Review article

Neglected vector-borne zoonoses in Europe: Into the wild

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ABSTRACT

Wild vertebrates are involved in the transmission cycles of numerous pathogens. Additionally, they can affect the abundance of arthropod vectors. Urbanization, landscape and climate changes, and the adaptation of vectors and wildlife to human habitats represent complex and evolving scenarios, which affect the interface of vector, wildlife and human populations, frequently with a consequent increase in zoonotic risk. While considerable attention has focused on these interrelations with regard to certain major vector-borne pathogens such as *Borrelia burgdorferi* s.l. and tick-borne encephalitis virus, information regarding many other zoonotic pathogens is more dispersed. In this review, we discuss the possible role of wildlife in the maintenance and spread of some of these neglected zoonoses in Europe. We present case studies on the role of rodents in the cycles of *Bartonella* spp., of wild ungulates in the cycle of *Babesia* spp., and of various wildlife species in the life cycle of *Leishmania infantum*, *Anaplasma phagocytophilum* and *Rickettsia* spp.

These examples highlight the usefulness of surveillance strategies focused on neglected zoonotic agents in wildlife as a source of valuable information for health professionals, nature managers and (local) decision-makers. These benefits could be further enhanced by increased collaboration between researchers and stakeholders across Europe and a more harmonised and coordinated approach for data collection.

1. Introduction

Wildlife has long been recognized to have a major role in the transmission and maintenance of zoonotic agents, as most emerging infectious diseases are of wildlife origin (Jones et al., 2008). However, knowledge of the pathogens that naturally occur in wild animals and their potential to spread to humans and domestic animals is still scarce (Thompson, 2013). This is particularly true for microorganisms transmitted by vectors, which have multi-component transmission cycles affected by the ecology as well as the dynamics and life cycles of both vectors and pathogens (Hollingsworth et al., 2015). Such transmission systems often include diverse wild vertebrate hosts, which can serve as reservoirs or amplification hosts for pathogens, as well as a food source for the hematophagous arthropods themselves.

Wildlife disease monitoring for emerging as well as for certain autochthonous, but neglected vector-borne diseases (VBD), is an essential component of surveillance systems, not only for public health, but also for veterinary and ecological health (Evensen, 2008; Braks et al., 2014). While the need for such wildlife disease monitoring programmes is internationally recognised (http://www.glews.net) as the emergence of infectious diseases of wildlife origin is frequently of global concern (Jones et al., 2008; Keesing et al., 2010; Olival et al., 2017), their surveillance, control and prevention chiefly require local actions. Work on the ground and allocation of resources is usually focused on local priorities and interests and subject to short-term planning. Any potential international surveillance programmes are further hampered by

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inconsistencies in case acquisition (capture and handling of animals), sampling strategies, diagnostics and data interpretation, and inadequate wildlife surveillance infrastructures (Stallknecht, 2007). Here we present the current state of knowledge of the role of wildlife in the emergence and ecology of a number of neglected vector-borne zoonoses in Europe. We hope that this critical review will help to promote future international collaborations focused on the detection, prevention and control of VBD in wildlife.

2. Wildlife population dynamics and their effects on vector abundance

The restoration of natural habitats under the European Union programme for protected areas (Natura 2000; http://ec.europa.eu/environment/nature/), aimed at establishing a connected network of natural habitats, as well as the legal protection and reintroduction of many wildlife species, and certain land use changes (Milner et al., 2006), are expected not only to benefit various wildlife species, but may also boost vector populations and allow them to spread and establish in new areas.

A much-cited example of how wildlife populations affect the abundance of vectors, is that of deer and *Ixodes ricinus* ticks. The last couple of decades have seen a dramatic increase in the abundance and geographic distribution of various deer species, particularly roe, red and fallow deer (Milner et al., 2006; Burbaitė and Csányi, 2009,2010). While immature stages may feed on a variety of wildlife hosts, including small rodents, insectivores and birds (Hofmeester et al., 2016), several studies have documented high infestation levels of deer with all developmental stages of ticks (Kiffner et al., 2010; Qviller et al., 2013). Deer species are thus considered the main determinants of tick abundance (Mihalca and Sándor, 2013). In fact, some investigations have reported a direct correlation between deer and tick numbers (Gilbert et al., 2012; Qviller et al., 2013). Others have found that once a deer population has reached a threshold level, the number of deer does not significantly affect tick density, indicating that spread rather than abundance is the main driver for boosting tick populations (Hofmeester et al., 2017). It is important, however, to differentiate between the overall abundance of ticks in a habitat and the expected number of ticks questing at any point in time. According to Dobson and Randolph (2011), the former is boosted by greater host abundance (particularly in areas recently colonized by deer), while the latter is expected to decline in areas with high deer densities, as unfed ticks quickly find a new host and spend less time questing. It is also necessary to stress that the specific level of tick infestation on hosts is dependent on the host's feeding and roaming behaviour. For example, moose (*Alces alces*), which mainly feed from branches on trees, harbour fewer ticks on their heads and ears than red and roe deer (Handeland et al., 2013); the latter two species are mainly ground feeders with ample opportunity to encounter all life stages of *I. ricinus*. In addition, deer represent important vehicles for tick distribution over long distances (Vor et al., 2010).

For other vectors populations, the effects of wildlife host dynamics have been less intensively studied. For example, sand flies are vectors of *Leishmania infantum*, phleboviruses and other pathogens in southern Europe, but there is a limited understanding of their spatial distribution of and relationship with wild host abundance. In particular, information is lacking on sand fly breeding sites, and trapping is mainly aimed at the adult stages (Feliciangeli, 2004). Adult female sand flies, which are the only developmental stage able to transmit pathogens as they require a blood meal to develop the eggs, may feed on a wide variety of wild mammal and bird species (Bongiorno et al., 2003; Millán et al., 2014). In rural areas, sand flies congregate in buildings housing domestic animals, such as sheep sheds, bird houses and dog kennels (Dantas-Torres et al., 2014; Risueño et al., 2017). However, they are also found in natural and abandoned habitats such as rabbit burrows, caves and old ruined buildings, where they rely on wildlife for food. The ability of wildlife to increase and sustain enormous sand fly

populations is demonstrated in the ongoing outbreak of human leishmaniosis in Fuenlabrada, Madrid, which is associated with an explosion in the population of hares (*Lepus granatensis*) in green areas integrated into a new housing development built on agricultural land (Molina et al., 2012; Carrillo et al., 2013).

While there are several studies on the role of wildlife on flea dynamics in North America, mostly focused on the ecology of the plague, such research is scarce in Europe. One survey reported that 70% of all flea species are found on rodents (Medvedev, 2002). For example, fleas in the Palaearctic region preferentially parasitize voles, gerbils and hamsters (Medvedev and Krasnov, 2006), and to a lesser extent other wildlife hosts such as hares and carnivores (mainly foxes) (Foley et al., 2017). Moreover, flea abundance positively correlates with host density in many flea-host associations (reviewed by Krasnov, 2008). On the other hand, more diverse host communities could lead to a decrease in flea prevalence. Krasnov (2008) divided fleas into three main categories: (i) fleas of poultry, livestock and pets; (ii) fleas of commensal birds and mammals (sparrows, pigeons, house martins, rats and mice); and (iii) fleas of wild birds and mammals. While the first two groupings show a relatively uniform flea species composition, species in the third category have a much more diverse pattern, depending on the specific wildlife composition in the region and its flea fauna.

All of these examples show that a rise in the number of certain wildlife hosts can increase the abundance and distribution of vectors. In some cases this situation results directly in an increase in VBD, as shown in the example of sand flies and hares in Spain. Many wildlife host/vector/pathogen relationships, however, are more complex, particularly if the wildlife host is not a competent pathogen reservoir and the vector is a generalist. In this case, a boost in wildlife host population can have a 'dilution' effect, i.e. it can reduce the pathogen prevalence in the vectors (Dudek, 2014). It has also been postulated that reduced biodiversity may favour transmission of vector-borne pathogens because many severely degraded environments of low biodiversity still abound in rodents (Dudek, 2014), many of which are competent reservoirs for a multitude of disease agents. Consequently, the declining biodiversity currently experienced in many habitats all over the world may be advantageous to certain pathogens and their vectors, potentially increasing the risk of pathogen exposure (Daszak et al., 2007). However, it should also be borne in mind that there are natural habitats of low biodiversity, such as bogland or tundra, which do not necessarily represent high risk VBD areas. Care must be taken therefore when extrapolating from the wildlife transmission dynamics of one pathogen to another.

3. Urbanization of wildlife and vectors

Green spaces and corridors in cities and (sub)urban areas not only improve human well-being (Hansen and Pauleit, 2014) but can also help to mitigate the negative effects of heat waves, air pollution, flooding and possible other health risks (IPCC, 2013). In addition, they can contribute to conservation strategies for wildlife and biodiversity. For example, forty-eight different mammal species, from bats to wild boars, have been recorded in Budapest (Tóth-Ronkay et al., 2015). Some mammal species, such as hedgehogs and squirrels, can reach higher densities in (sub)urban habitats than rural environments (Reeve, 1994; Tóth-Ronkay et al., 2015).

On the other hand, the trend in increasing urban green spaces and spatial expansion of urbanized areas into agricultural and nature habitats also increases the dispersal and abundance of vectors into urban areas and their contact with humans (Maetzel et al., 2005; Gassner et al., 2016; Paul et al., 2016; Vourc'h et al., 2016). As a matter of fact, *I. ricinus* (and to a lesser extent other tick species) are found in city parks, urban forests, private gardens and other green spaces in and around cities across Europe (Schorn et al., 2011; Buczek et al., 2014; Hornok et al., 2014; Mancini et al., 2014; Venclíková et al., 2014; Nelson et al., 2015; Starostzik, 2015; Szekeres et al., 2016). Although