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Modelling the effect of temperature on the seasonal population dynamics of temperate mosquitoes

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HIGHLIGHTS

- We model temperate mosquito species using delay-differential equations.
- Variable time delays incorporate effects of temperature on life stage duration.
- The effects of changing climate on mosquito seasonality are explored.
- Effects of seasonal temperature on abundance can be complex.
- An increase in mosquito abundance is expected under predicted UK warming.

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ABSTRACT

Mosquito-borne diseases cause substantial mortality and morbidity worldwide. These impacts are widely predicted to increase as temperatures warm and extreme precipitation events become more frequent, since mosquito biology and disease ecology are strongly linked to environmental conditions. However, direct evidence linking environmental change to changes in mosquito-borne disease is rare, and the ecological mechanisms that may underpin such changes are poorly understood. Environmental drivers, such as temperature, can have non-linear, opposing impacts on the demographic rates of different mosquito life cycle stages. As such, model frameworks that can deal with fluctuations in temperature explicitly are required to predict seasonal mosquito abundance, on which the intensity and persistence of disease transmission under different environmental scenarios depends. We present a novel, temperature-dependent, delay-differential equation model, which incorporates diapause and the differential effects of temperature on the duration and mortality of each life stage and demonstrates the sensitivity of seasonal abundance patterns to inter- and intra-annual changes in temperature. Likely changes in seasonal abundance and exposure to mosquitoes under projected changes in UK temperatures are presented, showing an increase in peak vector abundance with warming that potentially increases the risk of disease outbreaks.

1. Introduction

Climate change is expected to affect the distribution and seasonal dynamics of mosquito populations, with substantial implications for disease seasonality and persistence (Githeko et al., 2000). Globally, mosquito-borne diseases are a major public health concern (Gubler, 2002), and increasingly so in temperate climates, with disease caused by mosquito-borne pathogens including West Nile (Sambri et al., 2013), Chikungunya (Grandadam et al., 2011), Usutu (Weissenböck et al., 2002) and Toscana (Charrel et al., 2005) viruses being reported in Europe in recent years. A range of factors including societal, land use and habitat changes, have been linked to changes in exposure to mosquitoes, which vector these diseases (Gubler, 2002). These factors combine with widespread predictions that rising temperatures may increase mosquito population size, development rates and per host biting rate, producing increases in the incidence of mosquito-borne diseases (Mirski et al.,

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2012). The non-linear and opposing impacts of temperature on vector demographic rates require detailed modelling, incorporating the various biological processes at play, if we are to understand the likely impacts of climate change on vector abundance and whether predictions of increased exposure to vectors will be borne out (Rogers and Randolph, 2006).

To model disease seasonality and persistence it is essential that epidemiological models are coupled with accurate seasonal predictions of vector density (Lord, 2004). This is likely to become increasingly important in coming years, as the climate is expected to become more variable (Jones et al., 2009). Without accurate predictions of vector density, calculations of the basic reproduction number of the disease (R_0), which describes ability of a disease to persist in a susceptible population, will be subject to considerable error. However, many recent epidemiological studies of vector-borne disease do not account for seasonality in vector populations (Cruz-Pacheco et al., 2005; Bowman et al., 2005; Wonham et al., 2004). In this study we utilise a delay-differential equation (DDE) framework to explicitly model the effects of temperature on each of the life stages of the vector population. This gives valuable insight into how inter-annual variability in temperature may affect mosquito populations, which will have a direct effect on disease transmission.

There is considerable evidence showing that environmental drivers have a large impact on both the mosquito life and disease transmission cycles (Jian et al., 2014; Lebl et al., 2013; de Almeida Costa et al., 2006). Hence, understanding these mechanisms and resulting effects will aid our predictions for vector-borne diseases. Increasing temperature is known to decrease the length of time spent in each of the immature stages and to decrease the lifespan of adults (Madder et al., 1983; Loetti et al., 2011). Furthermore, the death rate of the immature stages is strongly linked to temperature (Ciota et al., 2014; Madder et al., 1983; Loetti et al., 2011) and increasing temperature leads to decreases in the lengths of both the gonotrophic cycle (the time required for location of a blood meal, embryonic development and egg-laying) (Madder et al., 1983; Vinogradova, 2000) and the extrinsic incubation period (time between an adult vector contracting a pathogen and becoming infectious, referred to as EIP) (Hartley et al., 2012). With photoperiod, temperature is also believed to control the induction and termination of diapause (Spielman and Wong, 1973; Madder et al., 1983). Overwintering behaviour is a vital aspect of disease transmission because diapausing mosquitoes may act as a pathogen reservoir between seasons when hosts are no longer infectious (Nasci et al., 2001). The winter survival of mosquitoes may therefore influence disease persistence and seasonal population dynamics. Diapause, which we consider in this study, has been ignored in previous DDE models as the focus has generally been tropical mosquito populations which do not exhibit this behaviour (White et al., 2010; Beck-Johnson et al., 2013). Clearly temperature exhibits complex and opposing effects on different parts of the mosquito life and transmission cycles. As such, mathematical models are needed which explicitly incorporate the impact of temperature on each life stage if we wish to understand its effect on seasonal abundance.

Stage-structured matrix population models allow populations to be broken down according to their life stages, with climate dependencies on each stage included, making them a popular tool for modelling mosquito populations (Lončarić and Hackenberger, 2013; Schaeffer et al., 2008). However, in many cases, these models make the assumption that development time for each stage is fixed (Schaeffer et al., 2008), when temperate species' generation times at high temperatures, can in fact exceed those observed at lower temperatures by a factor of more than four (Loetti et al., 2011). Combined with the effects of temperature on larval survival (Loetti et al., 2011), these models may substantially under- or overestimate population size. One solution is to split each stage into multiple sub-stages and allow temperature to influence transition probabilities (Lončarić and Hackenberger, 2013). This approach substantially improves upon the assumption of a fixed development time, however the transition probability remains dependent only on the current temperature and life stage, without accounting for temperatures experienced earlier in development. Similar problems are faced by models based on ordinary differential equations (ODEs) (Erickson et al., 2010; Alonso et al., 2010).

In contrast to discrete-time matrix-based approaches, and to allow the duration of each life stage to vary continuously, we can look to work carried out by Gurney et al. (1983), who advocated using a system of DDEs to model stage-structured populations. These DDEs are derived from continuous age-structured partial differential equations (PDEs) by assuming lumped age classes, which are appropriate for many insect species with distinct life stages. This formulation can then be extended as shown in Nisbet and Gurney (1983) to allow variation in stage duration dependent on biotic or abiotic factors.

The stage-structured DDE framework has recently been utilised to investigate ectotherm population viability under a climate warming scenario (Amarasekare and Coutinho, 2013) and to model the life cycle of *Anopheles*, a genus of tropical mosquito species that vector malaria (Beck-Johnson et al., 2013). To our knowledge, theirs is the first DDE model, applied to mosquitoes, where the total length of the immature life stages was assumed to be temperature-dependent. They used this model to make inferences about the ability of *Anopheles* to transmit malaria under various constant temperature scenarios. As previously alluded to, further complications arise for temperate mosquito species due to greater fluctuation in seasonal temperatures and overwintering behaviour. To simplify their model, Beck-Johnson et al. (2013) also assume that all immature life stages are affected by temperature in the same way, which allows the delay equations to be transformed onto the physiological timescale and reduced from three separate equations into one. Our review of the literature suggests that many temperate mosquito species have differential, temperature-driven rates of development and survival between life stages, so we allow each stage to have a unique relationship between temperature and vital rates.

The DDE modelling framework can be applied to any temperate mosquito species by choosing parameters and vital rate curves to fit the data available for that species. We focus our attention on modelling *Culex pipiens*, the most abundant potential vector of West Nile Virus (WNV) in the UK. WNV is the most significant cause of mosquito-borne disease in temperate regions including Europe and North America (Pervanidou et al., 2014; Barzon et al., 2013; Petersen et al., 2013) and substantial uncertainty remains about its seasonal dynamics (Golding, 2013).

Temperature is often considered to be the primary driver of mosquito development (Knies and Kingsolver, 2010). By developing a stage-structured model which explicitly captures its effects on each life stage we aim to understand how predicted seasonal temperature changes may affect mosquito seasonality. Whilst mosquito surveillance in the UK has increased in recent years (Townroe and Callaghan, 2014; Medlock and Vaux, 2015; Townroe and Callaghan, 2015) there remains a lack of publicly available empirical field data for UK *Cx. pipiens* populations, so accurate predictive modelling is needed to understand seasonal population dynamics and how vectors may be impacted by changing climate. We begin to address this issue here by providing testable theory on the impacts of temperature conditions on seasonal abundance of *Cx. pipiens*, to guide future laboratory or field studies and to highlight in precisely which areas this work is required. By