The Veterinary Journal 233 (2018) 25–34

Contents lists available at ScienceDirect

The Veterinary Journal

journal homepage: www.elsevier.com/locate/tvjl

Review

Domesticated animals as hosts of henipaviruses and filoviruses: A systematic review

Emma E. Glennon[a,*], Olivier Restif[a], Silke Riesle Sbarbaro[a], Romain Garnier[a], Andrew A. Cunningham[b], Richard D. Suu-Ire[c], Richard Osei-Amponsah[d], James L.N. Wood[a], Alison J. Peel[e]

[a] Department of Veterinary Medicine, University of Cambridge, Cambridge, UK
[b] Institute of Zoology, Zoological Society of London, Regent's Park, London, UK
[c] Accra National Zoo, Accra, Ghana
[d] Department of Animal Science, University of Ghana, Accra, Ghana
[e] Environmental Futures Research Institute, Griffith University, Nathan, Australia

ARTICLE INFO

Keywords:
Bat-borne viruses
Domesticated animals
Emerging zoonotic viruses
Filoviruses
Henipaviruses

ABSTRACT

Bat-borne viruses carry undeniable risks to the health of human beings and animals, and there is growing recognition of the need for a 'One Health' approach to understand their frequently complex spill-over routes. While domesticated animals can play central roles in major spill-over events of zoonotic bat-borne viruses, for example during the pig-amplified Malaysian Nipah virus outbreak of 1998-1999, the extent of their potential to act as bridging or amplifying species for these viruses has not been characterised systematically. This review aims to compile current knowledge on the role of domesticated animals as hosts of two types of bat-borne viruses, henipaviruses and filoviruses. A systematic literature search of these virus-host interactions in domesticated animals identified 72 relevant studies, which were categorised by year, location, design and type of evidence generated. The review then focusses on Africa as a case study, comparing research efforts in domesticated animals and bats with the distributions of documented human cases. Major gaps remain in our knowledge of the potential ability of domesticated animals to contract or spread these zoonoses. Closing these gaps will be necessary to fully evaluate and mitigate spill-over risks of these viruses, especially with global agricultural intensification.

Introduction

The list of bat-borne viruses known to cause morbidity and mortality in domesticated animals, wildlife and people continues to grow (Moratelli and Calisher, 2015). Many such viruses have pandemic potential and cause severe disease in recipient hosts, raising concern for public health, agriculture and conservation (Calisher et al., 2006; Plowright et al., 2015). The routes of associated spill-over events vary widely; ranging from sporadic bat-to-human Nipah virus (NiV) spill-over events over at least the last 15 years in Bangladesh (Luby et al., 2009; Lo et al., 2012) to the 1998–1999 pig-amplified NiV outbreak in Malaysia and Singapore, which resulted in the culling of >1,000,000 pigs and the deaths of more than 100 people (Chua et al., 2000; Chua, 2003). In Australia, outbreaks of disease caused by Hendra virus (HeV), which together with NiV and the closely related Cedar virus, comprises the genus *Henipavirus* (Marsh et al., 2012), have resulted from bat-to-horse transmission, with occasional spread among horses or transmission from sick horses to their veterinarians and handlers (Middleton, 2014). Henipavirus disease outbreaks have been characterised by stuttering chains of transmission, as have most outbreaks of filovirus diseases caused by Marburg virus (MarV) and ebolaviruses (Lloyd-Smith et al., 2009; Plowright et al., 2015). In contrast, the West African outbreak of Ebola virus (EbolaV) disease in 2013–2016 was characterised by sustained human-to-human transmission on an unprecedented scale. This outbreak, which caused a massive death toll and societal impact, may have resulted from a single bat-to-human spill-over event (Baize et al., 2014; Carroll et al., 2015; Spengler et al., 2016).

Domesticated animals used as food sources, companion animals or in the workforce are able to act as bridges for viral transmission between wildlife (including bats) and people (Reperant et al., 2016). Such animals link 'the field' and 'the home,' often having closer physical contact with both wildlife and

* Corresponding author.
E-mail address: eeg31@cam.ac.uk (E.E. Glennon).

https://doi.org/10.1016/j.tvjl.2017.12.024

people than wildlife and people typically have with one another. The context of intensive agriculture, in which livestock are held in large, dense and highly connected populations, provides an ideal opportunity for viral amplification, thereby increasing the risk of otherwise improbable spill-over events to people, as well as causing significant economic and animal health costs (Cleaveland et al., 2001; Hudson et al., 2002).

While clear examples exist for henipaviruses, the potential role of domesticated animals as bridging species for most filoviruses is less clear. This lack of clarity can be attributed in part to the different ecological and agricultural contexts of regions of documented henipavirus and filovirus spill-over events. For example, the type of intensive livestock production that facilitated NiV spill-over in Malaysia and possibly Reston ebolavirus spill-over in the Philippines (Barrette et al., 2009) is uncommon in sub-Saharan Africa, where most MarV and EbolaV disease outbreaks have occurred (Gilbert et al., 2015). Also, evidence for non-domesticated wildlife, such as apes and duikers, as bridging species for ebolaviruses has made the study of domesticated animals as hosts a less urgent priority (Leroy et al., 2004a, 2004b; Rouquet et al., 2005). Nonetheless, understanding the potential role of domesticated animals in filovirus transmission is important, particularly given the ongoing intensification of livestock production and its encroachment into new wildlife habitats in Africa (Gerber, 2005; Tilman et al., 2011; Herrero and Thornton, 2013; Perry et al., 2013; Pan et al., 2014).

The emergence of bat-borne henipaviruses and filoviruses has prompted frequent calls for a 'One Health' approach to mitigating their risk to people and animals, involving multidisciplinary collaboration to connect the health of wildlife, domesticated animals, people and the environment (Plowright et al., 2015; Roess et al., 2015; Lo Iacono et al., 2016).[1] Despite the importance of such an approach to zoonoses with complex life histories, few studies have explicitly considered the role of domesticated animals in the spill-over of bat-borne viruses. This omission creates a major gap in our understanding of the epidemiology and ecology of these viruses.

This paper systematically reviews the available literature on domesticated animals as hosts of two sets of bat-borne viruses with zoonotic potential, the henipaviruses NiV and HeV, and the filoviruses MarV and EbolaV, along with other ebolaviruses. It summarises the existing evidence for the abilities of domesticated animal species to host, sustain intraspecific transmission and act as interspecific spill-over species for each virus. This quantitative review is then used to define where research efforts has focussed, and to identify understudied domesticated animal species, regions and viruses, as well as more general knowledge gaps. Finally, we present a case study of filoviruses in Africa, considering the context of global capacity challenges, agricultural intensification and zoonotic disease emergence.

Materials and methods

Articles were gathered from a Web of Knowledge[2] search using the following terms and criteria: Topic = (morbillivirus OR Nipah OR Hendra OR henipavirus OR Ebola OR ebolavirus OR Marburg OR filovirus) AND Topic = (pig OR swine OR porcine OR cattle OR cow OR bovine OR sheep OR ovine OR goat OR caprine OR horse OR equine OR camel OR dog OR canine OR cat OR feline OR livestock OR domesticated OR pet OR poultry OR chicken OR galline OR duck OR anatine OR buffalo OR bubaline OR donkey OR asinine) AND Language = (English) AND Document Type = (Article OR Note). This search produced 1276 results as of 27 March 2017, of which 72 studies fitted the following inclusion criteria: (1) they pertained to henipavirus or filovirus infection in the selected set of domesticated animals (e.g. excluding laboratory rodents); (2) they do not represent comments, opinions or review articles; and (3) they have not been retracted or followed by an expression of concern. While perusing the papers identified by this search, additional unpublished or informally published reports were found (e.g. on government websites). Results from these additional reports are not included in any summary statistics or figures, but they were noted (and identified as outside of our search) if they provided additional relevant information or context.

Nipah viruses were categorised by clade (NiV-B for Clade I NiV originating in Bangladesh; NiV-M for Clade II NiV originating in Malaysia or elsewhere in Southeast Asia; Lo Presti et al., 2016), while ebolaviruses were categorised by species, such as *Zaire ebolavirus* (EbolaV) and *Reston ebolavirus* (Reston virus), where available; otherwise we used the narrowest classification provided by the study. Animal categories included were pigs, horses, cattle, small ruminants (sheep and goats), dogs, cats, buffaloes, donkeys and poultry (chickens and ducks). We included one entry in our database per animal–virus pair; as a result, some of the studies and some outbreaks appeared in multiple entries.

For each domesticated animal–virus species pair within each study, we evaluated whether any evidence, even if limited, was sought or provided for susceptibility, disease phenotype, a physiological or mechanical mechanism for virus transmission, demonstrated virus transmission to conspecifics, demonstrated inter-species virus transmission (where relevant, the other species infected were specified), natural (i.e. non-experimental) infection and a demonstrated role in zoonotic spill-over during the course of an outbreak. Studies were considered to provide evidence both for those characteristics that were tested directly and for those that were a prerequisite for the findings (e.g. we considered studies describing HeV transmission between horses as evidence of the susceptibility of horses to HeV). Where possible, we recorded negative findings as distinct from a lack of findings.

We accessed global domesticated animal counts by country in 2014 from FAOSTAT[3]; this database includes official national data, where available, supplemented by estimates from the Food and Agriculture Organization (FAO)[4] of the United Nations. We accessed filovirus disease outbreak data from the Centers for Disease Control and Prevention[5] to place research effort in Africa in the context of the distribution of past outbreaks. To compare the research effort applied to domesticated animals with that applied to bats, we collected studies that fitted criteria 2 and 3 above, applied to henipavirus or filovirus infection in bats in non-controlled settings in Africa, as returned by the following search terms: Topic = (Nipah OR Hendra OR henipavirus OR Ebola OR Marburg OR filovirus) AND Topic = (bat) AND Topic = (Africa OR Algeria OR Angola OR Benin OR Botswana OR Burkina Faso OR Burundi OR Cabo Verde OR Cameroon OR Central African Republic OR Chad OR Comoros OR Congo OR Cote d'Ivoire OR Djibouti OR Egypt OR Guinea OR Eritrea OR Ethiopia OR Gabon OR Gambia OR Ghana OR Kenya OR Lesotho OR Liberia OR Libya OR Madagascar OR Malawi OR Mali OR Mauritania OR Mauritius OR Morocco OR Mozambique OR Namibia OR Niger OR Nigeria OR Rwanda OR Sao Tome OR Principe OR Senegal OR Seychelles OR Sierra Leone OR

[1] See: http://www.agrifutures.com.au/wp-content/uploads/publications/16-001.pdf (accessed 1 January 2018).
[2] See: https://webofknowledge.com (accessed 1 January 2008).
[3] See: http://www.fao.org/faostat (accessed 1 January 2018).
[4] See: http://www.fao.org (accessed 1 January 2018).
[5] See: https://www.cdc.gov/vhf/ebola/outbreaks/history/chronology.html; https://www.cdc.gov/vhf/marburg/outbreaks/chronology.html (accessed 1 January 2018).

Somalia OR Sudan OR Swaziland OR Tanzania OR Togo OR Tunisia OR Uganda OR Zambia OR Zimbabwe) AND Language = (English). We produced plots using the *mapdata*,*ggplot2* and *treemap* packages in R.

Results

Susceptibility, clinical signs and natural infection

Available evidence for the capabilities of domesticated animal species to host, transmit, and contribute to the zoonotic spill-over of henipaviruses and filoviruses showed considerable species biases (Fig. 1). No MarV studies examined any domesticated animal as potential hosts. No studies examined camels, buffaloes or donkeys as hosts of any henipavirus or filovirus. No studies investigated any relationships between cattle or poultry and ebolaviruses, or directly tested the susceptibility of cattle or poultry to HeV. Experimental infection studies involving horses, goats and sheep suggest that these species are not highly susceptible to EbolaV infection (Kudoyarova-Zubavichene et al., 1999). All remaining animal–virus pairs demonstrated some level of susceptibility to henipaviruses or filoviruses (Fig. 1).

Of all domesticated animal species, pigs showed the most evidence for a significant role as amplifiers of zoonotic henipaviruses and filoviruses. They are demonstrated amplifiers of NiV-Malaysia (NiV-M), with serological studies of pigs, case-control studies of people and successful control via culling all supporting their critical role in the 1998–1999 NiV outbreak in Malaysia and Singapore (Chua, 2003). Pigs have also exhibited a high seroprevalence against NiV-Bangladesh in Bangladesh (Chowdhury et al., 2014). When experimentally infected with HeV, pigs demonstrate similar clinical signs, including fever and respiratory signs, as when naturally infected with NiV (Middleton et al., 2002; Li et al., 2010). About 5% of blood samples from pigs in two villages in Ghana

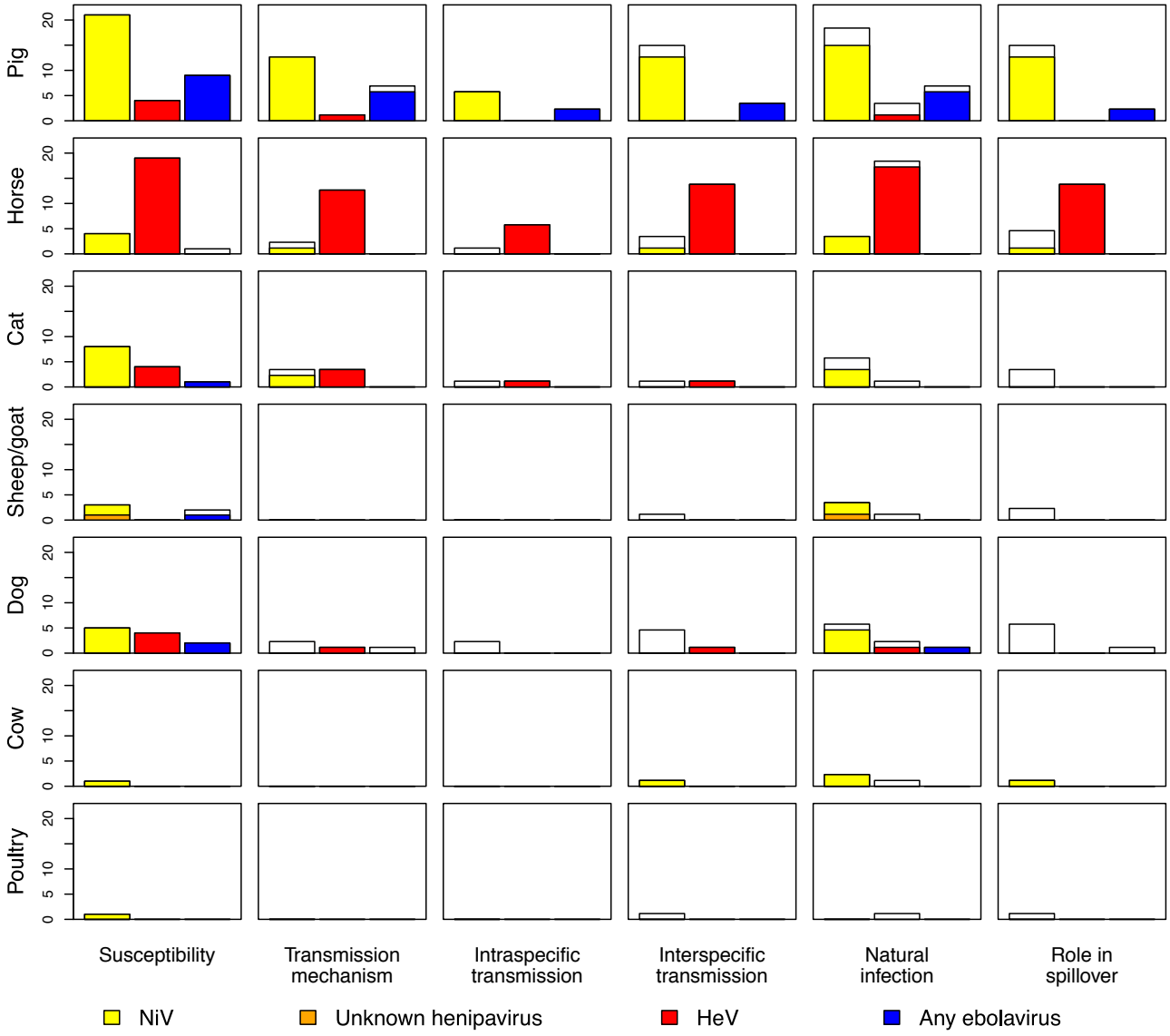

Fig. 1. Number of studies seeking (white) or providing (colour) evidence of domesticated animal species as hosts of Nipah virus, unknown henipaviruses (stacked with Nipah virus for visibility), Hendra virus or ebolaviruses. Marburg virus, camels, buffaloes and donkeys are excluded from the figure, since no associated studies were identified. Types of evidence considered include demonstrated susceptibility to each virus, demonstrated transmission mechanisms, evidence of transmission between animals of the same species, evidence of transmission from a domesticated animal species to some other species, evidence of natural infection (e.g. immunity during an outbreak or in a natural setting) and evidence of a role of spill-over to humans in a confirmed outbreak.

tested positive for non-neutralising antibodies to henipaviruses, suggesting natural henipavirus infections in pigs may have a geographical range outside South East Asia (Hayman et al., 2011).

When infected with the filovirus Reston virus, which occurs naturally in the Philippines, pigs exhibit no clinical signs (Barrette et al., 2009; Marsh et al., 2011; Sayama et al., 2012; Pan et al., 2014). However, upon experimental infection with EbolaV, pigs develop fever and pulmonary haemorrhage (Kobinger et al., 2011). Mass mortalities of bush pigs in Gabon have been reported concurrently with EbolaV disease outbreaks in people and other wildlife, but infection in pigs was not confirmed in these cases (Lahm et al., 2007).

Horses have exhibited susceptibility to NiV-M infection in experimental studies (Chua et al., 2000) and horses naturally infected with NiV in the Philippines have developed acute neurological disease, including circling and ataxia, as well as sudden death (Ching et al., 2015). The horse is a well-known host of HeV in Australia, apparently following direct or indirect infection from bats in multiple outbreaks (Halpin et al., 2011; Martin et al., 2015). However, infection in horses remains rare, with cross-sectional studies of unaffected horses and (informally published) investigations of clinically ill horses rarely showing evidence of past or current infection (Rogers et al., 1996; Ward et al., 1996). HeV infection in horses results in a wide range of clinical signs, often with severe respiratory and/or neurological disease, including pulmonary oedema and vascular lesions in the lungs and brain (Hooper et al., 1997a). High viral loads in response to HeV challenge have been confirmed experimentally (Williamson et al., 1998). The horse is not susceptible to EbolaV disease (Kudoyarova-Zubavichene et al., 1999).

There was serological evidence of natural NiV infection in goats, but not in sheep, during outbreaks of NiV infection in pigs and people in Malaysia and Bangladesh (Chua, 2003; Hsu et al., 2004; Chowdhury et al., 2014). Non-neutralising antibodies of an unknown henipavirus were reported from a sheep and a goat in Ghana (Hayman et al., 2011). No studies have examined or described henipavirus disease in these species. It appears that neither sheep nor goats are susceptible to ebolavirus disease; sheep exhibit a neutralising antibody response to immunisation with EbolaV glycoprotein (Dowall et al., 2016), but sheep and goats are insensitive to challenge with live EbolaV (Kudoyarova-Zubavichene et al., 1999).

Experimental infections of the domestic cat have demonstrated this species' susceptibility to HeV (Westbury et al., 1996; Hooper et al., 1997b; Williamson et al., 1998) and NiV (Middleton et al., 2002; Mungall et al., 2006, 2007). Cats infected with henipaviruses develop severe respiratory disease, with typical signs including pulmonary oedema and interstitial pneumonia (Hooper et al., 1997b). Natural infection of cats with NiV has also been reported; several cats died after eating the meat of NiV-infected horses in the Philippines in 2014 (Ching et al., 2015) and seropositive cats were detected during the index outbreak in Malaysia in 1999 (Chua et al., 2000). In contrast, serum neutralisation testing of blood from 64 cats following the first known HeV outbreak in Queensland, Australia, provided no evidence of exposure (Rogers et al., 1996). Of two cats sampled in Ghana during a wider study on henipavirus epidemiology, both tested seronegative to henipavirus (Hayman et al., 2011). The only investigation of the susceptibility of the domestic cat to any filovirus infection is an in vitro study (Han et al., 2016). This study assessed glycoprotein-mediated entry of EbolaV into primary feline cells and found they were more susceptible to EbolaV entry than canine cells, but less susceptible than human or primate cells (Han et al., 2016). We found no evidence that either natural or experimental infection of the domestic cat with EbolaV or any other filovirus has been investigated.

Several studies have reported high seroprevalences for NiV in the domestic dog during disease outbreaks in Malaysia (where up to 57% of tested dogs were seropositive; Mills et al., 2009) and the Philippines (where all four dogs in contact with sick horses were seropositive; Ching et al., 2015) in the absence of clinical disease. Dogs experimentally infected with HeV show few to no clinical signs, despite viral replication and excretion of viable virus in oral secretions and urine (Middleton et al., 2017). To date, however, only two dogs have been demonstrated to be naturally infected with HeV (Halim et al., 2015; Kirkland et al., 2015)[6]; both dogs were present on farms in Australia where there were HeV outbreaks in horses, showed minimal clinical signs and were euthanased as a precaution to protect public health. Post-mortem examination findings in one of these dogs revealed diffuse vasculitis (Kirkland et al., 2015). We could only find one investigation of filovirus infection in the domestic dog. The authors of this study reported a high seroprevalence of EbolaV-reactive antibodies in dogs in Gabon in the absence of clinical disease (Allela et al., 2005).

Minimal data exist for both poultry and cattle as hosts of henipaviruses and no data exist for either species as hosts of filoviruses. Contact with sick cattle has been associated with NiV seropositivity among people in Bangladesh (Hsu et al., 2004). A seropositivity of 6.5% against NiV glycoprotein was demonstrated in 6.5% of domesticated cattle in a NiV-prone region of Bangladesh (Chowdhury et al., 2014). This is the only study identified in which cattle were tested for evidence of exposure to NiV.

We identified two studies which examined NiV infection in poultry; one failed to find serological evidence of exposure during NiV outbreaks among a small ($n = 10$) sample of unspecified bird species (Hsu et al., 2004) and one demonstrated mortality in chicken eggs experimentally inoculated with NiV-M (Tanimura et al., 2006). We found one study that looked for evidence of natural HeV infection in cattle and poultry (following the first known outbreak of this disease); the authors failed to find serological evidence of exposure in 276 cattle or 21 species of poultry (turkeys, geese and chickens) (Rogers et al., 1996). No studies returned in our search have looked for evidence of susceptibility to, or infection with, filoviruses in either cattle or poultry, but one study that fell outside our search terms reported no evidence of EbolaV infection in tissues from fewer than five chickens collected in the Democratic Republic of the Congo and Cameroon (Breman et al., 1980).

Intraspecific and interspecific transmission

Interspecific transmission routes for which we found evidence of domesticated animal involvement are summarised in Fig. 2. Nipah virus circulation among pigs and transmission from pigs to people were documented in the 1998–1999 NiV outbreak in Malaysia and Singapore (Chua et al., 1999), but neither have been observed for HeV. Dogs and cats in contact with pigs became infected during this NiV outbreak (Chua et al., 2000). Phylogenetic and serological evidence suggest that Reston virus has circulated among pigs for decades (Barrette et al., 2009). Farmers and slaughterhouse workers in contact with infected pigs in the Philippines have tested seropositive to Reston virus antibodies, suggesting pig-to-human spill-over (Morris 2009; Sayama et al., 2012). Experimental studies have demonstrated the ability of pigs to transmit EbolaV to other pigs (Kobinger et al., 2011) and macaques (Weingartl et al., 2012).

A 2014 NiV outbreak in the Philippines involved multiple horses and their handlers, as well as people, cats and dogs that consumed

[6] Hendra virus, equine — Australia (18): (Queensland) Canine. ProMED-mail 20110727.2257. www.promedmail.org/post/799306 (accessed 1 January 2018).

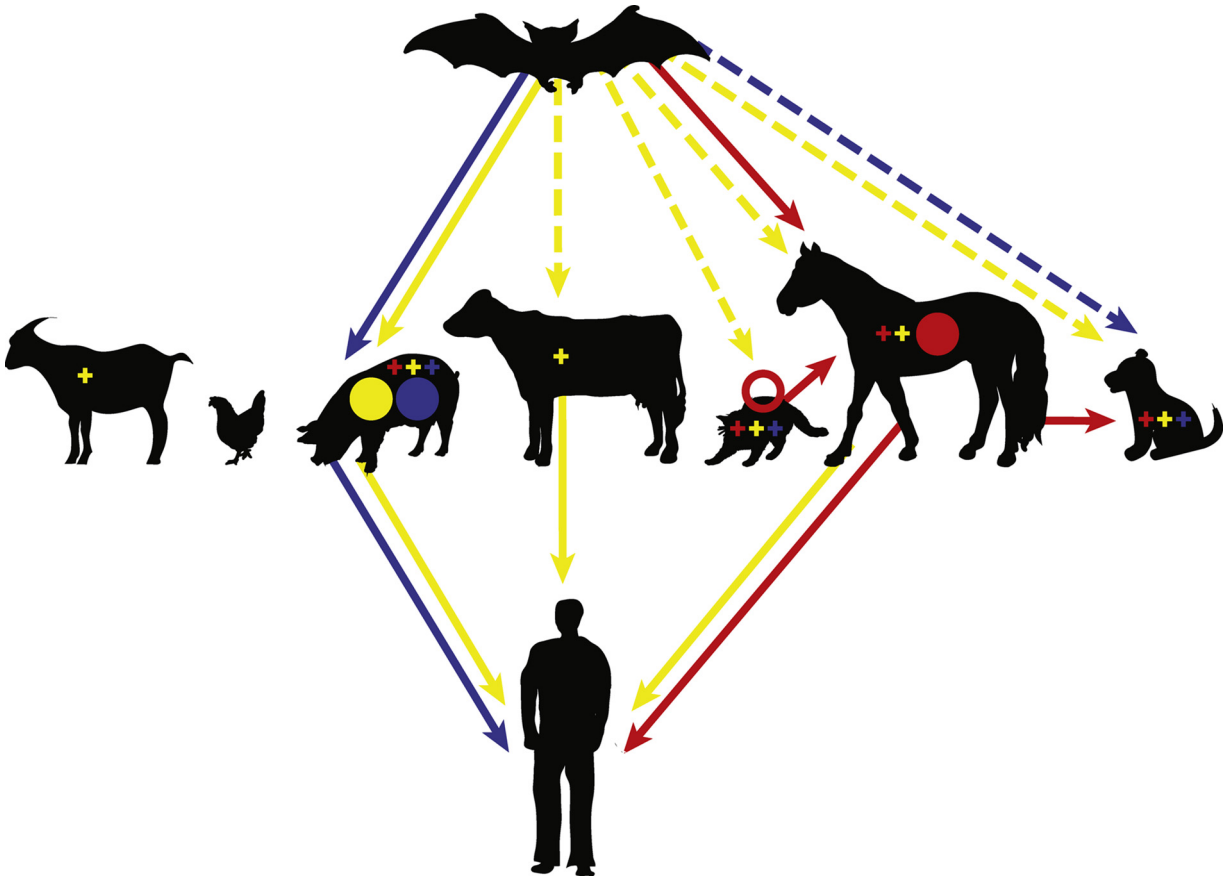

Fig. 2. Summary of suggested routes of interspecies transmission for Nipah virus (NiV; yellow), Hendra virus (HeV; red) and ebolaviruses (EbolaV; blue) to and from domesticated animals. The species represented are goats, poultry, pigs, dogs, cats, horses and cattle. Plus (+) symbols indicate known susceptibility to infection of a domesticated animal species, while filled and open/dashed circles indicate intraspecific transmission in natural and controlled settings, respectively. Solid and dashed lines represent transmission that has been observed or suspected in natural and experimental conditions, respectively. Carrion, rather than direct transmission from bats, has been suggested as a source of EbolaV infection in dogs (Allela et al., 2005). NiV-associated mortality has been demonstrated in chicken eggs, but not in live chickens. Known or suspected direct transmission from wildlife to people is not represented. We found no evidence of transmission from other wildlife host species (e.g. EbolaV from nonhuman primates) to domesticated animals.

horse meat; epidemiological evidence from this outbreak is highly suggestive of horse-to-human spill-over, but is inconclusive about horse-to-horse transmission (Ching et al., 2015). In addition to infecting their veterinarians and human handlers, HeV-infected horses have infected other horses with which they shared a stable, as well as at least one dog (Murray et al., 1995; Selvey and McCormack, 1995; Williamson et al., 1998; Field et al., 2010; Kirkland et al., 2015). This transmission was likely to be mediated by human handlers spreading the virus among horses or by environmental contamination, since outbreak reports suggest that direct horse-to-horse transmission is relatively inefficient (Field et al., 2010).

No intraspecific transmission has been demonstrated for any henipavirus among goats, sheep, poultry, dogs or cattle, but we found almost no research effort in this area. There is limited evidence from a questionnaire survey of an association between human NiV cases and exposure to sick cattle in Bangladesh (Hsu et al., 2004), although none of the sick cattle were tested for NiV infection. Dogs have been shown experimentally to be able to transmit HeV to ferrets (Middleton et al., 2017), and HeV-infected cats have infected other cats (Westbury et al., 1996) and horses (Williamson et al., 1998) in experimental settings. No transmission among adult cats or between cats and other species has been shown for NiV, although the isolation of NiV RNA from foetal tissues and placental fluid in an experimentally infected pregnant cat suggests that vertical transmission may be possible (Mungall et al., 2007).

No studies identified in our literature research tried to demonstrate the potential for intraspecific or interspecific ebolavirus transmission between domesticated animals (other than for pigs, as described above) and any other domesticated or wild species.

Research effort

A summary of all the studies investigating domesticated animals as hosts for a henipavirus or a filovirus returned by our search is shown in Fig. 3. Pigs and NiV comprised the most frequently studied domesticated animal–virus pair (25% of pairs studied). Most of these studies involved either analysis of the 1999 Malaysian NiV outbreak or experimental infection studies in controlled settings. Few studies investigated cattle (3% of studies), poultry (3%), or sheep/goats (7%). We found no studies that investigated filovirus infection in either cattle or poultry. For both henipaviruses and filoviruses, we found no cross-sectional studies of poultry and no experimental studies of cattle. Henipaviruses are much better-represented targets of domesticated animal studies than filoviruses; no study from our search looked at domesticated animals as potential hosts of MarV and only 19% of studies targeted ebolaviruses.

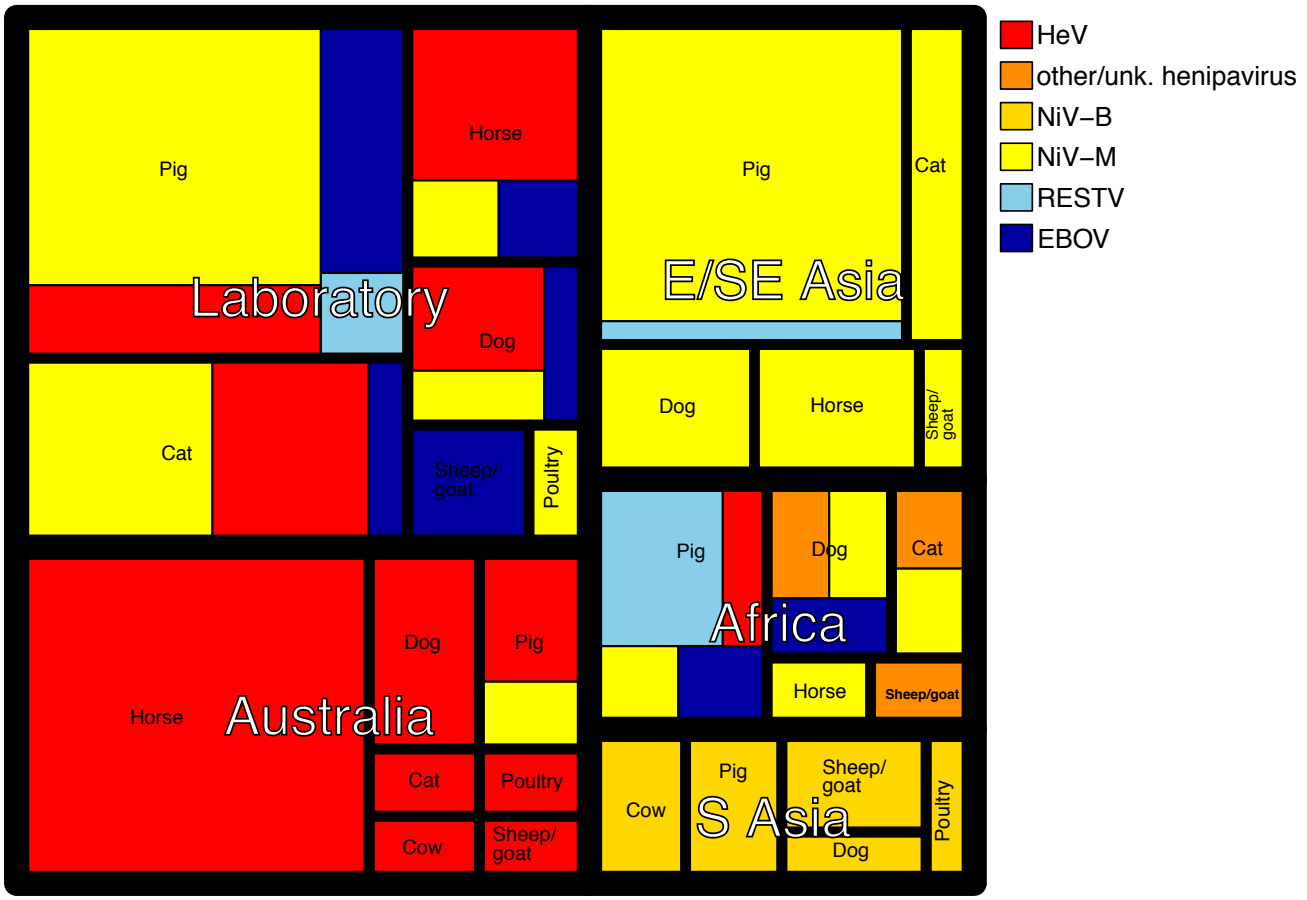

Fig. 3. Breakdown of studies returned in quantitative literature review by regions, species and viruses studied, where the area of each box is proportional to the number of studies looking at a given animal–virus pair in each region. Some studies cover multiple host-virus pairs and are therefore represented by a greater total area.

Apart from laboratory studies (for which locations were not always listed or relevant), Australia was the best-represented region, comprising 41% of geographically specific studies, followed by East and Southeast Asia (36%), Africa (18%) and South Asia (4.5%). Only one study in East/Southeast Asia investigated ebolaviruses (specifically Reston virus). Similarly, all but one study in Australia focussed on HeV; both studies in South Asia (for a total of eight species-specific investigations) focussed on NiV in Bangladesh. At least five domesticated animal species were studied per region.

Case study: filoviruses in Africa

Domesticated animals have received less attention as potential hosts of filoviruses than henipaviruses. Fewer than one fifth of studies returned in this review focussed on filoviruses; this is despite their profound impact on human health, as demonstrated by the 2013–2016 Ebola outbreak in West Africa (Carroll et al., 2015; Weyer et al., 2015; Spengler et al., 2016). Due to resource constraints and the importance of close contact human-to-human transmission in outbreak settings, domesticated animals have been relatively low priority targets of investigation (Spengler et al., 2016). Case investigations during outbreaks should continue to rule out known sources of EbolaV transmission before investigating speculative sources, such as domesticated animals, which have never been associated with previous outbreaks. A better understanding of the ecology of domesticated animals in relation to pathogen transmission nonetheless will be critical for long-term control of EbolaV disease in West Africa.

Research efforts on filoviruses in African bats are relatively well spatially matched to countries where zoonotic spill-over has occurred (Fig. 4A–D). In contrast, investigations of domesticated animals have only been conducted in Ghana, comprising one study on henipaviruses in pigs, goats, sheep, dogs and cats (Hayman et al., 2011), and Gabon, comprising two studies on ebolaviruses, one in pigs (Lahm et al., 2007) and one in dogs (Allela et al., 2005). Our current lack of knowledge about the potential of domesticated animals to host and transmit filoviruses is particularly striking given the ubiquity of large mammal livestock, and dogs and cats across the continent (Fig. 4E–F). There is limited evidence of susceptibility of pigs, sheep, goats, dogs and cats to some ebolaviruses. Pigs are a documented risk for Reston virus, with observed viral circulation among pigs and indirect evidence of transmission to their handlers in the Philippines (Barrette et al., 2009). Experimentally infected pigs are able to transmit EbolaV (Kobinger et al., 2011), the ebolavirus that has caused the most human mortality (Carroll et al., 2015; Weyer et al., 2015); the associated risk has not been evaluated adequately.

Both Reston virus spill-over in the Philippines and the major Malaysian NiV outbreak occurred in the context of highly intensive, high throughput pig production (Pulliam et al., 2012). The less intensive livestock production systems in Africa may, for now, reduce the risk of such amplification events (Gilbert et al., 2015). However, the potential for amplification is likely to rise along with economic development and agricultural intensification (Gerber, 2005; Herrero and Thornton, 2013; Perry et al., 2013); too little is known about the risk posed by dogs, despite their possible role as asymptomatic hosts, or livestock held in small holdings.

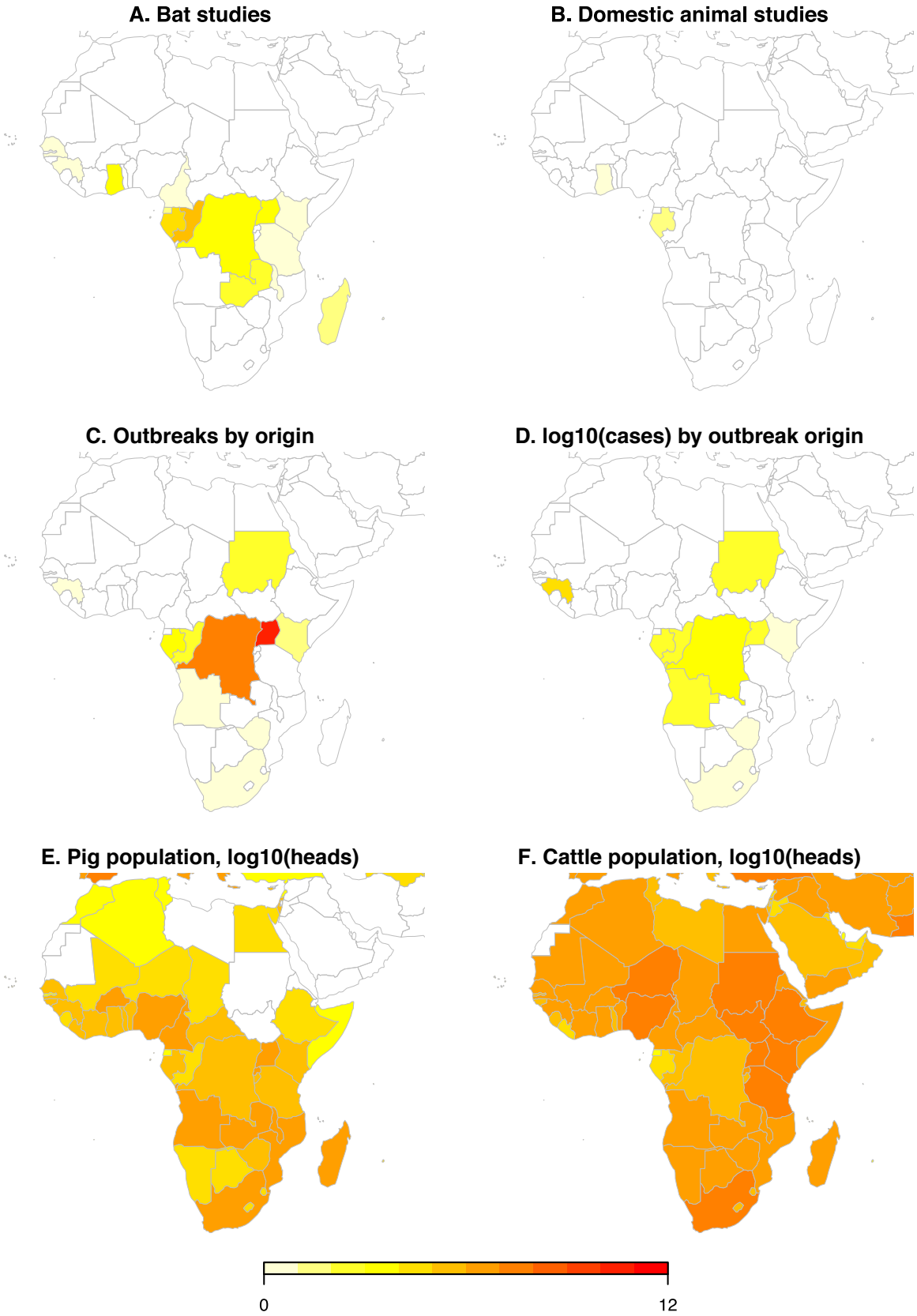

Fig. 4. Number of studies of henipaviruses and filoviruses in bats (A) and domesticated animals (B). Number of outbreaks (C) and confirmed human cases (D) of filoviruses by country of outbreak origin. Populations of pigs (E) and cattle (F) by country as reported by the Food and Agriculture Organization (FAO).[9]

[9] See: http://www.fao.org/faostat (accessed 1 January 2018).

Discussion

This review has summarised the current state of knowledge of domesticated animals as hosts of henipaviruses and filoviruses. Our findings have highlighted gaps in the research effort, particularly the paucity of studies of domesticated animals as hosts of filoviruses in Africa. South Asia represents a major geographic gap; direct bat-to-human transmission is a major spill-over route in Bangladesh. We identified two studies reporting evidence for a role of domesticated animals in NiV spill-over (Hsu et al., 2004; Chowdhury et al., 2014); further studies are warranted. The dearth of published studies on filoviruses in Oceania or Asia is also notable, given the known pig-mediated spill-over of Reston virus in the Philippines (Barrette et al., 2009). Only one study has been published on filoviruses in pigs in China (Pan et al., 2014), and none on any other domesticated animal, even though Reston virus has been detected in pigs in the country, China is in close proximity to known outbreaks of pig-mediated NiV outbreaks (e.g. in Malaysia) and considering that an estimated 65% of the world's domesticated pigs are in China. We recognise that additional studies in the above regions will have been published in non-English language journals, which were not included in our literature search.

The potential role of cats and dogs as intermediate hosts of zoonotic viruses also merits further study. Without isolation of viruses or clinical signs, the observed high seroprevalences in dogs of antibodies against NiV in Malaysia and the Philippines, and against EbolaV in Gabon, do not necessarily indicate any direct risk to human health. Nonetheless, further evaluation of that risk and of the possibility that dogs act as EbolaV carriers is warranted, particularly given the high frequency of close contact between people and dogs, and the use of dogs to hunt wildlife susceptible to EbolaV, such as duikers (Leroy et al., 2004a, 2004b; Allela et al., 2005). High viral loads and the presence of infectious secretions in HeV-infected dogs pose a potential zoonotic transmission risk. Further studies of the pathology and epidemiology of both henipaviruses and filoviruses in these species are justified.

Clarifying the role of domesticated animals as hosts of henipaviruses and filoviruses may help with the implementation of strategies to protect against outbreaks of these viruses, such as sentinel surveillance programmes. Whether domesticated animals act as amplifying or dead end hosts of a virus, detection of infection could indicate an increased risk of transmission to people before any active human infections occur. In many regions, deaths of domesticated animals are rarely investigated for emerging or novel pathogens (Zinsstag and Schelling, 2016). Due to the relatively small number of private veterinary practices in much of Central and West Africa (Christopher and Marusic, 2013),[7] where the risk of filovirus spill-over appears to be particularly high, partnerships with governmental agricultural and veterinary departments, and non-governmental organisations, may help in the dissemination of advice to farmers and other animal owners. Initiatives, such as the PREDICT project of the Emerging Pandemic Threats programme or the Dynamic Drivers of Disease in Africa (DDDAC) project, could help to establish surveillance capacity (Wood et al., 2012; Mandl et al., 2015; Gruber, 2017). In addition to acting as early warning systems, such programmes can build human capacity and generate data for additional research into these pathogens.

Few of the studies returned in our search examined domesticated animals as part of a wider ecosystem, although some studies outside the scope of our search (due to lack of specificity to a virus) have looked at behaviours of people (Mendez et al., 2014) or domesticated animals (Field et al., 2016) that potentially promote contact with bats or bridging species. Guided by a One Health approach, cross-scale studies assessing domesticated animals in the context of their potential interactions with bats, humans, wildlife and their environment represent another neglected area of research and could help with interpretation of the evidence described in this review.

Conclusions

Henipaviruses and filoviruses are among the better studied zoonotic bat-borne viruses, yet we have identified gaps in our knowledge of the past and potential roles of domesticated animals as hosts of these important pathogens. Due to our focus on formally published results, restrictions on the publication types and language included in our search, and a tendency, particularly in multidisciplinary outbreak investigations, to omit negative results, it is likely that we have underestimated the research effort expended on domesticated animal infections with henipaviruses and filoviruses. Nonetheless, the number of open questions remaining in this field is striking and underscores the need for continued emphasis on a One Health approach.

Conflict of interest statement

None of the authors of this paper have a financial or personal relationship with other people or organisations that could inappropriately influence or bias the content of the paper.

Acknowledgements

The silhouettes of animals used in Fig. 2 were provided by Jason C. Fisher, University of California Los Angeles, California, USA, and Jane Thomas, Joanna Woerner and Tracey Saxby, University of Maryland Center for Environmental Science, Maryland, USA.[8] This work was supported by a Gates Cambridge Trust Scholarship to Emma Glennon and a Queensland Government Accelerate Fellowship grant to Alison Peel.

References

Allela, L., Bourry, O., Pouillot, R., Délicat, A., Yaba, P., Kumulungui, B., Rouquet, P., Gonzalez, J.P., Leroy, E.M., 2005. Ebola virus antibody prevalence in dogs and human risk. Emerging Infectious Diseases 11, 385–390.

Baize, S., Pannetier, D., Oestereich, L., Rieger, T., Koivogui, L., Magassouba, N., Soropogui, B., Sow, M.S., Keïta, S., De Clerck, H., et al., 2014. Emergence of Zaire Ebola virus disease in Guinea. New England Journal of Medicine 371, 1418–1425.

Barrette, R.W., Metwally, S.A., Rowland, J.M., Xu, L., Zaki, S.R., Nichol, S.T., Rollin, P.E., Towner, J.S., Shieh, W., Batten, B., et al., 2009. Discovery of swine as a host for the Reston ebolavirus. Science 325, 204–206.

Breman, J.G., Johnson, K.M., van der Groen, G., Robbins, C.B., Szczeniowski, M.V., Ruti, K., Webb, P.A., Meier, F., Heymann, D.L., 1980. A search for Ebola virus in animals in the Democratic Republic of the Congo and Cameroon: Ecologic, virologic, and serologic surveys, 1979–1980. Ebola Virus Study Teams. Journal of Infectious Diseases 179 (Suppl), S139–S147.

Calisher, C.H., Childs, J.E., Field, H.E., Holmes, K.V., Schountz, T., 2006. Bats: Important reservoir hosts of emerging viruses. Clinical Microbiology Reviews 19, 531–545.

Carroll, M.W., Matthews, D.A., Hiscox, J.A., Elmore, M.J., Pollakis, G., Rambaut, A., Hewson, R., Garcia-Dorival, I., Bore, J.A., Koundouno, R., et al., 2015. Temporal and spatial analysis of the 2014–2015 Ebola virus outbreak in West Africa. Nature 524, 97–101.

Ching, P.K.G., de Los Reyes, V.C., Sucaldito, M.N., Tayag, E., Columna-Vingno, A.B., Malbas, F.F., Bolo, G.C., Sejvar, J.J., Eagles, D., Playford, G., et al., 2015. Outbreak of henipavirus infection, Philippines, 2014. Emerging Infectious Diseases 21, 328–331.

Chowdhury, S., Khan, S.U., Crameri, G., Epstein, J.H., Broder, C.C., Islam, A., Peel, A.J., Barr, J., Daszak, P., Wang, L.F., et al., 2014. Serological evidence of henipavirus

[7] See: http://www.oie.int/wahis_2/public/wahid.php/Countryinformation/Veterinarians (accessed 1 January 2018).

[8] See: ian.umces.edu/imagelibrary (accessed 1 January 2018).

exposure in cattle, goats and pigs in Bangladesh. Public Library of Science Neglected Tropical Diseases 8, e3302.
Christopher, M.M., Marusic, A., 2013. Geographic trends in research output and citations in veterinary medicine: Insight into global research capacity, species specialization, and interdisciplinary relationships. BMC Veterinary Research 9, 115.
Chua, K.B., 2003. Nipah virus outbreak in Malaysia. Journal of Clinical Virology 26, 265–275.
Chua, K.B., Bellini, W.J., Rota, P.A., Harcourt, B.H., Tamin, A., Lam, S.K., Ksiazek, T.G., Rollin, P.E., Zaki, S.R., Shieh, W., et al., 2000. Nipah virus: A recently emergent deadly paramyxovirus. Science 288, 1432–1435.
Chua, K.B., Goh, K.J., Wong, K.T., Kamarulzaman, A., Tan, P.S.K., Ksiazek, T.G., Zaki, S. R., Paul, G., Lam, S.K., Tan, C.T., 1999. Fatal encephalitis due to Nipah virus among pig-farmers in Malaysia. Lancet 354, 1257–1259.
Cleaveland, S., Laurenson, M.K., Taylor, L.H., 2001. Diseases of humans and their domestic mammals: Pathogen characteristics host range and the risk of emergence. Philosophical Transactions of the Royal Society of London Series B, Biological Sciences 356, 991–999.
Dowall, S.D., Callan, J., Zeltina, A., Al-Abdulla, I., Strecker, T., Fehling, S.K., Krähling, V., Bosworth, A., Rayner, E., Taylor, I., et al., 2016. Development of a cost-effective ovine polyclonal antibody-based product, EBOTAb, to treat Ebola virus infection. Journal of Infectious Diseases 213, 1124–1133.
Field, H., Schaaf, K., Kung, N., Simon, C., Waltisbuhl, D., Hobert, H., Moore, F., Middleton, D., Crook, A., Smith, et al., 2010. Hendra virus outbreak with novel clinical features. Australia.E merging Infectious Diseases 16, 338–340.
Field, H.E., Smith, C.S., De Jong, C.E., Melville, D., Broos, A., Kung, N., Thompson, J., Dechmann, D.K.N., 2016. Landscape utilisation, animal behaviour and Hendra virus risk. Ecohealth 13, 26–38.
Gerber, P., 2005. Geographical determinants and environmental implications of livestock production intensification in Asia. Bioresource Technology 96, 263–276.
Gilbert, M., Conchedda, G., Van Boeckel, T.P., Cinardi, G., Linard, C., Nicolas, G., Thanapongtharm, W., D'Aietti, L., Wint, W., Newman, S.H., et al., 2015. Income disparities and the global distribution of intensively farmed chicken and pigs. Public Library of Science One 10, e0133381.
Gruber, K., 2017. Predicting zoonoses. Nature Ecology and Evolution 1, 0098.
Halim, S., Polkinghorne, B., Bell, G., Van Den Berg, D., Sheppeard, V., 2015. Outbreak-related Hendra virus infection in a NSW pet dog. Public Health Research and Practice 25, e2541547.
Halpin, K., Hyatt, A.D., Fogarty, R., Middleton, D., Bingham, J., Epstein, J.H., Rahman, S.A., Hughes, T., Smith, C., Field, H.E., et al., 2011. Pteropid bats are confirmed as the reservoir hosts of henipaviruses: A comprehensive experimental study of virus transmission. American Journal of Tropical Medicine and Hygiene 85, 946–951.
Han, Z., Bart, S.M., Ruthel, G., Vande Burgt, N.H., Haines, K.M., Volk, S.W., Vite, C. H., Freedman, B.D., Bates, P., Harty, R.N., 2016. Ebola virus mediated infectivity is restricted in canine and feline cells. Veterinary Microbiology 182, 102–107.
Hayman, D.T.S., Wang, L.F., Barr, J., Baker, K.S., Suu-Ire, R., Broder, C.C., Cunningham, A.A., Wood, J.L.N., 2011. Antibodies to henipavirus or henipa-like viruses in domestic pigs in Ghana, West Africa. Public Library of Science One 6, e25256.
Herrero, M., Thornton, P.K., 2013. Livestock and global change: Emerging issues for sustainable food systems. Proceedings of the National Academy of Sciences of the United States of America 110, 20878–22088.
Hooper, P., Ketterer, P., Hyatt, A., Russell, G., 1997a. Lesions of experimental equine morbillivirus pneumonia in horses. Veterinary Pathology 34, 312–322.
Hooper, P., Westbury, H., Russell, G., 1997b. The lesions of experimental equine morbillivirus disease in cats and guinea pigs. Veterinary Pathology 34, 323–329.
Hsu, V.P., Hossain, M.J., Parashar, U.D., Ali, M.M., Ksiazek, T.G., Kuzmin, I., Niezgoda, M., Rupprecht, C., Bresee, J., Breiman, R.F., 2004. Nipah virus encephalitis reemergence, Bangladesh. Emerging Infectious Diseases 10, 2082–2087.
Hudson, P.J., Rizzoli, A.P., Grenfell, B.T., Heesterbeek, J.A.P., Dobson, A.P., 2002. Ecology of Wildlife Diseases. Oxford University Press, Oxford, UK 216 pp.
Kirkland, P.D., Gabor, M., Poe, I., Neale, K., Chaffey, K., Finlaison, D.S., Gu, X., Hick, P. M., Read, A.J., Wright, T., et al., 2015. Hendra virus infection in dog, Australia, 2013. Emerging Infectious Diseases 21, 2182–2185.
Kobinger, G.P., Leung, A., Neufeld, J., Richardson, J.S., Falzarano, D., Smith, G., Tierney, K., Patel, A., Weingartl, H.M., 2011. Replication, pathogenicity, shedding, and transmission of Zaire ebolavirus in pigs. Journal of Infectious Diseases 204, 200–208.
Kudoyarova-Zubavichene, N.M., Sergeyev, N.N., Chepurnov, A.A., Netesov, S.V., 1999. Preparation and use of hyperimmune serum for prophylaxis and therapy of Ebola virus infections. Journal of Infectious Diseases 179, 218–223.
Lahm, S.A., Kombila, M., Swanepoel, R., Barnes, R.F.W., 2007. Morbidity and mortality of wild animals in relation to outbreaks of Ebola haemorrhagic fever in Gabon, 1994–2003. Transactions of the Royal Society of Tropical Medicine and Hygiene 101, 64–78.
Leroy, E.M., Rouquet, P., Formenty, P., Souquière, S., Kilbourne, A., Froment, J.M., Bermejo, M., Smit, S., Karesh, W., Swanepoel, R., et al., 2004a. Multiple Ebola virus transmission events and rapid decline of central African wildlife. Science 303, 387–390.
Leroy, E.M., Telfer, P., Kumulungui, B., Yaba, P., Rouquet, P., Roques, P., Gonzalez, J.-P., Ksiazek, T.G., Rollin, P.E., Nerrienet, E., 2004b. A serological survey of Ebola virus infection in Central African nonhuman primates. Journal of Infectious Diseases 190, 1895–1899.
Li, M., Embury-Hyatt, C., Weingartl, H.M., 2010. Experimental inoculation study indicates swine as a potential host for Hendra virus. Veterinary Research 41, 33.
Lloyd-Smith, J.O., George, D., Pepin, K.M., Pitzer, V.E., Pulliam, J.R.C., Dobson, A.P., Hudson, P.J., Grenfell, B.T., 2009. Epidemic dynamics at the human–animal interface. Science 326, 1362–1367.
Lo, M.K., Lowe, L., Hummel, K.B., Sazzad, H.M.S., Gurley, E.S., Hossain, M.J., Luby, S.P., Miller, D.M., Comer, J.A., Rollin, P.E., et al., 2012. Characterization of Nipah virus from outbreaks in Bangladesh, 2008–2010. Emerging Infectious Diseases 18, 248–255.
Lo Iacono, G., Cunningham, A.A., Fichet-Calvet, E., Garry, R.F., Grant, D.S., Leach, M., Moses, L.M., Nichols, G., Schieffelin, J.S., Shaffer, et al., 2016. A unified framework for the infection dynamics of zoonotic spillover and spread. Public Library of Science Neglected Tropical Diseases 10 e0004957.
Lo Presti, A., Cella, E., Giovanetti, M., Lal, A., Angeletti, S., Zebender, G., Ciccozzi, M., 2016. Origin and evolution of Nipah virus. Journal of Medical Virology 88, 380–388.
Luby, S.P., Hossain, M.J., Gurley, E.S., Ahmed, B.N., Banu, S., Khan, S.U., Homaira, N., Rota, P.A., Rollin, P.E., Comer, J.A.M., et al., 2009. Recurrent zoonotic transmission of Nipah virus into humans, Bangladesh, 2001–2007. Emerging Infectious Diseases 15, 1229–1235.
Mandl, J.N., Ahmed, R., Barreiro, L.B., Daszak, P., Epstein, J.H., Virgin, H.W., Feinberg, M.B., 2015. Reservoir host immune responses to emerging zoonotic viruses. Cell 160, 20–35.
Marsh, G.A., de Jong, C., Barr, J.A., Tachedjian, M., Smith, C., Middleton, D., Yu, M., Todd, S., Foord, A.J., Haring, V., et al., 2012. Cedar virus: A novel henipavirus isolated from Australian bats. Public Library of Science Pathogens 8 e1002836.
Marsh, G.A., Haining, J., Robinson, R., Foord, A., Yamada, M., Barr, J.A., Payne, J., White, J., Yu, M., Bingham, J., et al., 2011. Ebola Reston virus infection of pigs: Clinical significance and transmission potential. Journal of Infectious Diseases 204 (Suppl), S804–S809.
Martin, G., Plowright, R., Chen, C., Kault, D., Selleck, P., Skerratt, L.F., 2015. Hendra virus survival does not explain spillover patterns and implicates relatively direct transmission routes from flying foxes to horses. Journal of General Virology 96, 1229–1237.
Mendez, D.H., Kelly, J., Buttner, P., Nowak, M., Speare, R., 2014. Management of the slowly emerging zoonosis Hendra virus by private veterinarians in Queensland, Australia: A qualitative study. BioMed Central Veterinary Research 10, 215–228.
Middleton, D., 2014. Hendra virus. Veterinary Clinics of North America: Equine Practice 30, 579–589.
Middleton, D., Riddell, S., Klein, R., Arkinstall, R., Haining, J., Frazer, L., Mottley, C., Evans, R., Johnson, D., Pallister, J., 2017. Experimental Hendra virus infection of dogs: Virus replication, shedding and potential for transmission. Australian Veterinary Journal 95, 10–18.
Middleton, D.J., Westbury, H.A., Morrissy, C.J., Van der Heide, B.M., Russell, G.M., Braun, M.A., Hyatt, A.D., 2002. Experimental Nipah virus infection in pigs and cats. Journal of Comparative Pathology 126, 124–136.
Mills, J.N., Alim, A.N.M., Bunning, M.L., Lee, O.B., Wagoner, K.D., Amman, B.R., Stockton, P.C., Ksiazek, T.G., 2009. Nipah virus infection in dogs, Malaysia, 1999. Emerging Infectious Diseases 15, 950–952.
Moratelli, R., Calisher, C.H., 2015. Bats and zoonotic viruses: Can we confidently link bats with emerging deadly viruses? Memórias do Instituto Oswaldo Cruz 110, 1–22.
Morris, K., 2009. First pig-to-human transmission of Ebola-Reston virus. Lancet Infectious Diseases 9, 149.
Mungall, B.A., Middleton, D., Crameri, G., Bingham, J., Halpin, K., Russell, G., Green, D., McEachern, J., Pritchard, L.I., Eaton, B.T., et al., 2006. Feline model of acute Nipah virus infection and protection with a soluble glycoprotein-based subunit vaccine. Journal of Virology 80, 12293–12302.
Mungall, B.A., Middleton, D., Crameri, G., Halpin, K., Bingham, J., Eaton, B.T., Broder, C.C., 2007. Vertical transmission and fetal replication of Nipah virus in an experimentally infected cat. Journal of Infectious Diseases 196, 812–816.
Murray, K., Rogers, R., Selvey, L., Selleck, P., Hyatt, A., Gould, A., Gleeson, L., Hooper, P., Westbury, H., 1995. A novel morbillivirus pneumonia of horses and its transmission to humans. Emerging Infectious Diseases 1, 31–33.
Pan, Y., Zhang, W., Cui, L., Hua, X., Wang, M., Zeng, Q., 2014. Reston virus in domestic pigs in China. Archives of Virology 159, 1129–1132.
Perry, B.D., Grace, D., Sones, K., 2013. Current drivers and future directions of global livestock disease dynamics. Proceedings of the National Academy of Sciences of the United States of America 110, 20871–20877.
Plowright, R.K., Eby, P., Hudson, P.J., Smith, I.L., Westcott, D., Bryden, W.L., Middleton, D., Reid, P.A., McFarlane, R.A., Martin, G., et al., 2015. Ecological dynamics of emerging bat virus spillover. Proceedings of the Royal Society B, Biological Sciences 282, 20142124.
Pulliam, J.R.C., Epstein, J.H., Dushoff, J., Rahman, S.A., Bunning, M., Jamaluddin, A.A., Hyatt, A.D., Field, H.E., Dobson, A.P., Daszak, P., et al., 2012. Agricultural intensification, priming for persistence and the emergence of Nipah virus: A lethal bat-borne zoonosis. Journal of the Royal Society Interface 9, 89–101.
Reperant, L.A., Brown, I.H., Haenen, O.L., de Jong, M.D., Osterhaus, A.D.M.E., Papa, A., Rimstad, E., Valarcher, J.F., Kuiken, T., 2016. Companion animals as a source of viruses for human beings and food production animals. Journal of Comparative Pathology 155 (Suppl. 1), S41–S53.
Roess, A.A., Winch, P.J., Akhter, A., Afroz, D., Ali, N.A., Shah, R., Begum, N., Seraji, H.R., El Arifeen, S., Darmstadt, G.L., et al., 2015. Household animal and human medicine use and animal husbandry practices in rural Bangladesh: Risk factors for emerging zoonotic disease and antibiotic resistance. Zoonoses and Public Health 62, 569–578.

Rogers, R.J., Douglas, I.C., Baldock, F.C., Glanville, R.J., Seppanen, K.T., Gleeson, L.J., Selleck, P.N., Dunn, K.J., 1996. Investigation of a second focus of equine morbillivirus infection in coastal Queensland. Australian Veterinary Journal 74, 243–244.

Rouquet, P., Froment, J.M., Bermejo, M., Kilbourn, A., Karesh, W., Reed, P., Kumulungui, B., Yaba, P., Délicat, A., Rollin, P.E., et al., 2005. Wild animal mortality monitoring and human Ebola outbreaks, Gabon and Republic of Congo, 2001–2003. Emerging Infectious Diseases 11, 283–290.

Sayama, Y., Demetria, C., Saito, M., Azul, R.R., Taniguchi, S., Fukushi, S., Yoshikawa, T., Iizuka, I., Mizutani, T., Kurane, I., et al., 2012. A seroepidemiologic study of Reston ebolavirus in swine in the Philippines. BioMed Central Veterinary Research 8, 82.

Selvey, L., McCormack, J., 1995. Infection of humans and horses by a newly described morbillivirus. Medical Journal of Australia 162, 642–645.

Spengler, J.R., Ervin, E.D., Towner, J.S., Rollin, P.E., Nichol, S.T., 2016. Perspectives on West Africa Ebola virus disease outbreak, 2013–2016. Emerging Infectious Diseases 22, 956–963.

Tanimura, N., Imada, T., Kashiwazaki, Y., Sharifah, S.H., 2006. Distribution of viral antigens and development of lesions in chicken embryos inoculated with Nipah virus. Journal of Comparative Pathology 135, 74–82.

Tilman, D., Balzer, C., Hill, J., Befort, B., 2011. Global food demand and the sustainable intensification of agriculture. Proceedings of the National Academy of Sciences of the United States of America 108, 20260–20264.

Ward, M.P., Black, P., Childs, A., Baldock, F., Webster, W., Rodwell, B., Brouwer, S., 1996. Negative findings from serological studies of equine morbillivirus in the Queensland horse population. Australian Veterinary Journal 241–243.

Weingartl, H.M., Embury-Hyatt, C., Nfon, C., Leung, A., Smith, G., Kobinger, G., 2012. Transmission of Ebola virus from pigs to non-human primates. Scientific Reports 2, 811.

Westbury, H., Hooper, P., Brouwer, S., Selleck, P., 1996. Susceptibility of cats to equine morbillivirus. Australian Veterinary Journal 74, 132–134.

Weyer, J., Grobbelaar, A., Blumberg, L., 2015. Ebola virus disease: History, epidemiology and outbreaks. Current Infectious Disease Reports 17, 1–8.

Williamson, M.M., Hooper, P.T., Selleck, P.W., Gleeson, L.J., Daniels, P.W., Westbury, H.A., Murray, P.K., 1998. Transmission studies of Hendra virus (equine morbillivirus) in fruit bats, horses and cats. Australian Veterinary Journal 76, 813–818.

Wood, J.L.N., Leach, M., Waldman, L., MacGregor, H., Fooks, A.R., Jones, K.E., Restif, O., Dechmann, D., Hayman, D.T.S., Baker, K.S., et al., 2012. A framework for the study of zoonotic disease emergence and its drivers: Spillover of bat pathogens as a case study. Philosophical Transactions of the Royal Society B: Biological Sciences 367, 2881–2892.

Zinsstag, J., Schelling, E. (Eds), 2016. The Future of Pastoralism. World Organisation for Animal Health (Office International des Épizooties), Geneva, Switzerland. Scientific and Technical Review 35(2), 1–720.