Ecological and Wind Analysis of Bluetongue Epidemics in Andalusia (Spain) in 2007

Yannan Shi
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by

Yannan Shi

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Specialisation: Environmental Modelling and Management

UNIVERSITY OF
Southampton

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Abstract

Bluetongue (BT) disease is an insect-borne, viral disease of ruminant livestock. *Culicoides* species are the main biting midges responsible for the transmission of BT. These movements are associated with the environment and midge flight dynamics and can be aided by mechanical means of transport. In this study we developed further the Spatio-temporal Wind-outbreak Trajectory Simulation algorithm (SWOTS) by implementing the relationship between climate and flight behaviour. In fact, the present SWOTS algorithm, takes into account only wind. Wind is considered as carrier of host semio-chemicals, for which the midges can respond flying upwind; or as carrier of infected midges themselves, for which the midges might act as small particles and hence dispersed passively. To complete, we define random midge flight when midge movement is independent from wind. Random flight can be combined with upwind and downwind movements as well. In this analysis, we implemented in SWOTS two parameters that affect the midge flight: temperature and precipitation.

The model are able to explain infection onset of 69 per cent of total 4,429 reported farms. We concluded that under the condition of temperature between 10°C and 25°C as well as precipitation less than 0.1mm per day, 35 per cent of outbreaks occurred through (presumable midge) movement of infections over distances greater than 31 km, 30 per cent between 5 to 31 km, and only 4 per cent of outbreaks within distance of 5 km. The modal distance covered by the midges was 15 km. Our analysis found that only 5 per cent of reported infection were infected by midge arriving in downwind movement while mixture movement type (i.e. none of the 5 types of movements considered was prevalent) was responsible for majority of farms (64 per cent of all cases). Compared with result of dataset of BTV-8 outbreak in 2007, we highlight the importance of relative speed between midge and wind therefore, further knowledge of midge flight behaviour in field situation is needed. Finally, the model returned an intrinsic incubation period of 15 days (with highest correlation value), which is consistent with the values described in the literature. We argue that better understanding of the movement of infected insect vectors is an important ingredient in the management of future outbreaks of BT in Europe, and other devastating vector-borne diseases elsewhere.

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1 Introduction

1.1 Background

Bluetongue (BT) is a non-zoonotic arbovirus disease of ruminants that has a significant global distribution, infecting certain cloven-hoofed ungulates (primarily sheep and including goats, cattle, buffalo, deer, and camels) (Maclachlan, 2011). It was first recognized and described more than 100 years ago in southern Africa (Ganter, 2013; Maclachlan, 2011; Takken et al., 2008), over the last decade BT has become one of the most important diseases of livestock, initiating a series of incursions into Europe (Szmaragd et al., 2009). BT is listed under the OIE Terrestrial Animal Health Code and must be reported to the World Organization for Animal Health ("What is Bluetongue (BT)?" Oie, 2013).

BT is caused by bluetongue virus (BTV), a non-contagious vector-borne arbovirus particularly transmitted by certain species of *Culicoides* biting midges. BTV extended an extensive geographic band nearby all the tropical, subtropical, and temperate region between the latitudes 40° North and 35° South (Ganter, 2013). Global warming and trade globalization may be one of important causes that virus northward extension in Europe (Rossi et al., 2013; Tsutsui, Hayama, Yamakawa, Shirafuji, & Yanase, 2011). In addition, ruminants' infections were found in area of Asia and west part of North America, where the BTV reaches as far as 50° North (Maclachlan, 2011).

Climate change has been implicated as a driver of this dramatic change in the global distribution and nature of BTV infection of livestock, because of its potential impact on the activity, abundance, and vectorial capacity of populations of *Culicoides* insects resident in affected areas (Mayo et al., 2012). To date, twenty six BTV serotypes have been recognized around the world (García-Lastra et al., 2012; Maan et al., 2012). It has been considered essentially to define serotypes, which helps a lot in developing of effective vaccines (Noad & Roy, 2009; Savini, MacLachlan, Sanchez-Vizcaino, & Zientara, 2008).

All the ruminants are likely infected by BTV but not all the infected have obvious signs. Usually, the most severe clinical signs are prevalent in domestic sheep, causing high morbidity and mortality.

Major signs of BT are high fever (40~41°C), superficial haemorrhages, hyperaemia of the skin, excessive salivation, weakness and weight loss, pregnant ewes may abort, the blue tongue after which the disease was named in seen only rarely in more serious clinical cases. The clinical sighs may vary depending on different virus serotype, age condition, resistance of the animal and so forth; other domestic ruminants for instance, the goats, generally show few or no clinical signs (García-Lastra et al., 2012; " Clinical Signs of Bluetongue Infection " BOVILIS, http://www.bovilis.com/diseases/bluetongue/clinical-signs.asp; "What is Bluetongue (BT)?" Oie, 2013).

BT can lead to severe consequence of a country or region both in agriculture and economy. The disease itself can cause disastrous losses to sheep populations. Mortality averages range from 2% to 30% but can peak as high as 70% and morbidity even reaches to 100% in highly susceptible sheep (Ganter, 2013; "What is Bluetongue (BT)?" Oie, 2013). The direct loss also includes the diagnosed cost and medicare for the sick ruminants, and milk yield reduction (Webb, 2008). And the indirect cost due to BT can be even worse. Ruminants

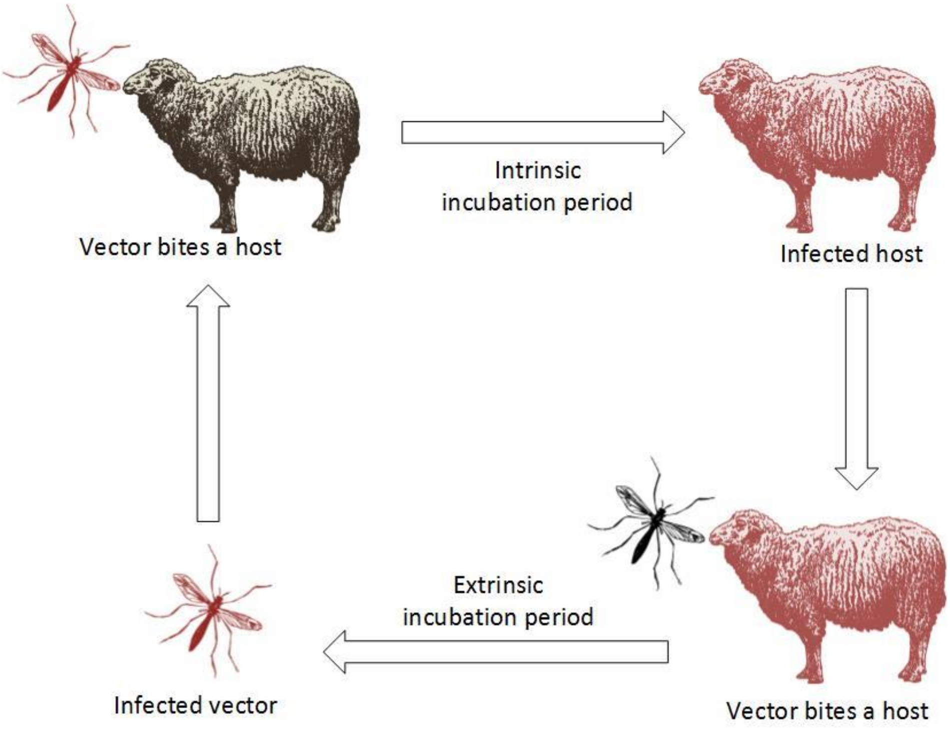

Figure 1: 'Vector-host' transmission cycle

in BT endemic areas are prohibited moving to those region considered BT-free through regulatory policy. BTV-8 outbreak in France was estimated to cost $1.6 billion, which were mainly because of such ‘trade barrier’ (Tabachnick, Smartt, & Connelly, 2014). Although BT is a life-threatening disease for ruminants, there is no public health risk related with BT ("What is Bluetongue (BT)?" Oie, 2013).

The flying insect vector plays an important role in transmission of Bluetongue between animals. Vector ingests virus when biting an infected ruminant. The extrinsic incubation period (EIP) is interval between the time of vector got infected and when it becomes capable in transmitting BTV to a new host. When the hosts survive long enough to ensure the completion intrinsic incubation period (IIP), the BTV in this area is established (Saegerman & Reviriego-gordejo, 2008). Biting female *Culicoides* midges serve as such a blood-feeder vectors to require protein for the production of eggs. Over 1,000 *Culicoides* species but less than 20 are considered competent vectors of BTV (Ganter, 2013; Zientara & Sánchez-Vizcaíno, 2013). BT invaded in Europe at intervals. The major vector in the incursion region (Spain, Portugal, Greek Islands of Lesbos and Rhodes) during 1956 to 1979 is *C.imicola*, which is connected with different BTV serotypes found already in Mediterranean states (Ganter, 2013; Mellor, Boorman, & Baylis, 2000). In southern Spain, the *C.imicola* is primarily responsible for the BTV-1 outbreak. From the table of capture frequencies of most abundant *Culicoides* species or groups of species in Andalusia during 2007 and 2008 outbreak, the *C.imicola* covers over 80% proportion of the whole captured *Culicoides* species in most of cities suffering BT incursion (J. M. Pérez, García-Ballester, López-Olvera, & Serrano, 2012). The geographical and seasonal distribution of *C.imicola* are consistent with those of the outbreaks of BT during epizootics in Spain (Brugger & Rubel, 2013). The *Culicoides* species is very small measuring from 1 to 3 mm (Wittmann and Baylis, 2000) in body lengths (Carpenter et al., 2008) thus they are easily carried by wind and fly for thousand miles away.

Once BTV is established in a region, it is difficult to control the spreading and may be impossible to eradicate. To date, vaccination focusing on different BTV serotypes is used widely as the most effective and practical measure to minimize losses caused by the disease (Goverment, 2014; Zientara & Sánchez-Vizcaíno, 2013), and to potentially interrupt the ‘vector-host’ transmission cycle (Figure 1). Other possible strategies for controlling BTV, such as livestock housing, movement restrictions which are based on animals, and targeting specific life stages of *Culicoides* midges which is based on vectors, also can be taken into account (García et al., 2009; Lorca-Oró et al., 2014).

1.2 Research problem

As discussed above, vector-borne diseases are sensitive to climate because the ecology of vectors and the development rate of pathogens within them are highly dependent on environmental conditions. Specifically, understanding the vector flight influenced by the climatic factors helps highly improve the accuracy predicting the BTV transmission. However, only a few models simulated the disease spreading by applying both the wind analysis and the metrological data with midge movements in a quantitative way. The algorithm called 'spatio-temporal wind-outbreak trajectory simulation' (SWOTS) identifies the possible important winds, related midge movements, and reports their correlation with the developing epizootic (L. Sedda et al., 2012a). By determining and adding the relevant climatic factors, the algorithm will be more developed and closed to the realistic transmission situation, which is possibly able to be applied in future vector-disease prediction, hence, better control and manage the disease transmission.

1.3 Research objectives

The aim of this study is by importing meteorological data related with midge flight behaviour, to develop the SWOTS model and build a robust statistical evaluation of wind fields and midge movements to analyse Bluetongue serotype 1 epizootic (2007) in Andalusia, Spain.

1.3.1 Specific objectives

I. To integrate the dataset of temperature, precipitation, and wind (including speed and direction) of Andalusia (Spain) in 2007.
II. To renew the assumption of midge flight behaviours and other relevant parameters based on new dataset.
III. To explore the highest correlations between wind fields and infected midges in R Project.
IV. To analysis the transmission both in spatial scale and temporal scale and offer suggestions.

2 Literature review

2.1 Bluetongue in Europe

Historically, although there were a few sporadic BT outbreaks occurred in the last century, such rare and short-lived invasion had never established itself in the long term (Guis et al., 2012). A dramatic change occurred in 1998 when BTV-9 was detected on four Greek islands, initiating the extensive and costly period of BTV incursion into Europe in recorded history (Carpenter, Wilson, and Mellor, 2009; Wilson & Mellor, 2009). Afterwards, BTV-1 invaded into mainland of Greece, and BTV-16 was detected in Turkey in 2000, occurring regularly in Israel as well. Prior to 2006, subsequent emerging of BTV novel strains in European area promoted the policymaker to envisage the broad spread and enormous economic loss the BTV had brought (Wittmann & Baylis, 2000).

In 2006 another even more spectacular outbreak in northern Europe surprised world in the history of BTV (Carpenter et al., 2008, 2009a), over 2,000 holdings in Netherlands, Belgium, Germany, France and Luxembourg were involved in. Distribution of BTV almost reached to 53°N that was the furthest north BTV had penetrated anywhere in the world (Meiswinkel, Goffredo, Leijs, & Conte, 2008). It may because that the 2006 was warmest on record and was favourable for BTV to become firmly established (A. J. Wilson & Mellor, 2009). After a short ceasing in winter, in 2007, the BTV resurfaced again covering all countries suffered in 2006 and, brought new cases in Denmark, Switzerland, the Czech Republic and UK. Nearly 60,000 holdings had been infected (Carpenter, Wilson, & Mellor, 2009b; De Koeijer et al., 2011; Saegerman & Reviriego-gordejo, 2008; Szmaragd et al., 2009; Wilson & Mellor, 2009).

In 2008, the new case of BTV-8 arose, probably detected on 8th January in northern Spain (Wilson & Mellor, 2009). After that the virus spread into new countries including Sweden, Hungary, Austria and Italy (Ander, Meiswinkel, & Chirico, 2012). Meantime BTV-1 had been extended incrementally northwards as far as Brittany in northern France and affected potentially in other NW European area. By the end of 2008, more than 86,000 holdings were reported to be affected by BTV-8, covering 14 countries (Pioz et al., 2012).

In 2009, new strains of BTV which were BTV-6 and BTV-11. were identified in Germany and Belgium respectively (Pioz et al., 2012). “In Europe, over 110,000 outbreaks were declared to the World Animal Health Organization (OIE) between 1998 and 2010; over 80,000 of these were owing to BT virus serotype 8.” (Guis et al., 2012). Such rapid spreading of BTV caused a great amount of economic losses.

2.2 Previous analysis of BT transmission

It is commonly admitted that the BTV transmitted among ruminants almost exclusively by the bites of the genus *Culicoides* (Pioz et al., 2012; Scolamacchia, Van Den Broek, Meiswinkel, Heesterbeek, & Elbers, 2014). Undoubtedly, the wind dominates the BTV spreading in vector-host transmission cycle (Figure 1). Some authors regarded the vectors as dust particles which can be carried by the wind passively and travel thousand miles away to achieve and enlarge the transmission (García-Lastra et al., 2012; Hendrickx et al., 2008; C. Pérez, Jm, & Jm, 2006; Christopher J. Sanders et al., 2011; A. J. Wilson & Mellor, 2009). However, the passive movements are insufficient to explain all the infected cases. For instance, during the BTV-8 outbreak in 2006, L. Sedda et al., (2012a) considered that upwind is much more important in short distance transmission. Midges can locate the host though smell within a certain radius, and the active flight of midges cannot be ignored (Graesbøll, Bødker, Enøe, & Christiansen, 2012; L. Sedda et al., 2012; Luigi Sedda & Rogers, 2013).

Apart from wind, other factors may have contributed to BTV spreading as well. Some strains of BTV can be transmitted directly from host to host such as transplacental, iatrogenic and oral transmission (Kirkland, Melville, Hunt, Williams, & Davis, 2004; Wilson & Mellor, 2009). In the local scale, the ‘random walk’ model was utilized to analysis the virus spread in an initial stage (Gerbier et al., 2008). The movement of infected livestock can introduce virus into a new area (Racloz, Venter, Griot, & Stärk, 2008) as well as unrestricted animal transport (De Koeijer et al., 2011). Pioz et al., (2012) illustrated that the land cover also affects the velocity of BT spread but with a slight effect. Edges of different land cover may provide meeting pints between hosts and vectors (Pioz et al., 2012). The human transport is likely served as and moving opportunity for infected midges to new regions (Mellor, Boorman, & Baylis, 2000; Mintiens et al., 2008).

As the midges in part determine the timing of outbreaks of insect-borne arbovirus outbreaks, the seasonal dynamic of adult *Culicoides* is of importance (Christopher J. Sanders et al., 2011). Most biting midges are crepuscular or nocturnal, with activity peaks during the evening and the first half of the night (Martínez-De La Puente et al., 2009), such period is also the peak transmission time of BTV (L. Sedda et al., 2012a). Light-trap experiments in BTV transmission analysis were mainly applied for *Culicoides* abundance surveillance thereby, to predict the BTV transmission. However, based on previous research, the light-trapping surveillance may underestimate the real population size of *Culicoides* species (Carpenter et al., 2008) and requires further development.

To reduce the transmission velocity, the surveillance about the climate change is necessary. The climate not only influences the whole lifespan of vectors but also helps more *Culicoides* species may be serve as an agent of BTV spread in Europe. Therefore, more complex epidemiological scenario for surveillance is needed (Ruiz-Fons, Reyes-García, Alcaide, & Gortázar, 2008). Beside this, avoiding cattle exposed during the time when *Culicoides* flights most actively helps lower the velocity of BT Spreading (Baylis et al., 2010; Pioz et al., 2012).

2.3 Life cycle of Culicoides

Biting midges in the genus *Culicoides* (Diptera: *Ceratopogonidae*) are distributed worldwide with more than 1,400 species (Martínez-De La Puente et al., 2009). The life cycle of *Culicoides* includes egg, four larval stages, pupa and imago (P S Mellor et al., 2000). The female require blood-meals to ingest enough protein for their eggs. Development from eggs to adults depends on the species and climatic conditions, varying from four or five days in the tropics to months in cool period. Most species diapause as fourth instar larvae during the overwinter period ("*Culicoides* midges - lifecycle," http://www.butox-info.com/ectoparasites/lifecycle-culicoides.asp.; Mellor et al., 2000; Saegerman & Reviriego-gordejo, 2008; Wittmann & Baylis, 2000). In Europe, competent vectors mainly include *C.imicola* in Mediterranean region, *C. obsoletus* and *C.scoticus* in central Italy and *C. pulicaris* in Sicily. *C. dewulfi* is recognized as a vector in northern Europe (Saegerman & Reviriego-gordejo, 2008; A. Wilson & Mellor, 2008).

2.4 Climatic effect on midge flight behavior

Served as vectors of arbovirus pathogens oral transmission, *Culicoides* are particularly sensitive to climate change because of the small size and poikilothermic attribute (A. Wilson & Mellor, 2008). Thus, to evaluate the potential risk of BTV it is key element to understand how climatic factors affect the *Culicoides* biting midges in BTV transmission system (A. J. Wilson & Mellor, 2009)

2.4.1 Distribution

The distribution of *Culicoides* varies a lot because some species can be more cold-adapted (Purse et al., 2004), which means the low temperature is more important to some extent. For instance, *C.imicola* were barely found in Netherlands, a country located in northern Europe but *C.obsolutus* Complex was abundant while these two species are both existed in Southern Europe (Baldet et al., 2008; Meiswinkel et al., 2008; Pioz et al., 2012).

Distribution of *Culicoides* is also associated with rainfall, but not directly. The seasonal availability and stability of midge's breeding sites are related with soil moisture result from a function of precipitation (Kirkland et al., 2004; A. Wilson & Mellor, 2008). Breeding sites would be destroyed because of the heavy rainfall (Wittmann & Baylis, 2000).

Besides these two environmental factors above, wind direction and speed also contribute to expend the distribution spatially. At a certain condition (e.g. 10 meters over the ground, less than 30°C temperature and relative humidity above 26%), the *Culicoides* can be alive for hundreds mile in air (García-Lastra et al., 2012; Luigi Sedda & Rogers, 2013). Moreover, landcover could be one of the factors that influence midge's distribution. Evidence shows that *C.obsoletus* group adults prefer shaded leafy habitats while the species *C.imicola* favours sparsely vegetated areas in full sunlight (Takken et al., 2008; A. Wilson & Mellor, 2008).

2.4.2 Vector population size

A slight rise in temperature can have further effect on local *Culicoides* population (A. J. Wilson & Mellor, 2009). Temperature is a driving force for immature vector developmental rate that influences the number of generations produced and the adult midge' population size that can result in a season (Mullens, Gerry, Lysyk, & Schmidtmann, 2004). As a support, Baldet et al., (2008) concluded that the low temperature and relatively heavy rains in northern Europe in August of 2006 likely had a negative impact on the populations of livestock-associated *Culicoides* due to inducing a decline in larval productivity. And the trap catches experiments also illustrated that larger catches are associated with higher temperatures, lower wind speeds and days without raining at sunset (Carpenter et al., 2008; Pioz et al., 2012; Christopher J. Sanders et al., 2011).

Ambient temperature determines the extrinsic incubation period (EIP) which happens during midges travel. The midges have to survive long enough to bite a suspect host after the competence (De Koeijer et al., 2011; García-Lastra et al., 2012). Higher temperature accelerates virus replication speed (Carpenter et al., 2008; A. J. Wilson and Mellor, 2009) and shortens the generation time of virus, hence leads to more susceptible bites to increase the opportunity of transmission. A small reduction in extrinsic incubation period (EIP) may greatly increases the vector abundance (A. Wilson & Mellor, 2008).

2.4.3 Flight behaviour

Temperature is unquestionably dominant climatic factor influencing the behaviour of these small midges. Their activities are highest between 13°C to 35°C and insignificant at temperatures below 10°C depending on different species (Kettle & Linley, 1969; Saegerman & Reviriego-gordejo, 2008; Sanders et al., 2011). Particularly, *C.obsoletus* are able to flight at minimum temperature ranging from 6°C to 12°C in cattle shed during winters (Saegerman & Reviriego-gordejo, 2008).

Some research found that the wind plays a significant role in midge's flight. Adult midge activity is almost entirely suppressed at wind speeds greater than 11 m/s (Hendrickx et al., 2008). If wind speed increases to 9 miles/h (approximately equals to 4m/s), the biting rate will be reduced by 90% (Kettle & Linley, 1969) which partially support the view of wind's effect. Moreover, heavy rainfall inhibited the vector flying (Gerry & Mullens, 2000). It is observed that highest velocities of BT spread happens when the monthly average of maximum daily temperature at the one month-lag between 21°C and 26°C with minimal monthly rainfall (Pioz et al., 2012). It seems that the interaction of temperature and precipitation is more vital instead of just one of climatic factors in midge's flight behaviour (Guis et al., 2012).

2.4.4 'Overwinter' phenomenon

The climate change may raise an 'overwinter' issue. A. J. Wilson & Mellor (2009) explained it as "In many temperate regions classical BTV transmission is almost completely interrupted for several months of the year by cold weather, but outbreaks often resume after interruptions far longer than the typical lifespan of an adult vector or the normal period of host infectiousness, a phenomenon termed 'overwintering'".

The virus could pass the winter and early spring in cattle like a reservoir, transmitted by vectors in short distance (García-Lastra et al., 2012). Some of the outbreaks in last decade years were result of novel introduction events, while others represented the successful overwintering of virus in local vector or host populations (L. Sedda & Rogers, 2013; A. Wilson & Mellor, 2008). Warm surroundings can enhance the overwinter success of *Culicoides* (Wittmann & Baylis, 2000). And *Culicoides* is also able to shelter from cold condition in farm building, for example, *C.obsoletus* could be active and feed indoors (Baldet et al., 2008), thus extends the period of active BTV transmissions. Meiswinkel et al., (2014) thinks that overwinter phenomenon may also because a vertebrate host infected quite late the previous season and which is infective to nulliparous midges active in late winter or early spring.

2.4.5 Virus competence

The variation in climate successfully reproduces many aspects of this past emergence (Guis et al., 2012). BTV appears unable to replicate when temperature is lower than 12°C (Mullens et al., 2004; A. J. Wilson & Mellor, 2009). Transmission declined in autumn is most likely due to the temperature getting lower instead of increasing the efficacy of the control measures (De Koeijer et al., 2011).

2.5 Future perspective

Understanding the ecology and behaviour of vector *Culicoides* species is a essential element in predicting the epidemiology of those pathogens they transmit. Therefore, it is necessary to take both biotic and abiotic factors into account (Guis et al., 2012). Basic data collection of *Culicoides* life cycle and ecology of potential arbo-virus victors are needed to be development. More complex and realistic models of transmission are required, such as separate transmission routes and seasonal vector dynamics, as well as multiple vector species and virus strains (Szmaragd et al., 2009). The successful example of UK in 2008 shows that vaccination implemented in advance could reduce the impact of incursion (Carpenter et al., 2009b). Furthermore, it is possible that still other species of temperate *Culicoides* may be served as vectors of BTV because of global warming. Establishing a flexible surveillance system covering the livestock, *Culicoides* species and climatic factor is impending and important (Racloz et al., 2008).

3 Methodology

3.1 Area of interest

Andalusia (Figure 2) (SW Europe: 38°42′-35°59′ N; 7°30′-1°38′ W) has a surface area of 87,597 square kilometres (33,821 sq. mi) ("Andalusia" Wikipedia, http://en.wikipedia.org/wiki/Andalusia). In general, Andalusia experiences a Mediterranean climate, varying considerably with dry, hot summers, and mild, rainy winters. It is worth mentioning that Andalusia's interior is the hottest area of Europe, some individual cities average above 36 °C (97 °F) in summer high temperatures. Even late evening temperatures persist around 35 °C (95 °F) up close to midnight, with day time highs of over 40 °C (104 °F). Altitudes range from sea level to 3,481 m above sea level. Annual precipitation ranges from 80 inches (2,000mm) to as little as 8 inches (200mm) (Ander et al., 2012). Mean relative humidity for an average year is recorded as 68.3% and on a monthly basis it ranges from 54% in July to 81% in December (Meiswinkel et al., 2008). Andalusia has rivers that both flow into the Atlantic and the Mediterranean. Those of Atlantic basin are tend to be long, run through mostly flat terrain with broad river valleys. In contrast, the rivers of the Mediterranean Basin are characteristically shorter, and more seasonal. Nowadays, Andalusia has been a traditionally agricultural region compared to the rest of Spain and the rest of Europe. Agriculture, together with livestock farming and fishing, accounts for more than 10% of the value of the Andalusian economy. From the data offered by Pioz et al., (2012), the most abundant livestock is sheep (2,670,810), then followed by domestic goats (1,072,458) and cattle (605,105) (2012).

3.2 Dataset

3.2.1 Epidemiological data

The data used for this analysis were the BTV-1 cases on farms obtained the Centre de Recerca en Sanitat Animal (CReSA) for the outbreak year 2007.

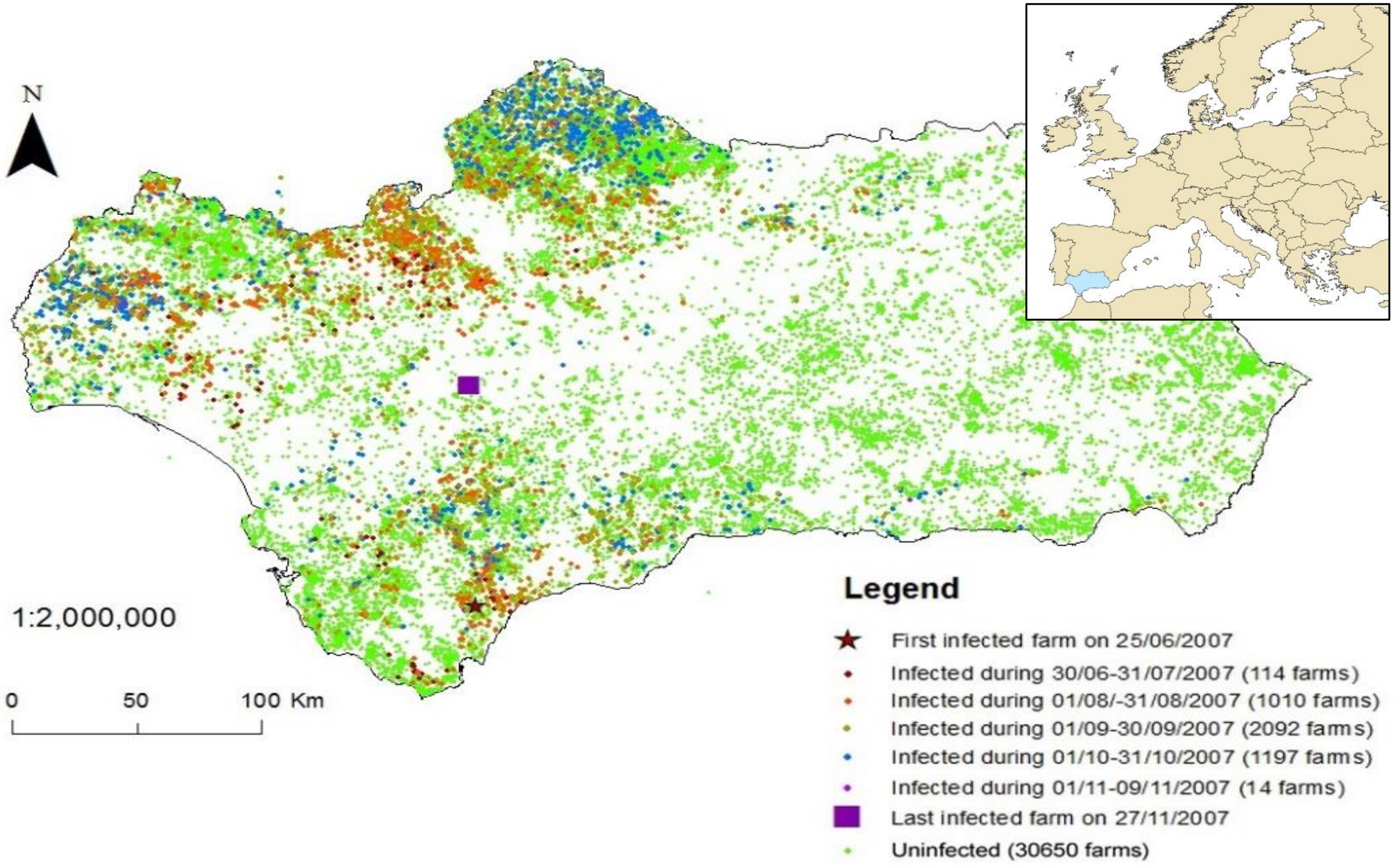

Figure 2: A map of Andalusia (Spain) with all farm locations.

35,079 farms were involved during this research including 4,429 infected farms and 30,650 uninfected farms. Of the infected cases, 527 were beef farms, 8 bullfighting farms, 62 dairy farm, and 70 mixture cattle farms, the rest were unclassified. The dataset includes the GPS coordinates of each of the infected farms and the date of the report of infection. In the entire dataset, the first confirmed report in 2007 was on 25th of June in Tarifa, and the last was on December 13 in Zalamea la Real. Figure 2 shows all the reported infections in Andalusia (Spain).

The minimum period between infection and reporting of BTV by a farmer is in theory equivalent to the time for an animal to develop clinical signs of BTV-1. Experimentally, clinical signs of BTV-1 (including hyperaemia of the buccal, labial and nasal mucosa, facial oedema and conjunctivitis) develop in Dorset Poll sheep only five days after needle inoculation of the virus (Darpel et al., 2007; Elbers et al., 2008). To this minimum period must be added a further delay of about one week between a farmer’s suspicion and veterinary confirmation of BTV-1 infection (Caporale et al., 2014; Meiswinkel et al., 2008).

3.2.2 *Culicoides* species involved in BTV serotype 1 outbreak

Candidate vectors in the outbreak region include the widespread and abundant *C. imicola*, *C. pulicaris* species and *C.obsoletus* (Allepuz et al., 2010; De Diego, Sánchez-Cordón, & Sánchez-Vizcaíno, 2013). Adult *Culicoides* are crepuscular, showing peak activity at dusk or dawn or during both periods (Pioz et al., 2012; Christopher J. Sanders et al., 2011). Variation in diurnal activity is much less well understood, but seems to be related to seasonal variation in humidity (Ander et al., 2012; Philip S. Mellor & Wittmann, 2002).

3.2.3 Wind data

The UK Met Office (http://www.metoffice.gov.uk) provided wind data generated by their numerical weather prediction model, the Unified Model (L. Sedda et al., 2012a) at the point locations of all farms that eventually became infected during the outbreak. The data consisted of hourly wind speed and direction estimates at a nominal height of 10 m for the period 1st May 2007 to 31st July 2008. These point estimates were interpolated from an original 12 km horizontal resolution grid. In order to apply these winds at a nominal height of 2m, relevant to midge take off ,the correction from (L. Sedda et al., 2012a) was used:

$$\tau_{j,\varepsilon}(2m) = \frac{\log\left(\frac{2}{l_0}\right) * \tau_{j,\varepsilon}(10m)}{\log\left(\frac{10}{l_0}\right)} \tag{1}$$

The outbreak was cross-correlated with wind vectors at each farm for five periods within each 24h cycle; period 1, 0000-0459h; period 2, 0500-1059h; period 3, 1100-1559h; period 4, 1600-2059h; and period 5, 2100-2359h.

The average speed in SWOTS was the arithmetic average of the speeds estimated for each day (or each period within each day) and the direction was determined by vector summation, using unit vectors for each period’s wind (use of unit vectors preserves direction but not speed).

Wind speed and direction histograms by 24 hours day (Figure 3, Figure 4) and by the five daytime periods listed above, averaged over all farms, and were derived for each farm from the hourly wind speed and direction data from the 1st of May 2007 through the 31st of July 2008. The modal average daily wind speed at the farms was between 2 and 3 m/s. The modal wind speed for each daytime category also fell within this range. For the wind direction, there were two modal daily directions, one at 0-20° (i.e. wind blowing from near NNE) and the other at 260-280° (i.e., near West). For each daytime period the modal wind directions were the same with one exception; during the 0500-1059h period the modal value was around 270°.

3.2.4 Precipitation data and temperature data

The two dataset are consisted of hourly precipitation and temperature data respectively for the period from 1st May 2007 to 31st July 2008. The average precipitation and temperature data in SWOTS was the average value estimated for each day (same each period within each day as wind data).

3.3 Assumptions about midge behaviour

The following assumptions are made about key aspects of midge behaviour.

3.3.1 Host distribution

Hosts are homogenously distributed within each farm, and all host species are equally susceptible to BTV infection (cattle, sheep etc.). This is a simplifying assumption because we are not weighting the disease according to the type of animal present in the farm (some *Culicoides* species are in fact more attracted to cattle than sheep (Bartsch, Bauer, Wiemann, Clausen, & Steuber, 2009), but according to the number of farms infected within certain spatial and temporal ranges.

3.3.2 Midge distribution

Midges are present at all infected farms and all species are equal with respect to activity, host preference, and vectorial capacity.

3.3.3 Midge infectivity

In most runs of SWOTS it was assumed that a midge, having left an infected farm, is infective by the time it arrives on an uninfected farm and is hence able immediately to transmit infection to animals on that farm. The effect was also explored of requiring a fixed extrinsic incubation period (EIP) before transmission by midges is possible.

3.3.4 Average midge lifespan

Each adult midge is assumed to be alive for between 1 and 21 days, the latter figure being the average lifespan of an adult (Gerry and Mullens, 2000; Mellor et al., 2000; Wittmann & Baylis, 2000).

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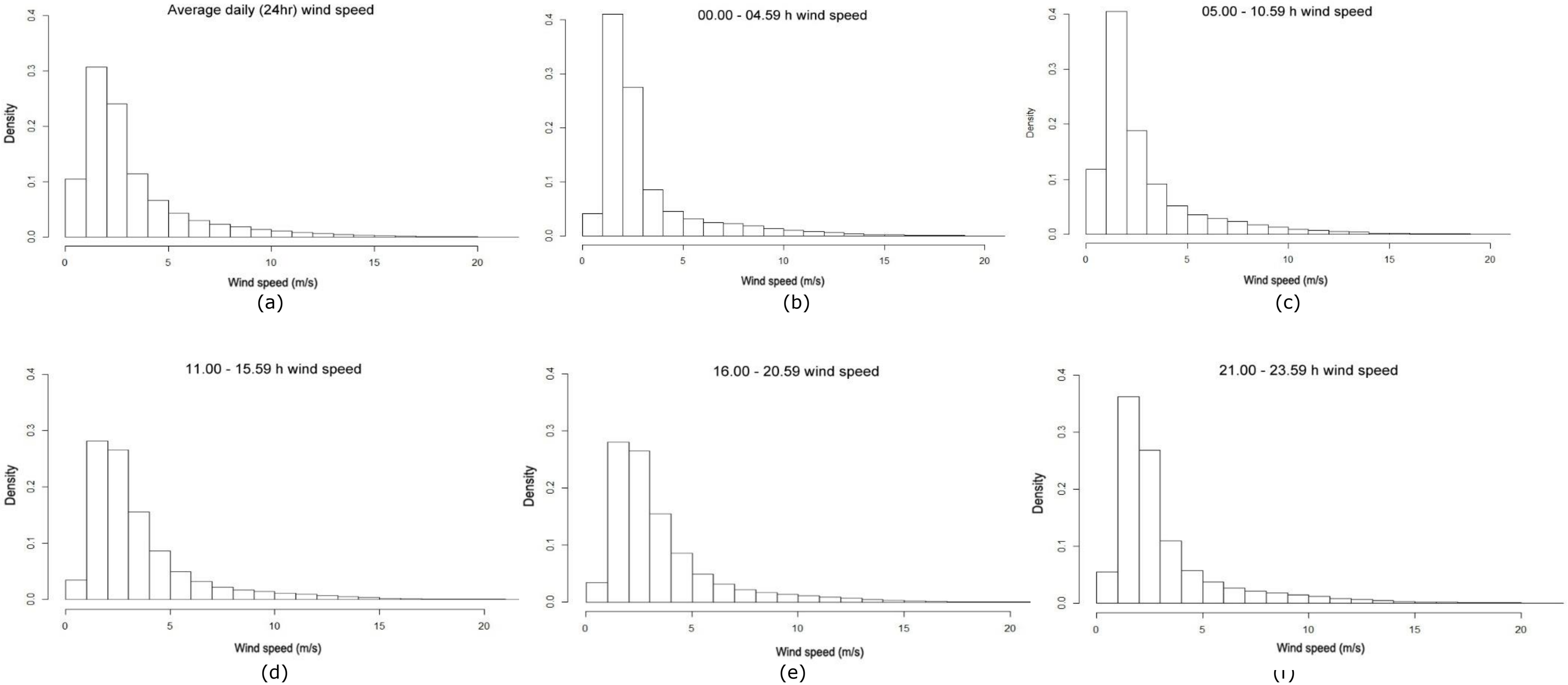
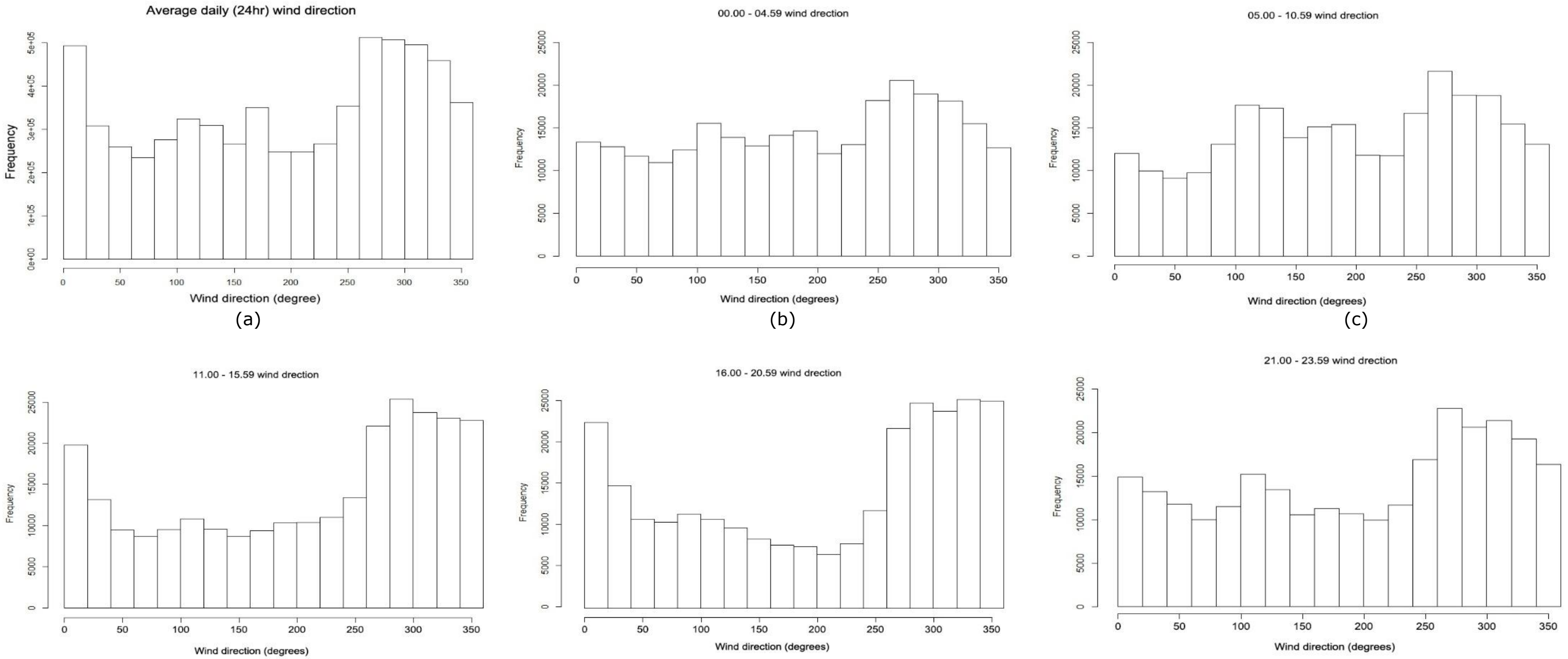


(a) (b) (c)

(d) (e) (f)

Figure 3: Histogram of average daily wind speed (m/s) from 1st of May 2007 to 31st of July 2008. (a) is the total average daily (24 hours) wind speed. Average wind speed in different time period are shown in (b) - (f) respectively. The total number of wind speeds used to produce daily average wind speed in (a) was 6,273,696.



(a) (b) (c)

(d) (e) (f)

Figure 4: Histogram of the average daily wind direction (degrees) from the 1st of May 2007 to 31st of July 2008. Directions are calculated clockwise from 0° = due North (East is +90o, and so on). (a) is the total average daily (24 hours) wind direction. Average wind direction in different time period are shown in (b) - (f) respectively. The total number of wind directions used to produce daily average wind direction in (a) was 6,273,696.

3.3.5 Midge behaviour

It is necessary to distinguish several sorts of midge movement and their defining parameters. A midge’s active flight speed is the speed at which it flies in still air. Its daily active displacement (the distance flown due to active flight in still air) depends upon the length of time for which it is airborne each day; the same daily displacement may be achieved by a slow active flight speed carried on for a long period within each 24 hours day, or a higher active flight speed carried on for a shorter period of time within the same 24 hours period. Daily movement is also carried out under the prevailing wind conditions; a midge with a fixed active flight speed and flying for a fixed period of time each day will achieve a higher daily rate of movement across the ground if it flies downwind rather than upwind

(1). Active midge flight speed

There are in the literature no recorded measures of *Culicoides* active flight speeds. These have to be inferred on the basis of recorded daily movements of midges, usually from rare mark-release-recapture experiments (T H Lillie, Kline, & Hall, 1985; P S Mellor et al., 2000) and making certain assumptions about midge behaviour. Midge catches are drastically reduced at wind speeds higher than 2 m/s, generating the idea that midges have active flight speeds of up to this amount (Baldet et al., 2008; Blackwell, 1997; Kettle & Linley, 1969). This figure, however, is probably an overestimate and has not been confirmed by direct (e.g. wind tunnel) flight measurements, a technique which shows that for similarly sized Diptera active flight speeds are less than 1m/s (for *Drosophila* see (Fry, Rohrseitz, Straw, & Dickinson, 2009); for sandflies see (Killick-Kendrick, Wilkes, Bailly, Bailly, & Righton, 1986)). We changed the midge flight speed from 0.5 m/s to 1m/s based on previous research (L. Sedda et al., 2012a).

(2). Amount and type of midge flight per day and the effect of climatic factors

I. The total daily flight duration of midges is unknown. The model assumes that midges fly for no more than ten hours per day in downwind and random movements, or four hours per day in upwind movement, when the average daily wind speed and direction is used; or up to four hours a day when the day is split into five time periods (see 3.2.2 Wind data, above).

II. Midges take off in the downwind direction only if the wind speed is less than 3 m/s (D. S. Kettle, Edwards, & Barnes, 1998) and in the upwind direction only if the wind speed is less than the active midge flight speed. Midges will stop flying (by landing) if winds are greater than 11 m/s (Hendrickx et al., 2008). Their activity is highest between 13°C to 35°C and insignificant at temperatures below 10°C depending on different species (Christopher J. Sanders et al., 2011). The suitable temperature range for midge flight in this case is from 10°C to 25°C. Heavy rainfall inhibited the midge's flying but they are not stopped by light rainfall ("Biting midges in Scotland", David Phillips, http://www.snh.org.uk/publications/on-line/advisorynotes/29/29.htm; Saegerman & Reviriego-gordejo, 2008). We assumed that midge only take off when the precipitation is lower than 0.1mm per day.

III. Midges attempt to fly upwind in response to host odours(Gillies, 1980; Grant & Kline, 2003; Logan & Birkett, 2007; Logan et al., 2008; Luntz, 2003) only in the boundary layer (Taylor, 1974). Their rate of movement across the ground is then equal to the difference between the wind speed and the active midge flight speed (e.g. if the wind speed is 0.1 m/s, the midge's upwind rate of movement is 0.4 m/s). Strong winds reduce host odours by diffusing and moving them from the lower strata of the air (Riffell, Abrell, & Hildebrand, 2008), so that upwind flight in response to host odours, even if it were possible at high wind speeds, is less likely to occur.

IV. Downwind movement occurs at a rate dependent on the sum of wind speed and active midge flight speed. At high wind speeds it is likely that midges use part of their energy to stay air-borne rather than actively to fly (Lehmann, 2004), but this is unlikely to create a problem in the model because the active flight speed of midges is relatively low compared with many of the predicted wind speeds in the area. The direction of downwind movement is assumed to be equal to that of the carrying wind (Arain et al., 2007; Gloster, Mellor, Burgin, Sanders, & Carpenter, 2007; A. M. Reynolds & Reynolds, 2009).

V. It is assumed that midges also have an option for flight initiated in random directions, i.e. irrespective of the current wind speed and direction, or the presence of wind turbulence. This results in a pure random walk process for the random movement, and is considered to occur in a uniform probability distribution around the upwind or downwind direction. The assumption of a flat-topped rather than Gaussian probability distribution of each random flight direction contrasts with that of previous models of random movement (Gerbier et al., 2008; Szmaragd et al., 2009) but is in agreement with random walk analyses (Marsh & Jones, 1988). Random movement occurs at a speed of 0.13 m/s (i.e. different from that in pure up- and down-wind flight), estimated using the method of Rogers (Rogers, 1977) applied to the data published by Thomas H Lillie, Marquardt, & Jones, (1981). It is assumed that this figure applies regardless of wind conditions (because no information about the wind is given in (Thomas H Lillie et al., 1981)). It is hence also the track speed (the across the ground speed). This figure of 0.13 m/s does not differ greatly from the rough estimate of 0.18 m/s or the dispersal coefficient value (L. Sedda et al., 2012a). In particular, Bishop et al. (2000) in a study of the spread of *Culicoides brevitarsis* into new areas within a season in Australia, estimated 138 days were necessary for *Culicoides* brevitarsis to cover 377 km (equivalent to a straight line flight speed of 0.18 m/s if flying for 4 hours a day) in a context of frequent high winds (>2.2 m/s).

(3). Midge track calculation

Once the various assumptions listed above had been made at different points in time in the model, the midges' track (the resulting across-the-ground movement) was determined by mathematical vector addition of the wind speed and direction and the midge's flight speed and direction. Each midge's location at the end of that period of movement could therefore be calculated and the midge was then deemed either to have arrived at a farm (criteria below) or else to have continued movement in the next time period.

3.3.6 Midge infection

A midge was considered to have arrived at a farm when its trajectory reached the neighbourhood of the farm plus the distance over which it can detect hosts. The neighbourhood is any part of a circle, radius 50m, centred on the farm's reported GPS coordinates. This rather generous figure allows for the fact that farm animals are not located precisely at each farm's GPS co-ordinate, but are likely to be distributed in the fields around the farm. It represents less than half of the shortest mean distance between any two farms in the region. Hence, allowing for detection of host odours (points 3.3.4, above and 3.3.7, below), model midges arriving anywhere within up to 1,050 m of a farm were considered to have arrived at that farm.

3.3.7 Host attraction

Midges are attracted to potential hosts by exhaled carbon dioxide or other semiochemicals (L. Sedda et al., 2012a). However, the distance over which such odour-mediated anemotaxis occurs is unknown. Mosquitoes can detect minute changes in carbon-dioxide levels at a distance of 200 metres from a source (Gillies & Wilkes, 1970). In the absence of other information, it was assumed that midges locate hosts by their odours at a maximum distance of 300 m.

3.3.8 Intrinsic incubation period in the vertebrate hosts

Based on previous research of (Saegerman, Berkvens, and Mellor, 2008; Hess, Howell, and Verwoerd, 2013; Darpel et al., 2007) we use IIP from 4 to 15 days. In fact, we note that the disease can be asymptomatic in cattle; hence the confirmation date for these hosts may include a longer delay than the equivalent dates for sheep (Philip S. Mellor, Baylis, Mertens, Maclachlan, & Gard, 2009).

3.4 Spatio-temporal Wind-Outbreak Trajectories Simulation (SWOTS) algorithm

In this paper, we develop the SWOT algorithm by adding two environmental parameters, temperature and precipitation, written by the authors in the R-language (R Development Core Team, 2011), It includes five types of *Culicoides* movement (downwind, upwind, random, downwind and random, plus upwind and random) and combines a search-fitting model with a stochastic simulation analysis.

As in L. Sedda et al. (2012), for clarity in what follows, we use the term 'infected midges' to indicate carriers of BTV-1 between farms. We use the term 'vector' in its mathematical sense, a variable with both magnitude and direction (e.g. as applied to wind, or the movement of infected midges). For the statistical part of the first stage of the model (see below) it was also necessary to define an 'infection vector' which is the mathematical vector between an already infected farm and a susceptible farm, usually close to it, that may be infected by it through the movement of infected midges (sometimes also referred to as `infecting/infectious` and `infected` farms respectively). Clearly a single infecting farm may have a number of infection vectors at any time, one to each of the surrounding, uninfected farms. The track of an infected midge over the landscape is referred to as a 'trajectory'.

SWOTS (Figure 5) is divided into three stages, for data preparation (first stage), statistical analysis (second stage) and modelling (third stage). The first stage is designed to turn the raw data of farm infections and wind trajectories into forms where comparison can be made between them, to investigate the likely routes of epizootic spread. In the first stage, therefore, the farm disease data (location and date of outbreak) were investigated to identify possible sources (infecting farms) and sinks (farms infected by them) of infection. Taking each infected farm in turn, from the date of its infection, the database was examined for every other farm infected at some future date. The distance (x-y co-ordinates), time (between calendar dates of possibly infecting and infected farms' reported infection dates) and angular direction (from possibly infecting to infected farm) were recorded. At this stage some spatial and temporal filtering was applied to the data, allowing a minimum period between the two infection dates (that allows for the intrinsic incubation period (IIP) of the disease in the newly infected hosts and the time spent by the midge in the air (DT) to reach the uninfected farm) so that only likely possible infection sources and sinks remained. In practice, IIP and DT operate as follows: IIP is subtracted from the recorded date of infection (t) on each farm to obtain the latest possible date of arrival (t') of an infected midge on that previously uninfected farm (thus $t' = t -$ IIP). To arrive at that farm on that date the infecting midges from possible source (i.e. infected) farms had necessarily spent DT days in transit. Source farms must therefore themselves have been infected DT days before infected midges originating from them could have arrived at uninfected farms, to infect them. Similarly sink farms could not be infected by any source farm that was not infected at least DT days previously.

At this point in the first stage, every possible (filtered) pair of source and sink farms was in the database; that is to say, all possible infection pairs were in the database and all impossible ones had been filtered out. For each infected farm and time period (e.g. for DT = 20 days after the corrected farm date of outbreak, t') a combined

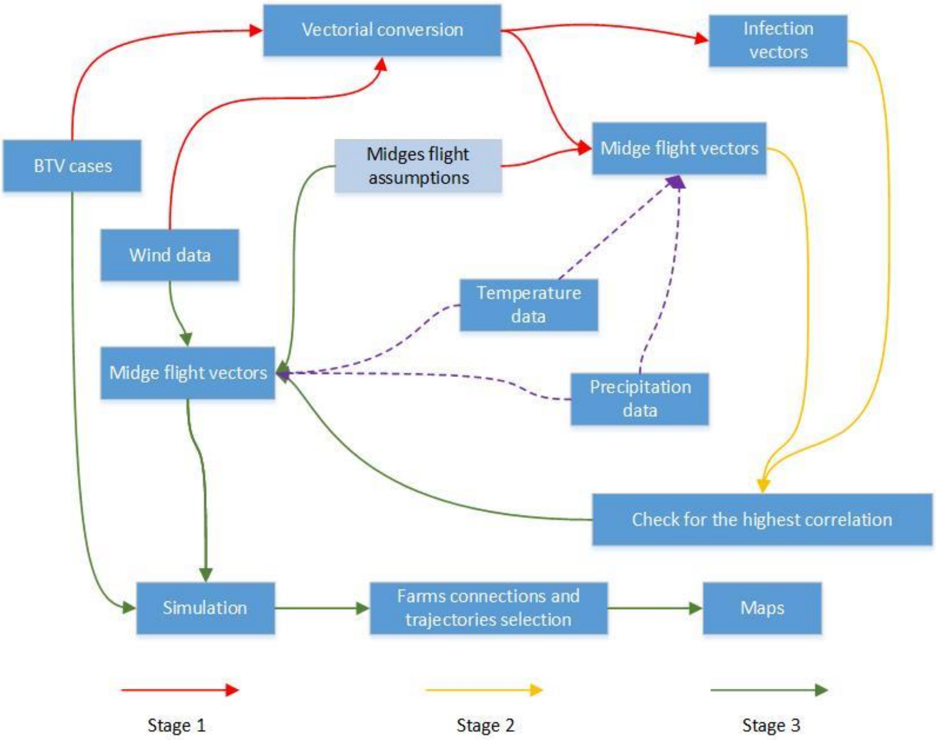


Figure 5: Simplified diagram of the SWOTS algorithm. The purple dash lines indicate the two new meteorological parameters were used to generate the midge flight vectors.

infection vector was then calculated. This was obtained by vector addition of all the individual (farm-to-farm) infection trajectories arising from that farm in the period concerned. This resulting vector had distance (x- and y-co-ordinates), speed (mean distance divided by time) and a variable that here we call the 'direction tendency' which is the proportion of all contributing individual infection vectors that were within ±45 angular degrees of the resulting vector. This variable was introduced as a measure of the central tendency of individual vectors to cluster around their resulting 'mean' value (it is possible, for example, for a combined infection vector to be in a quite different direction from the individual vectors contributing to it). The combined infection vector for each farm therefore encapsulates important features of the epizootic spread from that farm to other farms possibly infected by it. The results for each farm were stored in terms of four dimensional vectors (where the dimensions are the x- and y-co-ordinates, the direction tendency, tt, and speed, v), called $\boldsymbol{b}$. Next, the wind data were treated in a similar way. From each already infected farm, wind vectors were calculated over subsequent periods of time (from t' to $t' +$ DT), using conditions (location, wind speed and direction) at the start of each time period to predict the location at the end of each time period of any object carried passively by that wind. The location of the object after T days (or T-periods of each day) was obtained by mathematical addition of the wind vectors for all days (periods) involved. The wind vectors are called $\boldsymbol{w}$. Wind were converted in midge movements for each farm and temporal threshold, then midge movements were summed to a unique ($\boldsymbol{X}$ farms) midge movement vector. At the end the matrix $\boldsymbol{W}$ contained the vectors "midge movements" and the same parameters of matrix B. During the conversion the temperature and precipitation are considered in order to create the vector or not.

At this stage each farm, j, was associated with the vectors $\boldsymbol{b}$ and $\boldsymbol{w}$. Each vector was then converted into spherical polar coordinates (four dimensions are described by three angles that are then converted into four Cartesian coordinates): $\alpha_{1,j}^{b}$, $\alpha_{2,j}^{b}$, $\alpha_{3,j}^{b}$, $\alpha_{4,j}^{b}$ for vectors $\boldsymbol{b}$, and $\alpha_{1,j}^{w}$, $\alpha_{2,j}^{w}$, $\alpha_{3,j}^{w}$, $\alpha_{4,j}^{w}$for vectors $\boldsymbol{w}$. These values were ordered in matrices, B (for infection vectors $\boldsymbol{b}$) and W (for midge vectors $\boldsymbol{w}$), in which the rows are the farms and the columns the four Cartesian coordinates.

This entire first stage of SWOTS was repeated for different values of the intrinsic incubation period (IIP), the time interval between the time of infectiousness of the infecting farm and the infection of the susceptible farms (DT), the time of day of the wind field (TOD), generating in each case a new set of B and W matrices.

The second stage of SWOTS involved two steps, the first looking for significant relationships between the infection and midge vectors and the second taking only the highest correlation between infections and midge vectors. This two-step approach was based on the assumption that wind is likely to have been involved in disease spread, as other authors have claimed (Hendrickx et al., 2008; Mehlhorn et al., 2007; Pedgley, 1983; Sellers & Maarouf, 1989, 1990; A. J. Wilson & Mellor, 2009) and that this occurred through wind transport of midges behaving in a limited variety of biologically realistic ways, something that previous authors have not tried to quantify or model. Thus the SWOTS algorithm first searched through the data to detect the strongest correlation between the infection and midge matrices ($\mathbf{B}$ and $\mathbf{W}$ respectively). The correlations (r) were calculated using the technique of vector 'angular' correlation analysis (Johnson & Wehrly, 1976; Stephens & Correlation, 1979):

$$\boldsymbol{Q} = \frac{\boldsymbol{B}'\boldsymbol{W}}{n} \tag{2}$$

$$\lambda = \boldsymbol{eigenvalues\ of\ Q'Q} \tag{3}$$

$$|\boldsymbol{Q}| \begin{cases} < 0 \ \ r = \left(\sum_{i=1}^{p-1} \sqrt{\lambda_i}\right) - \sqrt{\lambda_p} \\ < 0 \ \ r = \left(\sum_{i=1}^{p} \sqrt{\lambda_i}\right) \end{cases} \tag{4}$$

Where $\boldsymbol{Q}$ is the matrix defined by (3), $\boldsymbol{Q'}$ is its transpose and $|\boldsymbol{Q}|$ its determinant; n is the number of farms in the present group and p is the number of variables (four in SWOTS) being compared in the two matrices.

Each calculated correlation was tested via spatial bootstrapping to ensure sensitivity and to reduce error (Loh, 2008). The spatial bootstrapping allows for the definition of the level of significance, here taken to be 99%. The highest correlation between the $\mathbf{B}$ and $\mathbf{W}$ matrices was 0.6. The third stage then explores, through simulation, the consequences of a variety of midge behaviours recorded in the literature, using both the values of IIP, TOD and DT estimated in the second stage, and upon which the epizootiological outcome of those behaviours (direction and distance of movement of infected midges) depended.

In the final, third stage of SWOTS, the optimal values of IIP, DT and TOD obtained in Stage 2, and the modelled wind conditions, were used to estimate midge trajectories. As detailed above, midges are imagined to use a variety of movement strategies, up- and downwind, random and mixed movements. Assuming each of these strategies in turn, and a mixture of these strategies, a variety of resulting midge trajectories were produced, called $\boldsymbol{w}_{\mathrm{D}}, \boldsymbol{w}_{\mathrm{U}}, \boldsymbol{w}_{\mathrm{R}}, \boldsymbol{w}_{\mathrm{DR}},$ and $\boldsymbol{w}_{\mathrm{UR}}$ (where the subscript refers to downwind movement D, upwind movement U, random movement R, mixed downwind and random, DR, and mixed upwind and random UR).

At this stage a stochastic component for both wind speed and direction was added. These two parameters were assumed to be random variables centred on their modelled values. Introduction of such variation was motivated by the fact that the wind can show a considerable variation in speed and direction within a few hours. Thus, for each known location (farm), s, at time, t, we produced a value of wind direction, $\delta^*_{s,t}$ (expressed in radians), and speed, $\tau^*_{s,t}$ (expressed in m/s) from the following distributions:

$$\begin{gathered}\delta^*_{s,t} \sim N\left(\bar{\mu}_{s,t}, \sigma_{s,t}\right) \ \text{ with } \ \delta^*_{s,t} \propto [0, 2\pi] \\ \tau^*_{s,t} \ \sim \chi^2(\varsigma_{s,t}, \varphi_{s,t}) \\ for \ \ s = 1, 2, \dots, N \ \ and \ t = 1, 2, \dots, T\end{gathered} \tag{5}$$

where $\bar{\mu}$ and σ are the mean and the standard deviation of the normal distribution of wind direction; and ζ and φ are the degrees of freedom and non-centrality parameter of the chi square distribution (χ^2) for wind speed.

In the present analysis $\bar{\mu}_{s,t}$ was equal to the average value of wind direction from the original dataset (i.e. the UK Met. Office wind model) for a specific farm on a specific day (or daytime period) (i.e., the modelled value $\delta_{s,t}$) and $\sigma_{s,t}$ was ± 0.5 standard deviations of this mean value. The wind speed had $\zeta_{s,t}$ equal to the average value of wind speed from the original dataset ($\tau_{s,t}$) for a specific farm on a specific day (or daytime period) and the non-centrality parameter, $\varphi_{s,t}$ was set to zero; given that wind speed is chi-square distributed, a mean value of 15 may therefore give realised values in the approximate range of zero to 50.

Once $\delta^*_{s,t}$ and $\tau^*_{s,t}$ were calculated for each farm, the five types of midge movement (trajectories) were simulated (applying the kriged values of wind speed and direction in between farms, as explained above). This was repeated 1,000 times for each infected farm.

For each newly infected farm we therefore had a set of trajectories arriving from different, already-infected farms. The probability p_{f-m}, that farm f was the source of infection for farm m was defined as the proportion of all trajectories arriving at farm m that originated from farm f:

$$p_{f-m} = \frac{\text{number of trajectories from } f \text{ to } m}{\text{totalnumber of trajectories reaching } m \text{ from all possible infecting farms}} \tag{6}$$

The farm, f, with the highest probability was selected as the most likely source of infection of farm m. The probability, p_w, that midge movement of type w caused that infection was then calculated in an analogous way from:

$$p_w = \frac{\text{number of } w \text{ typetrajectories from } f \text{ to } m}{\text{totalnumber of trajectories from } f \text{ to } m} \tag{7}$$

Once again, the highest probability was selected from the five different values of p_w , and only values of 0.9 and above were considered meaningful (no standard statistical test exists for this calculation). Table 2 indicating that SWOTS is able to describe the origins and routes of infection in 69% of farms.

4 Result and discussion

4.1 The main types of midge movements explaining the outbreak in 2007

We keep using the finer resolution surface wind information (at the heights of 2 and 10m rather than 1 km). Based on the more biologically realistic assumptions of midge movement types (upwind, downwind, random, upwind and random, as well as downwind and random) mentioned previously, our simulation shows that in 2007, all types of midge movement considered here were found to be correlated with the BTV-1 outbreak (Table 1): upwind movement (correlation value 0.2129), downwind movement (correlation value 0.2256) and random movement (0.9640). Because SWOTS model simulated the trajectories for thousands times, the highest correlation values were generated as a final result. Although the upwind and downwind movements are with lower correlation values, it is possible that a couple of trajectories were closed to a susceptible farm and the midge were able to arrive and infect it. The result is reasonable in our simulation.

Table 1: Highest correlation value between BTV-1 infection and midge movement types/vectors

	Upwind movement	Downwind movement	Random movement	Wind vector	Midge vector
Correlation value	0.2129	0.2256	0.9640	0.6080	0.9720

The wind speed histogram (Figure 3 (a)) concluded that the most frequent average daily wind speed was between 2 to 3 m/s. We assumed that midges are almost entirely suppressed or cease flying when wind speeds are greater than 11m/s (Hendrickx et al., 2008). In our study, at period from 0500 to 1059 h which belongs to midge peak activity time (Christopher J. Sanders et al., 2011), the wind speeds of 2 m/s with the highest density provides the midge more options of movement types. Hence, the higher correlation between infection and midge random movement may result from that midges fly relatively freely with the low speed of wind and can locate hosts by olfaction.

The average direction of all infection (see Figure 7) connected by SWOTS is 98° from north (where compass direction north is 0°), which signifies the mean direction of the BTV-1 spreading is approximately east-southeast. The mean direction of midge movement is 74°. Other directions with highest correlation are 98°, 185° and 6° of random, upwind, and downwind movements respectively. Result from all movement types together, the mean direction of midge flight has slight deviation of 24° off the infection. The consequence shows that the direction midge vectors random movements were virtually identical with which of disease transmission. It suggests that for the BTV-1 outbreak in 2007, the midge random movement is more remarkable.

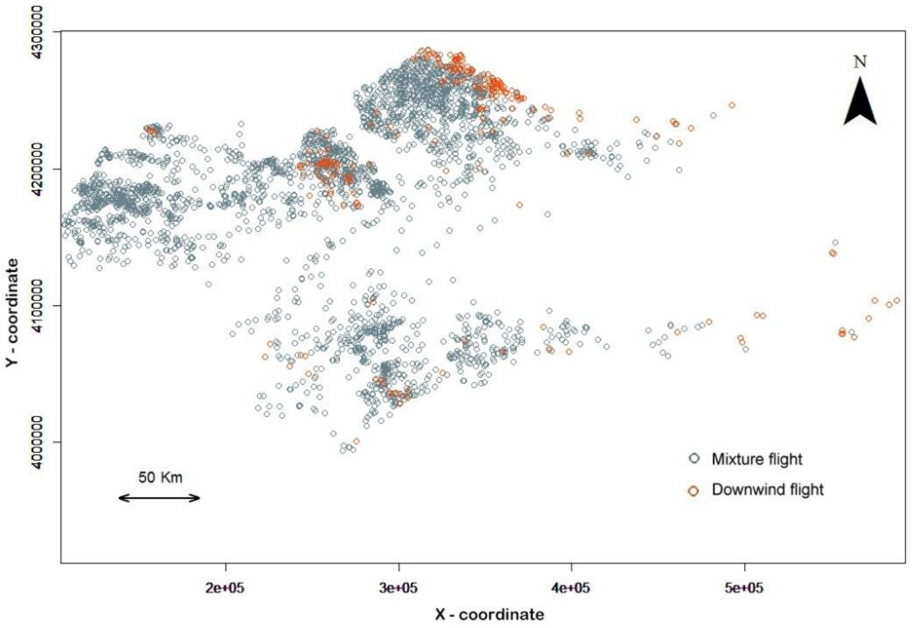


Figure 6: Farm classification according to the way the midges arriving. 2,830 farms were infected by midge mixture flight type; 222 farms were infected mainly by downwind flight type.

For any particular farm-to-farm infection, we found that the single type of midge movement was not enough to complete the transmission of the BTV-1 (see Figure 6 and Table 2). Of the explained 3,052 farms, only 222 farms (5 per cent of all epizootic cases) were infected by midges arriving prevalently in downwind movement (trajectories showed in Figure 9). Most of the farms (2830 farms, 64 per cent of all infection) were infected from mixtures of midges movements which means none of the 5 types of movements considered was prevalent (trajectories showed in Figure 8). 31 per cent of all infections remain unexplained by the model.

In all cases, the distances midges travelled were longer than the straight-line distances between farms. Because wind directions varied greatly and the midges were easily influenced by the wind. Thus, midge trajectories show various degrees of 'zig-zag' movement. This

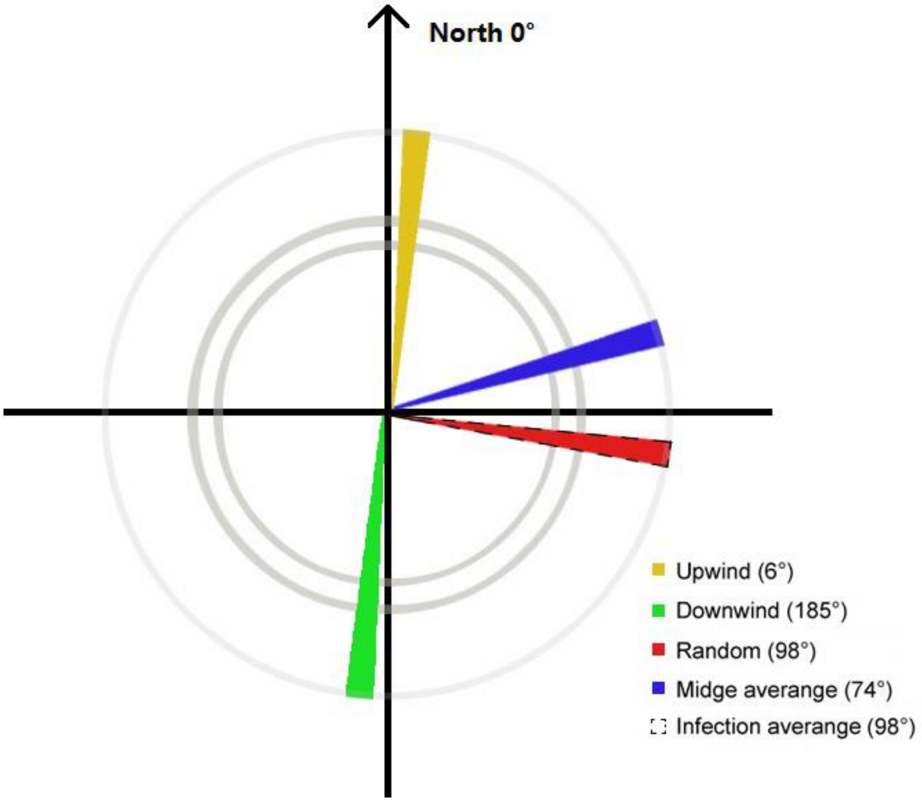


Figure 7: A diagram shows the highest correlations between infection and direction of different movement type. The yellow, green and red indicate the direction of midge upwind, downwind and random movements respectively. Blue indicates the average direction of midge flight. Black dash lines indicate the average direction of BTV-1 infection, and it is the same direction with which of highest midge random movement.

movement was combined with upwind, downwind and random (including cross-wind) movements which are usually not the straight lines connecting two farms, therefore, resulted in midges covering larger distances before arriving at the next uninfected farm.

4.2 Spatial spreading of BTV-1 between farms

As the category described by Hendrickx et al. (2008), of the 69 per cent of all outbreaks explained by SWOTS model, most of the farms (35 per cent of infected farms) were found within long-range transmission, 30 per cent in their medium-range transmission, and only 5 per cent were located on the short-range transmission. We analysed the midge movement types within each transmission scales and found that, of 222 farms infected by midge downwind movement, over half (120 farms) were infected at medium-range transmission, followed by long-range with 91 farms and only 11 farms infected by downwind movement were with in short-range (Figure 10 and Table 2).

The high proportion of medium and long range dispersal occupied in downwind movement supports that the midges are able to reach to further area by virtue of the wind, as for the short distance, the downwind movement seems to contribute less frequent as longer distance. However, from a general view of infected farms, the mixture flight cannot be ignored. Even in medium and long-range distance the majority of farms were infected by midge arriving as mixture flight rather than downwind, while the downwind movement is described as a main flight type for long-range dispersal in (García-Lastra et al., 2012) and (Hendrickx et al., 2008).

The different result compared with the two models above is because that in HYSPLIT model, the data implied for backward wind trajectories were obtained at 10, 500 and 1,000 meters above the ground level while we were focusing on the wind under (including) 10 meter's height. García-Lastra et al. (2012) mentioned that HYSPLIT model has some limitation related to the low vertical and horizontal resolution of the relevant data. In like manner, wind density model used the wind fields recorded at an average altitude of 1,450 m instead of the much lower altitudes that is surface layer conditions applied in current analysis. Winds tend to move faster and stronger (L. Sedda et al., 2012) at high altitudes than those nearer the ground and are much more stable. Such wind can also have negative effect on midge's abundance (Martínez-De La Puente et al., 2009), thus, leading to a possible overestimate of long-range effects.

Culicoides are usually sampled at low altitudes. For instance the *C.imicola*, incriminated as the main vector for BTV-1 outbreak, is never found at high altitudes in temperate regions. And C J Sanders et al. (2011) analysed the composition of insects in the air (sampling conducted for three/four weeks in July from 1999 to 2007, excluding 2001 and 2003) showed that only 14 *Culicoides* were caught at 170/200 m altitude over the entire sampling period. However, evidence shows that large populations of *C.obsoletus* Complex can be found in European areas above 1,000m (Pioz et al., 2012). It is possible that midges are willing to fly at a higher altitude although the presence of vectors does not imply viral activity. We do not deny that some *Culicoides* species (and many other insects) occur at altitudes up to 1km or are even flying higher; for further research we query the epizootiological and epidemiological importance of such records and require exact data in detail.

Table 2: Farm amount and proportion of midge mixture and downwind movements respectively.

	Midge mixture movement		Midge downwind movement		Total	
Item	Number of farms	Proportion of all reported cases	Number of farms	Proportion of all reported cases	Number of farms	Proportion of all reported cases
Short-range distance	145	3%	11	<0.5%	156	4%
Medium-range distance	1,209	27%	120	3%	1,329	30%
Long-range distance	1,476	34%	91	2%	1,567	35%
Total	2,830	64%	222	5%	3,052	69%

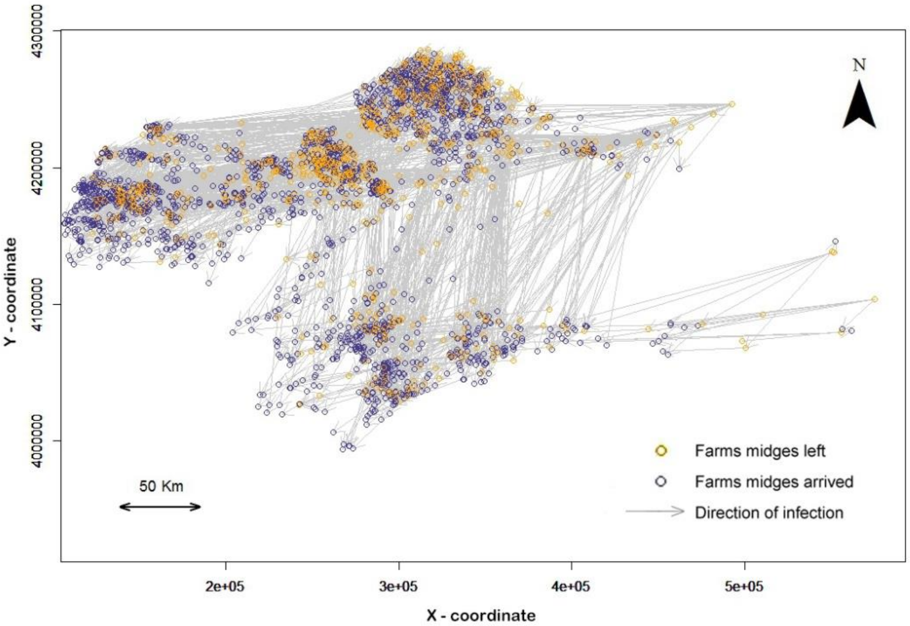


Figure 8: A map showing farms infected by midge mixture movement. The arrows indicate the direction of infection movement from infected farms (arrow origins) to farms that they infect (tips of arrows).

The pie chart (Figure 10) shows that in this outbreak, the short distance (less than 5km) occupied the lowest proportion. The downwind movement were not significant within this distance while more mixture movement was responsible for the infection. Majority of the farms within short-range distance were infected by the midge active flight which is similar with the random dispersal in local scale (Gerbier et al., 2008).

In terms of the distances between farms in SWOTS, the modal distance covered by the midges was 15km (see Figure 12). The most frequent infection range shows an alarming message with the possible radius that midges are able to cover and infect. For potential infection we simulated the transmission ability of vectors measured by distance of midge flight covering (Table 3). Although the random movement is the highest correlation between infection and midge vector, the low velocity of this single movement is not strong enough for longer distance transmission of without carried by wind.

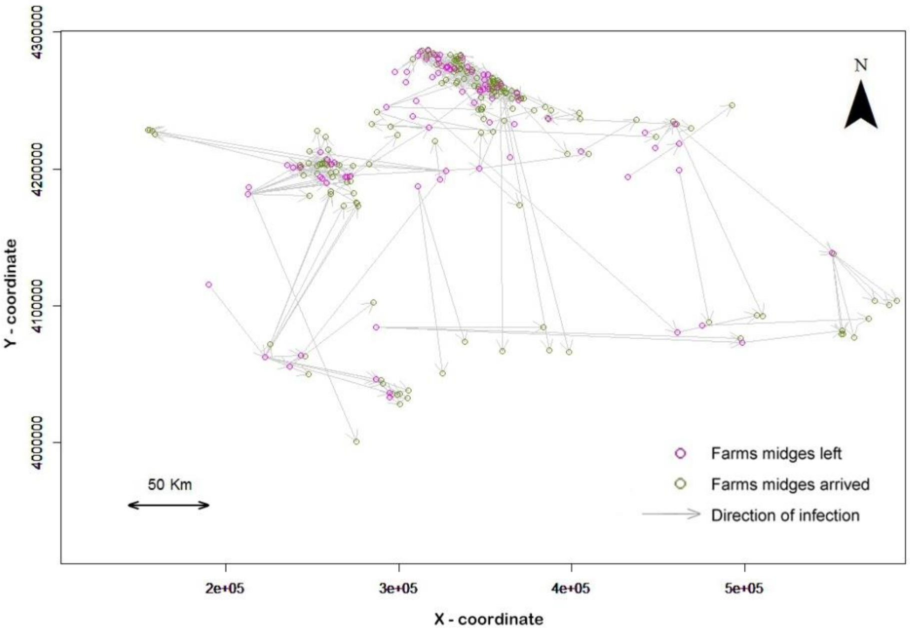


Figure 9: A map showing farms infected mainly by midge downwind movement. The arrows indicate the direction of infection movement from infected farms (arrow origins) to farms that they infect (tips of arrows).

Meanwhile, the downwind type is significant for further transmission, requiring surveillance of meteorological and climate research institutes. We suggest the farm owners to report susceptible infection cases as soon as possible. The sooner diagnosing the quicker to control subsequently possible infections.

4.3 The temporal scale and the estimated intrinsic incubation period during the outbreak

Because the SWOTS model simulates the time course of the infections during the season, processing data not only in spatial but also temporal way. Among the 5 period within 24 hours, we found that the highest correlation between farm infection and midge vector is at time from 05.00 to 11.00 h, rather than at any other time of day. Our study shows that the during 05.00 – 11.00 h when peak midge activity occurs, the highest infection is likely a result from the higher bite rate brought by the higher midge abundance (A. C. Gerry, Sarto i Monteys, Moreno Vidal, Francino, & Mullens, 2009).

As for IIP, a significant etiological parameter, SWOTS model estimated that the strongest correlation between the infection and midge vector is maximum 15 days. It means that that if a farm was deemed to be infected, for instance, any livestock showed a BTV clinical signs and were able to infect a midge after being bited for the first time on 16th May, we assumed that the infectious (or infecting) midges had arrived this farm on 1st May, which before 15 days (IIP) ago. In relevant literatures the intrinsic incubation period (IIP) was described as ranging from 4 to 20 days (Saegerman, Berkvens, and Mellor, 2008; Hess, Howell, and Verwoerd, 2013; Darpel et al., 2007) depending on ambient conditions and different species of ruminant. Therefore we considered the estimated value of IIP which as the highest correlation is reasonable and consistent with previous researches. Midges need to be on air between 1 to 10 days flying from a farm to reach subsequent farms. The average travel time calculated in SWOTS is approximately 10 days (the travel time can be less than 10 days if the distance between two farms is short).

Table 3: Probability of midge movement types flight to further distance based on current database.

Movement types/midge vectors	Midge random movement	Midge downwind movement	Midge upwind movement	Midge vectors
Probability[1] (%)	114	13,595	16,550	26,396

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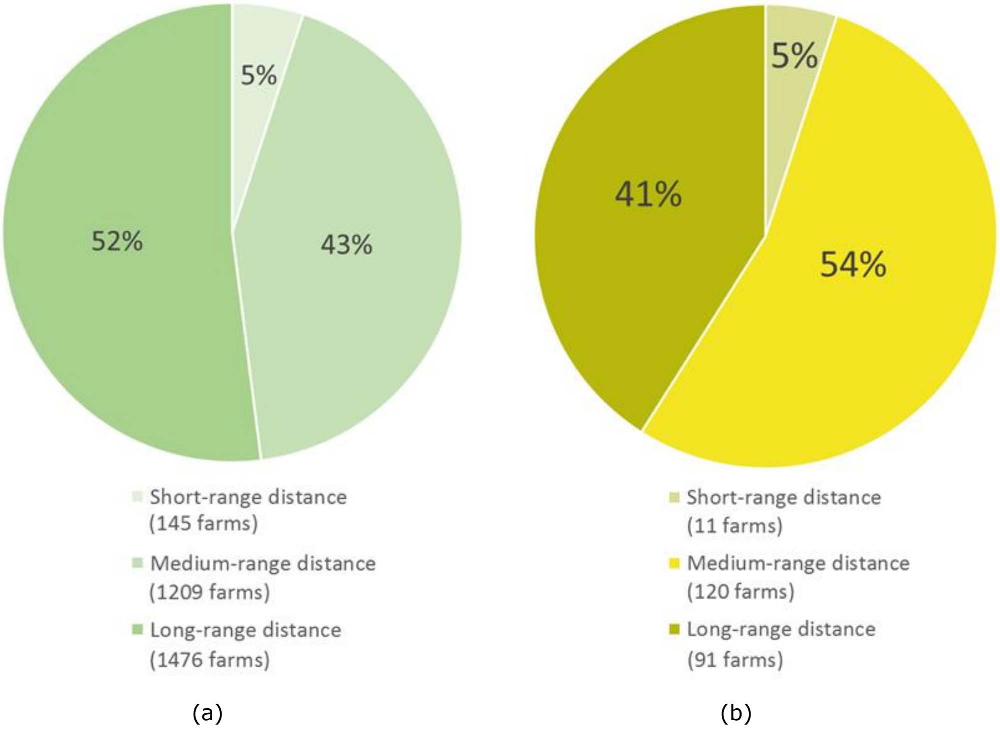
[1] 'Probability' is potential distance that midges are able to cover. 'Midge vector' is converted by wind speed and direction. For example, if the midge transmitted the disease to a farm located in 1km away, as showed in simulation result, with 114% probability of midge random movement, the midge are able to transmit the disease to a distance of 1.14km only by random movement. But the midge vectors can transmit the disease to much further distance with 26,396km.



(a) (b)

Figure 10: Pie diagram showing proportion of distance covering in different movement types. Hendrickx et al. defined the short-range distance is less than 5km, medium-range distance is between 5 to 31 km, and long-range distance is greater than 31km. (a) indicates the covering distance proportion of midge mixture flight and (b) indicates the covering distance proportion of downwind flight.

Of 3,052 farms connected in SWOTS, the mean distance estimated between infected farms is 85 km in 2007 BTV-1 outbreak year. From the first reported infection case, the epizootic spread through the wide area in Andalusia at 0.5 km of average speed per day, the infection even reached as far as 63 km within one day. The furthest distance that infection could influence was over 400 km after only 10 days vector flight. This result is supported by (García-Lastra et al., 2012) that an active infection in medium-long distance regions, wind with suitable speed, altitude and trajectory, and appropriate weather can lead to outbreaks of BTV-1 not only over the sea but also over the land. We considered during the over 100 km distance, the midges were not simply carried by wind, the random movement contributed a lot. The high proportion of mixture-flight infection in long-range distance suggests that such a long distance flight may not be accidental (García-Lastra et al., 2012). The long-distance flight of midges is an action of migration (Chapman, Drake, & Reynolds, 2011; Eagles et al., 2014; D. R. Reynolds, Chapman, & Harrington, 2006), which result in the extensive spatial spreading of BTV-1.

4.4 Further consideration of the extrinsic incubation period

To simplify the model, we did not take the midge’s extrinsic incubation period (EIP) into account. The assumption is that, when midges leave an infected farms they are infectious or else, being infected. In other words, the midges complete development of BTV, becoming infectious during the time on flight and as long as they reach a susceptible farm, they are able to infect it. The SWOTS model estimated that 94 per cent (Figure 11) of connected farms have a flight time (DT) range from 7 to 10 day (65 per cent of all reported farms). As literatures described, the Extrinsic incubation period (EIP) in *C.imicola* is range from 4 days to 10 days (Saegerman and Reviriego-gordejo, 2008) depending on ambient temperature. Because minimum temperature required for BTV replication is 11-13°C (Carpenter et al., 2011), in our study we assumed that the midge vector only take off at temperature between 10-25°C. Thus the 10 days travel time along with suitable ambient temperature is a guarantee of that the EIP be able to have been completed before midges arrive at and infect the next target farm.

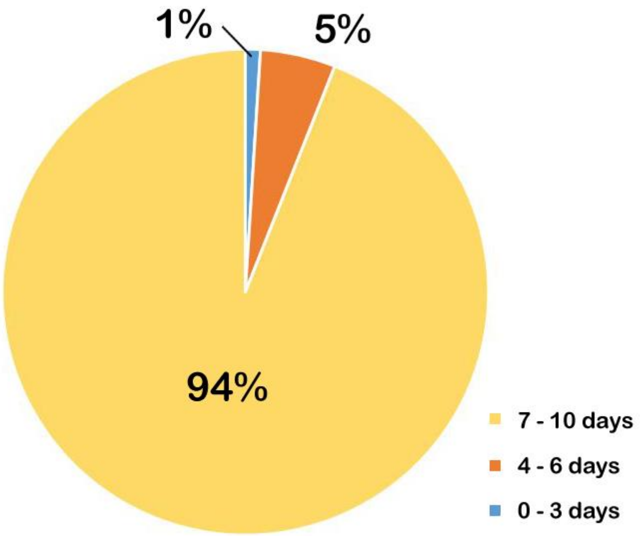


Figure 11: Pie chart shows the proportion of extrinsic incubation period (EIP) in 3,052 connected farms in SWOTS.

Because the Andalusia is located the South-coast of Spain and the average temperature is rather high, during the infection period the highest temperature reached 38°C. A C. Gerry & Mullens, (2000) described that the EIP could beshorter to 4 days at ambient temperature of 32°C. In our study, only 1 percent of connected farms in SWOTS remain with DTs less than the possible shortest EIP (4 days). In terms of all the epizootic farms the effect is rather small.

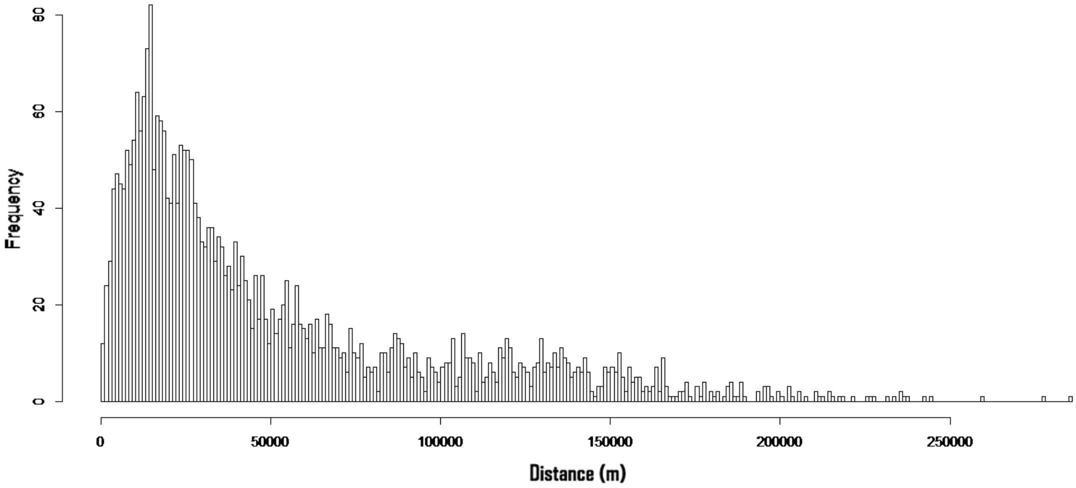


Figure 12: SWOTS estimated the distance the midges are able to cover. In terms of the distances between farms, the modal distance covered by the midges was 15km.

Figure 13: The map shows the infectious farms and 'end point' farms.**Figure 12**: SWOTS estimated the distance the midges are able to cover. In terms of the distances between farms, the modal distance covered by the midges was 15km.

4.5 Implications for disease control and management

The transmission of vector-borne disease is greatly affected by wind speed and direction as a result of the small size of vectors. Thus, understanding the different types of midge movements as a role in epizootic is significant for the disease surveillance and control. In the outbreak year 2007, 35 per cent of infected farms are considered as long-distance transmission which is over 31km (Table 2); 12 per cent (522 farms) are over 100 km. We used the wind data at 2 and 10 m height above the ground however, evidence show that adult midges usually make 'swarms' for reproduction which could be elevated 10 m above the ground by air updrafts (García-Lastra et al., 2012). For this reason we cannot exclude the possibility that the midges can be carried by the wind at high altitude and transmitted to further region. Under a certain condition for example, wind speed with 3-11 m per second, temperature less than 30°C and relative humidity above 25% related with precipitation, the midge are able to survive long enough to transmit the disease as far as 100-400 km (García-Lastra et al., 2012).

These long-range movements were investigated that midges can actively initiate and maintain it, or finished it either (if insects cease to move their wings and descend). This is likely the case of oversea transmission because the midges can reach up to 700 km away with the help of wind under certain condition characterized by the different factors of atmospheric turbulence, surface roughness and the availability of midge food (L. Sedda et al., 2012a). Previous model about the long-range models tended to regards the midges as a dust particle to fly in long-range distance (García-Lastra et al., 2012; Hendrickx et al., 2008; Pérez, Jm, and Jm, 2006; Sanders et al., 2011; Wilson and Mellor, 2009). It is concluded in our study the

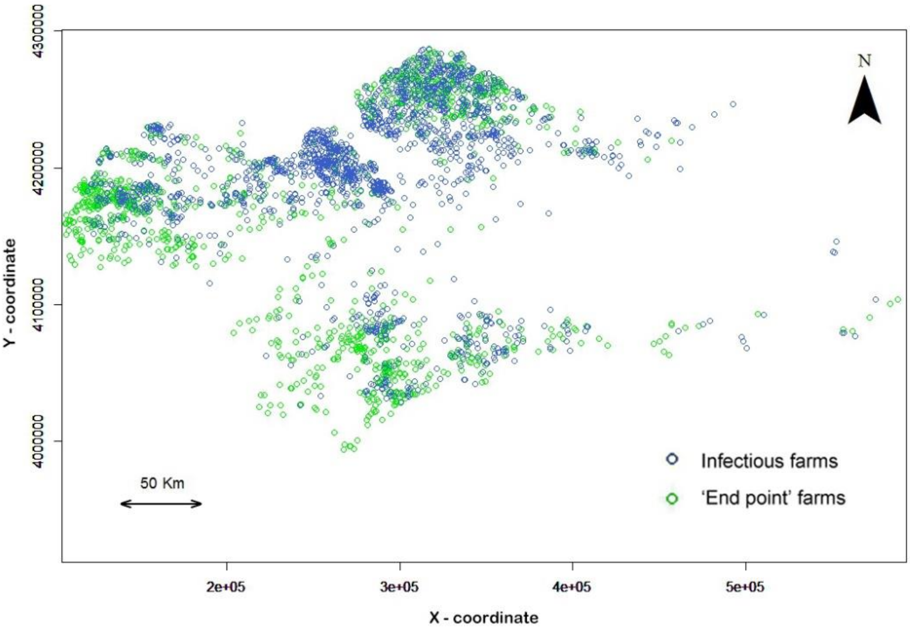


Figure 13: The map shows the infectious farms and 'end point' farms.

midge transmitting the disease in long-range happened not only passively but also actively. Midge flight over miles is a potential threatening to enlarge the epizootic. As long as the virus established in a new region, the neighbour local farms are possibly infected from those infected by long distance spread. As suggested by L. Sedda et al. (2012), the local farms are deemed as "stepping" stone to infect the sequent farms, helping the virus transfer to nearby area or even, midge and take off again when under a proper condition, transmit the virus into another continent. We also suggest that having an accurate estimation of the local dissemination velocity can help to control the longer transmission due to the infected farms and meanwhile, managing the long-range transmission contributes to the control the highly possible target to area by inhibiting the establishment of virus. Neither can exist effectively without the other.

According to our analysis, 1,069 farms (38 per cent of total infected farms in 2007) are infectious, the rest (1,303 farms) of explained case in SOWTS were infected by the initial infected farms as transmission 'end points' (see Figure 13) and infect no farms (the cross infected happened as well among the primal 1,069 infectious farm). The map shows that generally, the 'end points' are located on the edge of the whole infection region (far from the infectious farm gathering area). It is probably because of the spatial position relative to other farms that after long-range flight the midges scattered over the farms with low abundance which is not strong enough to continue infecting and the prevailing wind condition changed that the midges cannot to be carried to another farms or, simply the transition period was waning to close that the ambient temperature cannot support to provide more infections (brought about by on-coming winter conditions. Hence, we have reasons to believe some farms are more important as source of infection than others in respect of any control or intervention strategy.

SWOTS is an advanced alternative for investigating and predicting flying insect-borne disease outbreak events (or even insect-related damage to crops or vegetation). At the primary stage the model need to be provided with more initial information, for example in our study, we need to know the prior estimates of incubation period, time of the day of vector activity, etc. through the whole infection period. If the parameters are unable to get, and so must be estimated from the existing data. At such a stage of simulating any new outbreak, parameter estimated are likely to be quite variable and so will need to be updated as more data accumulate. However, the model updates can be imported with the previously estimated parameter values thus reducing algorithm running times.

Although the SWOTS took a considerable time to run on the current dataset (simulation in our studying cost more than 10 days), its application can to extend to beyond just simple wind-epizootic outbreak. If any other relevant environmental factors can be converted to analogous geometric vectors (representing fluxes or directional gradients, etc.). The improvement of SWOTS model in this study makes the result closer to real epizootic situation and helps control the vector-borne and other diseases in many respects. The spatial and temporal scales of epizootic spreading may help the public health actors and veterinary health managers to increase the efficacy of monitoring, surveillance and intervention for potentially forthcoming outbreaks. The meteorological elements imported may contribute to the entomological and physical scientist more information knowing better about the flight speed and time of midges within a day in the air, or their willingness or otherwise to fly at high altitude. The vector movement types may lay the foundation of prospective BT (and other vector-borne disease such as

Table 4: Comparison of relevant parameters between current SWOTS model and previous SWTOS model.

	Current SWOTS model (used to explain BTV-1 outbreak in 2007)	Previous SWOTS model (used to explain BTV-8 outbreak in 2006)
Temperature for midge vector flying	Between 10°C to 25°C	NA
Precipitation for midge vector flying	Under 0.1mm per day	NA
Highest density of wind	2 – 3 m/s	3 – 5 m/s
Assumption of midge free-fly speed	1 m/s	0.5 m/s
Mixture movements proportion	64%	17%
Explained cases	69%	94%

Schmallenberg disease, African Horse Sickness, Foot-and-mouth disease and so forth (P S Mellor et al., 2000)) research for epidemiological scientists considering the correlation between infection and winds. Further work is needed estimate these relevant parameters correctly and, by better development can SWOTS frameworks be applied in the future.

4.6 Limitations in SWOTS model

Focusing on different cases of outbreaks we change relevant parameters, making the model fit the infection better. We analysed the two winds dataset in 2006 and 2007 respectively and found that the different movement type in two BTV epizootic outbreak is possibly due to the midge and wind 'relative speed.' In 2006 of BTV-8 outbreak, the highest density of wind was between 3 to 5 m/s and we made an assumption of midge active flight speed as 0.5 m/s, the result shows that the downwind and upwind occupied 77 per cent of all infections (L. Sedda et al., 2012a). We changed the parameter of midge active flight speed from 0.5 to 1 m/s in this study and the simulations indicates that only 5 per cent of reported farms were infected by midges arriving in downwind (Figure 3 shows that the highest density of wind happened between 2 to 3 m/s), and mixture movement type is main transmission driver. The comparison of two sets of data concludes that the former wind speed is relatively greater than the latter, which also supports the view that the greater the midge's active flight speed, the greater in the non-downwind component of disease spread.

The unexplained portion of the BTV-1 epizootic (31% of the reported infected farms) might be due to human transport of midges or virus, to the animal movement, or simply to erroneous estimation of the date of infection. The role of wild ruminant's transportation in the dissemination of BTV-1 in Andalusia may have been significant. Allepuz et al. (2010) stated that BTV is widespread among red deer in southern Spain, and these species can act as reservoirs in the transmission and maintenance of virus which are of importance in the dissemination of BT, especially in the areas where livestock and wild ruminants share the same habitat. Apart from red deer, widespread circulation of BTV exists in fallow deer and mouflon as well (García-Bocanegra et al., 2011). These wild ruminants could be acting as a confounding factor more than as a risk factor itself (Allepuz et al., 2010), therefore, sero-surveillance would be useful to detect virus circulation and control the potential transmission.

Compared with analysing BTV-8 in outbreak 2007 year by using same model, we considered more about the climatic factor which influence the vector flight behaviour widely. However, lacking of the epidemiological and entomological knowledge about the vector behaviour can cause bias in our study in some way. We assume that the midge only take off at temperature between 10°C and 25°C, but we cannot exclude the possibility that the midges are able to fly and bite a susceptible host at temperature out of this range. For example, with the shelter *C.obsolutus* Complex are able to survive at 6°C (Saegerman & Reviriego-gordejo, 2008). During the late transmission period it is possible that the midge survive longer enough and continue transmission activity at lower than 10°C. Lebl, Brugger, & Rubel, (2013) suggest that lagged time intervals are better adapted to describe the midges abundance than point lags. As we assuming the midge fly when precipitation is lower than 0.1mm per day may generate error in estimating the correlation. Hence, further information in meteorological aspect the relationship with midges is desired.

Based on these consideration above, we expect that our modelling approach will have predictive power until it also incorporates characteristic of not only meteorological data but also the wildlife population (their distribution, abundance, movement patterns and infection status), quite different from those of domestic stock, to improve the model better.

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5 Conclusion

The SWOTS model analysed the data of BTV epizootic outbreak in 2007, suggests that on the condition of temperature range from 10°C to 25°C and precipitation lower than 0.1mm per day, the spatial and temporal pattern of BTV serotype 1 movement across the Andalusia, Spain was mainly driven by midge mixture movement type (i.e. none of the single movement type is significant). Only a small proportion of farms were infected by midge downwind movement type, happening mostly within medium and long-range distance. In terms of the distances between farms, the modal distance covered by the midges was 15km. Our model is able to describe 69 per cent of the total of 4,429 reported infection cases. We recognize that certain critical assumptions had to be made necessarily in this simulation result from the insufficient knowledge of the life cycle of *Culicoides* species and detailed relevant parameter of meteorological factors. Key among these, and for which we require further information to develop our model's predictions are, the midge population parameters (reproductive status, age, local population density), weather (humidity, relevant climatic factor which decide the mortality of midges such as maximum wind speed, precipitation, and temperature) midge flight properties (the altitude they are willing to reach, flight behaviour at different wind speed and directions) as well as other etiological parameters (accurate IIP and EIP time).

This model explained specifically in one picture of one disease outbreak, but can be used over other different types of insect-borne disease spreading and come up with conclusions about vector flight behaviour with winds at multiple spatial and temporal scales, to understand completely the transmission drivers and unfolding events of a major disease epizootic. By calling into question the claims previously made for the frequency and therefore importance of relationship between infection and random movements, the down-wind only infection events within medium and long-range during the 2007 BTV serotype 1 outbreak, the importance of the midge reaction of climate factors and for the importance of high rather than low-altitude wind fields, our study highlights the importance of finding our more about hitherto little known and understood aspects of *Culicoides* behaviour. Only better knowledge of this behaviour, within a robust model framework, will prepare us for future similar outbreaks and provide the tools for implementing effective control.

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