An overview of the challenges and methods for defining the wildlife-disease interface in the context of disease spread modelling, including concepts of infectious diseases epidemiology

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Abstract

The wildlife-domestic interface is a key concept helping us to understand how diseases affect both wild and domestic animal populations, yet how to define and measure it remains a challenge. One tool which can contribute to our understanding of the wildlife-domestic interface is disease spread modelling. This can provide insight into how diseases spread within and between populations, and guide decision-making for disease control, response and surveillance programs. Specifically, quantitative estimation of contact rates permits such disease spread models to be developed and used confidently. Here we present a case study of the potential spread of rabies (an exotic disease in Australia) within the wild dog-domestic dog ecosystem of northern Australia to illustrate the concept of the wildlife-domestic interface and disease transmission. Over a period of 10 years, free-roaming domestic dogs and wild dogs in the Northern Peninsula Area (NPA) of Cape York, Queensland were studied. Key findings included identification of a small but important group of domestic dogs which regularly roam in bushland areas; peri-urban wild dog activity, particularly in the dry season, likely driven by the availability of food sources; and the potential for interaction between hunting dogs and wild dogs in remote areas, particularly during the wet season. These observations can be used to inform disease spread models and identify strategies to mitigate the risks of disease transmission. However, the collection and incorporation of data into such models needs more consideration regarding what information is usable (such as contact rates) and the best ways to collect it. The scarcity of such models incorporating the wildlife-domestic interface suggests that integrated epidemiological-ecological studies are needed to fill this gap.

Key words: Wild-domestic interface; Dingo; Dog; Infectious disease model

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The wildlife-domestic interface is a key concept for understanding how diseases affect both wild and domestic animal populations, and how diseases within one population can affect another population. Despite its importance in animal health, the wildlife-domestic interface remains a challenge to define and to measure. Disease spread models of wildlife-domestic animal ecosystems attempt to characterise this interface and provide insight into how diseases spread within and between populations, and guide decision-making for disease control, response, and surveillance programs. Here we discuss the concept of the wildlife-domestic interface and disease transmission, present the basics of disease spread models, and provide a case study of the potential spread of rabies (an exotic disease) within the wild dog-domestic dog ecosystem of northern Australia. We conclude with recommendations to improve research of the wildlife-domestic interface to facilitate our understanding of disease spread and its implications.

1. The wild-domestic interface

Interfaces between populations are important in infectious disease epidemiology because they are spatiotemporal points of contact at which transmission of microbes between populations could occur, leading to spill-over events and potentially, the emergence of infectious diseases (Magouras et al., 2020). Understanding the characteristics of such interfaces, how contacts and microbe transmission occurs, and can be influenced is critical to prevent disease spread (Hassell et al., 2017).

The wildlife-domestic interface represents risks of transmission of microbes between wild and domestic animals. Because such interfaces involve domestic animals, they are usually anthropogenic, occurring when people and their activities encroach on wildlife habitat (for example, agriculture (Jori et al. (2021) or deurbanization (Ward et al., 2004)), people bring wildlife into built environments (for example, wildlife farming and markets; Brookes et al. (2022); Wikramanayake et al. (2021)), or wildlife become adapted to built environments (Bradley & Altizer, 2007).

Established wildlife-domestic interfaces for infectious disease spread include rabies virus between wild and domestic dog populations (Lushasi et al., 2021), Japanese encephalitis virus between waterbirds, pigs and poultry (Mulvey et al., 2021; Walsh et al., 2022), and tuberculosis between badgers and cattle (Chambers et al., 2014). These examples demonstrate the diversity of reservoir and other host species, as well as ecological landscapes in which interfaces occur. The need to understand interfaces involving wildlife and how disease transmission events occur has become more important over the previous few decades as increased anthropogenic pressure on wildlife populations and their habitats have intensified the risk of microbe transmission, resulting in increased frequency of emergence of infectious diseases (Cunningham et al., 2017). Recent – and well-defined – wildlife-domestic interfaces include those at which henipaviruses have emerged, including Hendra virus from bats to horses and Nipah virus from bats to pigs (Field et al., 2007); but there are also less well-defined or unknown interfaces in which a disease of animal origin might have arisen from wildlife with a domestic livestock or farmed wildlife intermediate. Examples of the latter include SARS and COVID-19 (SARS-CoV and SARS-coV2, respectively) in which wildlife and interfaces with farmed animals at markets are implicated but the specific interfaces (for example, which species were involved) are unknown (Shi & Hu, 2008; Worobey et al.).

Disease spread models can provide insights about the circumstances in which wildlife-domestic interfaces become important, and factors that could limit the transmission between populations at these interfaces. A critical limitation of such models is that they are dependent on adequate data to produce meaningful and useful predictions. Recent reviews demonstrate that the data required for such models or about specific interfaces can be limited (Brookes et al., 2022; Gabriele-Rivet et al., 2019). Defining such interfaces in terms of the species and pathogens involved, and the extent of the interface (for example, spatially and temporally, the abundance or density of species involved, and the prevalence of potential pathogens) are minimum requirements, but fundamental to useful models is quantification of the probability or rate of effective contact such that microbe transmission could occur between individuals.

In the following sections, we review the concepts of infectious disease epidemiology in the context of disease spread models, then illustrate the types of data required using the example of rabies modelling in northern

Australia and the quantification of contacts that would be required to determine rabies spread between wild and domestic dog populations.

2. Disease transmission and the application of disease spread models

Disease spread involves the transmission of a pathogen (or a microbe with pathogenic potential) from one individual to another. In some cases, the event during which transmission occurred can be identified (for example, a sexually transmitted disease such as *Campylobacter fetus venerealis* in cattle, or a disease such as rabies in which the bite was observed). However, unequivocal identification of the transmission event is rare; most diseases have several routes of transmission, and microbes, by definition, are usually invisible to the naked eye. Typically, an individual becomes infected, and a range of time, places and methods by which transmission could have occurred are identified, with the certainty of these estimates dependent on the epidemiology of the disease and the information available about the individual case. Identification of transmission events in wildlife populations - which might be rarely observed or hide from people - is even more challenging.

When considering the epidemiology of infectious diseases, it is useful to think in terms of the 'infectious diseases triad' which includes features about the pathogen, hosts, and the environment. As well as describing the distribution of disease in terms of where and in whom it occurs, these three domains determine the situations in which 'effective contact' can occur. Effective contact is the situation in which disease could successfully transmit between two individuals if one were infected and the other susceptible. The least complex infectious disease triad combination involves pathogens with a single host and a limited or non-existent environmental stage. Examples include herpes viruses, such as infectious bovine rhinotracheitis virus and equine herpes virus 1, and lente viruses such as caprine arthritis encephalitis virus. Combinations of factors – and hence the range of possible circumstances, or routes, in which effective contact could occur – increase if the pathogen can survive in the environment (for example, foot and mouth disease virus on fomites, foodborne bacteria such as *Salmonella* spp, and the spore-forming bacteria that cause clostridial diseases), there is a mechanical or biological vector (for example, *Stomoxys* flies and porcine reproductive and respiratory syndrome virus, and ornithodorid ticks and African swine fever virus), and there is more than one host (for example, many parasitic diseases, and zoonoses). In any disease transmission event between two individuals (one infected, the other susceptible), there is both a probability of a route of transmission given the combination of factors that could have occurred, and a probability that pathogen transfer and infection then occurred.

Disease spread models are a useful tool to generate insights about how the dynamics of a particular disease in a population can be influenced by control methods. At a population level, models are useful to explore how disease spreads, given the probabilities of the range of effective contact possibilities and subsequent transmission and infection. The simplest disease spread model can be defined in terms of only 2 states in which an individual can be either susceptible or infected, and therefore, the population is divided between these two states. In this simple model, the assumption is that once an individual is infected, they remain infected. The model is dynamic, because the risk of infection for individuals who are susceptible (S) depends on the relative proportion or number of infected individuals. To start with, when there are very few infected individuals, the overall risk of infection is low, and the rate of transition of the population from S to I is low. However, this rate increases as the number in I grows, and then decreases again as the number of S falls. Unpacking the mathematical basis of this dynamic change in rate of infection demonstrates the importance of defining effective contact in disease spread models, and the type of field data that is required for parameterisation.
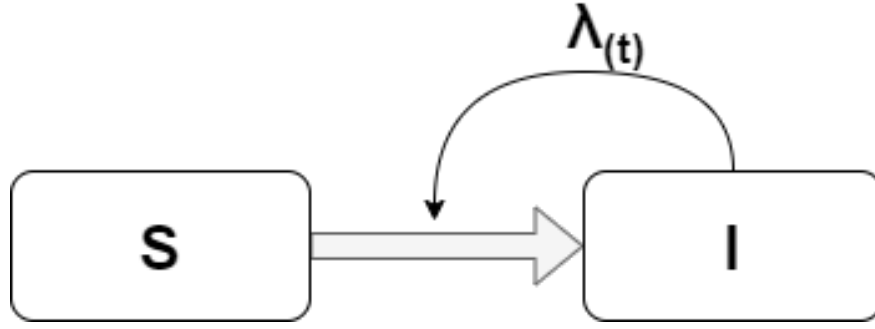
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$$\lambda_{(t)}$$

Figure 1: Compartmental SI model of disease spread, in which S = susceptible group, I = infectious group, and λ = risk (or force) of infection which determines the rate of transition of the population from S to I.

We use differential equations to illustrate the process of disease transmission as a continual process, although difference equations using a time-step process could also be used (Vynnycky & White, 2010). The risk of infection, known as $\lambda_{(\tau)}$, is the rate at which susceptible individuals become infected and is dependent on both the number or proportion of infected individuals in the population, $I_{(t)}$, and the effective contact rate (*ecr*), or *ß* , more formally defined as the per capita rate at which two specific individuals come into effective contact per unit time (Equations 1 and 2).

$$\lambda_{(t)} = \ \beta.I_{(t)} \ \text{Equation 1}$$

$$\beta \ = \ ecr/N \ \text{Equation 2}$$

The disease model can then be defined in terms of 2 equations in which the S compartment loses individuals and the I compartment gains individuals as disease spreads (Equations 3 and 4; Figure 2).

$$\frac{dS_{(t)}}{dt} = \ - \ \beta.I_{(t)}. \ S_{(t)} \text{Equation 3}$$

$$\frac{dI_{(t)}}{dt} = \ \beta.I_{(t)}.S_{(t)} \text{Equation 4}$$

We can further define effective contact by considering the basic reproductive rate, R_0 . This is the number of infected individuals that arise from one typically infectious individual during their entire infectious period when introduced to a totally susceptible population. Therefore, R_0 is equivalent to the effective contact rate (*ecr*) multiplied by the duration of infectiousness, D (Equation 5), and the per capita rate at which two specific individuals come into effective contact per unit time is described in Equation 6.

$$R_0 = ecr \ . \ D \ \text{Equation 5}$$

$$\beta = \ R_0/(N \ . \ D) \ \text{Equation 6}$$

Further modification of equations to describe effective contact depend on whether we assume contacts are dependent on the density of the population, or are limited to a finite number of contacts between two individuals (Begon et al., 2002). This is determined by our understanding of the disease transmission process. The former is called density dependent transmission, the latter frequency dependent transmission. The density dependent assumption is generally considered appropriate for animal diseases in which the population is constrained within a given space. This might be the case for livestock, and perhaps also many wild animal species. The frequency dependent assumption might be more appropriate in the case of sexually-transmitted diseases, or human or companion animal diseases in which contact is determined by social networks and constraints, rather than population size.

To produce a realistic output, data to parameterise the effective contact rate is essential (Kirkeby et al., 2020). Without knowing details about the way in which the disease is transmitted, a modeller can use previous or current outbreak data to determine the likely duration of infectiousness of individuals and R_0 .

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However, relevant outbreak data are often unavailable, and although it might be possible to generalise R_0 and the duration of infectiousness from other situations, R_0 depends on local context (for example, the R_0 of measles is estimated to range from 12 to 18; Guerra et al., 2017). Instead, the frequency of contact at disease transmission interfaces and the probability of transmission given the potential routes of transmission can be used to infer an effective contact rate. This approach is often used when building models in contexts in which outbreaks are yet to occur and the model is being used to predict the pattern of disease spread and the efficacy of control measures. A range of experimental and observational data might be used, for example, laboratory transmission experiments to define transmission probability, and field telemetry data to define contact rates. In the next section we describe a range of methods that have been used in rabies spread models in free-roaming domestic and wild dogs in northern Australia to parameterise the effective contact rate using the probability of contact (bite) and the probability of rabies virus transmission, given a contact.

Models become more complex and data requirements increase for diseases with multiple routes of transmission because each route has a probability of effective contact (more than one ß) for which species-specific data about the probability of contact needs to be collected, as well as disease-specific data such as the probability of infection associated with the route. For disease transmission between populations, such as at a wildlife interface, population density, distribution, and the behaviour of the populations such as pack size, home range and seasonality, or spatial variation of movements might be required, to reflect the nature of interaction between the populations. This contact heterogeneity (rather than homogenous mixing) can be important for valid predictions of disease spread patterns and assessment of control options.

Population dynamics are also needed to derive birth and death rates (which could also be seasonal), and knowledge of the progression of disease in individuals is required to parameterise the rate of transition between states other than susceptible to infected (for example duration of infectiousness to determine rate of recovery in an SIR model). Finally, uncertainty can be reflected by introducing stochasticity of events so that outputs represent a range of possibilities (for example, the number of individuals infected, or the duration of an outbreak), and by using distributions of parameters to represent known natural variability (for example, in disease parameters such as latent period or in population parameters such as group size) or limited knowledge (the influence of such parameters can be assessed using sensitivity analysis).

3. Case study: potential disease (rabies) spread between wild and domestic dogs in northern Australia

Rabies in people is almost invariably fatal. The greatest burden of this disease is in Africa and Asia, where nearly all cases are attributable to a bite from a rabid dog (Hampson et al., 2015). Although rabies can be prevented in people by timely treatment of bite wounds and administration of post-exposure prophylaxis, vaccination of dog populations – both owned and unowned – is recognised as the key to controlling rabies within a One Health framework (Fahrion et al., 2017; Ward and Brookes, 2021).

During the past few decades, rabies has spread to areas in Southeast Asia where historically it was not present (especially islands), and incidence has increased in some areas where rabies was previously controlled. This (re)emergence of rabies is typified by the spread of rabies in the eastern islands of Indonesia – including Bali, Flores and Ambon – increasing the risk of a rabies incursion in northern Australia (Ward and Brookes, 2021). Dog-mediated rabies has never been reported from Australia (except for a suspected outbreak in Hobart in 1866-1867) (Rupprecht et al., 2010). Given a lack of experience with rabies and its control, the large populations of roaming domestic dogs and wild dogs, existing disease spread pathways and its remoteness and subsequent challenges for surveillance, modelling of the spread of rabies in northern Australia - should an incursion occur - has become a priority (Sparkes et al., 2015). Models of how rabies might spread within wild dog populations (Johnstone-Robertson et al., 2017; Gabriele-Rivet et al., 2021a) and domestic dog populations (Durr and Ward, 2014; Brookes et al., 2019) in the Northern Peninsula Area (NPA) of Cape York, Queensland and on islands in the Torres Strait have been developed. These models have focused on each population and have generated information about how rabies might best be controlled; for example in domestic dog populations in Indigenous communities (Hudson et al., 2019a, b).

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Despite potential interactions between wild and domestic dogs (the *wild-domestic interface* ; Bombara et al., 2017a, 2017b; Gabriele-Rivet et al., 2019a; Ward et al., 2021), integrated modelling of rabies spread between free-roaming domestic dog and wild dog populations has not been undertaken. Interactions at this interface can potentially occur via domestic dog forays into bushland areas, wild dogs attracted to focal points within communities as a food resource (for example refuse dumps and abattoirs) and through hunting with domestic dogs in bushland areas (Ward et al., 2021). Here we review research that has been conducted on free roaming domestic dog populations and wild dog populations, separately and focused on contact patterns, to inform disease spread modelling. We further review research that contributes to the definition of the interface between free-roaming and wild dog populations, with the aim of identifying research gaps and making recommendations for further research at the wildlife-domestic interface.

3.1. Study area

The Northern Peninsula Area (NPA) is a local government area situated at the tip of Cape York, Queensland, Australia and adjacent to the Torres Strait to the north. Further to the north lies Papua New Guinea. The NPA is 105,207 hectares in size and incorporates the Indigenous communities of Bamaga, Injinoo, New Mapoon, Seisia and Umagico. Outside of these five communities, the vegetation and landscapes are diverse – including woodlands, grasslands, tropical rainforests, heathlands, wetlands and large river systems. It is a biodiverse subequatorial region (Gabriele-Rivet et al., 2020; Ward et al., 2021).

3.2. Contact structure: domestic dogs

For the transmission of lyssavirus (the cause of rabies) between dogs, the probability of transmission given contact (a bite) has been estimated to be 49% (95% CI, 45-52%) (Hampson et al., 2009). The epidemiology of transmission is not subject to great uncertainty because the parameter estimate is not highly variable: this is information that can be obtained through controlled laboratory studies and detailed field observations. Therefore, understanding rabies spread at the wild-domestic interface depends on knowledge of the pattern of contacts between domestic and wild dogs. Canine rabies lyssavirus can only be transmitted between live animals, so the role of the environment in indirect transmission is not relevant. Thus, with documented knowledge of the probability of transmission given contact, the challenge to model rabies spread within populations and between populations at the wild-domestic interface is to characterise and measure effective contact.

Within Indigenous communities across Australia, it is common practice to allow domestic dogs to roam freely both within and around the communities, with some individuals traveling to more distant bushland areas (Bombara et al., 2017a; Hudson et al., 2017; Maher et al., 2019). Such roaming behaviours increase the likelihood of disease spread within and between communities, as well as creating an opportunity for disease transmission beyond communities via interactions with wild dogs.

In northern Australia, and specifically within the NPA, the roaming distributions of domestic dog - and inferences regarding contacts - have been studied extensively. For domestic dogs, the approach has used GPS units attached to collars (Figure 1A). With periods of monitoring from 3 days up to 2 months, GPS data (Figure 1B) allow dogs' home ranges (HR) and utilisation distributions (UD) to be estimated (Figure 1C). The Biased Random Bridge (BRB) analytical method has application to such GPS data in which the period between GPS fixes is semi-regular but there can be considerable time periods when no fix is recorded (for example, a dog lying underneath a car). The BRB method places kernel functions over each movement of the dog between two consecutive GPS fixes, therefore more realistically tracing the dog's movements. Kernel smoothing is carried out considering not only recorded GPS fixes, but also interpolated locations. The dog is assumed to move between two successive fixes according to a biased random walk, i.e. the roaming pattern has a drift along each track, represented by a diffusion parameter (Durr and Ward, 2014). The estimated UD has a probabilistic interpretation; for example, at the 95% isopleth, this is the area in which the dog spent 95% of its time during the monitoring period.

In initial studies in the NPA, Durr and Ward (2014) estimated UDs for roaming dogs of up to 20 ha (95% isopleth). In addition, within this short-term study dogs were recorded to be taken in vehicles on hunting

trips of up to 25km in distance and 6 hrs in duration (Durr and Ward, 2014). In another study, seven community dogs were identified with an estimated HR > 20 ha (maximum 40 ha), which included the bushland surrounding these Indigenous communities, areas in which many dogs were observed to spend considerable periods of their time (Bombara et al., 2017a). In a study using longer monitoring periods (up to 67 days), three classes of domestic dogs were characterised: stay-at-home, roamers and explorers (Hudson et al., 2017). Explorer dogs showed large variability in their roaming patterns, but their HRs continued to increase as the monitoring period increased. In further analyses, Maher et al. (2019) examined the temporal activity of roaming domestic dogs and found that dogs roamed further during the dry season and that their daily roaming behaviour peaked between 1700 and 1800 hours. Some dogs were recorded up to 2.5 km from their residence in this study. The studies conducted in the NPA suggested that mostly, domestic dogs remained within their communities with ample opportunities to contact other domestic dogs. However, it was also observed that some of these dogs could roam considerable distances from their communities into bushland areas, demonstrating a potential wildlife-domestic interface.

3.3. Contact structure: wild dogs

Wild dogs in Australia might act as a reservoir of rabies if an incursion of this exotic disease occurred. The presence of a wildlife reservoir would make rabies eradication difficult and have far reaching economic and social implications (Sparkes et al., 2015).

Existing data to inform rabies spread modelling in wild dog populations are scarce. In a scoping review of wild-living dog ecology and biology in Australia to inform parameterisation for disease spread (Gabriele-Rivet et al., 2019b), lack of data on density and contacts are major research gaps in the literature: only a small number of recent studies on these topics (14 and 12, respectively) was found, with few quantitative estimates. Even for home range, only 24 studies were identified that provided usable evidence. Information from equatorial and tropical climate zones of northern Australia – a high-risk area for a rabies incursion – to inform disease spread is even more limited. Within these zones, no studies reporting information on contact rates were found, and only one study reporting wild dog home range was identified.

In the case of wild dogs, measuring home ranges and inferring contact rates is challenging, particularly in the context of the equatorial and tropical climate zones of northern Australia. Gabriele-Rivet et al (2020) used a camera trap survey to monitor the wild dog population in the NPA. Wild dog density and home range size estimates were derived via maximum-likelihood, spatially explicit, mark–resight models. Densities varied from 0.135 animals/km^2 (95% CI = 0.127–0.144) during the dry season to 0.147 animals/km^2 (95% CI = 0.135–0.159) during the wet season. Although densities were relatively uniform during the year, suggesting a stable population, estimated home range sizes were highly variable (7.95–29.40 km^2). Of note, these home ranges are comparable to some of the estimated HRs of roaming domestic dogs in the NPA (Durr and Ward, 2014; Hudson et al., 2017; Bombara et al., 2017a).

3.4. Characterising the wild-domestic interface

In a camera trap study conducted around NPA communities (Ward et al., 2021), wild dogs and unsupervised domestic dogs accounted for the majority of dog triggers, 40.7% and 44.5%, respectively (N = 2,317 photo series). Wild dogs were most frequently observed at night around a waste site and less frequently around campground and beach locations. They were generally observed with other wild dogs, as well as domestic dogs occasionally. This observational study demonstrates that wild dogs are active in peri-urban community areas in northern Australia.

In the camera trap survey used to monitor the wild dog population in the NPA, Gabriele-Rivet et al (2020) also found the spatial use and daily activity patterns of wild dogs and free-roaming community dogs showed substantial temporal activity overlap and spatial correlation, especially during the dry season. This highlights the potential risk of disease transmission at the wild–domestic interface in an area of biosecurity risk in equatorial northern Australia.

Data from this camera-trap study were further used to explore spatial and seasonal opportunities for in-

teractions between wild dogs and unsupervised domestic dogs (Gabriele-Rivet et al., 2021b). A detection event was defined as the capture of one individual in a photograph. For each dog type (wild dog *versus* unsupervised domestic dog), the (standardised) relative activity index (detection events / capture effort) was calculated at each camera station and for each season.

Unsupervised domestic dogs were mostly (86% and 84% in the dry and wet seasons, respectively) active in proximity (< 1 km) to the five Indigenous communities in the NPA. A peak of unsupervised domestic dog activity was noticeable in areas that lay further away from the communities towards the tip of the peninsula, which was more pronounced during the wet season compared to the dry season. This finding is most certainly related to hunting excursions (Gabriele-Rivet et al., 2019a).

Compared to unsupervised domestic dogs, the activity of wild dogs was more spatially homogeneous across the study area, although more activity was found around the communities, especially during the dry season, and in distant areas where hunting trips frequently occur, especially during the wet season.

The higher level of wild dog activity around the communities during the dry season implies a higher risk of interaction with free-roaming domestic dogs; indeed, significant spatial correlation between wild dogs and unsupervised domestic dogs has been found early in the dry season (Gabriele-Rivet et al., 2019a). In contrast, wild dogs are 1.6-times more active >10km from the communities in the wet season. This coincides with domestic dog activity in these areas due to hunting, increasing the likelihood of interactions between both populations. Thus, the location and nature of the domestic-wild interface varies by season in this equatorial climate zone.

3.5. *Hunting increases the wildlife-domestic dog interface*

Cooperative hunting (most commonly for feral pigs) involving several hunters and their domestic dogs is common across Australia, and within Indigenous communities is a traditional practice that contributes to food security. Contact opportunities between wild and hunting dogs during hunting can create a wildlife–domestic interface for disease transmission of shared pathogens (Fiorello et al., 2006; Hughes and Macdonald, 2007), such as canine parvovirus (Meers et al., 2007; Kelman et al., 2020). Generally, hunting provides an opportunity for spatial translocation of disease over large distances (Sparkes et al., 2016), contributing to disease spread and complicating disease control. Hunting dogs can also provide a link between wild dogs (and other wildlife) and humans.

To further investigate this potential interface, a cross-sectional survey of 13 hunters from communities of the NPA was undertaken (Gabriele-Rivet et al., 2019a). More than half these hunters had experienced at least one wild dog encounter during hunting in the year prior to the interview. Wild dogs were seen mostly on the roads when driving before or after their hunting trip, and during hunting trips wild dogs were reported to keep their distance from the hunting group (hunting dogs often barked at or chased wild dogs during encounters). Generally, 1–2 wild dogs travelling together were observed, but sometimes packs of 3–6 wild dogs, including puppies, were seen. Hunters reported practicing hunting activities more frequently during the wet season compared to the dry season (median of 12 vs 7.2 hunting trips per season, respectively). Mapping of the relative risk of interactions between wild and hunting dogs during hunting trips allowed the identification of high-risk areas in the NPA, based on the combination of high wild dog density and frequency of hunting trips. These areas, towards the tip of the NPA region, are characterised by dense rainforests. Results from this study, when combined with those from a camera trap survey in the NPA in which a peak of unsupervised domestic dog activity was noticeable in areas that lay further away from the communities towards the tip of the peninsula in the wet season (Gabriele-Rivet et al., 2019a), support the potential for disease transmission at the domestic–wild dog interface through contacts between hunting dogs during hunting activities.

3.6. *Summary of findings*

Insights from this case study suggest that interactions between domestic dogs and dingoes, and hence risk for disease transmission at the wild-domestic interface, are more likely to occur around the communities during

the dry season, whereas the risk seems to be increased in bush areas away from the communities during the wet season. The former is likely driven by the availability of freely accessible food sources which attracts wild dogs and the presence of roaming domestic dogs, and the latter is apparently driven by an intensification of hunting activities with domestic dogs coupled with a higher level of wild dog activity in these same areas. These two potential disease pathways need to be incorporated into any model of disease spread within this ecosystem.

Monitoring of roaming domestic dogs at the study site demonstrates that most dogs will "stay at home" and only explore their immediate surroundings. However, there is a proportion of the population (estimated to be 29% by Hudson et al. (2017)) which will explore their surroundings, including areas of bushland where contact with wild dogs is possible. Dog factors such as age, sex, and neuter status do not appear to be strong predictors of this roaming behaviour. However, recognition of the heterogeneity of roaming behaviour in populations of roaming dogs in Indigenous communities presents an opportunity to reduce disease spread at the wild-domestic interface (Hudson et al., 2016).

Wild dogs often reside near human settlements (Allen *et al.* 2013; Sparkes *et al.* 2016) and their home range can be configured around supplementary food sources, such as mine sites and refuse facilities (Allen *et al.* 2013; Newsome *et al.* 2013; McNeill et al., 2016). It is likely that sites are more frequented when wild dogs have unrestricted access to resources such as food, water and vegetation coverage (Sparkes *et al.* 2015). Therefore, locations such as waste disposal sites pose a risk because higher wild dog activity around human-provided resources could increase contact opportunities with free-roaming domestic-type dogs (Fleming *et al.* 2001; Newsome *et al.* 2013; Bombara *et al.* 2017b; Hudson et al., 2016; Hudson et al., 2017), and provide opportunity for disease transmission between the two dog populations. The findings of hybridisation studies also support the existence of this wild-domestic interface (Bombara et al., 2017a; Gabriel-Rivet et al., 2021c). In addition, greater activity in wild dog populations between dusk and dawn have been observed, due to aversion to human activity and more profitable foraging opportunities following dusk (Allen *et al.*2013; Newsome *et al.* 2013; Ward et al., 2021). Thus contacts are more likely during these times of the day. The presence of community-associated food resources which attract wild dogs – particularly during the dry season - need to be incorporated into disease spread models. Monitoring of these sites to estimate contact rates is a priority for such research.

The role that hunting might play at the study site, and more broadly across northern Australia, needs more investigation. During hunting trips, dogs can travel in the bush for long distances (up to 4 km) and for a considerable amount of time (up to 9 h), whilst being remotely monitored by hunters using GPS technology. This hunting behaviour can increase the chances of encountering wild dogs (Gabriel-Rivet et al., 2019a). Studies in the NPA (Gabriel-Rivet et al., 2021b) indicate that opportunities for encounters are likely, which is consistent with the results of a previous survey of Australian hunters (Sparkes et al., 2016), in which 50% of the hunters interviewed witnessed at least one encounter with wild dogs throughout their hunting experience. However, the probability or rate of effective contact needs quantification for the purpose of disease spread modelling to determine the relative risk posed by this interface compared to others such as the wild-domestic peri-community interface.

4. Conclusions and Recommendations

The wildlife-domestic interface defines if and how infectious diseases will spread between wildlife and domestic populations. Understanding of this interface involves detailed field studies on the context and nature of interactions between populations. Such knowledge can be incorporated into disease spread models to understand how diseases might behave at the wildlife-domestic interface. Specifically, quantitative estimation of contact rates permits such disease spread models to be developed and used confidently.

Over a period of 10 years, free-roaming domestic dogs and wild dogs in the Northern Peninsula Area (NPA) were studied with the objective of understanding the potential consequences of an incursion of rabies in this area, and more broadly in northern Australia. Key epidemiological findings included identification of a small but important group of domestic dogs which regularly roam in bushland areas; peri-urban wild dog

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activity, particularly in the dry season, likely driven by the availability of food sources; and the potential for interaction between hunting dogs and wild dogs in remote areas, particularly during the wet season. Such disease spread pathways must be incorporated into models to realistically represent the potential outcomes of a disease incursion within this ecosystem. Furthermore, these studies have generated quantitative information on home ranges, utilisation distributions, and the overlap in activity of domestic and wild dogs. This information can be used to infer contacts between these two populations and thus model disease spread at the wild-domestic interface.

The roaming behaviour of domestic dogs in northern Australian Indigenous communities is a recognised feature of these communities, and this characteristic is determined by cultural norms as well as structural disadvantage (Brookes et al., 2020; Degeling et al., 2018). Studies on the roaming behaviour of domestic dogs are therefore important as input to disease spread models. Recognition of the heterogeneity in roaming behaviour in these populations presents an opportunity to control disease spread at the wild-domestic interface (Hudson et al., 2016). Strategies to mitigate transmission could focus on restricting movement of domestic dogs to limit potential interactions with wild dogs during risk periods (Ward et al., 2021). However, whether the behavioural characteristic of exploring is specific to certain dogs, and methods to reliably identify "explorer" dogs, are research questions which need to be resolved via low-term monitoring of these populations.

Another strategy would be to reduce the activity of wild dogs around communities. This could be done by restricting access to food sources – for example better fencing of waste disposal sites (Ward et al., 2021). This would have maximum benefit during the dry season. Ongoing monitoring of such sites would generate information on which wild dogs are part of this interface, the relationship between dog activity and resource availability, and whether breeding season is a driver of these contacts, with implications for potential disease spread. This requires more than *ad hoc* research studies. In addition, studies that employ genetic analysis can provide useful information to develop an understanding of the wild-domestic interface (Bombara et al., 2017a; Gabriele-Rivet et al., 2021c).

Whilst hunting might contribute to the wild-domestic interface, characterising and measuring contacts is problematic. Hunting trips often occur during nocturnal hours, and hunting dogs travel out of sight during hunting activities (Gabriel-Rivet et al., 2019a; Sparkes et al., 2016). Hunters can also sometimes lose their dogs. Therefore, contacts between hunting and wild dogs are difficult to observe, record and measure. To contribute to more realistic disease spread models, more field research is needed to estimate contact rates, and identify when, where and under what circumstances these occur as a result of hunting. For example, roads within otherwise densely vegetated areas might act as potential contact hotspots (Gabriele-Rivet et al., 2021b; Vernes et al., 2001). Additional field methods and study designs are needed to understand such characteristics of the wild-domestic interface.

Disease spread models are valuable to help us understand the wildlife-domestic interface. However, to produce insights that can be used to mitigate the effects of disease spread such models require parameterisation of effective contact, which is defined using fundamental knowledge of the underlying system and field data. We have summarised a decade of research conducted to understand one such interface, the wild-domestic dog interface at one site in northern Australia, for the purposes of exploring the impact of one specific disease, rabies. Further development of disease spread models that focus on this interface is the catalyst needed to generate field data to inform these models and provide a deeper understanding of the wildlife-domestic interface.

5. References

Allen, B.L., Goullet, M., Allen, L. R., Lisle, A., Leung, L. K.-P. Dingoes at the doorstep: preliminary data on the ecology of dingoes in urban areas. *Landscape and Urban Planning* 2013; 119: 131-135.

Begon, M., Bennett, M., Bowers, R.G., French, N.P., Hazel, S.M., Turner, J. A clarification of transmission terms in host-microparasite models: Numbers, densities and areas. *Epidemiology and Infection* 2002; 129(1): 147-153.

Bombara, C., Durr, S., Gongora, J., Ward, M.P. Roaming of dogs in remote Indigenous communities in northern Australia and potential interactions between community and wild dogs. *Australian Veterinary Journal* 2017a, 95: 182-188.

Bombara, C., Durr, D., Machovsky-Capuska, G.E., Jones, P.W., Ward, M.P. A preliminary study to estimate contact rates between free-roaming domestic dogs using novel miniature cameras. *PLoS One* 2017b; 12(7): e0181859.

Bradley, C.A., Altizer, S. Urbanization and the ecology of wildlife diseases. *Trends in Ecology and Evolution* 2007; 22(2): 95-102.

Brookes, V.J., Durr, S., Ward, M.P. Rabies-induced behavioural changes are key to rabies persistence in dog populations: investigation using a network-based model. *PLoS Neglected Tropical Diseases* 2019; 13(9): e0007739.

Brookes, V.J., Ward, M.P., Rock, M., Degeling, C. One Health promotion and the politics of dog management in remote, northern Australian communities. *Scientific Reports* 2020; 10(1): 12451.

Brookes, V.J., Wismandanu, O., Sudarnika, E., Roby, J.A., Hayes, L., et al. A scoping review of live wildlife trade in markets worldwide. *Science of The Total Environment* 2022; 153043.

Chambers, M.A., Carter, S.P., Wilson, G.J., Jones, G., Brown, E., et al. Vaccination against tuberculosis in badgers and cattle: an overview of the challenges, developments and current research priorities in Great Britain. *Veterinary Record* 2014; 175(4): 90-96.

Cunningham, A.A., Daszak, P., Wood, J.L.N. One Health, emerging infectious diseases and wildlife: two decades of progress? *Philosophical Transactions of the Royal Society London B Biological Sciences* 2017; 372: 1725.

Degeling, C., Brookes, V., Lea, T., Ward, M.P. Rabies response, One Health and more-than-human considerations in Indigenous communities in Northern Australia. *Social Science & Medicine* 2018; 212: 60-67.

Durr, S., Ward, M.P. Roaming behaviour and home range estimation of domestic dogs in Aboriginal and Torres Strait Islander communities in northern Australia using three different methods. *Preventive Veterinary Medicine* 2014; 117:340-357.

Fahrion, A.S., Taylor, L.H., Torres, G., Muller, T., Durr, S., et al. The road to dog rabies control and elimination - What keeps us from moving faster? *Frontiers in Public Health* 2017; 5:103

Field, H.E., Mackenzie, J.S., Daszak, P. Henipaviruses: emerging paramyxoviruses associated with fruit bats. *Current Topics in Microbiology and Immunology* 2007; 315: 133-159.

Fiorello, C.V., Noss, A.J., Deem, S.L. Demography, hunting ecology, and pathogen exposure of domestic dogs in the Isoso of Bolivia. *Conservation Biology* 2006; 20: 762–771.

Fleming, P.J., Corbett, L.K., Harden, R. et al. Managing the impacts of dingoes and other wild dogs. Bureau of Rural Sciences, Canberra, 2001.

Gabriele-Rivet, V., Brookes, V.J., Arsenault, J., Ward, M.P. Hunting practices in northern Australia and their implication for disease transmission between community dogs and wild dogs. *Australian Veterinary Journal* 2019a, 97: 268-276

Gabriele-Rivet, V., Arsenault, J., Wilhelm, B., Newsome, T., Ward, M.P., Brookes, V.J. A scoping review of dingo and wild-living dog ecology and biology in Australia to inform parameterisation for disease spread. *Frontiers in Veterinary Science* 2019b; 6: 47

Gabriele-Rivet, V., Arsenault, J., Brookes, V.J., Fleming, P.J., Nury, C., Ward, M.P. Dingo density estimates and movements in equatorial Australia: Spatially explicit mark–resight models. *Animals* 2020; 10: 5

11

Gabriele-Rivet, V., Ward, M.P., Arsenault, J., London, D., Brookes, V.J. Predicted spatiotemporal spread of rabies in dingo populations in northern Australia. *PLoS Neglected Tropical Diseases* 2021a, 15(2): e0009124.

Gabriele-Rivet, V., Brookes, V.J., Arsenault, J., Ward, M.P. Seasonal and spatial overlap in activity between domestic dogs and dingoes in remote Indigenous communities of northern Australia. *Australian Veterinary Journal* 2021b, 99: 114-118

Gabriele-Rivet, V., Brookes, V.J., Stephens, D., Arsenault, J., Ward, M.P. Dingo-dog hybridisation in a wild dog population surrounding Indigenous communities in northern Australia. *Australian Veterinary Journal* 2021c, 99: 388-391.

Guerra, F.M., Bolotin, S., Lim, G., Heffernan, J., Deeks, S.L., et al. The basic reproduction number (R_0) of measles: a systematic review. *Lancet Infectious Diseases* 2017; 17(12): e420-e428.

Hampson, K., Dushoff, J, Cleaveland, S., Haydon, D.T., Kaare, M,, et al. Transmission dynamics and prospects for the elimination of canine rabies. *PLoS Biology* 2009; 7(3): e1000053..

Hampson, K., Coudeville, L., Lembo, T., Sambo, M., Kieffer, A., et al. Estimating the global burden of endemic canine rabies. *PLoS Neglected Tropical Diseases* 2015; 9, e0003709.

Hassell, J.M., Begon, M., Ward, M.J., Fevre, E.M. Urbanization and disease emergence: Dynamics at the wildlife-livestock-human interface. *Trends in Ecology and Evolution* 2017; 32(1): 55-67.

Hudson, E., Dhand, N., Durr, S., Ward, M.P. A survey of dog owners in remote northern Australian indigenous communities to inform rabies incursion planning. *PLoS Neglected Tropical Diseases* 2016, 10(4): e0004649.

Hudson, E, Brookes, V., Durr, S., Ward, M.P. Domestic dog roaming patterns in remote Australian indigenous communities and implications for disease modelling. *Preventive Veterinary Medicine* 2017, 146: 52-60.

Hudson, E., Brookes, V.J., Durr, S., Ward, M.P. Modelling targeted rabies vaccination strategies for a domestic dog population with heterogeneous roaming patterns. *PLoS Neglected Tropical Diseases* 2019a; 13: e0007582.

Hudson, E, Brookes, V.J., Durr, S., Ward, M.P. Targeted pre-emptive vaccination strategies in a susceptible domestic dog population with heterogeneous roaming patterns. *Preventive Veterinary Medicine* 2019b; 172: 104774.

Hughes J., Macdonald, D.W. A review of the interactions between free roaming domestic dogs and wildlife. *Biology and Conservation* 2013; 157: 341–351.

Johnstone-Robertson, S.P., Fleming, P.J., Ward, M.P., Davis, S.A. Predicted spatial spread of canine rabies in Australia. *PLoS Neglected Tropical Diseases* 2017; 11(1): e0005312.

Jori, F., Hernandez-Jover, M., Magouras, I., Durr, S., Brookes, V.J. Wildlife-livestock interactions in animal production systems: what are the biosecurity and health implications? *Animal Frontiers* 2021; 11(5): 8-19.

Kelman, K., Harriott, L., Carrai, M., Kwan, E., Ward, M.P. , Barrs, V.R. Phylogenetic and geospatial evidence of canine parvovirus transmission between wild dogs and domestic dogs at the urban fringe in Australia. *Viruses* 2020; 12: 663.

Kirkeby, C., Brookes, V.J., Ward, M.P., Durr, S., Halasa, T. A practical introduction to mechanistic modeling of disease transmission in veterinary science. *Frontiers in Veterinary Science* 2020; 7, 546651.

Lushasi, K., Hayes, S., Ferguson, E.A., Changalucha, J., Cleaveland, S., et al. Reservoir dynamics of rabies in south-east Tanzania and the roles of cross-species transmission and domestic dog vaccination. *Journal of Applied Ecology* 2021; 58(11): 2673-2685.

McNeill, A., Leung, L. Goullet, M. Gentle M., Allen, B. Dingoes at the doorstep: home range sizes and activity patterns of dingoes and other wild dogs around urban areas of north-eastern Australia. *Animals* 2016; 6: 48.

Magouras, I., Brookes, V.J., Jori, F., Martin, A., Pfeiffer, D.U., Durr, S. Emerging Zoonotic Diseases: Should We Rethink the Animal–Human Interface? [Opinion]. *Frontiers in Veterinary Science* 2020; 7: 748.

Maher, E.K., Ward, M.P., Brookes, V.J. Investigation of the temporal roaming behaviour of free-roaming domestic dogs in Indigenous communities to inform rabies disease incursion preparedness. *Scientific Reports* 2019; 9: 14893

Meers J., Kyaw-Tanner M., Bensink, Z. et al. Genetic analysis of canine parvovirus from dogs in Australia. *Australian Veterinary Journal* 2007; 85: 392–396.

Mulvey, P., Duong, V., Boyer, S., Burgess, G., Williams, D. T., et al. The ecology and evolution of Japanese Encephalitis *Viruses and Pathogens* 2021; 10(12): 1534.

Natalini B., Gennuso, S., Beldomenico, P.M., Rigonatto, T., Kowalewski, M.M. Parasitologic examination and associated risk factors of domestic dogs at the domestic-wildlife interface in the Ibera wetlands Ecoregion, Argentina. *Veterinary Parasitology: Regional Studies and Reports* 2020; 20:100378.

Newsome, T.M., Ballard, G-A., Dickman, C.R. et al. Home range, activity and sociality of a top predator, the dingo: a test of the Resource Dispersion Hypothesis. *Ecography* 2013; 36: 914–925.

Rupprecht, C.E., Freuling, C.M., Mani, R.S., Palacios, C., Sabeta, C.T., Ward, M. Chapter 1, *A history of rabies—The foundation for global canine rabies elimination* . In: Rabies, Scientific Basis of the Disease and Its Management. Fourth Edition, Anthony R. Fooks and Alan C. Jackson (editors). Academic Press, ISBN 978-0-12-818705-0; pp. 1-44. 2010.

Shi, Z., Hu, Z. A review of studies on animal reservoirs of the SARS coronavirus. *Virus Research* 2008; 133(1): 74-87.

Sparkes, J., Fleming, P.J.S., Ballard, G., Scott-Orr, H., Durr, S., Ward, M.P. Classical rabies in Australia: A review of preparedness and research needs. *Zoonoses and Public Health* 2015, 62: 237-253.

Sparkes, J., Ballard, G., Fleming, P.J.S. Cooperative hunting between humans and domestic dogs in eastern and northern Australia. *Wildlife Research* 2016; 43: 20-26.

Vernes K, Dennis A, Winter J. Mammalian diet and broad hunting strategy of the dingo (Canis familiaris dingo) in the wet tropical rain forests of northeastern Australia. *Biotropica* 2001; 33: 339–345.

Vynnycky E., White, R.G. An Introduction to Infectious Disease Modelling. Oxford University Press, 2010

Walsh, M.G., Pattanaik, A., Vyas, N., Saxena, D., Webb, C., et al.. High-risk landscapes of Japanese encephalitis virus outbreaks in India converge on wetlands, rain-fed agriculture, wild Ardeidae, and domestic pigs and chickens. *International Journal of Epidemiology* 2022; https://doi.org/10.1093/ije/dyac050

Ward, M.P. , Brookes, V.J. Rabies in Our Neighbourhood: Preparedness for an Emerging Infectious Disease. *Pathogens* 2021, 10: 375.

Ward, M.P. , Guptill, L.F., Wu, C.C. Evaluation of environmental risk factors for leptospirosis in dogs: 36 cases (1997-2002). *Journal of the American Veterinary Medical Association* 2004, 225: 72-77.

Ward, M.P., Qing-Ling Sivieng, K., Brookes, V. The wild-domestic dog interface: implications for disease spread. *Australian Zoologist* 2021, 41: 388-407.

Wikramanayake, E., Pfeiffer, D.U., Magouras, I., Conan, A., Ziegler, S., et al.. A tool for rapid assessment of wildlife markets in the Asia-Pacific Region for risk of future zoonotic disease outbreaks. *One Health* 2021; 13: 100279.
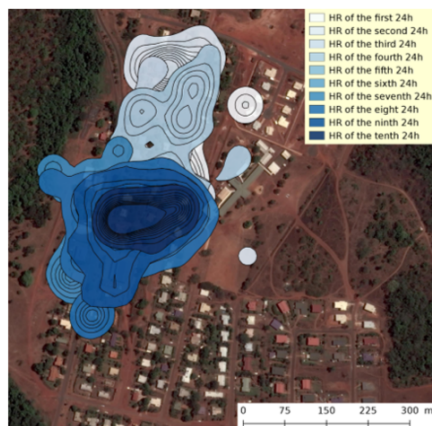
Worobey, M., Levy, J.I., Serrano, L.M., Crits-Christoph, A., Pekar, J.E., et al. The Huanan Seafood Wholesale Market in Wuhan was the early epicenter of the COVID-19 pandemic. *Science* 2022; https://doi.org/doi:10.1126/science.abp8715
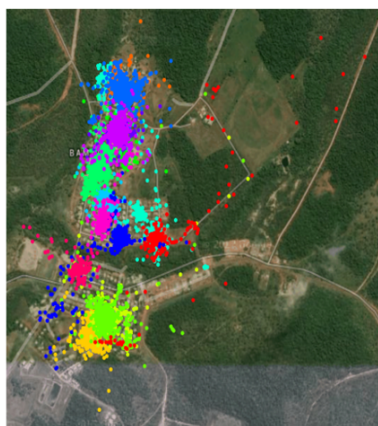
The use of GPS units (A) with domestic dogs in northern Australian Indigenous communities to collect GPS data (B) used to estimate utilisation distributions and home range (C).