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Bluetongue in the Mediterranean: prediction of risk in space and time

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Abstract

Bluetongue virus (BTV) causes an infectious, non-contagious disease of ruminants and is transmitted by *Culicoides* biting midges. Currently an unprecedented epidemic of bluetongue (BT) is sweeping the Mediterranean Basin and a large number of countries are now involved in managing the disease. Therefore the development of new methods for accurate prediction of BT risk in space and time is essential. The life-history parameters of *Culicoides* and other parameters of the BTV transmission cycle are highly sensitive to climatic conditions. Thus the potential exists to define the limiting conditions and likelihood of spread of BTV, using geographical information systems (GIS) to combine vector, virus and environmental information. This paper reviews the progress and current status of GIS and remote sensing (RS) as applied to BTV in the Mediterranean Basin. These analytical tools have aided the determination of the relative roles of different *Culicoides* vectors in BTV transmission across the region and have facilitated prediction of the wide-scale distribution of the major field vector *C. imicola* from RS climate variables. On the basis of findings and lessons from statistical models of vector distribution, a strategy for development of dynamic biological or process-based models of BT risk is suggested.
Keywords: Bluetongue virus; Mediterranean; *Culicoides obsoletus*; *Culicoides pulicaris*; *Culicoides imicola*; distribution; climate; remote sensing; risk map

Bluetongue virus, its vectors and the changing face of bluetongue epidemiology in the Mediterranean

Bluetongue virus (BTV) causes an infectious, non-contagious disease of ruminants (bluetongue, BT) and is transmitted between its vertebrate hosts by *Culicoides* biting midges (*Diptera*: *Ceratopogonidae*). Although severe disease is restricted to certain breeds of sheep and some species of deer (Taylor 1986), it has been estimated that BTV causes losses of US $3 billion a year to trade in animals and animal products. Thus BT is classified as a List-A disease by the Office International des Epizooties (OIE). *Culicoides* are significant as arbovirus vectors since they inhabit a wide range of moist habitats, rapidly reach high abundances under suitable climatic conditions, and are passively dispersed on the wind, producing rapid spread of *Culicoides*-borne diseases (Mellor, Boorman and Baylis 2000). *Culicoides* broadly require the presence of host for blood meals and moist breeding sites for egg and larval development. Their life-history parameters and other parameters of the BTV transmission cycle (rates of

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BTV infection and virogenesis, efficiency of gut barriers to infection in the midge) are highly influenced by climatic factors, especially temperature and moisture (Mellor, Boorman and Baylis 2000). *Culicoides* development and survival rates are temperature-dependent as adults and larvae, and fecundity is inversely related to temperature once the lower temperature threshold has been exceeded (Wittmann and Baylis 2000, and refs. therein). Larvae may be desiccated by low soil moisture but equally may drown if breeding sites are flooded. Adults, being small, are susceptible to desiccation at low humidity (Murray 1991) and thus require moist microhabitats for shelter as well as oviposition. Only a handful of *Culicoides* species are of transmission importance and different vectors operate in different continental episystems within the global distribution of BTV (Mellor, Boorman and Baylis 2000).

Considering the Mediterranean Basin, only brief periodic incursions of BTV and the closely related *African horse-sickness virus* (AHSV) occurred before 1998, with only one or two countries affected at a time and one viral serotype being involved in each epidemic (Figure 1a, see Colour pages elsewhere in this book). Also, prior to the current series of outbreaks only one main vector species was known to be involved in BTV transmission - *Culicoides imicola sensu stricto* (Linto et al. 2002), a member of the *C. imicola* Kieffer species group. All outbreaks before 1998 caused by BTV and AHSV occurred within the region delineated by the known northern distribution limit of this species (Figure 1a, see Colour pages elsewhere in this book). However, between 1998 and 2003, an unprecedented BT epidemic has occurred (Baylis 2002; Mellor and Wittmann 2002), affecting many countries in both the east and west Mediterranean areas, including many that were unaffected in previous outbreaks. BTV has expanded northwards (over 700 km) and beyond even the updated northern distribution limit of *C. imicola* (Figure 1b, see Colour pages elsewhere in this book), in northwest Greece, Bulgaria, west European Turkey and parts of Italy (Mellor and Wittmann 2002; Baylis and Mellor 2001). Therefore, novel *Culicoides* vectors must now be involved in transmission, possibly the widespread *C. obsoletus* Meigen and *C. pulicaris* Linnaeus complexes (Mellor and Wittmann 2002). Indeed, BTV has previously been detected in wild-caught *C. obsoletus* in Cyprus (Mellor and Pitzolis 1979) and, more recently, in southern mainland Italy (Savini et al. 2003) and in wild-caught *C. pulicaris* in Sicily (Caracappa et al. 2003). The current epidemic has persisted for six years to date (affecting Italy for four consecutive years since 2000) and several viral serotypes are circulating. With over a million sheep dead so far (Mellor and Wittmann 2002; Calistri and Caporale 2003) and many Mediterranean countries now forced to manage BT, it is essential to develop methods for accurate prediction of BT risk in space and time.

Prediction of where and when disease might spread involves three main steps (Rogers and Randolph 2003). First, the pathogen and its routes of transmission must be identified; secondly, the patterns of disease in space and time must be recorded in relation to the environment. Finally, it is imperative to understand the dynamic processes of transmission that ultimately determine the observed patterns.

During previous BT epidemics in the Mediterranean Basin, the identity of the vector, *C. imicola,* was determined by periodic local vector surveillance in the infected areas (Mellor et al. 1983; Jennings, Boorman and Ergun 1983; Boorman and Wilkinson 1983; Boorman 1986) in combination with virus isolations from wild-caught adult *Culicoides* (Mellor et al. 1990; Mellor and Pitzolis 1979). Following the advent of GPS technology, spatio-temporal patterns of *Culicoides*-borne virus transmission and *Culicoides* abundance have been recorded more systematically within Geographical Information Systems (GIS) and compared over extensive areas at

a fine resolution. These new analytical tools retrospectively supported the role of *C. imicola* in BTV transmission in Morocco and Iberia (Rawlings et al. 1997; Baylis et al. 1997; Capela et al. 2003). At a local scale, the relative roles of *C. imicola* and novel *Culicoides* vectors in BTV transmission in Sicily have recently been investigated (Torina et al. 2004). Vector and disease information can now be integrated with information about the environment, including both ground-based weather-station and remotely sensed (RS) climate variables, within the same geographical framework. Statistical models have been developed, at different spatial scales, to elucidate the relationship between environmental factors and vector *Culicoides* presence in sampled locations to permit prediction of the distribution of BTV and *Culicoides* in unsampled locations. This paper reviews the relatively short history of GIS and RS for prediction of BT risk in space and time in the Mediterranean. We show that RS climate variables can be used to predict the wide-scale distribution of *C. imicola*, with thermal requirements being particularly important at this species' northern range limit. Lessons learned in the development of statistical models can direct us towards a strategy for dynamic biological or process-based models that are much more versatile for disease prediction (Rogers and Randolph 2003).

Wide-scale determinants of *Culicoides* distribution

Climate models based on weather-station data

A preliminary attempt to relate the distribution of BTV and vector *Culicoides* to environmental factors at a continental scale was made by Sellers and Mellor (1993) and was based on the thermal requirements for BTV transmission over winter. BTV probably has no long-term vertebrate reservoir or trans-ovarial transmission (Mellor, Boorman and Baylis 2000). Thus persistence between years should only be possible where adult *Culicoides* vectors are present year-round and are of sufficient abundance and competence to permit continual host-midge cycling of BTV over winter (Mellor and Boorman 1995). Sellers and Mellor (1993) found an average daily maximum temperature of the coldest month of 12.5ºC across locations where BTV persisted in Turkey over the winters of 1977-1978 and 1978-1979. The 12.5ºC isotherm for the average daily maximum temperature of the coldest month of the year was then super-imposed on the distribution of outbreaks and *Culicoides* across the Mediterranean. This isotherm broadly delineated the areas where adult *C. imicola* could survive year round and hence where overwintering of BTV was possible.

Wittmann, Mellor and Baylis (2001) showed that the Mediterranean distribution limits of *C. imicola* could be broadly predicted from a model of this species' thermal requirements. These authors compared historic (1931-1960) monthly weather-station-derived temperature, saturation deficit, rainfall variables and altitude in sites in Iberia where *C. imicola* was known to be present versus those where it was known to be absent. The resultant logistic regression model correctly predicted *C. imicola* distribution at 83% of sites in Iberia and included the average temperature of the coldest and the warmest month and the number of months with mean temperature ≥ 12.5°C but did not include any rainfall variables. The predicted distribution for *C. imicola* (Figure 2, see Colour pages elsewhere in this book) showed broad correspondence to the current distribution limits, indicated by the red line in Figure 1 (see Colour pages elsewhere in this book).

Why are RS climate databases useful for prediction of the distributions of vector *Culicoides*?

In the search for predictors of the distributions of a range of vectors, climatic databases have been superseded by RS databases derived from the Advanced Very High Resolution Radiometer (AVHRR) on the National Oceanic and Atmospheric Administration's (NOAA) meteorological satellites (Hay et al. 2000; Rogers and Randolph 1991; Rogers et al. 1997; Rogers 2000; Randolph 2000; Hendrickx et al. 2001). From RS imagery, continuous layers of environmental information can be derived at high spatial (8 km by 8 km and 1 km by 1 km) and temporal resolutions (10-day cloud-free images are produced). This information, in contrast to ground-based weather-station data, requires no interpolation for extensive prediction across environments not sampled on the ground. Weather-station data may seem easier to interpret biologically, but processing of RS imagery from different spectral channels produces variables that are highly relevant to insect microhabitats, namely: Normalized Difference Vegetation Index (NDVI), Middle Infra-Red Reflectance (MIR), Land Surface Temperature (LST) and Air Temperature (TAIR). For example, NDVI specifically measures chlorophyll abundance and light absorption, but is correlated with soil moisture, rainfall and vegetation biomass, coverage and productivity (Campbell 1996). MIR is correlated with the water content, surface temperature and structure of vegetation canopies (Boyd and Curran 1998). LST is a general index of the apparent environmental surface temperature (whether soil or vegetation) and TAIR is an estimate of the air temperature a few metres above the land surface (Goetz, Prince and Small 2000). The biological relevance of these variables can be further enhanced by Fourier-processing monthly time series of variables (Rogers, Hay and Packer 1996), a technique that extracts information about their seasonal cycles in terms of their annual, biannual and triannual cycles, each described by their phase and amplitude. This can be carried out for each pixel, so that geographical patterns in the seasonal variations of the environment can be related to vector distributions.

RS climate models for explanation and prediction of *C. imicola* distribution

Initially, at a national level, within Morocco, Baylis et al. (1998) found a significant positive relationship between *C. imicola* abundance in 22 sampled sites and annual minimum of NDVI. The best two-variable regression model of these authors also contained average wind speeds (to which abundance was negatively related, probably due to adverse affects of wind on adult activity rates, mortality and trap efficiency) and accurately predicted *C. imicola* abundance at a further 27 sampled sites in Iberia (Baylis and Rawlings 1998). Predictions were less accurate in northerly sites, where *C. imicola* was absent despite high NDVIs. This is again suggestive of thermal limitation of this species at its northern range margin.

Two studies have confirmed the relevance of NOAA RS climate variables at different resolutions (8 km – Baylis et al. 2001; 1 km – Tatem et al. 2003), for prediction of the distribution of *C. imicola* at a continental scale - across the Mediterranean Basin. With both of these models, sites in Iberia were divided into high, medium and low *C. imicola* abundance categories on the basis of surveillance data (a different set of such data being used in each case). Non-linear discriminant analysis was used to identify which of the 40 temporally Fourier-processed RS variables and altitude best divided the Iberian sites into the observed abundance categories. Coefficients from the models were then used to predict *C. imicola* abundance elsewhere across Europe and North Africa in unsampled pixels, with

predictions restricted to pixels that were broadly similar in environment and climate to the original training set. These predictions are shown in Figures 3a and 3b. Both models are of high accuracy, correctly predicting *C. imicola* distribution in 93% and 87% of sites respectively, and predicted *C. imicola* presence in areas such as southern Iberia, northern Morocco, northern Algeria, northern Tunisia, Mallorca, Menorca, Sardinia, Sicily, Lazio, Tuscany and Calabria (in mainland Italy), the eastern and western edges of mainland Greece, Lesbos, Rhodes, western Turkey, Syria and Cyprus. In the absence of fine-scale surveillance data from the northern edge of the *C. imicola* range, these models also highlight countries or provinces where BT has recently occurred, but where *C. imicola* is predicted to be rare or absent. Such information supports the involvement of novel vector species of *Culicoides* in BTV transmission in many geographical locations during the current epidemic, e.g. in Croatia, Bosnia-Herzegovina, Kosovo, Serbia, Montenegro, Macedonia, Bulgaria and north-west Greece.

The predicted distribution of *C. imicola* from Tatem et al. (2003) corresponds particularly well with the new observed northern distribution limit of *C. imicola* (Figure 1, see Colour pages elsewhere in this book), including pixels near Barcelona, the southern coast of France in Alpes-Maritimes (J. Delacolle pers. comm., http://blue-tongue.cirad.fr/) and the northwest coast of Italy. Neither model predicts the recently observed presence of *C. imicola* in southern Switzerland (Ariane Cagienard pers. comm.), suggesting that the thermal requirements of this species in some marginal populations may differ from those further south or that the Swiss finding is based upon wind-borne vagrants. In addition, the effect of recent climatic changes on the expansion of *C. imicola* in Europe may not have been captured in these analyses since they were based only upon RS variables derived from NOAA imagery from 1982 to 1994. The training set of sites used by Tatem et al. (2003) were located only in Portugal whilst those used by Baylis et al. (2001) were spread across Iberia and in Morocco. However, the finer resolution of imagery available to Tatem et al. (2003) and the larger number of trap sites meant that this model was based upon a wider range of climatic or environmental conditions across both *C. imicola*-suitable and *C. imicola*-unsuitable areas. In turn, this model could be used to predict the potential distribution of *C. imicola* across a much larger proportion of pixels in the Mediterranean, i.e. in Figure 3b (see Colour pages elsewhere in this book) the grey, unpredictable areas are much less extensive than in Figure 3a (see Colour pages elsewhere in this book). This illustrates the importance of defining the relationship between vector abundance and climate on the basis of large vector surveillance data sets and up-to-date, fine-resolution imagery, extending across a wide range of environmental conditions.

What is the biological basis for the relationship between *C. imicola* abundance and NDVI?

The single most important remotely sensed predictor of *C. imicola* abundance in both models was the timing of the annual peak of vegetation abundance (i.e. NDVI), which is itself related to soil moisture levels. In Portugal, between 2000 and 2002, *C. imicola* occurred in high abundance where the NDVI peaked in mid-March but was rare or absent where the NDVI peaked in late April (Tatem et al. 2003). It is essential to consider the biological basis for these relationships with NDVI, i.e. what NDVI-correlated, environmental factor is determining vector distribution and abundance on the ground? The most robust ecological explanations are those founded on demographic processes (births and deaths), whose rates determine population

performance (Randolph 2000). Since *C. imicola* breeds in wet, organically rich soil and mud (Braverman, Galun and Ziv 1974; Braverman 1978), recruitment to the population in spring will depend on early availability of moist breeding habitat and temperature-dependent immature development and survival rates. In some areas, the number of completed generations in summer and thus the annual total of recruitment may be increased by such early availability of breeding sites. Vegetation abundance and NDVI in spring will similarly increase with early availability of moist soil conditions, hence the relationship between the timing of the annual peak of NDVI and *C. imicola* abundance.

RS climatic determinants of distribution differ between *Culicoides* vectors

However, a recent study of the distributions of both *C. imicola* and potential novel vector *Culicoides* across 268 sites in Sicily has revealed that the RS climatic determinants of distribution are species-specific, presumably due to the differing life-history requirements of different species of *Culicoides* (Purse et al. 2004). This is indicated by the different rank and order of climatic variables added to the discriminant, presence–absence model for each potential vector (models were developed from 1km by 1km NOAA data as in Tatem et al. (2003) and are shown in Table 1). The distributions of the *C. obsoletus* group and *C. newsteadi* were predicted by temperature variables (LST, MIR and TAIR). *C. obsoletus*, a northern Paleoarctic species on the southern margin of its range in Sicily, preferred warmer, less variable thermal regimes whilst *C. newsteadi,* a southern Paleoarctic species, was associated with high values of MIR and TAIR. The distributions of *C. pulicaris* and *C. imicola* were determined mainly by NDVI. *C. pulicaris,* a wet soil and bog breeding species, was associated with high, stable, levels of moisture (high, less variable NDVI) for optimal survival and development. These species-specific models produced strikingly different predicted distributions when extrapolated to unsampled environments in mainland Italy (Figure 4, see Colour pages elsewhere in this book), which, should they prove accurate, will have important implications for disease prediction, surveillance and control. For example, the predicted continuous presence of *C. pulicaris* along the Appenine Mountains, from north to south Italy, suggests BTV transmission may be possible in a large proportion of this region. Thus traditional seasonal transhumance between mountainous *C. imicola*-free areas and the coast may not be as safe as had been suggested by Conte et al. (2003) since it could provide a mechanism for hand-over of BTV between the traditonal vector (*C. imicola*) and the novel vector (*C. pulicaris*) (Mellor and Boorman 1995). *C. obsoletus*, another potential vector, is predicted to be widespread across Italy, including areas where *C. pulicaris* is predicted to be absent or rare, i.e. along the Adriatic coast and in Tuscany, and further increases the area of Italy at risk of BTV incursion. Consequently, predictive risk maps for BT derived entirely from the distribution of the main European vector, *C. imicola*, will omit extensive regions at risk of transmission via other vector species.

Table 1. The first four of ten variables, ranked in order of importance, which best allocated Sicilian trap sites to the observed *Culicoides* species presence–absence classes (Purse, unpublished data)

Rank	C. obsoletus	K	C. newsteadi	K	C. pulicaris	K	C. imicola	K
1	LST mean	0.24	MIR mean	0.26	NDVI mean	0.42	LST tri-ann. phase	0.04
2	LST variance	0.32	LST ann. amp.	0.30	NDVI tri-ann. amp.	0.47	MIR tri-ann. phase	0.26
3	MIR bi-ann. amp.	0.38	TAIR min.	0.37	NDVI variance	0.50	NDVI ann. phase	0.45
4	TAIR min.	0.41	LST min.	0.39	LST variance	0.48	NDVI mean	0.49

Key: K = Kappa value for the model at the step when the variable was added; LST = land surface temperature; NDVI = Normalized Difference Vegetation Index; MIR = Middle Infrared; TAIR= air temperature xm above ground; DEM = altitude derived from Digital Elevation Model; amp. = amplitude; ann. = annual; bi-ann. = bi=annual; tri-ann = tri-annual.

Local-scale determinants of *Culicoides* distribution

Models of *Culicoides* abundance incorporating RS correlates of temperature and moisture have successfully predicted the countries and regions at risk of BT. However, these models perform only moderately well when validated at a finer scale, for example at a farm level. For example, the model of Baylis et al. (2001) successfully predicted the *C. imicola* abundance category of only 51.4% of those sites in Portugal sampled after the training set, in 2000 and 2001 (Capela et al. 2003). The Sicilian model of *C. imicola* distribution (Purse et al. 2004), previous RS climate models (Baylis et al. 2001; Tatem et al. 2003) and a model based on interpolated weather-station data (Conte et al. 2003) all predict *C. imicola* to be much more widely distributed across Sicily than is observed to be. It is probable that in Sicily the restricted distribution of *C. imicola* is caused by environmental factors other than climatic ones – factors that may influence its breeding requirements. For example, a negative relationship has been found between *C. imicola* abundance and soil sandiness in South Africa (Baylis, Meiswinkel and Venter 1999). Similarly, Calistri and Caporale (2003) suggest that the porous, freely draining volcanic soils with a poor moisture content that predominate in Sicily are unsuitable as *C. imicola* breeding sites.

Being dependent on the rate of recruitment from breeding sites, *Culicoides* population sizes are highly heterogeneous at a local scale, and will vary in response to host and breeding-site factors in addition to climatic ones. This is likely to be reflected in significant variation in the risk of BTV transmission at a local scale. The size and quality of breeding sites may depend on soil type, slope of terrain, rate of dung removal from animal holdings and availability of water sources – irrigation pipes and channels, leaky taps etc. Host variables that may affect vector biting rates include the number and type of livestock and ease of access to them (e.g. Meiswinkel, Baylis and Labuschagne 2000). Thus, some factors that affect important parameters of the BTV transmission cycle (e.g. recruitment rate and biting rate) will not be measurable by RS, even using fine-resolution imagery (e.g. SPOT or MODIS). Although data collection can be expensive and time-consuming, it is imperative to determine the relative role of climate and farm-level factors at a local scale. Such local processes

may contribute to the distribution of BTV and *Culicoides* at broad scales, and, if unaccounted for, produce inaccuracies in broad-scale predictive models.

Future directions

Improvements to statistical models

Errors in BT risk maps based on statistical models of vector abundance may arise for several reasons, one of which is that the input data may be wrong or inaccurate. Given that adult vector *Culicoides* activity and trap efficiency can depend on daily climatic conditions, the estimate of vector abundance per site should be based on several catches made during the peak of *Culicoides* abundance (Baylis and Rawlings 1998). Also, given the species-specific climatic requirements of different *Culicoides* vectors, the distribution of each potential vector species should be modelled individually. In addition, for extrapolation across wide geographic areas and accurate determination of the relationship between vector abundance and climate, the model training set should include observations across a wide range of environmental and climatic conditions, preferably across the entire geographic range of the vector. The use of finer-scale RS data such as that derived from MODIS imagery (0.5 km) will provide a more accurate assessment of climatic factors. The statistical models reviewed here and the wide range in vector seasonal incidence between countries (Mellor, Boorman and Baylis 2000) indicate that the climatic requirements of *C. imicola* and other vectors may vary across their ranges. When constructing continental-scale models, regional heterogeneity in eco-climatic conditions and the response of *Culicoides* vectors to them can be accounted for using ecozonation (Hendrickx et al. 1999). This involves the division of pixels into clusters of environmental similarity prior to analysis and the development of a separate model for each eco-zone.

Why are biological process-based models of BT risk required and how can they be developed?

Rogers and Randolph (2003) pointed out that risk maps based on statistical models often indicate larger areas 'at risk' than are known to be affected by the disease at present, because a vector or disease will not occupy all 'suitable' habitats. Similarly, BTV does not occur across the entire distribution of *C. imicola, C. obsoletus* and *C. pulicaris* in the Mediterranean Basin and may not depend solely on the abundance of these vectors but also on spatio-temporal variations in other factors. Firstly, BTV transmission is seasonal being related to the timing of peak abundance of *Culicoides* vectors in different areas (Mellor, Boorman and Baylis 2000). There is compelling evidence that vector competence for BTV varies widely between different vector species of *Culicoides* and even between populations of the same species, for example, for *C. obsoletus* in Europe (Simon Carpenter, unpublished data). This may be due either to genetic differences in susceptibility to infection between populations (Tabachnick 1991) or to differences in the climatic regimes to which populations are subjected (affecting infection rates, rates of virogenesis or the efficacy of infection barriers) or to both (Mellor, Boorman and Baylis 2000). Additionally, whether BTV titres develop to transmissible levels in the vertebrate host and the vector depends also on the strain or type of BTV circulating. Indeed, most ruminant hosts of BTV do not develop clinical signs of infection, and so, generally speaking, evidence of BT in a vertebrate population is a very poor indicator of the level of BTV transmission. Where a species of *Culicoides* is in the process of expanding its range, its populations may

not permanently occupy all suitable habitats, due to isolation from source populations. For example, in New South Wales, Australia, near the southern range limit of the BTV vector *C. brevitarsis*, colonization of marginal sites occurs seasonally by passive wind dispersal when climatic conditions are suitable for population multiplication, but population establishment only occurs if conditions also facilitate survival over winter. Bishop, Barchia and Spohr (2000) found that between-population movements of *C. brevitarsis* over 8 years depended on wind direction, wind speeds (allowing adult activity) and temperature during vector movements.

Given these considerations, only biological-process-based models of *Culicoides* population dynamics and BTV transmission dynamics will permit integration of predictions between spatial scales (local and continental) and time scales (ecological and evolutionary). Given the high-temporal resolution of RS data, the same data that are used to describe the patterns of *Culicoides* or BTV abundance can be correlated with key transmission-cycle parameters in intensive studies, and used to generate predictions extensively (Rogers and Randolph 2003). Considering the vector and virus surveillance data available from the current BT epidemic, there is potential to model seasonal rates of *Culicoides* population change in relation to RS climate variables, as has already been done successfully for ticks and tsetse flies (Rogers 2000; Randolph 2000). This would enable prediction of the geographical and annual variation in the timing of spring appearance and winter disappearance of adult vectors and BTV, and the location of any seasonal dispersal from overwintering foci. The distribution and timing of new outbreaks could be examined in affected countries in the first year of the current epidemic, i.e. when clinical signs are severe and most BTV transmission is likely to be manifested as outbreaks. Rates of movement of BTV in space and time could then be correlated with wind speed and direction data and RS climate data to determine the factors affecting the probability of dispersal of infected midges during an epidemic. Collection of appropriate data on other parameters of the transmission cycle, especially biting rates, via the design of intensive field experiments should be considered a priority.

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