



The role of wildlife in bluetongue virus maintenance in Europe: Lessons learned after the natural infection in Spain



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ABSTRACT

Bluetongue (BT) is a re-emergent vector-borne viral disease of domestic and wild ruminants caused by bluetongue virus (BTV), a member of the genus *Orbivirus*. A complex multi-host, multi-vector and multi-pathogen (26 serotypes) transmission and maintenance network has recently emerged in Europe, and wild ruminants are regarded as an important node in this network. This review analyses the reservoir role of wild ruminants in Europe, identifying gaps in knowledge and proposing actions. Wild ruminant species are indicators of BTV circulation. Excepting the mouflon (*Ovis aries musimon*), European wild ungulates do not develop clinical disease. Diagnostic techniques used in wildlife do not differ from those used in domestic ruminants provided they are validated. Demographic, behavioural and physiological traits of wild hosts modulate their relationship with BTV vectors and with the virus itself. While BTV has been eradicated from central and northern Europe, it is still circulating in the Mediterranean Basin. We propose that currently two BTV cycles coexist in certain regions of the Mediterranean Basin, a wild one largely driven by deer of the subfamily *Cervinae* and a domestic one. These are probably linked through shared *Culicoides* vectors of several species. We suggest that wildlife might be contributing to this situation through vector maintenance and virus maintenance. Additionally, differences in temperature and other environmental factors add complexity to the Mediterranean habitats as compared to central and northern European ones. Intervention options in wildlife populations are limited. There is a need to know the role of wildlife in maintaining *Culicoides* populations, and to know which *Culicoides* species mediate the wildlife–livestock–BTV transmission events. There is also a clear need to study more in depth the links between *Cervinae* deer densities, environmental factors and BTV maintenance. Regarding disease control, we suggest that research efforts should be focused on wildlife population and wildlife disease monitoring.

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1. Introduction

Bluetongue (BT) is a vector-borne viral disease of ruminants that causes high socio-economic and sanitary consequences. Bluetongue virus (BTV) is a member of the genus *Orbivirus* of the family *Reoviridae* (Verwoerd and Erasmus, 2004) with 26 serotypes (Hofmann et al., 2008; Maan et al., 2011a,b, 2012; Schwartz-Cornil et al., 2008). Bluetongue causes high morbidity and mortality rates in naïve sheep and some wild ruminants, e.g. pronghorn antelope *Antilocapra americana*, bighorn sheep *Ovis canadensis*, American bison *Bison bison*, European bison *Bison bonasus* and mouflon *Ovis*

aries musimon, while other ruminant species – e.g. cattle and *Cervinae* deer species – usually exhibit subclinical disease (López-Olvera et al., 2010; Maclachlan et al., 2009; Mellor, 2012; Murray and Trainer, 1970; Verwoerd and Erasmus, 2004). Transmission of BTV is mainly mediated by several species of biting midges belonging to the *Culicoides* (Diptera: *Ceratopogonidae*) genus (du Toit, 1944; Mellor and Wittmann, 2002), although transmission by other vectors (Bouwknegt et al., 2010; Gerdes, 2004; Luedke et al., 1965), through bites or skin wounds (López-Olvera et al., 2010) and mother-to-foetus transmission (De Clercq et al., 2008) are also possible.

During the second half of the 20th century, BTV distribution changed dramatically and expanded northwards into Europe, where serotypes 1, 2, 4, 6, 8, 9, 11, 16 and 25 have been reported (Enserink, 2008; Eschbaumer et al., 2010; Maclachlan and Guthrie, 2010; Maclachlan and Mayo, 2013; Purse et al., 2005; Rodríguez-Sánchez et al., 2008; Saegerman et al., 2008; Toussaint et al.,

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2006). Outbreaks of BTV1, 4 and 8 in Europe in the beginning of the 21st century allowed the detection of infected livestock and wildlife in countries that had never reported BT (see Falconi et al., 2011). European countries affected by the different BTV serotypes in the 2000s implemented strict BT control schemes and therefore several European countries managed to eradicate BT from livestock and currently BT in livestock is limited to the Mediterranean Basin (http://ec.europa.eu/food/animal/diseases/controlmeasures/bluetongue_en.htm).

The wide range of wild ruminants susceptible to BTV infection, the changes in wildlife population densities (e.g. Ripple and Beschta, 2012), the apparently long-lasting viraemia experienced by red deer infected by different BTV serotypes (López-Olivera et al., 2010), and the ongoing BT outbreaks in livestock in Mediterranean countries (<http://www.rasve.es>) have increased the awareness about the role of wildlife as BTV reservoirs in Europe (Falconi et al., 2011). Bluetongue virus may have nowadays established endemically in the Mediterranean Basin and epidemiological studies in wildlife from Spain (García-Bocanegra et al., 2011; Lorca-Oró et al., unpublished) point to the current existence of interconnected domestic and wild cycles that could account for the maintenance of BTV. Therefore, the aim of this review was to analyze the implication of wild ruminants in the complex multi-vector and multi-host BTV epidemiology in Europe, with particular emphasis in Spain, as well as identifying gaps in knowledge on the ecology of BTV and the risks of wildlife-mediated re-emergence of BT in livestock. Determining the potential reservoir role of wildlife and its consequences for BT eradication is essential to the implementation of new effective disease control strategies and the improvement of current surveillance schemes.

2. Factors modulating bluetongue virus infection in wildlife

The complex epidemiology of BTV – which may be influenced by vector and host community composition, density and distribution, climatic conditions and virus traits – causes that wild and domestic hosts may play different roles depending on particular regional features. Demographic, behavioural, genetic, physiological and pathological traits of wild hosts may modulate their relationship with BTV vectors and with the virus itself. This section summarizes ecological traits of wild hosts, vectors and pathogen modulating exposure of wild hosts to BTV vectors and the outcome of BTV infection that could be of relevance for understanding the ecology of BTV.

2.1. Host population factors

In Europe, the red deer (*Cervus elaphus*) is considered the most relevant wild ungulate host for BTV, among other factors (e.g. geographic distribution and BTV infection patterns) due to its high abundance (Falconi et al., 2011; Ruiz-Fons et al., 2008). The current demography of red deer in Europe shows an increasing distribution and density trend (Acevedo et al., 2011; Apollonio et al., 2010; Gortázar et al., 2012, 2000; Mattioli et al., 2011), in part due to an insufficient hunting harvest of deer populations in Europe (Milner et al., 2011). Red deer densities may overtake livestock densities in some European regions, reaching up to 70 deer per square kilometre (Acevedo et al., 2008). These high densities may offer BTV vectors an abundant and widespread food resource (Bartsch et al., 2009) and therefore may enable red deer to play a relevant role in BTV vectors' population dynamics (as already evidenced for ticks; e.g. Ruiz-Fons and Gilbert, 2010) and in the maintenance of BTV in a wild cycle (Falconi et al., 2012; García-Bocanegra et al., 2011; Lorca-Oró et al., unpublished). Bluetongue virus may benefit from the high

availability of susceptible hosts in time and space in dense continuously distributed red deer populations, therefore increasing its chances to persist. Indeed, areas with higher red deer density have been identified to display higher BTV prevalence in Spain (García et al., 2009). The roe deer (*Capreolus capreolus*) – belonging to the subfamily *Capreolinae* – is abundant in certain European regions and also displays an increasing distribution range and demographic trend (Acevedo et al., 2005; Apollonio et al., 2010) that could have implications in BTV epidemiology. However, either BTV vectors do not feed frequently on roe deer or this ungulate has a low susceptibility to BTV infection in comparison to red deer (according to postulates from Rossi et al., 2014) because BTV seroprevalence in roe deer populations from areas with high BTV prevalence in livestock are consistently low (Corbière et al., 2012; Linden et al., 2010; Rossi et al., 2014; Ruiz-Fons et al., 2008). No experimental infection study has been undertaken in roe deer, so particular traits of the BTV–roe deer relationship are completely unknown. In other vector–pathogen systems (e.g. LIV in the Scottish Highlands; see Gilbert et al., 2001), hosts that are non-target for the pathogen (mountain hares *Lepus timidus* and red and roe deer in LIV example) but that are relevant hosts for the vectors (the tick *Ixodes ricinus* in this example), may have a highly relevant role in pathogen maintenance when they coexist with hosts that efficiently replicate the pathogen (red grouse *Lagopus lagopus scoticus* in the LIV example). Therefore, predicting any role of roe deer in the epidemiology of BTV even at local/regional scales is currently difficult. The same could apply to other BTV hosts such as fallow deer, mouflon or Spanish ibex (*Capra pyrenaica*).

Host aggregation at particular sites has been consistently identified as a highly relevant behavioural pattern linked to increased transmission of infectious diseases (Gortázar et al., 2006). Aggregation may occur naturally due to seasonal variation in availability of food or water resources (e.g. seasonal acorn production by oaks) or as a consequence of particular traits of the host life history (e.g. mating), but it may also come from inadequate management practices (Gortázar et al., 2006). The red deer is a social gregarious species that may use indistinctly forested and open habitats (Clutton-Brock et al., 1982; Ruiz-Fons and Gilbert, 2010). Males and females form separate groups outside the rutting season in late summer–early autumn, when both sexes mix for mating (Acevedo et al., 2008). During the rutting season – which coincides with the main annual activity period of many BTV vectors – large groups of red deer tend to aggregate in open habitats, perhaps favouring interaction with *Culicoides* midges and increasing exposure to BTV and transmission of the infection. However, seasonal variations in the interaction between deer and BTV vectors and the effect of this behaviour on BTV transmission are currently unknown. In contrast to red deer and to fallow deer (*Dama dama*), also belonging to the subfamily *Cervinae*, the roe deer does not usually form large social groups (Chapman et al., 1993), which could perhaps be in part related to the lower BTV seroprevalences reported in the literature.

Host community composition may influence BTV dynamics by offering both BTV vectors and the virus a complex net of hosts, but this has been not well explored for the moment. Particular interaction features of any host with BTV vectors in the community would modulate, together with climate and other environmental factors, the abundance and distribution of BTV vectors (see Acevedo et al., 2010). At the same time, the variable interaction among different ruminant species and BTV could account for either the maintenance of the virus through boosting replication or its clearance through dilution effects if hosts targeting the major part of infected vector bites are unable to replicate BTV at the threshold rate required for maintenance. Bluetongue virus prevalence in wildlife correlated with BTV distribution in livestock; García-Bocanegra et al. (2011), García et al. (2009), Lorca-Oró et al. (2011), Rossi et al. (2014) and Ruiz-Fons et al. (2008) established higher BTV prevalence in wildlife

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