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REVIEW

Introduced deer and their potential role in disease transmission to livestock in Australia

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ABSTRACT

1. The transmission of pathogens between wildlife and livestock is a globally recognised threat to the livestock industry, as well as to human and wildlife health. Wild cervids are susceptible to many diseases affecting livestock. This presents a challenge for wildlife and domestic animal disease management because the frequent use of agricultural areas by wild cervids may hamper the effectiveness of disease control strategies.
2. Six deer species have established wild populations in Australia and are expanding in range and abundance. A comprehensive literature review of diseases impacting deer and livestock was undertaken, resulting in consideration of 38 pathogens. A qualitative risk assessment was then carried out to assess the overall risk posed by the pathogens to the livestock industry.
3. Five diseases (bovine tuberculosis, foot and mouth disease, malignant catarrhal fever, surra, and screw-worm fly infestation) ranked highly in our risk assessment. Of these five diseases, only one (malignant catarrhal fever) is currently present in Australia, but all five are notifiable diseases at a national level. Data on these diseases in deer are limited, especially for one of the most abundant species, the sambar deer *Rusa unicolor*, highlighting a further potential risk attributable to a lack of understanding of disease epidemiology.
4. This paper provides a detailed review of the pathogens affecting both cervids and livestock in Australia, and applies a qualitative framework for assessing the risk posed by deer to the livestock industry. The qualitative framework used here could easily be adapted to assess disease risk in other contexts, making this work relevant to scientists and wildlife managers, as well as to livestock industry workers, worldwide.

INTRODUCTION

The transmission of pathogens between wildlife and livestock is globally recognised as a threat to the livestock industry, as well as to human and wildlife health. The frequency of emerging (and re-emerging) infectious diseases in wildlife reservoirs has increased, posing new questions about disease pathogenesis and epidemiology (Rhyan &

Spraker 2010). Human-driven changes in land use, encroachment into wildlife habitat, increasing distribution and abundance of invasive alien species, climate change, and intensified livestock production practices are all factors that can increase the potential for disease outbreaks. Anthropogenic landscape modifications create new interfaces between livestock and wildlife, potentially exacerbating processes that favour pathogen transmission (Miller et al. 2013). The transmission of an infectious agent at the wildlife/livestock interface may occur directly, through interspecies contact, or indirectly, through shared space or vectors. Overabundance of native or invasive exotic species may exacerbate the risk of transmission through increased population densities and increases in host contact rates (Gortázar et al. 2006).

Multi-host pathogens are very prevalent among the infectious agents of domestic mammals; estimates suggest that 77% of pathogens infecting mammalian livestock are generalists that can infect multiple host species (Cleaveland et al. 2001). For parasites, the incidence of host sharing is variable but can be high: between 14 and 76% of nematode species found in various taxa of wild hosts also infect domestic hosts, and between 42 and 77% of nematode species in various domestic hosts are recorded as infecting wild hosts (Walker & Morgan 2014). As deer (family Cervidae) are ungulates, closely related to economically important livestock species including cattle *Bos taurus*, sheep *Ovis aries* and goats *Capra hircus*, it is unsurprising that they share many pathogens, including several of major agricultural importance. Wild cervids present a unique challenge for wildlife disease management, as they frequently share habitats and resources with domestic livestock. Previous reviews by Conner et al. (2008) in North America and Böhm et al. (2006) in the UK have covered many of these shared cervid–livestock infectious diseases in detail, but with a focus on the implications for those local contexts. The potential role of deer as vectors of diseases and pathogens in Australia was highlighted by Davis et al. (2016) but has not been examined in depth. Australian agriculture currently experiences substantial benefits due to its freedom from many epidemic diseases that impact livestock industries in other parts of the world. The issue of cervid-transmitted disease in Australia is highly significant, as exotic disease incursion or outbreaks of emerging or endemic disease could cause serious production losses, resulting in substantial economic impacts. Transmission of disease by cervids could also prevent effective control, management or eradication of a livestock disease, resulting in prolonged epidemics.

Globally, deer have been introduced to many countries and have become established in multiple areas outside their native range (Clout & Russell 2008). Australia is no exception – in the mid-1800s, multiple species were introduced to Australia from Europe and Southeast Asia, and now populations of six deer species, chital *Axis axis*, hog deer *Axis porcinus*, red deer *Cervus elaphus*, fallow deer *Dama dama*, Javan rusa *Rusa timorensis*, and sambar deer *Rusa unicolor*, are well-established and increasing in geographic range and abundance (Davis et al. 2016). There are no reliable estimates of deer abundance in Australia, but populations appear to be increasing in size. For example, deer harvest statistics in the state of Victoria show that the reported number of deer harvested has increased by an average of 15% per year since 2009, despite reduced harvest effort over this time (Moloney & Turnbull 2018). There are several issues associated with population increases of deer (reviewed by Burgin et al. 2015, Davis et al. 2016), including the expansion of deer into new areas and consequent increases in disease risk, especially as these species have not yet reached their maximum potential geographic ranges in Australia. Currently, wild deer are most commonly found in south-eastern Australia, however, Davis et al. (2016) showed that deer have the potential to occupy many parts of Australia from which they are currently absent, including parts of the arid interior (Fig. 1). In northern Australia, 75% of land is devoted to livestock production. This land contains almost 50% of Australia's cattle population (PricewaterhouseCoopers 2011). If pathogens of agricultural significance become established in wild deer populations, they will present a significant threat to livestock production and markets.

We set out to review the global literature on diseases of agricultural significance known to occur in wild deer populations, or to have documented potential to be transmitted to, and hosted by, any of the six Australian deer species, as well as economically important livestock species, predominantly sheep and cattle, but also pigs *Sus scrofa domesticus*, goats and horses *Equus caballus*. We do not review the impact on farmed deer, as they comprise only a small percentage (<0.05%) of livestock. In 2010–2011 (the latest year for which data are available), 45073 deer were farmed in Australia (Animal Health Australia 2017). In comparison, there are over 25 million cattle and 67.5 million sheep across the continent (Meat and Livestock Australia 2017). A large number of pathogens are theoretically hosted by both deer and livestock; it has been necessary to restrict this review to those diseases that have been relatively well studied or are of major economic importance. We conducted a qualitative risk assessment by compiling information to assess the potential risks of each disease to the Australian livestock industry, based on current understanding. The information we provide from our risk assessment could assist decision-making around disease prioritisation, management, and surveillance, both in Australia and elsewhere in the world where deer and domestic livestock interact. Hence, this disease risk assessment framework could easily be adapted and used within other contexts.

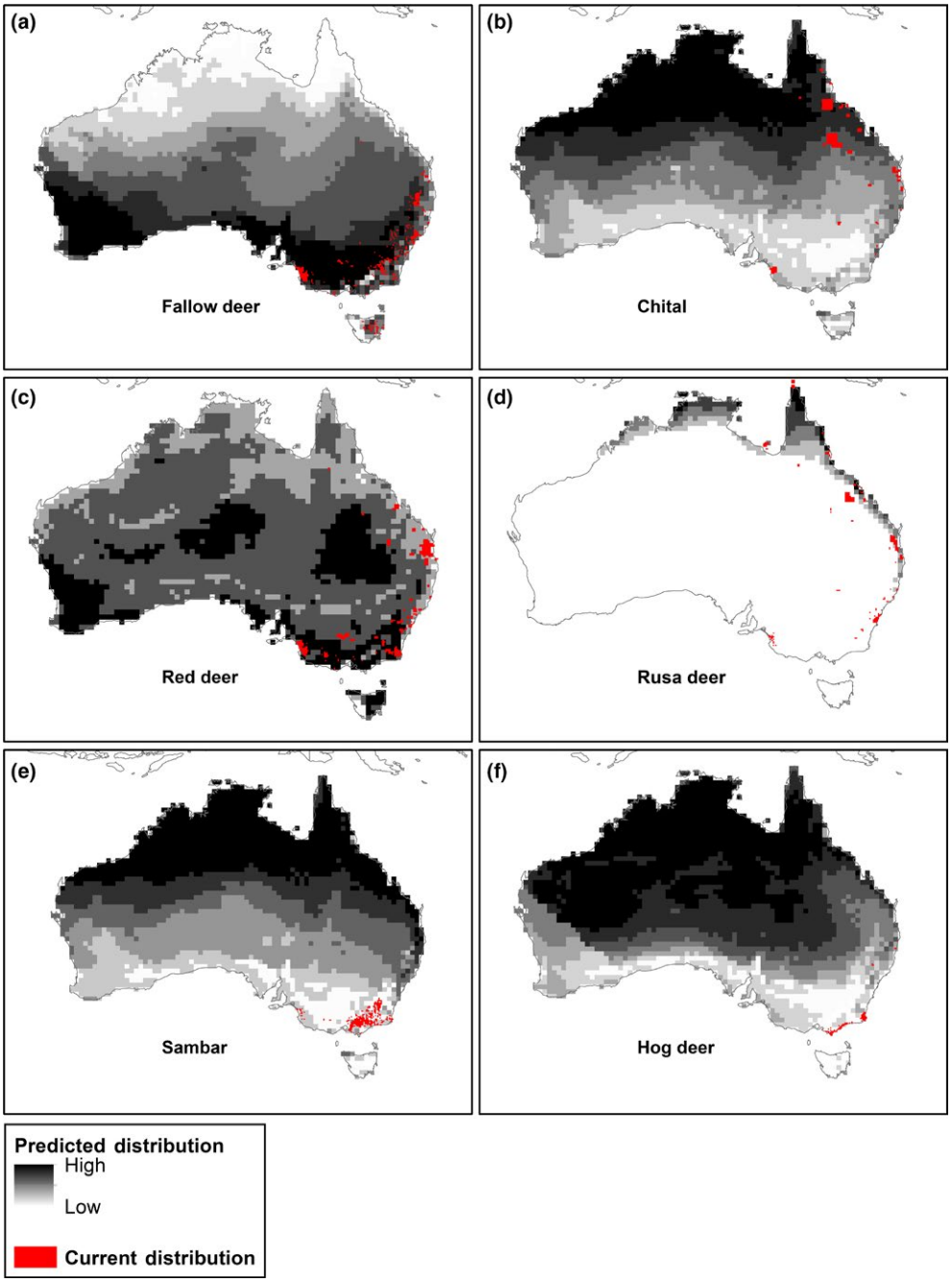

Fig. 1. Current (red; West 2011) and potential distribution (greyscale) of the six deer species established in the wild in Australia (republished from Davis et al. 2016). The potential distributions were estimated using the Climatch algorithm (Invasive Animals CRC 2011).

METHODS

Literature review

We identified peer-reviewed and grey literature from studies worldwide that have reported pathogens infecting wild deer (Cervidae) populations and known or potential transmission risks to economically important ungulate livestock in Australia. Our assessment, out of necessity, included pathogens not known to occur in Australia, but known to infect both livestock and wild Cervidae elsewhere. We briefly report on important literature regarding each parasite or pathogen fulfilling these criteria. Our intention was to cast the widest possible net and to identify

pathogens that fulfil the stated criteria for inclusion, without providing a thorough assessment for arrival or establishment risks in Australia. We also consulted earlier reviews on this topic from within Australia (Animal Health Australia 2011, Davis et al. 2016) and elsewhere (Simpson 2002, Böhm et al. 2006, Conner et al. 2008) to identify pathogens of interest. Previous reviews on this topic from Australia have been relatively brief – our work expands on these by conducting a thorough assessment of the literature to compile potential diseases shared by deer and livestock, and then prioritising the risk to the livestock industry through a risk assessment process.

We searched online databases (Web of Science, Scopus, Google Scholar) for references using combinations of the following search strings: 'deer', 'cervidae', 'spillover', 'disease', 'livestock', 'pathogen', 'parasite', 'source', and 'infection'. We also used the terms 'deer ("pathogen name")' and 'cervidae ("pathogen name")'. Full search strings are provided in Appendix S1.

We use the term 'maintenance hosts', for directly transmitted pathogens only, to describe hosts in which the disease persists by vertical transmission (mother to offspring) or by horizontal transmission (from one individual to another) within the species, without the need for any external source of reinfection. We use 'spillover hosts' to describe where the occurrence of the disease within a host population requires an external source of reinfection. Spillover hosts may further be characterised as 'dead-end' hosts if they play no further role in disease transmission (Coleman & Cooke 2001). Disease in spillover and dead-end hosts typically disappears, as disease is eliminated from the maintenance host. However, in some cases spillover hosts can act as amplifying hosts, increasing the transmission risk to other wildlife hosts or to livestock. The transmission of infection across the wildlife/livestock interface tends to occur predominantly through a spillover effect (livestock infect wildlife) or via a spillback effect where wildlife reinfect livestock (Conner et al. 2008).

Disease risk assessment

We evaluated several criteria (likelihood of deer being susceptible, being infected, transmitting the disease to livestock, and being infected by livestock) to rank the overall risk posed by the selected pathogens to the livestock industry, using a similar approach to Hartley et al. (2013). We expressed these qualitative 'likelihood scores' as high, medium, or low. With the first category ('susceptible'), we evaluated the degree to which there is certainty that the six deer species we considered are susceptible to the pathogen. With 'infected' we evaluated the likelihood of the deer species acquiring the infection, given that they are exposed to the pathogen. The 'transmitting the disease to livestock' criterion was used to express the likelihood that, once it was present in deer populations, the pathogen would be transmitted to livestock species. We used a gradient of likelihood scores, where we considered pathogens that are transmitted exclusively by direct physical contact to have a lower score than pathogens that are transmitted indirectly (for example by environmental contamination, which only requires shared habitat to spread the infection), which in turn were considered to have a lower likelihood than infections that are spread by vectors (where the assumption was made that suitable vectors exist in Australia). Our reasoning for this is that we consider very close physical contact of deer and livestock to be rarer (although anecdotal evidence indicates that it does sometimes occur) than situations where pasture or supplemental food is shared, for example, the use of feed troughs by deer. The category 'being infected by livestock' reported the likelihood of deer becoming infected, given that a disease is present in livestock. Factors that we took into consideration included whether management actions would be put in place to control infection in livestock, which may consequently also reduce the risk of infection to deer.

In contrast to Hartley et al. (2013), we separated the category 'infected' into three intermediate steps to allow a more transparent assessment, as well as to facilitate an update of our assessment when new information becomes available. The three steps were then combined to obtain an average 'infected' score. We detail these intermediate steps as follows:

Presence: whether the pathogen is present in Australia (or alternatively, the likely risk of it being introduced and becoming established). For pathogens not yet present, likely risks were assessed (as described in Appendix S2) using information that is publicly available through Biosecurity Import Risk Analyses (Australian Department of Agriculture and Water Resources 2018).

Distribution: we considered the geographical distribution (based on detected cases) of pathogens already present in Australia, or, alternatively, the likelihood of them becoming widespread should they arrive in Australia. We paid particular attention to whether the known (or potential) distribution of the pathogen would match the known and potential distribution of deer.

Transmission: the route of transmission plays an important role in the probability of transmission of diseases, as well as in disease management. We focussed on transmission within each deer species (i.e. intra-species transmission) and its influence on the epidemiology of the disease (e.g. highly contagious diseases were given higher scores).

In addition to the criteria used by Hartley et al. (2013), we included 'impact', where we attempted to predict the

potential additional economic impact that a disease would have on livestock farming (in this case, the economic impact on the predominant livestock farmed in Australia, sheep and cattle), should deer become an additional route of transmission to those already recognised. The impact depends on the clinical consequences of the disease, the management actions (e.g. containment, stamping out, slaughter, vaccination), and the costs resulting from these. Generally speaking, diseases that are currently common, and whose management would not dramatically change if deer were implicated in their transmission, were scored as having a low impact, while exotic diseases that would require extensive intervention or cause dramatic loss were scored as high.

We did not carry out a separate disease risk assessment for each deer species. However, we report notable differences when we expect these to occur. Most deer species found in Australia are known to use agricultural land (Lindeman & Forsyth 2008), especially when this occurs adjacent to, or is interspersed with, native forest areas, which are preferred deer habitat. Disease susceptibility and social behaviour were the two main factors evaluated when assessing differences between species. With the exception of sambar and hog deer, the deer species in Australia are gregarious, which generally facilitates higher contact rates and the spread of highly transmissible pathogens (Sah et al. 2018). In the absence of information on the relative abundance of deer, we therefore assumed that in situations of equivalent density, these gregarious species would pose a greater risk to livestock.

The overall risk assessment ranking was calculated using an average rating of the probability of occurrence (through combining the scores from the 'susceptible', 'infected', 'infecting livestock', and 'being infected by livestock' categories) and then ranking this against the potential 'impact' of the pathogen, using the risk assessment matrix shown in Table 1.

Table 1. Risk assessment categories used for assessing the overall risk (a combination of the probability of occurrence and the impact) posed by pathogens infecting wild deer for the livestock industry in Australia. The probability of occurrence was a combined score from the 'susceptible', 'infected', 'infecting livestock', and 'being infected by livestock' categories (see text for details)

	Impact		
Probability of occurrence	Low	Medium	High
Low	Low	Low	Medium
Medium	Low	Medium	High
High	Medium	High	High

RESULTS

Literature review

In total, we documented eight bacterial, eight viral, and one prion disease known to infect both the deer species that occur in Australia and livestock. All species of deer host a wide range of parasites, and we documented 19 endoparasites (13 helminths and six protozoans) and two ectoparasites which are known to infect both livestock and the deer species of interest. For each disease, we documented the host species, the transmission routes, whether the disease is present in Australia, and a list of relevant references from the literature (Table 2).

Disease risk assessment

From the list of documented pathogens (Table 2), the overall risk assessment (combination of probability of occurrence and impact) was assessed as 'high' for five pathogens, 'medium' for 11 pathogens and 'low' for 21 pathogens (Table 3). We describe below details on those diseases ranked as 'high', while comprehensive information and literature on the remaining pathogens (scored as 'low' or 'medium') can be found in Appendix S3.

Mycobacterium bovis (bovine tuberculosis)

Mycobacterium bovis, the causative agent of bovine tuberculosis (bTB), has one of the broadest host ranges of all known pathogens (O'Reilly & Daborn 1995). Bovine tuberculosis is primarily a respiratory disease and a prominent disease of cattle. It is found in most livestock species (cattle, sheep, goats, pigs, deer, and horses) and can become zoonotic. It is transmitted primarily by direct contact via infectious aerosols in farmed deer and livestock, but can also be spread through contact with urine and faeces in wild deer (Böhm et al. 2006). *Mycobacterium bovis's* broad host range includes many wildlife species such as common brushtail possums *Trichosurus vulpecula* in New Zealand (Coleman 1988), European badgers *Meles meles* in the UK (Gallagher & Clifton-Hadley 2000), bison *Bison bison* in Canada (Nishi et al. 2006), and African buffalo *Syncerus caffer* in southern Africa (Cross & Getz 2006). Epidemiological studies of bTB in wild deer populations have occurred in New Zealand (Nugent 2011), Europe (de Mendoza et al. 2006), and the USA (Schmitt et al. 1997).

There is evidence that *Mycobacterium bovis* strains can spillover from livestock into wild deer hosts (particularly fallow deer and red deer), and then spillback, reinfecting domestic livestock (Coleman & Cooke 2001, de Mendoza et al. 2006, Nugent 2011). There is also evidence that bTB can be maintained in free-ranging cervid populations

Table 2. Pathogens and parasites of concern for both deer and livestock species in Australia, and their likely transmission routes. Vertical transmission takes place from mother to offspring

Pathogen	Disease	Host deer species	Host domestic species	Transmission route	Present in Australia?	References
Bacterial						
Mycobacterium bovis	Tuberculosis	Red deer, fallow deer, chital	Cattle, sheep, goats, pigs, deer, horses	Respiratory, faecal–oral, urinary–oral, contact with infected skin/ wounds	No	Coleman and Cooke (2001) Simpson (2002) Böhm et al. (2006) Siembieda et al. (2011) de Lisle et al. (2001)
Mycobacterium avium spp. complex	Johne's disease, Paratuberculosis	Red deer, fallow deer, chital, sambar	Cattle, sheep, goats, pigs, deer	Faecal–oral, vertical	Yes	Mackintosh et al. (2004) Simpson (2002) Böhm et al. (2006) Siembieda et al. (2011) Coelho et al. (2013)
Leptospira spp.	Leptospirosis	Red deer, fallow deer	Cattle, sheep, goats, pigs, deer, horses	Urinary–oral, ingestion (e.g. water)	Yes	Mackintosh et al. (2002) Böhm et al. (2006) Siembieda et al. (2011) Miller et al. (2013) Ellis (2015)
Salmonella spp.	Salmonella	Red deer	Cattle, sheep, goats, pigs, deer, horses	Faecal–oral, ingestion	Yes	Mackintosh et al. (2002) Sanchez et al. (2002) Böhm et al. (2006)
Brucella spp.	Brucellosis	Red deer	Cattle, sheep, goats, pigs, deer, horses	Reproductive-oral	Yes	Corbel (1997) Böhm et al. (2006) Conner et al. (2008)
Bacillis anthracis	Anthrax	Red deer, fallow deer	Cattle, sheep, goats, horses	Ingestion (e.g. soil, water)	Yes	Mackintosh et al. (2002) Siembieda et al. (2011)
Yersinia spp.	Yersiniosis	Red deer, fallow deer, chital	Cattle, sheep, goats, pigs, deer, horses	Faecal–oral, ingestion	Yes	Mackintosh et al. (2002) Jerrett et al. (1990) Böhm et al. (2006) Mair (1973)
Chlamydia spp.	Chlamydiosis	Red deer, fallow deer	Cattle, sheep, goats, pigs	Faecal–oral, urinary–oral	Yes	Mohamad and Rodolakis (2010) Salinas et al. (2009)
Viral						
Aphthae epizooticae	Foot-and-mouth disease	Red deer, fallow deer, sambar	Cattle, sheep, goats, pigs, deer	Respiratory, faecal–oral, urinary–oral	No	Haigh et al. (2002) Simpson (2002) Sutmoller et al. (2003) Böhm et al. (2006)
Flavivirus	Louping ill	Red deer	Sheep, cattle (occasionally), pigs, horses, deer	Vector-borne (tick)	No	Simpson (2002) Callan and Van Metre (2004) Böhm et al. (2006)
Orbivirus	Epizootic haemorrhagic disease, bluetongue	Red deer, fallow deer	Cattle, sheep, deer	Vector-borne (midge)	Yes	Haigh et al. (2002) Maclachlan et al. (2015a) Maclachlan et al. (2015b)
Ephemerovirus	Bovine ephemeral fever	Red deer	Cattle	Vector-borne (unknown)	Yes	St George (1988) Nandi and Negi (1999) Haigh et al. (2002)
Pestivirus	Bovine viral diarrhoea disease	Red deer, fallow deer	Cattle, sheep, goats, deer	Faecal–oral, urinary–oral, reproductive-oral, vertical	Yes	Haigh et al. (2002) Simpson (2002) Böhm et al. (2006)
Parapoxvirus	Parapoxvirus	Red deer	Cattle, sheep, goats, deer	Contact with infected skin/ wounds	Yes	Horner et al. (1987) Haigh et al. (2002) Scagliarini et al. (2011)

(Continued)

Table 2. (Continued)

Pathogen	Disease	Host deer species	Host domestic species	Transmission route	Present in Australia?	References
Gammaherpesvirus	Malignant catarrhal fever	Red deer, fallow deer, sambar, hog deer	Cattle, sheep, pigs, deer	Respiratory, vertical, wind-borne	Yes	Heuschele et al. (1984) Mackintosh (1992) Haigh et al. (2002)
Alphaherpesvirus	Infectious bovine rhinotracheitis, cervid herpesvirus	Red deer, fallow deer	Cattle, deer	Respiratory, vertical	Yes	Nettleton et al. (1988) Engels and Ackermann (1996) Haigh et al. (2002) Callan and Van Metre (2004)
Prion diseases	Chronic wasting disease	Fallow deer*, red deer	NA	Respiratory, faecal–oral, urinary–oral, contact with infected material	No	Williams et al. (2002) Williams (2005) Hartley et al. (2013)
Parasites – Nematodes						
Ostertagia spp.		Red deer, fallow deer	Cattle, sheep, goats, deer.	Faecal–oral	Yes	Presidente (1978) Bisset (1980) Barth and Matzke (1984) Taylor et al. (2007)
Haemonchus spp.		Red deer, fallow deer, hog deer	Cattle, sheep, goats, deer	Faecal–oral	Yes	McKenzie (1985) Ferté et al. (2000) Taylor et al. (2007) Chintoan-Uta et al. (2014)
Spiculopteragia spp.		Red deer, fallow deer, sambar	Cattle, sheep, goats, deer	Faecal–oral	Yes	Andrews (1973) Rehbein and Haupt (1994)
Cooperia spp.		Red deer, fallow deer, sambar	Cattle, sheep, goats, deer	Faecal–oral	Yes	Taylor et al. (2007) Tapia-Escárate et al. (2015)
Dictyocaulus spp.		Red deer, fallow deer, sambar	Cattle, deer	Faecal–oral	Yes	Simpson (2002) Johnson et al. (2003) Taylor et al. (2007)
Oesophagostomum spp.		Red deer, fallow deer, sambar	Cattle, sheep, goats, pigs, deer	Faecal–oral	Yes	Andrews (1973) Taylor et al. (2007) Tapia-Escárate et al. (2015)
Trichostrongylus spp.		Red deer, fallow deer, sambar, hog deer	Cattle, sheep, goats, pigs, deer	Faecal–oral	Yes	Taylor et al. (2007) Tapia-Escárate et al. (2015)
Elaphostrongylus cervi		Red deer	Sheep, goats, deer	Intermediate host (gastropod)	No	Handeland et al. (2000) Böhm et al. (2006) Taylor et al. (2007)
Parasites – Trematodes						
Fasciola spp.	Liver flukes	Red deer, fallow deer, sambar	Cattle, sheep, deer	Intermediate host (gastropod)	Yes	Samuel et al. (2001) Taylor et al. (2007) Malcicka (2015)
Dicrocoelium dendriticum	Lancet fluke	Red deer, fallow deer	Sheep, deer	Intermediate hosts (gastropods and ants)	No	Samuel et al. (2001)
Paramphistomes	Rumen flukes	Red deer, fallow deer	Cattle, sheep, deer	Intermediate host (gastropod)	Yes	Skuce and Zadoks (2013) O'Toole et al. (2014)
Parasites – Cestodes						
Taenia hydatigena		Red deer, fallow deer, sambar	Cattle, sheep, goats, deer	Faecal–oral	Yes	Samuel et al. (2001) Taylor et al. (2007)

(Continued)

Table 2. (Continued)

Pathogen	Disease	Host deer species	Host domestic species	Transmission route	Present in Australia?	References
Echinococcus granulosus		Red deer, fallow deer	Sheep	Faecal–oral	Yes	Jenkins (2005) Taylor et al. (2007)
Parasites – Protozoa						
Giardia spp. and *Cryptosporidium* spp.[#]	Giardiasis, Cryptosporidiosis	Red deer, sambar	Cattle, sheep, goats, pigs, deer, horses	Faecal–oral	Yes	Samuel et al. (2001) Ryan and Power (2012)
Neospora caninum	Neosporosis	Red deer, fallow deer	Cattle, sheep, goats, pigs, deer, horses	Faecal–oral, vertical	Yes	Donahoe et al. (2015) Dubey (1999)
Trypanosoma evansi	Surra	Sambar, hog deer	Cattle, sheep, goats, pigs, deer	Vector-borne (tabanid flies)	No	Reid (2002) Desquesnes et al. (2013)
Sarcocystis spp.		Red deer	Cattle, sheep, goats, pigs, deer	Faecal–oral	Yes	Levine and Tadros (1980) Kutkienė (2003)
Eimeria spp.		Red deer, fallow deer	Cattle, sheep, goats, pigs, deer	Faecal–oral	Yes	Daugschies and Najdrowski (2005)
Parasites – Ectoparasites						
Rhipicephalus microplus	Cattle tick infestation	Red deer	Cattle	Direct	Yes	George (1990) Barré et al. (2002)
Chrysomya bezziana	Screw-worm fly infestation	Fallow deer, sambar	Cattle, sheep, goats, pigs, deer	Direct	No	Spradbery and Tozer (2013) Welch et al. (2014)

*Infected under experimental transmission only.
[#]combined due to similar epidemiology and clinical signs.

without infected livestock involvement (Schmitt et al. 1997, O'Brien et al. 2006), although there is a scarcity of data showing this for red, fallow, sambar, or hog deer. Wild deer populations appear to have the capacity to act as maintenance hosts for *Mycobacterium bovis,* particularly if they reach high densities (Coleman & Cooke 2001, Nugent 2011), or are highly aggregated (Ramsey et al. 2014), leading to outbreaks of bTB in livestock (Schmitt et al. 1997, Ramsey et al. 2014). Evidence from New Zealand suggests that deer could play a role in initiating new outbreaks of bTB outside infection areas through dispersal, or can reinitiate infection after it has been eliminated in other hosts by acting as a long-lived reservoir of infection (Ryan et al. 2006, Nugent et al. 2015).

Bovine tuberculosis formerly occurred in livestock in Australia, but was eliminated through an intensive test and slaughter programme (Cousins & Roberts 2001). An integral part of the success of the eradication program was the culling of wild water buffalo *Bubalus bubalis*, which reduced this species to low numbers and eliminated it as a maintenance host and source of reinfection for cattle (Cousins & Roberts 2001). A lack of other established wildlife hosts was also seen as a crucial factor for this success. Failure to eradicate bTB elsewhere (New Zealand, the UK) has generally been attributed to the presence of a significant wildlife reservoir (i.e. possums and badgers) causing continual spillback of disease to livestock populations (Tweddle & Livingstone 1994, Palmer 2007). There has only been one known outbreak of *Mycobacterium bovis* in deer in Australia, which occurred in three farmed herds of fallow deer and was successfully eliminated through a test and slaughter programme (Robinson et al. 1989).

Successful bTB control strategies tend to focus around test and slaughter or segregation of infected animals, although these strategies are complicated when there is a wildlife reservoir involved. Culling may decrease transmission by decreasing the population density of the reservoir host. However, it may not always be an effective method in controlling outbreaks, or be publicly supported (O'Brien et al. 2011). Vaccination of livestock against *Mycobacterium bovis* tends to occur when test and slaughter campaigns are not feasible, but the effectiveness of vaccination in wildlife hosts is yet to be proven (Siembieda et al. 2011). Any outbreak of bTB in wild deer populations would present a significant risk to the Australian livestock industry and would be costly to eradicate, resulting in substantial financial losses.

Table 3. Qualitative assessment of disease risk for deer and livestock in Australia. The pathogens and parasites are listed in Table 2, the method for the overall assessment is explained in Table 1. 'Susceptible' refers to the degree to which there is certainty that the six deer species considered are susceptible to the pathogen. 'Infected' refers to the likelihood of these deer species acquiring the infection given that they are exposed to the pathogen (based on whether the pathogen is present or has a likely risk of being introduced into Australia, the geographical distribution of the pathogen and its route of transmission). Risks are tabulated for the likelihood that, once present in deer populations in Australia, this pathogen will infect livestock, and conversely, the likelihood of deer being infected if the pathogen is present in livestock. 'Impact' refers to the potential additional economic impact that a disease would have on Australian livestock farming, should deer become an additional route of transmission

Pathogen	Disease	Susceptible	Infected	Infecting livestock	Being infected by livestock	Impact	Overall assessment
Bacterial							
Mycobacterium bovis	Tuberculosis	High	Medium	Medium	Low	High	High
Mycobacterium avium spp. complex	Johne's disease, Paratuberculosis	High	High	Medium	Low	Low	Medium
Leptospira spp.	Leptospirosis	High	High	Low	Medium	Low	Medium
Salmonella spp.	Salmonella	Medium	High	Low	Medium	Low	Low
Brucella spp.	Brucellosis	Medium	High	Low	Medium	Low	Low
Bacillis anthracis	Anthrax	High	Medium	Low	Low	Medium	Medium
Yersinia spp.	Yersiniosis	Medium	High	Low	Low	Low	Low
Chlamydia spp.	Chlamydia	Medium	High	Low	Medium	Medium	Medium
Viral							
Aphthae epizooticae	Foot-and-mouth disease	High	High	Medium	Medium	High	High
Flavivirus	Louping ill	Low	Low	Low	Low	Low	Low
Orbivirus	Epizootic haemorrhagic disease, bluetongue	High	Medium	Low	Low	Medium	Medium
Ephemerovirus	Bovine ephemeral fever	High	Medium	Low	Low	Low	Low
Pestivirus	Bovine viral diarrhoea disease	High	High	Medium	Medium	Low	Medium
Parapoxvirus	Parapoxvirus	High	Medium	Low	Low	Low	Low
Gammaherpesvirus	Malignant catarrhal fever	High	Medium	Low	Medium	High	High
Alphaherpesvirus	Infectious bovine rhinotracheitis, cervid herpesvirus	High	High	Low	Low	Low	Low
Prion diseases							
	Chronic wasting disease	High	High	Low	Low	Low	Low
Parasites – Nematodes							
Ostertagia spp.		High	High	Low	Medium	Low	Medium
Haemonchus spp.		High	High	Low	Medium	Low	Medium
Spiculopteragia spp.		High	High	Low	Low	Low	Low
Cooperia spp.		High	High	Low	Low	Low	Low
Dictyocaulus spp.		High	High	Medium	Low	Low	Medium
Oesophagostomum spp.		High	High	Low	Low	Low	Low
Trichostrongylus spp.		High	High	Low	Low	Low	Low
Elaphostrongylus cervi		High	Medium	Low	Low	Low	Low
Parasites – Trematodes							
Fasciola spp.	Liver flukes	High	High	Medium	Medium	Low	Medium
Dicrocoelium dendriticum	Lancet fluke	High	Medium	Low	Low	Low	Low
Paramphistomes	Rumen flukes	High	High	Low	Low	Low	Low
Parasites – Cestodes							
Taenia hydatigena		High	High	Low	Low	Low	Low
Echinococcus granulosus		High	High	Low	Low	Low	Low
Parasites – Protozoa							
Giardia spp. and *Cryptosporidium* spp.	Giardiasis, Cryptosporidiosis	High	High	Low	Medium	Low	Medium
Neospora caninum	Neosporosis	High	High	Low	Low	Low	Low
Trypanosoma evansi	Surra	High	Medium	High	Medium	High	High
Sarcocystis spp.		High	Medium	Low	Low	Low	Low
Eimeria spp.		Low	Medium	Low	Low	Low	Low
Parasites – Ectopasites							
Rhipicephalus microplus	Cattle tick infestation	Low	Medium	Low	Low	Low	Low
Chrysomya bezziana	Screw-worm fly infestation	High	High	High	High	Medium	High

Aphthae epizooticae (foot and mouth disease)

Aphthae epizooticae, causing foot and mouth disease (FMDV), is a highly contagious viral pathogen that spreads rapidly among livestock, particularly when animals are housed close together. It affects cattle, sheep, goats, pigs, and farmed deer, and is spread via the respiratory route, although small quantities of the pathogen are excreted in the faeces, urine, saliva, and other fluids of infected hosts. There are seven different viral serotypes of FMDV that are disease-causing, and they can persist in the environment for long periods of time when conditions are favourable (Davies 2002). Although most infected hosts can recover, outbreaks in livestock can have significant economic impacts (Knight-Jones & Rushton 2013). Infected animals can excrete the virus for up to four days before showing clinical signs. FMDV tends to have a higher transmission rate in cattle than in sheep, as cattle tend to be more susceptible to the disease (Keeling et al. 2001). Outbreaks have historically occurred in several parts of the world, including Europe, Africa, Asia, and the Middle East, and attempts to control FMDV have a long history (Sutmoller et al. 2003).

Although FMDV has been detected in many wildlife species, it appears to cause clinical disease almost exclusively in livestock (Weaver et al. 2013). Experimental studies in the 1970s showed that all deer species in the UK, including red and fallow deer, were susceptible to FMDV transmission when exposed to infected cattle, and could transmit the disease within their own species as well as to sheep and cattle (Sutmoller et al. 2003). Susceptibility of deer species to FMDV can vary and, while infection in red and fallow deer is generally subclinical (Simpson 2002), disease persistence can be high in these two species, increasing transmission risk to livestock. Red deer, for example, shed similar amounts of the virus to sheep and cattle (Haigh et al. 2002). FMDV infection has been recorded in six deer species including red and fallow deer (Haigh et al. 2002), and in captive sambar deer (Weaver et al. 2013). While there is clear experimental evidence of disease transmission between wild cervids and domestic livestock and vice versa, there is, however, limited evidence of this occurring under natural conditions (Weaver et al. 2013, Dhollander et al. 2016). Outside of Africa, where African buffalo are maintenance hosts, FMDV is maintained mainly in domestic ruminants, and wildlife occasionally become infected accidentally by spillover (Bengis et al. 2002). Epidemiological modelling of FMDV spread in deer in Europe has concluded that cervid populations are unlikely to be able to maintain FMDV for long periods of time without reinfection from domestic hosts (Dhollander et al. 2016). However, virus circulation may be prolonged when cervid population densities are high. Disease transmission between deer and domestic livestock is most likely to occur through direct contact between hosts.

Australia is currently free of FMDV and it is a notifiable disease in all states and territories. The introduction of this disease would have enormous economic impacts, with the costs of an outbreak of FMDV in Australia estimated to be up to A$5.2 billion (Buetre et al. 2013). Due to concerns around these economic impacts, epidemiological modelling for FMDV spread in feral pigs in Australia has been undertaken (Pech & Hone 1988, Doran & Laffan 2005), and suggests that very high culling rates of pigs would be required for eradication of FMDV. No literature could be located documenting comparable modelling of FMDV infection in deer in Australian. FMDV excretion can peak before clinical signs occur, which means the disease would be very difficult to contain or eradicate if there was an incursion into Australia, as its spread is rapid.

In livestock, FMDV control methods are normally focused around intensive culling (slaughter and disposal of susceptible livestock) on infected farms and surrounding farms, vaccination, and strict biosecurity controls for personnel who have contact with infected animals (Sutmoller et al. 2003). There has been widespread use of vaccination programmes in Europe to control the disease, which can be effective if maintained. As different serotypes are dominant in different parts of the world, control through vaccination can be difficult because vaccines that are effective against one serotype will not protect against others. Epidemiological modelling has been used to support decision-making processes during FMDV outbreaks in livestock, particularly in the UK (Keeling 2005), and could be a useful tool for modelling similar outbreaks in wildlife. Control strategies for FMDV outbreaks in wildlife are varied. Culling programmes to remove infected animals and reduce density have been used in Mongolian gazelles *Procapra gutturosa*, while fencing has been successfully used to manage FMDV transmission between African buffalo and livestock (Weaver et al. 2013).

Herpesviruses (malignant catarrhal fever)

Malignant catarrhal fever (MCF) is an infectious viral disease in the gammaherpesvirus group, often affecting domestic cattle and deer. Three types of the MCF herpesvirus have been identified as causing disease, with sheep and wildebeest *Connochaetes* spp. identified as asymptomatic carriers or natural hosts (Heuschele et al. 1984). These two natural hosts act as reservoirs, causing spillover infection in other species that then experience severe clinical disease. A feature of MCF in cattle is that outbreaks are unpredictable and sporadic, and infection typically occurs following close contact with sheep that are actively

shedding (Callan & Van Metre 2004). Transmission is predominantly respiratory, and direct contact with a natural host is not necessarily required – wind-borne infection has also been documented (Haigh et al. 2002). Vertical transfer of infection between a female and her offspring (transplacentally) can also occur. All herpesviruses can establish latent infections (where there is a dormant phase to their life cycle, Engels & Ackermann 1996), which allows the virus to persist in a population for long periods, with periodic reactivation, then posing a risk for transmission to domestic or wild animals.

Wildlife hosts infected with MCF include mostly wild ruminants (Heuschele et al. 1984) and there is abundant evidence that MCF occurs in free-ranging cervids (Heuschele et al. 1984, Li et al. 1996). Indeed, MCF is considered one of the most important diseases of farmed deer due to its high mortality rates (Reid & Buxton 1984). MCF has been reported in 14 species of deer, including five of the Australian species – red, fallow, chital, sambar, and hog deer (Heuschele et al. 1984, Semiadi et al. 1994, Haigh et al. 2002). Stress seems to play a significant role in disease outbreaks, with infection peaking when conditions are crowded and during winter and spring, when deer may be in poorer condition (Haigh et al. 2002). Deer appear to be particularly susceptible and death often occurs within 48 hours of the first clinical signs (Jesser 2005). However, the evidence suggests that deer are not significant maintenance hosts, but tend to be spillover hosts, acquiring the infection primarily from sheep (Reid et al. 1979).

Malignant catarrhal fever occurs sporadically in Australia and mainly in cattle. Outbreaks in captive deer have been documented in Australia (Tomkins et al. 1997), and lesions consistent with MCF were described by Presidente (1978) in captive Javan rusa deer in Victoria, but the virus could not be isolated and confirmed as that causing MCF. No effective treatment or vaccine for MCF has been described. In the absence of a vaccine, the best strategy appears to be limiting contact between susceptible species, for example, deer and the natural host, sheep (Callan & Van Metre 2004).

Trypanosoma evansi (surra)

Trypanosoma evansi is a protozoan that causes the disease trypanosomiasis or surra in vertebrate animals. *Trypanosoma evansi* is transmitted mechanically by various species of tabanid flies (horseflies). It is found over a wide range of climates, but is more common in the tropics. The main host species affected by *Trypanosoma evansi* depends on the predominant mammalian species in a region, as it has a wide host range (Reid 2002). *Trypanosoma evansi* has become established in wild reservoirs all over the world, mostly as a consequence of moving infected livestock. Deer, including sambar and hog deer (Desquesnes et al. 2013), are susceptible to *Trypanosoma evansi*, however, reports of surra in deer are not particularly common. As deer may tolerate a heavy burden of *Trypanosoma evansi* without showing any clinical signs, they can be an efficient reservoir of the pathogen (Reid et al. 1999).

The only known introduction *of Trypanosoma evansi* into Australia was in camels *Camelus dromedarius* and *Camelus bactrianus* imported from India to Port Hedland, Western Australia, in 1907 (Reid 2002), and this incursion was rapidly eradicated through the slaughter of infected animals. Today, the likely route of introduction would be via eastward spread into Papua New Guinea and then across the islands of the Torres Strait (Reid 2002). *Trypanosoma evansi* is a substantial threat for Australia and has the potential to become endemic, firstly because tabanid vectors are common, and secondly because there are large populations of potential reservoir hosts, such as feral pigs, in many areas where livestock occur (Reid 2002). It is a notifiable disease in all states and territories. Although small outbreaks of surra have been eradicated in Australia and elsewhere, no country is known to have eliminated the disease once it has become well established (Desquesnes et al. 2013). Increasing populations of feral deer would be likely to act as reservoirs and could contribute to disease establishment, should it reach Australia.

Chrysomya bezziana (screw-worm fly infestation)

The Old World screw-worm fly *Chrysomya bezziana* is a parasitic insect pest that is endemic to the tropical regions of Asia, the Middle East, and Africa. The insect reproduces by laying its eggs in open wounds and mucus membranes of mammals. Upon hatching, the fly larvae eat the living flesh of the host, causing injury (cutaneous myiasis), secondary infections, and in extreme cases, death. *Chrysomya bezziana* has been found in free-ranging sambar deer in India (Radhakrishnan et al. 2012) and in captive Persian fallow deer (*Dama dama mesopotamica,* Mombeni et al. 2014). In Papua New Guinea, Javan rusa deer are likely to be maintenance hosts of *Chrysomya bezziana* (Spradbery & Tozer 2013). No literature on its occurrence in other wild deer species could be located. Currently the Australian mainland is free of *Chrysomya bezziana*, and although its distribution is relatively static, its range includes Australia's tropical northern neighbours such as Indonesia, Malaysia, and Papua New Guinea. Due to the close geographical location of *Chrysomya bezziana* range and the shipping traffic to and from Australian ports, there is a risk of introduction of this species to Australia through importation of the insect, particularly in northern Australia (Welch

et al. 2014). Increasing populations of wild deer would be likely to act as reservoirs and further contribute to spread of the parasite, should it reach Australia.

DISCUSSION

Diseases of deer and potential threats to Australian livestock

In total, we considered eight bacterial, eight viral, one prion, thirteen helminth, six protozoan, and two ectoparasitic diseases (Table 2, Appendix S3) affecting deer and livestock species. Many of the pathogens are zoonoses and pose a risk of disease in humans as well. There is substantial literature describing infectious diseases in deer, but very little of this is focused on deer in Australia. Indeed, there is a scarcity of recent information describing basic screening of diseases in deer found in Australia. Also of note was the deficiency of information available in the literature about the pathogens infecting Asian deer species, such as sambar deer or hog deer, which makes it difficult to assess their susceptibility and their potential contribution to disease risk in Australia. By far the overwhelming majority of studies of cervid diseases relevant to Australia have come from research in the UK on red and fallow deer (reviewed by Böhm et al. 2006).

We focused this review on a range of infectious agents that have the potential to be shared between domestic livestock and wild deer and are likely to be of economic importance to livestock farming. Given the current paucity of information, we found it particularly difficult to estimate the impact of diseases that are currently present within Australia, and for which an increase in deer abundance or range may affect their incidence. The overall disease risk for the majority of pathogens was found to be low, which was supported by the lack of evidence for clinical infection in deer to date. However, some diseases, such as anthrax and bluetongue, which are currently present in Australia, are considered to be medium risk based on a relatively low risk of transmission to or from livestock and the moderate potential economic impacts they could have if wild deer were to play a role in future outbreaks. Risk may be greatly underestimated if there is significant uncertainty around diseases scored as 'medium' or 'low' due to limited knowledge of these diseases. The impact of variation in knowledge and disease ranking would be worthy of further investigation.

Of the pathogens we considered, the majority are transmitted by contact with, or ingestion of, contaminated excretory products in the environment, mostly via the faecal–oral route. Experimental and natural transmission studies in deer have provided disease-specific evidence for the transmission of many of the pathogens we examined. However, common susceptibility to a disease does not necessarily equate to shared infection. Few studies have examined the natural transmission of pathogens between livestock and deer, and modes of transmission are still not fully understood in many cases (Frölich et al. 2002). The existence of a pathogen in either wild deer or domestic ruminants is irrelevant to establishment of the disease in the other if the two populations do not interact, either directly or indirectly (Hartley et al. 2013). A recent review by Pruvot et al. (2014) also suggests that transmission route can be important when assessing the risk of pathogens spreading between domestic and wild animals; indirectly transmitted pathogens are more easily shared between species than directly transmitted ones, because they do not require a strict temporal or spatial sympatry. Future work in Australia should focus on quantifying contact rates between deer and livestock, in order to improve estimates of infection likelihood. This can be done by using proximity loggers or animal-borne cameras, as demonstrated by Lavelle et al. (2014), or by using molecular markers (Streicker et al. 2010, Allison et al. 2013, Faria et al. 2013).

Influence of deer ecology and density on disease risk

The behavioural ecology of each deer species influences its exposure risk to different diseases. Sharing of habitat with livestock, as has been reported in sambar deer in Victoria, Australia (Lindeman & Forsyth 2008), increases the risk of transmission via fomites, vector, and aerosol spread. Riparian habitat within agricultural regions can exacerbate disease risk, as deer may concentrate in these areas, increasing between-group contact rates and spatial overlap (Nobert et al. 2016). Social behaviour affects transmission between wild deer, as the number of contacts between conspecific individuals influences the ability of a disease to become established (Hartley et al. 2013). Most deer species present in Australia are gregarious (with the exception of sambar deer and hog deer), forming large groups and thus increase the probability of disease spread (Animal Health Australia 2011, Sah et al. 2018). This may be especially relevant for two of the highly ranked diseases, bovine tuberculosis and foot and mouth disease. Male cervids may contribute disproportionately to the risk of transmission, through contact with multiple females during the breeding season across a range of spatial scales; or through contact with infectious agents at scent stations (Conner et al. 2008). Moreover, breeding interactions may leave male deer in poor condition and susceptible to disease.

The size of the host's home range influences the potential for disease transmission to livestock and other deer

herds, as it indicates the likely extent of movement of individual infected animals, and therefore the geographical range over which each animal could transmit disease. In cervids, juvenile males disperse from their natal home range, which could also contribute to the spread of disease and movement of infection into new areas (Conner et al. 2008). Seasonal changes in food availability may result in animals frequently making short-distance movements to more suitable habitats or food sources (Conner et al. 2008), which may bring them into contact with livestock or cause them to transmit disease to deer in uninfected areas. Unfortunately, little is known about the home range sizes and seasonal movements of any of the deer species in Australia.

Current and future range expansions of deer into new locations may result in disease establishment there, as these new environmental conditions may be more suitable for certain diseases. Range expansions will also increase the risk of deer encountering other cervid species, livestock and farmed deer. If deer expand into areas of high livestock density, disease establishment and maintenance in the host deer population and spillback to livestock will become more likely (Böhm et al. 2006). The risk of both direct and indirect disease transmission will be influenced by host density, and there is likely to be a greater risk of transmission in areas of both high livestock density and high deer density. Increasing deer abundance means an increased number of hosts available for the transmission of disease, and a higher contact rate between hosts. These issues are likely to be particularly relevant for three of the highly ranked diseases, bovine tuberculosis, foot and mouth disease, and malignant catarrhal fever, because high host densities can result in the disease becoming established in the deer population. When sympatric host species share the same infectious disease, multiple transmission pathways are possible (Woolhouse et al. 2001, Barron et al. 2015). Under such circumstances, multiple hosts can act as one large heterogeneous host population, potentially exacerbating disease transmission and spread (Dobson 2004). Consequently, increases in deer abundance may exacerbate the potential for disease persistence and spread in livestock-deer communities.

CONCLUSION

Deer have the potential to play a significant role in the epidemiology of multiple livestock diseases, both those that are currently present in Australia, and those that are absent but have the potential to become established in the future. Of the 38 pathogens we reviewed, five of these classify as of a high risk for transmission by deer to Australian livestock. Of these five diseases, only one (malignant catarrhal fever) is currently present in Australia, but all five are notifiable diseases at a national level. Our review has revealed that there is little understanding or discussion of disease risks in deer within the Australian literature. This is especially concerning as deer populations are large and expanding, and it is likely that the eradication of exotic diseases through culling would be very challenging. Furthermore, sambar deer and hog deer pose potential risks due to the dearth in understanding of the ecology and disease epidemiology of these two species.

Our disease risk assessment can assist decision-makers by outlining high, medium, and low risks of diseases of concern. However, improvements in disease monitoring of Australian deer are required to provide timely knowledge on disease incursion and spread, in order to minimise the risk of impacts on both humans and livestock. At present, there are no disease surveillance programmes targeting deer in Australia. Hence, the feasibility of large-scale surveillance strategies for detecting incursions of exotic disease or outbreaks of endemic disease in Australian deer populations should be investigated. Large-scale surveillance programmes of wild deer could be based on hunter-harvested deer or on other forms of passive surveillance (e.g. public reporting of moribund or dead deer). Successful examples of such passive surveillance programs utilising hunter-harvested deer include bovine tuberculosis surveillance programs in France (Rivière et al. 2015) and in lower Michigan, USA (O'Brien et al. 2006). These programmes could serve as models for a surveillance programme in Australia.

We apply the disease risk assessment to the Australian context, and provide a framework that can easily be adapted to different contexts. For example, in other locations where livestock farming is less extensive than in Australia, the three categories ('presence', 'distribution', and 'transmission') which are used to calculate the 'infected' score, can be altered as required. Our review highlights how a qualitative risk assessment can be used to ascertain which diseases pose the highest risk and where gaps in knowledge inhibit our understanding and risk of disease transmission, making our approach relevant to scientists, wildlife managers, and livestock industry workers worldwide.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Web of Science, Scopus, and Google Scholar search terms used to review the literature on the pathogens of deer and livestock and disease risk.

Appendix S2. Notes on the process of assessing the risk of disease entry into Australia.

Appendix S3. Summary details on diseases ranked as 'low' or 'medium' in the disease risk assessment.