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The Daubenton's Bat (*Myotis daubentonii*, Kuhl, 1817) and Its Role as a Reservoir for Europe Bat Lyssavirus Type-2

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Abstract

The Daubenton's bat is found on a geographical cline from Western Europe, including the British Isles, across Central Europe and Asia, and as far east as Japan. The species is insectivorous and uses echolocation to detect and catch prey, with the distinct behaviour of hunting over water bodies such as lakes and rivers. The other distinctive feature of Daubenton's bats is that they appear to be the principal species of bat that harbours European bat lyssavirus type-2 (EBLV-2). The lyssaviruses, a group of viruses that includes the rabies lyssavirus, are generally associated with bats. Many are zoonotic with EBLV-2 being responsible for two human deaths. Reports of EBLV-2 in Daubenton's bats have been made from countries across Europe although the majority have been from England. This chapter will consider the biology of the Daubenton's bat, the association of EBLV-2 with this particular species and discuss the interaction between bat and virus.

Keywords: Daubenton's bat, European bat lyssavirus type-2, Europe, virus transmission

1. Introduction

Europe has 45 bat species considered indigenous to the continent (<http://www.batlife-europe.info/about-batlife-europe/european-bats/>, accessed 8 November 2017). This number is being constantly revised as new and cryptic species are identified. All are small- to medium-sized insectivorous bat species although colonies of the Egyptian fruit bat (*Rousettus aegyptiacus*) are known to colonise islands of the Mediterranean Sea [1]. The role of bats as a source of zoonotic viruses has been recognised over the past three decades with the emergence of viruses such as Hendra virus, Nipah virus and SARS-coronavirus [2]. However, European bats are nocturnal

so contact with humans is minimal making them both an elusive species to study and a rare source of zoonotic pathogens [3]. Key amongst these is the European bat lyssaviruses (EBLVs), members of the genus *Lyssavirus*, family *Rhabdoviridae*. The type species of the genus is rabies lyssavirus (RABV), the virus responsible for virtually all cases of rabies in the world. The genus contains a growing number of viruses, the majority associated with bat species [4] (Table 1).

All can cause encephalitis in mouse models of infection and it is suspected that all are capable of causing rabies in humans. Of these, five have been reported from Europe. European bat lyssavirus type-1 (EBLV-1), EBLV-2, West Caucasian bat lyssavirus (WCBV), Bokeloh bat lyssavirus (BBLV) and Lleida bat lyssavirus (LLEBV). Despite the close association with bats, the first recognised isolation of EBLV-2 was derived from a human case of rabies. The patient was a bat ecologist working in Finland when he developed rabies [5]. Shortly afterward, a related virus was isolated from the brain of a pond bat (*Myotis dasycneme*). Since then there has been one further case of EBLV-2 infection in a human [6] and continual reports of the virus infection of Daubenton's bats (*Myotis daubentonii*).

The ability to discriminate between different lyssaviruses was only achieved with the advent of monoclonal antibody panels that show different binding patterns to particular viruses. This first alerted researchers that the viruses present in European bats were distinct from RABV found in North American bats [7]. Antigenic typing has now been superseded by genetic

Virus species	Bat reservoir	Human infection
Rabies lyssavirus	Numerous insectivorous, frugivorous and hematophagous bat species	Yes
Lagos bat lyssavirus	Various species including <i>Eidolon helvum</i> and <i>Rousettus aegyptiacus</i>	No
Mokola lyssavirus	Not known	Yes
Duvenhage lyssavirus	<i>Nycteris thebaica</i>	Yes
European bat lyssavirus type-1	<i>Eptesicus serotinus</i>	Yes
European bat lyssavirus type-2	<i>Myotis daubentonii</i>	Yes
Bokeloh bat lyssavirus	<i>Myotis nattereri</i>	No
Aravan lyssavirus	<i>Myotis blythii</i>	No
Irkut lyssavirus	<i>Murina leucogaster</i>	Yes
Khujand lyssavirus	<i>Myotis mystacinus</i>	No
West Caucasian bat lyssavirus	<i>Miniopterus schreibersii</i>	No
Australian bat lyssavirus	Various species including <i>Pteropus alecto</i> and <i>Saccolaimus flaviventris</i>	Yes
Shimoni bat lyssavirus	<i>Hipposideros commersoni</i>	No
Gannoruwa bat lyssavirus	<i>Pteropus medius</i>	No
Taiwan bat lyssavirus	<i>Pipistrellus abramus</i>	No
Lleida bat Lyssavirus	<i>Miniopterus schreibersii</i>	No

Table 1. Known lyssaviruses and their association with particular bat species.

discrimination based on genome sequencing [8] and the first complete genome sequence for EBLV-2 was reported in 2007 [9]. Of the other lyssaviruses detected in European bats, WCBV and LLEBV represent single isolations of virus so little is known about the epidemiology of these viruses. The most commonly encountered lyssavirus in European bats is EBLV-1 and almost all detections of this virus are from serotine bats (*Eptesicus serotinus*) [10]. A more recent addition is Bokeloh bat lyssavirus that is predominantly associated with Natterers bats (*Myotis nattereri*) from Germany and France [11].

The first report of EBLV-2 in the UK resulted from the discovery of an adult female bat in the cellar of a public house in Newhaven, Sussex in 1996 [12]. Virus was isolated from brain tissue removed from the bat. Subsequently, reverse transcription polymerase chain reaction (RT-PCR) and sequencing confirmed the virus species by comparison with sequences derived from lyssaviruses known at the time. It was speculated that the bat may have flown across the English Channel but subsequent isolations of virus from other locations in England suggested that the virus was actually endemic long before cases were detected [13]. All detections of EBLV-2 in bats in the UK (isolation of virus or detection of virus in a salivary swab) have been from Daubenton's bats. This pattern has been reflected across Europe with occasional bat-associated cases reported in The Netherlands [14], Germany [15], Switzerland [16], Finland [17] and Norway [18].

The following sections discuss the biology and ecology of the Daubenton's bat, research on the relationship between EBLV-2 and its reservoir host and a discussion on the transmission of the virus between conspecifics that might explain the persistence of this virus in European bat populations.

2. The Daubenton's bat

The Daubenton's bat was first described by the German naturalist and zoologist, Heinrich Kuhl [1797–1821] in his monograph, *Die deutschen Fledermäuse*, published in 1817. The name selected for the species was derived from the French naturalist Louis Jean-Marie Daubenton [1716–1800]. Kuhl went on to take part in an expedition to Java to study the islands fauna but developed a fever that subsequently killed him. He was buried in the Botanical Gardens of Bogor to the south of Jakarta where his gravestone can still be located.

Daubenton's bats are considered a medium-sized insectivorous bat with an adult wingspan of up to 27.5 cm and a body length up to 5.5 cm. Adults weigh between 7 and 12 g and have a reddish brown pelt. The common name of the species is the 'water bat' due to its feeding habit. This involves flying low across the surface of water bodies such as lakes, rivers and canals, feeding on a range of water-associated flies. These include chironomid midges, caddisflies and mayflies. Daubenton's bats echolocate in a call range between 35 and 85 kHz, and generally feed within 6 km of their roost. Roost sites range from natural sites such as tree holes to man-made structures, including houses [19]. During the summer, there is a degree of segregation between maternity colonies, dominated by a single male and bachelor roosts [20]. Hibernation takes place over the winter months, usually in caves, tunnels and mines.

Daubenton's bats are found from Ireland in the west, across Europe, Asia and the islands that form the Japanese archipelago. In Europe, the species can be found in the Iberian Peninsula and north of the Alps. Populations are also reported as far north as southern Sweden and Finland, almost as far as the Arctic Circle. Mating occurs in late autumn and is preceded by a behaviour termed swarming where bats congregate and fly near the entrance to a hibernation site. Daubenton's bats are not the only species that demonstrate this behaviour but they are commonly found early in the swarming season. In Britain, this is typically between August and October [21]. The behaviour is thought to be a form of lekking due to the male bias observed during trapping at swarming sites and may proceed mating.

Investigation into the population structure of the Daubenton's bat, based on genetic data, between UK bats and those on the European mainland suggests that there is regular movement of bats across the English Channel [22]. This suggests panmixia between the two populations with no barriers to the spread of genetic haplotypes, and in theory to the transmission of EBLV-2. A similar situation has been proposed for the straw-coloured fruit bat, *Eidolon helvum*, and its association with certain zoonotic viruses across its range in Africa [23].

The first report of EBLV-2 in a Daubenton's bat occurred in Denmark in 1986 [24, 25]. The virus from this account was not isolated. Subsequently, EBLV-2 was isolated from pond bats from the Netherlands in 1987 [8] and Daubenton's bats from Switzerland in 1992 [16]. Descriptions of initial encounters with EBLV-2 infected bats typically report grounding, particularly near rivers or canals, although occasionally bats are reported to fly in daylight. Live bats vocalise, show signs of distress and can bite aggressively although this may in part be a result of distress caused by captivity. Infected bats often appear emaciated and dehydrated despite attempts at rehabilitation [26].

3. European bat lyssavirus type-2 and its relationship with the Daubenton's bat

Phylogenetic analysis on early isolations of EBLV-2 confirmed that the virus was a lyssavirus related to rabies lyssavirus [27]. However, many questions remained about the transmission of the virus between bats and the pathogenesis in its reservoir host. Early reports indicated that infected bats exhibited signs suggestive of rabies including aggression, inability to fly and vocalisation. One of the earliest questions was the distribution of virus in an infected bat. Rabies lyssavirus is neurotropic, meaning that it targets neurons within the peripheral and central nervous system. The application of sensitive RT-PCR and virus isolation detected virus predominantly in the brain but also in other organs of an EBLV-2 infected Daubenton's bat [13]. However, quantitative RT-PCR demonstrated that the virus was most abundant in the brain and spinal cord of the bat [28] in a pattern like that observed for RABV. Virus detected in other tissue was likely to be derived from innervating nerves. The presence of virus in salivary glands and tongue suggested that this was likely the point of virus egress and that biting was the means of transmission between bats. A similar conclusion was made for the transmission of RABV in North American bats [29]. Experiments in a mouse model attempting to

demonstrate aerosol transmission were unsuccessful for EBLV-2 [30]. However, once in the brain, EBLV-2 shows similar characteristics to rabies lyssavirus, infecting neurons, stimulating innate immune responses [31] and triggering signs of viral encephalitis [32, 33]. In order to confirm some of these observations, a series of experimental studies were established to investigate the methods of EBLV transmission in bats and characterised EBLV-induced disease in the natural host [34–36]. These studies demonstrated that subcutaneous inoculation was the most efficient means of infecting insectivorous bats with EBLVs. Clinical signs exhibited by infected bats ranged from sudden death with no apparent disease to a spectrum including weight loss and rapid progression to paralysis [35].

Field studies in the UK in response to the human case of EBLV-2 in 2002 provided evidence of virus circulation within the Scottish Daubenton's bat population [37]. Seroprevalence levels ranging from 0.05 to 3.8% were detected in colonies from across the country although oral swabs taken coincident with blood samples were all negative for EBLV-2. Subsequent surveillance in Daubenton's bat colonies in England found similar seroprevalence levels [38] suggesting that the virus affects bat populations across the country. This is supported by population genetic analysis of English Daubenton's bats [22] and the detection of EBLV-2 infected bats from locations across England, Scotland and Wales [39]. One location where EBLV-2 infected bats have been repeatedly detected is Stokesay Castle in Shropshire [40]. The tower of the castle (**Figure 1**) is known to host a summer maternity roost and there have been three bats found in the castle that have been infected with EBLV-2. Another infected bat was submitted from the nearby location of Newtown. A further practical question, bearing in mind the zoonotic potential of EBLV-2, was whether current vaccines developed against rabies lyssavirus would be protective against exposure following a bat bite. Cross-neutralisation and cross-protection studies in mice indicated that rabies vaccines would be protective [41].



Figure 1. A photograph of Stokesay Castle where EBLV-2 infected bats have been repeatedly detected. The site offers a number of features attractive to bats including the main tower where bats were roosting, a large pond in the foreground that could provide a feeding site and extensive woodland that would provide alternative roosts.

This lead to the public health recommendation that individuals that are in close contact with bats should be vaccinated, in addition to simple measures such as wearing gloves whilst handling bats. Furthermore, post-exposure vaccination could be offered to those that were bitten or had inadvertently been in contact with bats. This could also be extended to domestic animals, particularly cats that catch bats.

4. Discussion

All evidence to date suggests that the Daubenton’s bat is the wildlife reservoir for EBLV-2. However, many questions remain concerning the persistence of EBLV-2 within the Daubenton’s bat population in Europe. The virus is only detected sporadically. In the UK, this equates to a single isolation a year but this meagre number is presumably the tip of the iceberg of what must be constant virus transmission events occurring whilst the bats are active. With the exception of two bats submitted in May, the majority of submissions in the UK occur in late summer and early autumn (**Figure 2**). The incubation period, the time from exposure to the development of disease or death, for lyssaviruses in bats is highly variable. By their nature, this cannot be established in wildlife populations as the timing of the transmission event is not known. In a unique case, EBLV-2 was detected in a bat that had been held in captivity for 9 months [42]. Captive studies in Daubenton’s bats reported an incubation period of 33 days [35] after infection by the sub-dermal route. The later study involving EBLV-1 infection of serotine bats gave incubation periods between 17 and 26 days following sub-dermal or intramuscular infection [36]. This suggests that the incubation period varies from just over 2 weeks to over 9 months, with factors such as virus dose and route of exposure influencing the time to development of disease. The presence of virus in the salivary glands and taste buds of infected bats implicates biting as the main means of transmission. This could presumably occur at a number of points in the Daubenton’s bat life cycle including swarming and mating just prior to hibernation, to the formation of colonies during the summer months. The composition of UK

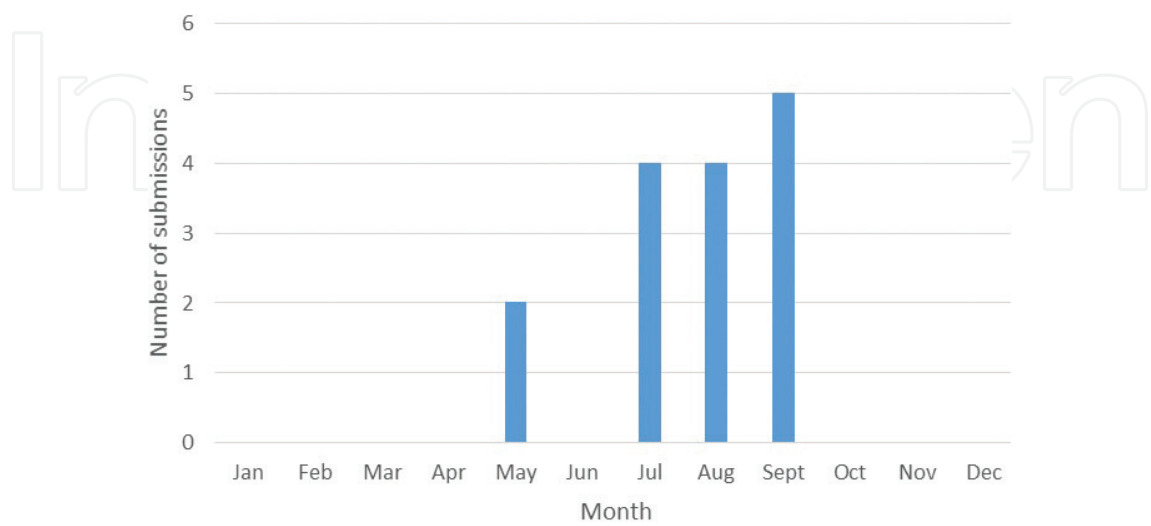


Figure 2. Seasonal distribution of EBLV-2 infected Daubenton’s bats submitted for rabies testing in the UK (1996–2017).

submissions of EBLV-2 bats gives little help in resolving this. Although based on low numbers, 15 cases, there is no gender bias (7 males versus 8 females). There does appear to be a relatively higher proportion of juveniles submitted (8 versus 6 adults, where data is known), perhaps favouring transmission in maternity colonies and shorter incubation periods of 2–3 months. This would be supported by the repeated submission of EBLV-2 infected bats from the colony at Stokesay Castle. However, the means by which the virus persists through hibernation is not known and may rely on long incubation events in a proportion of cases. Modelling of rabies infection in North American bat populations suggests that this is critical for long-term persistence of rabies lyssavirus [43].

The geographical spread of EBLV-2 infected bats in the UK is also a mystery with cases submitted from disparate locations with no obvious link in time or space. A virus such as EBLV-2, which kills its host, should struggle to persist in small populations of bats. It is possible that a virus could persist in areas where Daubenton's bats are abundant and there is movement of individuals between colonies [44]. Alternatively, the virus could move across the wider landscape moving between populations as observed for rabies lyssavirus in common vampire bat (*Desmodus rotundus*) populations in Latin America [45]. In continental Europe, similar challenges have been encountered due to the uneven distribution of EBLV-1 in the serotine bat population [10, 46] and the sporadic nature of BBLV in Natterers bats [11]. A better understanding of Daubenton's bat behaviour, particularly how populations interact and move across the landscape may help in formulating hypotheses that could explain this distribution. Migration and dispersal, particularly by males may be a key feature driving virus persistence within bat populations. This is also considered to be critical for the spread of rabies in European red fox (*Vulpes vulpes*) populations. Bats may use rivers and valleys to provide corridors for long distance migration [47]. This would seem highly appropriate for a bat species that uses water bodies for feeding.

5. Conclusions

When the second case of EBLV-2 infection occurred in a human in 2002, very little was known about the biology of the virus and its relationship with its bat reservoir leading some authors to describe the relationship as an ecological enigma [48]. Since then advances have been made in the detection of more lyssavirus species in bat populations, the virus distribution in the bat host, the derivation of the complete EBLV-2 genome and the establishment of clear public health measures aimed at protecting those that handle bats. This includes the wearing of gloves to prevent exposure to virus and the knowledge that current vaccines against rabies will prevent infection with EBLV-2. However, much is not known, in part due to the difficulties in studying a protected, nocturnal, flying mammal. Lyssaviruses form intimate relationships with particular bat species that maintain the virus in the environment [49]. This could imply adaptation to the host that favours continued transmission in that host but limiting the viruses' ability to infect another species. Alternatively, host behaviour such as roosting, dispersal and mating could be drivers for conspecific transmission. Indeed, both may function to restrict particular viruses to

a single bat species. It is clear that further multidisciplinary research will be needed to answer fundamental questions on the maintenance of EBLV-2 in the Daubenton's bat.

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