0 at $p < 0.05$; italic at $p < 0.1$

Population pair ^d	FN	FW	SF	SN	SW	WN	NN	SS	WW	FF
Parameter										
intercept	0.6892	1.2299	0.3531	1.5042	-0.9466	1.9432	2.2912	-0.3038	0.6407	2.6243
t_{crit}	0.0035	0.0012	0.0050	0.0040	0.0030	0.0037	0.0037	0.0020	-0.0032	0.0032
ivA^a						0.0015				
$p_{\delta 2}A$	0.4605	0.4583					0.8683	0.3974		
$p_{base}A$							0.3854			
q_1A	0.0033	<i>0.0065</i>	-0.0009	-8.0×10^{-6}	0.0031	0.0002	-0.0053	-0.0012	0.0014	0.0051
σ_1A	<i>0.0192</i>	0.0367	-2.2×10^{-5}	0.0051	0.0633	-0.0116	-0.0134	0.0439	0.0134	0.0325
q_2A	0.0002	<i>-0.0098</i>					-0.0019			-0.0122
σ_2A	0.0025	0.0357					-0.0067		0.0287	
ivB	0.0001			0.0043		-0.0004				
$p_{\delta 1}B$	0.6287		0.5158	<i>1.0992</i>		0.9311				
$p_{base}B$	-0.2474			0.4752		<i>-0.9815</i>				
q_1B	-0.0033	0.0009	0.0017	-0.0038	-0.0006	-0.0033				
σ_1B	-0.0031	0.0376	0.0234	-0.0179	0.0166	-0.0025				
q_2B	0.0001		-0.0009	-0.0010		-0.0001				
σ_2B	-0.0072		0.0082	0.0150		0.0135				
Model R²	0.49	0.18	0.42	0.43	0.12	0.38	0.43	0.18	0.16	0.21
F	6.3860	2.4470	8.0773	6.8205	2.5784	5.4278	8.7258	7.2392	6.0249	4.1449
p	<0.0001	0.0191	<0.0001	<0.0001	0.0313	<0.0001	<0.0001	0.0002	0.0008	0.0010

^a A indicates the first population in the pair, B the second. For example, in the FN pair the fall-spring population is population A, but in the SF pair it is population B.

Table 4

Regression models for other output variables. Analysis was restricted to those simulation runs which were epidemic (i.e., number of epidemics >0)

Population pair	Model R ²	F	p ^a	Number of significant parameters ^b	Significant parameters in regression model ^c
Accumulated infection in birds					
FN	0.58	8.42934	<0.0001	3	$epi, t_{crit}, p_{base}Bd$
FW	0.48	7.04768	<0.0001	4	$epi, q_1B, q_2A, \sigma_2A$
SF	0.61	14.39898	<0.0001	4	$epi, q_1B, q_2B, \sigma_1B$
SN	0.79	29.59942	<0.0001	2	$epi, p_{base}B$
SW	0.51	11.89657	<0.0001	4	$epi, \sigma_1A, \sigma_1B, q_1B$
WN	0.52	8.731253	<0.0001	4	$q_1A, epi, p_{base}B, p_{\delta_1}B$
NN	0.66	19.41283	<0.0001	2	$epi, p_{base}A$
SS	0.79	55.59629	<0.0001	1	$t_{crit}E$
WW	0.28	2.152498	<0.0001	1	epi
FF	0.40	6.799444	<0.0001	2	epi, σ_2A
Day of peak bird infection					
FN	0.99	519.0268	<0.0001	3	$t_{crit}, p_{\delta_2}B, q_2B$
FW	0.98	470.2992	<0.0001	1	t_{crit}
SF	0.98	490.017	<0.0001	2	t_{crit}, q_1A
SN	0.93	123.4455	<0.0001	3	$t_{crit}, p_{base}B, \sigma_2B$
SW	0.96	371.3185	<0.0001	2	t_{crit}, q_1B
WN	0.98	349.9512	<0.0001	3	$t_{crit}, p_{base}B, \sigma_2B$
NN	0.99	753.3523	<0.0001	3	$t_{crit}, p_{base}A, \sigma_2A$
SS	0.96	336.5778	<0.0001	1	t_{crit}
WW	0.99	800.2194	<0.0001	1	t_{crit}
FF	0.95	206.7994	<0.0001	1	t_{crit}

^a p value for overall regression model.

^b Significantly different from 0 at $p < 0.05$.

^c As in Table 3, A indicates the first population in the pair and B the second. Doubled populations are listed as population A.

^d epi, number of epidemics in simulation.

^eNote that all runs in the SS set had 0 (not epidemic) or 1 epidemic; thus there was no variation in ept in the regression model.