Quantifying effects of wild dogs, domestic dogs and humans on the spread of rabies in Australia

Jessica Louise Sparkes

Bachelor of Animal and Veterinary Bioscience (Hons), Sydney University, 2008

Graduate Certificate in Public Administration, University of Canberra, 2009

This thesis is presented for the degree of Doctor of Philosophy

The University of New England

School of Environmental and Rural Science

December 2015

Declaration

I certify that the substance of this thesis has not already been submitted for any degree and is not currently being submitted for any other degree or qualification.

I certify that any help received in preparing this thesis and all sources used have been acknowledged in this thesis.

[redacted]

Jessica Sparkes

12 December 2015

Date

Abstract

Rabies is a preventable viral zoonosis that causes inflammation of the brain, and eventually death, in infected mammals. With few exceptions, including Australia, terrestrial rabies can be found worldwide. More than 55,000 deaths from rabies infection are reported annually; these are mainly in Asia and Africa where the primary reservoir is the domestic dog.

Despite ongoing control efforts in Indonesia, canine rabies remains a disease of critical concern there. Although rabies is not endemic in Australia, at less than 300km away in Indonesia, a rabies incursion is a likely and imminent threat.

To improve preparedness for a canine rabies outbreak in Australia, I collected data on a number of extant dog populations in northern and eastern Australia. I used a range of methods including self-administered questionnaires, GPS telemetry collars, camera trapping and mark-recapture studies. Using my own data and parameters collected from the wider literature, I developed state-transition models to determine how rabies could spread through these dog populations. Finally, I used these same models to evaluate a range of control strategies, including dog removal and vaccination, to identify the most effective options for reducing impacts in Australian communities following a rabies incursion.

Model outputs suggested that rabies will progress differently within functionally different dog populations present within Australia. Restrained domestic dogs posed limited risk for rabies transmission, because interactions with other dogs were limited and generally supervised by owners. Free-roaming domestic and hunting dogs will likely play an important role in rabies transmission in some situations only, primarily based on their ability to roam, access to other free-roaming dogs and their interactions within and between dog groups. Wild dogs (including dingoes) proved the most critical type of dog for rabies spread and maintenance in Australia, because they are widely distributed, often in high abundance, roam over large distances and frequently interact.

I found that time to detection for rabies in wild dogs will likely be lengthy, probably due to low infection rates prior to an epidemic and limited contact with humans, relative to the other categories of dog that I studied. Further, the capacity of authorities to implement effective control strategies for wild dogs will likely be restricted because of limited access to individual animals. The economic costs of controlling a rabies

outbreak involving wild dogs will be substantial and likely equivalent to the costs for extensive aerially-based wild dog control that are currently used in some areas of Australia (~Aus$34 km^{-2}).

Australia’s current plans to address rabies incursions, which were developed in the 1990s are clearly outdated. My findings reveal that revision of these plans, taking specific account of relevant differences between restrained domestic dogs, free-roaming domestic dogs and extensive wild dog populations is necessary to ensure that Australia is adequately prepared for the arrival of canine rabies.

Acknowledgements

I could not have completed this doctoral thesis without support from my family, friends and work colleagues. To each and every one of you, I am endlessly grateful for all your support, friendship and guidance.

First and foremost, I would like to sincerely thank Guy Ballard for taking me on as a student and for your patience, support, help and advice throughout this project. Without this, I would never have gotten through one of the toughest challenges of my life. The faith you entrusted with me has driven me to aim for the absolute best. Throughout the many highs and lows I have faced over the last few years, your encouragement and belief in me has never wavered and has gotten me through some pretty hairy situations! I look up to you as a mentor, colleague and friend and hope I have done you proud.

A great thanks must also go to Wendy Brown for all her behind the scenes, thankless and tiring work she has put in to helping get to this point. Without your enthusiasm, support and many contacts, I would not have realised many of my goals.

Thank you to Peter Fleming for all your tireless work in securing funding, reviewing work and most of all, for supporting and encouraging me to develop in this career path. The proffering of your extensive knowledge has allowed me to grow and achieve feats I never dreamed of!

To Gerhard Körtner, who has always grounded me and encouraged me to question everything. Your generosity in sharing your knowledge, skills and time know no bounds. You have taught me many new skills I never dreamed I could have gained. Without your computer programs, I would still be sorting my data!

To Paul Meek, who has been a good friend, colleague and mentor. Your support and faith, particularly through the tough times gave me strength to continue, when I was so close to calling it quits.

To my family away from home, my PhD family; Catie, Sarah, Michal, Helen, Fran, Trent, Huw, Heidi and Mariette, you have shared your skills, knowledge and expertise with me. You have all opened my eyes to a myriad of possibilities and thought processes and provided support and advice that only other PhD students would know or understand. Thanks to everyone that helped catch dogs, post surveys and check cameras with me! Despite some boggings, bites and scratches, we are all still standing!

Thanks to all my other beautiful friends for putting up with me over the past three and a half years. Your moral support and distractions from the PhD life have been greatly appreciated and kept me sane. A special mention to Ainslie and Michella for opening your houses to Toby and me while undertaking fieldwork. Despite rocking up muddy and filthy, and sometimes with dead animals, you were always there and willing to share a wine or chocolate to get me through those long days.

I wish to thank all the NPWS, SF and LLS staff; in particular, Gina, Lisa, Mark, John, Andy, Holly, Emma, Felicity and Dean who have supported and helped me complete my fieldwork. To AMRRIC, for helping create networks and providing fantastic growth opportunities within Indigenous communities. To all the landholders and dog owners that were such willing participants. Without your support and participation, our research would be dead on the ground.

To Steve, Gerhard, Greg and Remy, I am endlessly grateful for all your programming, modelling and statistical assistance; especially in the last year. Without your willingness to help, I would still be stuck in R (or somewhere else unpleasant)!

None of this work would even be possible if it weren't for generous financial contributions from the Department of Agriculture, Fisheries and Forestry (Wildlife Exotic Disease Preparedness Program), the Northern Rivers Regional Organisation of Councils (thanks Angus), the University of New England's Indigenous scholarship and the Australian Postgraduate Award.

Finally, I would like to thank my family for their understanding and support. To Andrew, Mum and Dad, Brian, Tracey and Leo, thank you so much for your encouragement, love and support, I am so lucky to have such a wonderful family. You always had faith that I would finish!

See every difficulty as a challenge,

a stepping stone,

and never be defeated by anything or anyone

Eileen Caddy

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Abbreviations

ABLV Australian Bat Lyssavirus

AEC Animal Ethics Committee

AMRRIC Animal Management in Rural and Remote Communities

AR Activity Range

CTN Camera Trap Nights

E Exposed

GPS Global Positioning Satellite

I Infectious

LGA Local Government Authority

LLS Local Land Services

MCP Minimum Convex Polygon

NPWS National Parks and Wildlife Service

NSW New South Wales

ORV Oral Rabies Vaccination

PEP Post Exposure Prophylaxis

PNG Papua New Guinea

R Immune or Removed

S Susceptible

SEIR Susceptible-Exposed-Infectious-Removed

SF Forestry Corporation of NSW

WA Western Australia

1 Introduction

Rabies is an acute, fatal, viral zoonosis, most commonly transmitted to people through the bite of an infected dog (Warrell & Warrell 2004). Worldwide, more than 55 000 people die of rabies annually (Knobel *et al*. 2005), with more than half of these deaths occurring in Asia (World Health Organization 2005). The Australian continent is currently free of terrestrial rabies, but some experts believe that a zoonotic outbreak is a realistic and imminent threat from South-East Asia (e.g. Murray *et al*. 2012).

Although Australia has a strong quarantine record and has developed disease preparedness plans (AUSVETPLANs) to address incursions of exotic diseases, such as rabies (Animal Health Australia 2011), experience has shown that such incursions still occasionally happen (e.g. equine influenza; Schemann *et al*. 2014 and rinderpest; Turner 2011).

Despite this, limited research has been undertaken to update Australia's preparation to address a rabies incursion since the 1990s. Previous rabies research was primarily focused on the red fox (*Vulpes vulpes*), as this species was considered of greatest concern for maintenance and spread of the disease in Australia (O'Brien & Berry 1992). More recently, the canine rabies virus strain has spread through Indonesia's dog populations and is considered the strain most likely to reach Australia (Cookson *et al.* 2012, Drewitt 2012, World Organisation for Animal Health 2012).

Were it to reach Australia, rabies' most significant host would likely be dingoes, domestic dogs and their crossbreeds (*Canis lupus familiaris*). Although dingoes were previously thought to be a separate subspecies, the most recent taxonomic deliberation confirms that all dogs, including dingoes, pets and pariah dogs should be called *Canis familiaris* (Jackson & Groves 2015). Because this change is recent, some of the published papers comprising this thesis use previously asserted Latin names (e.g. *Canis dingo*) as well as the current deliberation. Consequently, I have also used the terms 'hybrid' and 'crossbreed' interchangeably.

If rabies does enter Australia, it has the potential to have a greater impact on the continent, in social, ecological and economic terms, than any previous incursion of an exotic disease. This is because although Australia is unusually free of rabies, compared to other populated continents, it has an extensive assemblage of susceptible dogs. These animals range from totally restrained individuals who are wholly dependent on anthropogenic resources and care, through to totally independent, free-ranging dingoes.

To help Australia prepare for a rabies outbreak, I aimed to identify and address some key knowledge gaps in population dynamics, ecology and behaviour of domestic and wild, free-living dogs. Specifically, my objectives were to:

1. Review the literature to identify current status of knowledge about rabies, Australian free-roaming dogs and requirements for rabies preparedness in Australia,
2. Identify and then quantify population and contact parameters, within and between Australian wild and domestic dog populations and
3. Use my derived and other, already published, parameters in epidemiological models to illustrate their use for predicting potential rabies spread in Australia.

Achieving these objectives is an important step towards improving Australia's preparedness for a rabies incursion and informing responses to outbreaks and subsequently, preventing spread through susceptible dog populations and to the human population.

1.1 Thesis structure

The chapters within this thesis are presented in the format of scientific papers. Some are already published (Chapters 2, 4 and 5), while others have been submitted to journals for publication (Chapters 3, 6 and 7). The structure of the thesis includes an initial chapter to establish the reasons for undertaking the work and a logical framework for data collection in following chapters. Each chapter comprises one or more papers, each containing its own methods, and addressing parameter estimation for different components of Australia's dog populations. Therefore, there is no separate Methods chapter and there is some unavoidable repetition of Introductions and Methods among chapters. The work culminates in the application of the parameters from the previous data chapters in rabies simulation models.

The thesis is presented as follows:

In Chapter 2, I undertook a comprehensive review of rabies literature to contextualise the extent of rabies as a problem, to identify knowledge gaps and to determine priorities for research. Hypothesised social, ecological and economic consequences of endemic rabies in Australia are also presented in this chapter.

Next, to enumerate dog ownership and align current official records with true population estimates for domestic dogs, results of a survey of residents in north-east New South Wales is presented. Roaming behaviour and dog attacks were also quantified to determine the extent of the problem if rabies were to breach Australian borders (Chapter 3).

Following the survey of residents, I present details of an intensive study to assess population dynamics and sociality of free-roaming domestic dogs in an Aboriginal Island community (Chapter 4). Mark-recapture estimates and GPS telemetry were used to quantify population numbers, dog behaviour and contact rates for use in models.

To understand the potential role of hunting dogs in a rabies outbreak, a survey of hunters was developed and administered through online hunting forums, hunting stores and various government agencies (Chapter 5). Human mediated dog movements and interactions between hunting dogs and wild dogs were quantified, highlighting the potential for rabies spread in highly populated areas ahead of the disease front.

Chapter 6 focuses on the potential of dingoes and other wild dogs to spread rabies through free-ranging dog populations. The potential of free-roaming domestic dogs to interact with wild dogs and spread disease at the wildlife-domestic interface are also quantified and discussed. Within this chapter, contact rates and population dynamics of wild and domestic dogs in north-east NSW were quantified.

In Chapter 7, I used population parameters derived in Chapters 3 to 6 to model the spread of rabies in communities. I present a Susceptible-Exposed-Infectious-Removed model, incorporating previously published values, along with my own derived values. This model was used to predict the likely outcomes of a rabies incursion and to identify optimal response strategies to combat such an outbreak.

Finally, the limitations and management implications of the research are discussed and future research requirements highlighted, to aid better predictions and management of rabies spread within Australia.

2 Canine rabies in Australia

Canine rabies is exotic to Australia. With just one likely incursion, in 1867, this is unique among populated continents. The absence of rabies is perhaps even more surprising given the presence of a widespread free-ranging dog population, which includes the naturalized dingo, feral domestic dogs and dingo-dog crossbreeds. Just 300km to Australia's north, rabies has recently spread within the Indonesian archipelago, with outbreaks occurring in historically rabies-free islands to the east including Flores (1997), Ambon (2003), Bali (2008) and the Tanimbar Islands (2010) (Windiyaningsih *et al*. 2004, Putra *et al*. 2013, Ward & Hernandez-Jover 2015).

Australia relies on strict quarantine protocols to prevent importation of rabid animals, but the risk of illegal animal translocations, by fishing and recreational vessels circumventing quarantine, remains. Predicting where rabies is most likely to enter Australia is important but understanding dog population dynamics, including contact rates in and around human populations is essential. The interactions within and between Australia's large populations of wild, free-roaming and restrained domestic dogs require quantification for rabies incursions to be detected and managed effectively.

The imminent risk of rabies breaching Australian borders makes the development of disease spread models that will assist in the deployment of cost-effective surveillance, improve preventive strategies and guide disease management protocols, vitally important.

At the outset of this research, I conducted two reviews of rabies-related literature. In the first manuscript, I critically review Australia's preparedness for rabies, discuss prevailing assumptions and models, identify knowledge deficits with respect to free-roaming dog ecology and rabies maintenance, and speculate on the likely consequences of endemic rabies within Australia. In the second manuscript, I discuss the social and economic implications for rabies in Australia. Combined, these reviews are integral to establishing the context for my research, highlighting potential consequences for a rabies outbreak and discussing future research requirements to ensure Australia is suitably prepared.

2.1 Canine rabies in Australia: a review of preparedness and research needs

This Section has been written in the format of a scientific paper and has been published in Zoonoses and Public Health (Appendix 2-1) with the following citation:

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

2.1.1 Summary

Australia is unique as a populated continent in that canine rabies is exotic, with only one likely incursion in 1867. This is despite the presence of a widespread free ranging dog population, which includes the naturalised dingo, feral domestic dogs and dingo-dog cross-breeds. To Australia's immediate north, rabies has recently spread within the Indonesian archipelago, with outbreaks occurring in historically free islands to the east including Bali, Flores, Ambon and the Tanimbar Islands.

Australia depends on strict quarantine protocols to prevent importation of a rabid animal, but the risk of illegal animal movements by fishing and recreational vessels circumventing quarantine, remains. Predicting where rabies will enter Australia is important but understanding dog population dynamics and interactions, including contact rates in and around human populations, is essential for rabies preparedness. The interactions among and between Australia's large populations of wild, free-roaming and restrained domestic dogs require quantification for rabies incursions to be detected and controlled.

The imminent risk of rabies breaching Australian borders makes the development of disease spread models that will assist in the deployment of cost-effective surveillance, improve preventive strategies and guide disease management protocols vitally important.

Here, we critically review Australia's preparedness for rabies, discuss prevailing assumptions and models, identify knowledge deficits in free-roaming dog ecology relating to rabies maintenance, and speculate on the likely consequences of endemic rabies for Australia.

2.1.2 Impacts

- The current national rabies preparedness plan (AUSVETPLAN) is largely based on overseas fox rabies research and Australian fox ecological studies, and has largely ignored Australia's ubiquitous and often locally abundant free-ranging dog populations.
- Realistic and sophisticated models of dog rabies spread, incorporating the movement and ecological parameters of the many different dog populations throughout Australia are required for robust, accurate and cost-effective preparedness planning.
- We propose the development of an ecological database for each Australian dog population because their different behavioural and social patterns are likely to represent a range of risk profiles for rabies susceptibility, transfer and persistence.

Keywords

Rabies, dingo, free-ranging dog, peri-urban dog, epidemiologic models, preparedness

2.1.3 Introduction

Rabies is an acute, fatal, viral zoonosis, most commonly transmitted to people through the bite of an infected dog (Warrell & Warrell 2004). More than 55 000 people die of rabies annually (Knobel *et al.* 2005), with more than half of those deaths occurring in Asia (World Health Organisation 2005). The Australian continent is currently free of terrestrial rabies but a zoonotic outbreak is a realistic and imminent threat from South East Asia, where canine rabies is endemic and known to be spreading eastward along the Indonesian archipelago (Putra *et al.* 2009, Tenzin & Ward 2012, Putra *et al.* 2013). Despite culling programs and mass vaccination campaigns in Indonesia, canine rabies is now less than 300km from the Australian mainland (Tenzin & Ward 2012).

Australia has disease preparedness plans to address the incursions of exotic disease, such as rabies (Animal Health Australia 2011). Australia's most recent rabies review occurred in 1999 (Saunders 1999) and the most recent exercise for rabies preparedness and contingency planning was a 1990 test of the AUSVETPLAN for fox rabies (O'Brien & Berry 1992). At that time, the threat of dog rabies to Australia was largely discounted, although Newsome and Catling (1992) identified that dingoes (*Canis lupus dingo*: synonyms *C. familiaris dingo* and *C. dingo*) and other dogs (*C.l. familaris*: synonym *C. familiaris*, and cross-breeds *C.l. dingo* X *C.l. familiaris*) of northern Australia should be given the highest priority in rabies preparedness. Despite best efforts and the rabies AUSVETPLAN, Australia remains underprepared for rabies because of insufficient and outdated information about free-roaming canid interactions and importation risks.

It is most probable that rabies will enter northern Australia by a subclinically infected dog travelling on a fishing vessel or pleasure craft. With a potentially long incubation period (Warrell & Warrell 2004, Wandeler *et al.* 2013), the disease would probably spread undetected through the dog population for many months, as recently occurred in Indonesia (Clifton 2010).

Following the introduction of rabies, large populations of free-roaming dogs in and around remote communities, outstations and mining camps would be likely contact points for zoonotic rabies transmission. Translocation of subclinically infected domestic dogs between communities will likely accelerate the spread of the disease, increase human exposure to infected dogs and create multiple, disparate foci for reactive management programs. Domestic dogs in more urban areas will also play a significant role in the zoonotic transmission of rabies (Warrell & Warrell 2004), and their interactions with urban and peri-urban wild dogs will likely accentuate spread of rabies between closely settled eastern Australian communities.

Developing our understanding of the roles that dogs, other potential ‘spillover’ hosts and the broader environment may play in the spread of rabies in Australia is vital to facilitate informed management plans and the development of useful epidemiological models of the disease in Australia.

We reviewed the literature from rabies endemic countries and the ecology of Australia’s free-roaming dogs to provide a contextual framework for rabies transmission in Australia. Furthermore, we speculate on the likely consequences of endemic rabies for Australia and identify knowledge gaps that require further research.

2.1.4 Rabies

Canine rabies is caused by the classical rabies virus, Genotype 1 of the genus Lyssaviruses within the Rhabdoviridae family, and causes acute encephalitis in mammals (Burgos-Caceres 2011). Other Lyssavirus genotypes, including the Australian bat lyssavirus, an emerging disease that continues to threaten human health (Moore *et al.* 2010), cause bat-related rabies. With a few exceptions, including Australia and New Zealand, rabies occurs worldwide and the number of clinical cases continues to rise

(Warrell & Warrell 2004, World Health Organisation 2005). The focus of this review is on the canine rabies virus (Genotype 1), which is likely to have great impacts on Australian society because Australians are unfamiliar with and fearful of canine rabies.

Rabies is usually transmitted through saliva by the bite or scratch of an infected animal. Once the rabies virus enters the body, it replicates in the tissue surrounding the bite wound. Within hours to days, the virus invades peripheral nerve endings, proceeding along axons to the central nervous system (Schnell *et al.* 2010). Clinical signs are observed once the virus reaches the central nervous system, and at this point, the disease is fatal.

The incubation period can range from several days to several years, depending on the susceptibility of the host and the location of infection (Smith 1996, Koprowski 2009). In dogs and cats (*Felis silvestris catus*), incubation typically ranges from 10 days to six months, with most cases apparent between two weeks and three months after initial infection (Warrell & Warrell 2004, Center for Food Security and Public Health 2009). The only definitive test currently available to diagnose rabies is by examination of brain tissue post-mortem (World Health Organisation 2005).

2.1.4.1 Hosts and clinical signs

Rabies can infect all mammals. However, there are multiple strains (biotypes) of the virus, each associated with a particular maintenance (reservoir) host. The canine biotype of the rabies virus is the most widely distributed in the world (Paweska *et al.* 2006). Transmission cycles within reservoir species are common, as they are generally extremely sensitive to their rabies virus biotype, but less so to those of other species (Bingham 2005). Spillover hosts, such as humans, livestock and ungulate wildlife species are dead-end hosts that cannot maintain an independent rabies cycle. Death is inevitable once rabies progresses to the central nervous system and clinical signs are apparent, with death usually occurring within 10 days after the onset of clinical signs (Alkali *et al.* 2002, Tepsumethanon 2005).

Rabies is maintained and characterised by two distinct epidemiologic cycles; an urban and a sylvatic cycle:

- **Urban cycle**: dogs are the main reservoir host and the dog virus biotype prevails. This cycle is common where the proportion of unvaccinated and free-roaming dogs is high, such as in Africa and Asia (Forman 1993, Tenzin & Ward 2012)

- **Sylvatic cycle**: circulates through wildlife populations and is more important where the urban cycle is well controlled, such as in Europe and North America (Holmala & Kauhala 2006, Burgos-Caceres 2011)

Importantly, Australia has the potential for a sylvatic cycle where the wildlife involved would be free-ranging dogs (including dingoes), which are widespread, locally abundant and conspecific (Fleming *et al.* 2006, Fleming *et al.* In press). This is a key difference for Australia because multiple biotypes and multiple species are usually involved in sylvatic rabies epidemiology elsewhere (Holmes *et al.* 2002, Blanton *et al.* 2012). The exceptions are North America, where a sylvatic cycle of the dog biotype is sometimes maintained between domestic dogs and coyotes (*Canis latrans*) (e.g. Sidwa *et al.* 2005, Shwiff *et al.* 2008), and possibly South Asia where jackals (*Canis spp.*) are a minor species implicated in zoonotic rabies infections (Tenzin & Ward 2012) and it is likely that they are infected with the dog biotype. In Australia, all wild-living dogs are generally considered 'wildlife' and dingoes are considered 'native', but their presence and interactions with urban dogs (Allen *et al.* 2013) will likely result in overlap between urban and sylvatic cycles.

Although the clinical manifestation of rabies (clinical signs can be classified into the furious and dumb [paralytic] forms and can change during disease progression, Laothamatas *et al.* 2008, Thanomsridetchai *et al.* 2011, Susilawathi *et al.* 2012) varies greatly between individuals and species, an increase in aggression and a tendency to bite (and therefore transmit the virus) is reported to be associated with rabid carnivores, including dogs (Silva *et al.* 2004, Hampson *et al.* 2009). Hampson *et al*. (2009) reported that the biting behaviour of rabid dogs was highly variable, highlighting that a small number of individuals can disproportionately drive rabies transmission. However, recent studies (e.g. Tepsumethanon *et al.* 2010, Wang *et al.* 2011) have cast doubt on the relationship between aggression and rabies infection in pets (particularly cats and dogs).

Other studies have continued to highlight the relationship between rabid wildlife and aggressive behaviour (Rosatte *et al.* 2006, Wang *et al.* 2010a, Wang *et al.* 2010b, Wang *et al*. 2011). However, only suspect rabid animals were included in these studies and as such, aggressive behaviour of wild animals may be over reported compared with clinical signs of dumb rabies (i.e. if animals exhibit the dumb form, they are less likely to bite and be found, and therefore may go unreported).

2.1.4.2 Control options

Although many countries are reducing rabies incidence (e.g. Freuling *et al.* 2013), incidence continues to rise worldwide despite much being known about the epidemiology of rabies and the control options that are available. Canine rabies is reported in over 80 countries, predominantly in developing nations where lack of knowledge and capacity limits the uptake of control options (World Health Organisation 2005).

2.1.4.2.1 Domestic animals

Canine rabies has been eradicated from domestic canine populations in North America (Velasco-Villa *et al.* 2008), Western Europe (Müller *et al.* 2012), Japan (Takahashi-Omoe *et al.* 2008) and parts of South America (Schneider *et al.* 2007). Effective control strategies typically involve mass vaccination campaigns along with epidemiological surveillance, dog population control and modification of relevant human behaviour, such as improved domestic animal management, refuse disposal and an increased awareness in zoonotic diseases through education programs.

Campaigns to vaccinate domestic dogs have proven to be the most successful method for controlling and eradicating the canine rabies virus in parts of Europe and North America. Parenteral vaccination programs are widely implemented in rabies endemic regions. Oral vaccination of domestic dogs has also proved useful in controlling rabies in free-roaming and largely unsupervised dog populations, such as those present in many developing nations (World Health Organisation 2007). Mass culling of animals to eradicate rabies – as occurred in China (Yang & Dong 2012) and parts of Indonesia (Hutabarat *et al.* 2003, Clifton 2010) – was ineffective because insufficient animals were culled to eliminate the disease and account for compensatory recruitment of individuals to the population. Alternatively, owners removed their (subclinically infected) dogs to prevent them being killed and consequently spread the disease (Clifton 2010). A coordinated and integrated approach including dog management, animal birth control programs and widespread vaccination are more likely to achieve the desired outcome (World Health Organisation 2005, Clifton 2011) and has also been recommended as a key measure in developed countries (Adedeji *et al.* 2010, Putra *et al.* 2013). These recommendations have direct application to some remote communities in

Australia where relationships with free-roaming dogs are analogous to the situation in developing countries.

2.1.4.2.2 Wildlife

The control of rabies in wildlife has proven more difficult than in domestic animals because interactions between humans and animals are more stochastic and largely unquantified, and there may be large communities of multiple reservoir species and numerous spillover host species.

Vaccination of wildlife through delivery of oral baits has proven effective in some countries, including in the eradication of fox rabies from European countries (Wandeler *et al.* 1988, Müller *et al*. 2012, Freuling *et al*. 2013). Similar successes have been replicated in Ontario, Canada, and parts of North America in the elimination of the raccoon rabies variant and the canine rabies variant, respectively (Sterner *et al.* 2009). However, the area treated in these countries is relatively small compared to many endemic regions and only a single animal reservoir species was targeted (Smith 1996). To maintain these rabies-free regions or minimise the spread in wildlife populations, oral rabies vaccination campaigns continue to be implemented at high costs (Smith 1996, Warrell & Warrell 2004, Sterner *et al*. 2009).

Similar to the widespread culling of domestic dogs, reducing the population size of wildlife host species has not been effective in eradicating rabies. Indeed, the removal of large numbers of host species has been implicated in increasing the spread of the rabies virus (Rupprecht *et al.* 1995, Morters *et al.* 2013) due to compensatory survival of recruits and removal of mature animals that caused disruption of social groups, increased dispersal of younger hosts, increased territory disputes and higher host-host contact rates (e.g. Smith 1996). This in turn, can result in a greater potential to spread the disease. However, the proportional reduction in wildlife population size and the density of remaining animals after culling, as in Fleming (1997), is seldom reported (Saunders *et al.* 2010). This is essential information for assessing the effectiveness of culling programs in halting a disease, because, unless substantial reductions in population size and density are made, compensatory births and survival of young may ensure that population parameters are unaffected in the long-term.

2.1.5 Canine rabies in Australia

Although Australia is currently free of terrestrial rabies, in 1867 a single, probable occurrence of rabies transmission occurred in Tasmania [the large island-state in south-eastern Australia]. A child was bitten by a dog that was assumed rabid after the child, several dogs and a pig died shortly after the onset of clinical signs (Pullar & McIntosh 1954). No further outbreaks have been recorded in Australia since (Geering 1992). Two confirmed reports of rabies in humans in Australia have been documented (1987 and 1990) but the disease was contracted outside of Australia (Bek *et al.* 1992, Grattansmith *et al.* 1992).

The Australian Government, in consultation with state and territory governments and industry bodies, has developed a technical response plan (AUSVETPLAN) for use in the advent of a rabies outbreak in Australia (Animal Health Australia 2011). The rabies AUSVETPLAN outlines key control measures to be implemented and highlights policies, coordination requirements and emergency management plans to ensure rapid detection and containment of the disease. The technical response plan is continually reviewed and updated as new information becomes available and relies on realistic incursion scenarios. In an attempt to reduce the risk of disease incursions, regular surveys for exotic diseases, including rabies, are carried out under the Northern Australian Quarantine Strategy in Australia and neighbouring countries (Department of Agriculture Fisheries and Forestry 2011).

2.1.5.1 Incursion scenarios

We can only speculate on how rabies will be introduced to Australia and spread, once introduced. The epidemic size could range from rapid fading out of the disease to nation-wide disease spread. There remains a constant possibility of illegal importations of rabid animals through visits from boats continuing Australian-South East Asian cross-cultural traditions that were established pre-European settlement, unauthorised fishing vessels and itinerant yachts. This is particularly relevant across northern Australia where the coastline is vast and sparsely populated by humans (Australian Bureau of Statistics 2012), limiting our ability to detect an initial outbreak. Recent outbreaks in Indonesia (Flores, Bali, Ambon and the Tanimbar Islands) have also increased the risk of rabies entering Australia (Drewitt 2012, World Organisation for Animal Health 2012).

Once an infected animal has breached northern Australian quarantine, it would first have to encounter and bite a resident dog, for an outbreak to begin. This first contact is a realistic threat because most coastal communities have populations of unrestrained domestic dogs and wild free-ranging dogs are relatively numerous across northern Australia (see Figures 3.42 and 3.43 in West 2008).

In the rabies-endemic eastern islands of Indonesia that are closest to Australia, rabies exists as a ‘street dog’ urban cycle of transmission (Putra *et al*. 2013), with transmission to owned dogs from free-ranging street dogs. An owned and usually restrained dog, once infected could then be placed on a boat bound for Australia. The introduction of a live, infected dog travelling with humans who avoid quarantine is the most plausible incursion scenario for Australia (Forman 1993, Cookson *et al.* 2012).

Time-to-detection will be a critical factor affecting the extent of rabies infection in Australia. A long incubation period increases the risk that rabies will spread undetected for some time and could infect many dog populations prior to disease detection. Disease awareness of rabies in northern Australia is expected to be minimal because of the historical absence of rabies. Further, the occurrence of coincident endemic diseases such as canine distemper in remote-community dogs and a lack of active surveillance of wild dog populations for disease events will likely mask rabies and extend the time to first detection.

Effective surveillance is essential to minimise time-to-detection. However, little is known about the size and abundance of many susceptible populations in northern Australia, the contact rates between them and the movement of dogs between communities. Further research in these fields is required to gain information not only on potential rabies spread but also to refine surveillance programs. Multiple pathways for incursion exist and two likely scenarios are described as examples.

2.1.5.1.1 Northern incursion scenario 1: the Top End of the Northern Territory

Yachts regularly travel through the islands of Maluku province, Indonesia and it is possible that one might contain a subclinically infected dog. If the yacht illegally lands along the coast of Arnhem Land, the dog could escape (still without having shown clinical signs) and make contact with wild dogs, or contact free-ranging dogs associated with a remote coastal community, or it could become visibly sick and be abandoned.

Similarly, the source could be a subclinically infected dog brought by South East Asian people maintaining ancient cultural ties with Northern Territory peoples. The spread of rabies in Australia would begin through contact between such an infected animal and wild or domestic free-roaming dogs and then spread through the region. Movement of the disease from the initial source could be facilitated by human transport of one or more subclinically infected dogs to other communities.

2.1.5.1.2 Northern incursion scenario 2: Cape York Peninsula

The Indonesian province of Maluku is adjacent to the province of West Papua. If rabies spreads to West Papua province (currently believed to be rabies free), there is no natural barrier to protect Papua New Guinea (PNG) from the disease. The central mountainous terrain of this island might slow spread, but is unlikely to prevent the eventual diffusion of rabies through PNG.

Several communities are located in the Northern Peninsula Area of Australia, including those on the Torres Strait Islands. Strong cultural links exist between some of these communities and those on both the mainlands of PNG and Australia. Should rabies spread to PNG, a viable pathway exists via the movement of people and their dogs through the Torres Strait to Cape York Peninsula communities.

2.1.5.2 Potential hosts

Australia contains substantial numbers of suitable domestic and wild host populations including domestic and wild dogs, cats, foxes (*Vulpes vulpes*), pigs (*Sus scrofa*), water buffalo (*Bubalus bubalis*) and native mammals (West 2008). Although it is expected that a rabies incursion into Australia will be in the form of the canine rabies biotype originating in Indonesia, consideration should also be given to the potential spread of the disease into other mammals.

Foxes and possums, particularly brush-tailed possums (*Trichosurus vulpecula*), are widespread over much of Australia, are often found within urban areas (Marks & Bloomfield 1999, Eymann *et al.* 2006), have close associations with domestic animals and human habitation.

The susceptibilities of possums and other Australian native fauna, including carnivorous quolls (*Dasyurus spp.*) is unknown, but due to presumed low abundance and limited distributions, native carnivorous mammals have not been considered a high risk for rabies transmission in Australia (Garner 1992). Although New Guinea marsupials, such as sugar gliders (*Petaurus breviceps*), which are also found in Australia, have been experimentally infected with rabies virus (Banks 1992, Geering 1992, Newsome & Catling 1992), most Australian marsupials are expected to be dead-end hosts (Newsome & Catling 1992). However rabies, once established, may have important implications for long term persistence of marsupials.

2.1.6 Wild canids in Australian landscapes

Wild dogs and red foxes are prominent pest species in Australian rangelands (Fleming *et al*. In press) and could facilitate the maintenance and spread of rabies. While the illegal or accidental importation of the fox biotype into Australia is considered unlikely and hence foxes are an unlikely threat for initial rabies establishment and spread (Saunders 1999, Animal Health Australia 2011), Forman (1993) highlighted the potential of dogs to become infected and maintain both a sylvatic and urban rabies cycle within Australia, so we concentrate on dogs here.

2.1.6.1 Wild dogs

Free-ranging dogs, some of which are unowned or ‘wild’ dogs, are a feature throughout mainland Australia (Fleming *et al.* 2001, Fleming *et al*. In press). Dingoes, descendants of grey wolves (*Canis lupus*) (Pang *et al.* 2009, von Holdt *et al.* 2010) were brought to Australia from Asia approximately 4,000 years ago (Corbett 2001, Oskarsson *et al.* 2012) and Europeans first introduced modern domestic dogs in the late 18th Century (Fleming *et al*. 2001, Fleming *et al.* 2012).

Dingoes and domestic dogs have since interbred (Wilton *et al.* 1999, Stephens 2011) and now populate much of mainland Australia (Fleming *et al*. In press) (Figure 2-1). Food, water and vegetation coverage are the most important factors influencing the distribution and abundance of wild dogs (Newsome *et al.* 2013) but management and control does limit their distribution (Fleming *et al*. 2001).

[redacted]

Figure 2-1 Distribution of free-ranging dogs in Australia in 2012

Grey represents presence and white represents absence or no data. The black lines are government maintained dog barrier fences. Data are from standardised expert surveys (From Fleming *et al*. In press)

2.1.6.2 Wild dog ecology

The size and structure of wild dog social groups, their density, home range size and movement behaviour of individuals and groups will all impact upon how quickly rabies will spread in Australia. Studies of social organisation among wild dogs have mostly been done in pen studies of dingoes (exception Thomson 1992b) and extrapolated to field situations and all wild dogs (Corbett 1988, Fleming *et al*. 2001). The structure of dingo packs is matrilineal, with a dominant bitch mating with an alpha male and regulating the reproductive success of subordinate females, which are usually her offspring (Corbett 1988). However, these social structures are fluid; with dominance being constantly contested and changing (Corbett 1988, Thomson 1992b) and sometimes breaking down altogether when superabundant anthropogenic food is available (Newsome *et al*. 2013). Aggressive interactions within and among groups of wild dogs are likely affected by resource availability and distribution, which are often determined by human activities such as refuse disposal and provision of water points for livestock.

Determining the abundance of wild dogs is always difficult (Fleming *et al*. 2001) but density estimates (i.e. abundance per unit area) are critical for modelling disease transmission and implementing effective rabies surveillance and control strategies. Disease transmission is likely to be at least partly density-dependent and the number of animals present at any location will impact on contact rates (both inter- and intra-species interactions). Wild dog densities vary with primary productivity, ranging from about 0.08 per km^2 in arid areas to between 0.14 and 0.3 per km^2 in higher-rainfall areas (Fleming *et al*. 2001). Greater densities have been observed at focal anthropogenic resources (Newsome *et al*. 2013).

Home ranges (the area in which an individual normally resides; Burt 1943) are important for defining areal denominators when quantifying contact rates and identifying locations of spatial overlap where disease transmission can occur. Wild dog's home range sizes vary depending on the environment and resource availability (Fleming *et al*. 2006). Generally they are larger in the more arid regions (Thomson 1992b, Thomson & Marsack 1992, Newsome *et al*. 2013) and smaller in higher-rainfall habitats such as northern and eastern Australia (Harden 1985, Claridge *et al*. 2009) and near anthropogenic food (0.7—10.9km^2 near arid zone mine sites *cf* 79.5-999km^2 in surrounding arid areas, Newsome *et al*. 2013) as would be expected in northern Australian remote communities.

Individual free-ranging dog home ranges often overlap spatially (Claridge *et al*. 2009, Allen *et al*. 2013, Newsome *et al*. 2013), particularly where there is a shared focal resource such as a water source or foraging area (Meek 1999, Newsome *et al*. 2013) or during the breeding season (Corbett 2001).

High densities of susceptible host species increase the risk of a rabies epidemic but long dispersal distances and forays have also been known to increase the rate of spread (Jin & Wang 2005). Importantly, resource rich areas with many overlapping home ranges may allow rabies to rapidly spread through a population, infecting a large number of dogs in a relatively short timeframe. In contrast, in resource poor areas, where home ranges are larger and densities smaller, rabies may take longer to infect the same number of dogs, but may infect a larger land mass before detection and persist in the environment for longer. Consequently, understanding host dispersal, including frequency of movements and distance travelled will contribute to our understanding of rabies spread (Jin & Wang 2005).

The roaming behaviour and home range sizes of wild dogs in remote Australia are generally understood (Whitehouse 1977, Thomson & Marsack 1992, Thomson *et al.* 1992a, Thomson *et al.* 1992b, Newsome *et al*. 2013). Few studies have examined ranging behaviours in higher-rainfall coastal regions (Harden 1985, Claridge *et al*. 2009, Robley *et al.* 2010, Allen *et al*. 2013) and none have been undertaken in northern Australia where first contact with rabies is more likely. Genetic analysis could be used to quantify dispersal rates and contact rates between populations via studies of relatedness among individuals and groups (e.g. Cullingham *et al.* 2008) and genetic mutation rates.

2.1.7 Community dogs

Dogs in many parts of Australia are often associated with remote and indigenous communities (Hardaker 2008). These dogs are typically free-roaming and often found searching for food around local townships. In some communities, dogs are considered sacred, with some individual animals holding spiritual significance.

Due to their free-roaming behaviour, uncontrolled dog populations are often in poor health because of the remoteness from veterinary support and lack of resources and many dogs in central and northern Australia spread disease and parasites to both humans and wildlife (Meek 1999, Bradbury & Corlette 2006, Barker *et al.* 2012, Hii *et al.* 2012). Further, it is not uncommon for dogs to be translocated between neighbouring communities, transferring disease with them (Hardaker 2008).

Subsidised dog health programs have been implemented in a number of remote communities in northern Australia over the past few decades in an attempt to reduce dog numbers and improve animal and human health, with varying success (Bradbury & Corlette 2006). Successful programs that improve human health and animal health and welfare, usually incorporate some form of surgical de-sexing and anthelmintic treatments of dogs and educational programs (Currie 1998, Bradbury & Corlette 2006, Hardaker 2008). Due to the cultural significance placed on dogs within communities, cultural sensitivity and empathy should be employed when implementing animal management strategies. Any attempt to deal with dog health issues inappropriately (for example, through enforced mass euthanasia) will likely be met with resistance and a lack of support, inhibiting any real permanent change (Constable *et al.* 2010) and potentially impeding the uptake of rabies control programs in the future.

Information on the roaming behaviour and home range sizes of free-roaming community dogs in Australia is limited to two small studies (Meek 1999, Allen *et al.* 2013). Meek (1999) studied the movements of free-roaming dogs from an Australian indigenous community in south-eastern New South Wales (NSW) (n=10) during 1994 and 1995. Half of the collared dogs undertook forays of 8 to 30km into nearby riparian habitat. Home ranges of these dogs varied from 1.4 to 24.5km^2 (mean 9.3km^2). In contrast, the remaining dogs spent the majority of their time within close proximity to the community, with an average home range of 0.026km^2 (Meek 1999). Using GPS logging collars on peri-urban wild dogs in south-east Queensland, Allen *et al.* (2013) also found small home ranges (<4km^2, n= 9), that were all within 700m of residential homes at all times and that 72% of their time was spent in urban habitats. Contacts among the study dogs and between them and domestic animals were not measured. In Bali, where plentiful food waste was available, mean home ranges were found to be 0.1km^2 for male free-roaming dogs and 0.05km^2 for females (Gunata 2011). There was, however, variation in the home ranges of urban, peri-urban and rural dogs.

2.1.8 Pet dogs

The domestic dog plays a critical role in contemporary Australian society (Australian Companion Animal Council 2010) and has cultural and familial importance. Human reliance on and engagement with the domestic dog is reflected through increasing dog ownership across the globe (Burgos-Caceres 2011).

In Australia, the pet dog population was estimated to be 3.4 million in 2009, with 2.9 million (36%) households owning a dog (Australian Companion Animal Council 2010). Although all Australian States and Territories have laws pertaining to dog ownership, not all dogs are adequately registered and restrained and as such, management of dogs is complex, difficult and often conflicted and this may have negative implications for the control of rabies in Australia.

Stray dogs (i.e. pet dogs roaming unsupervised) can pose a critical risk for rabies transmission between sylvatic and urban cycles (Woodroffe & Donnelly 2011). Limited studies have assessed the roaming behaviour of stray dogs in Australia. Coman and Robinson (1989) investigated the roaming behaviour of stray dogs on the outskirts of Bendigo, a city in central Victoria. Of the 80 straying dogs observed, 47 travelled less than 2km, 31 travelled between 2 and 6km and two stray dogs undertook a foray of more than 11km. Dogs living in the outer suburbs were found to be more likely involved in forays into surrounding bush or farmland compared with inner city dogs and may therefore be at greater risk of contracting and transmitting rabies.

2.1.9 Role of the working dog

Working dogs' roles in society have diversified over the centuries and they are now used widely throughout the world for law enforcement, search and rescue, assisting the disabled, herding, stock protection, hunting and other recreational activities. However, population data and the behavioural characteristics of these working dogs is lacking (Miklosi 2007). Understanding these different groups of domestic dogs and how they interact with other animals is essential in understanding inter- and intra-species interactions that will likely influence the spread of rabies.

Stock-working dogs are used on some northern Australian cattle stations, and contractors transport groups of working dogs between stations. Property managers using contracted working dogs are less likely to implement broad-scale lethal wild dog control activities due to the high risk to un-muzzled working dogs. This scenario of free-ranging and working dogs using and potentially interacting within the same landscape provides contact points for the transmission of rabies. Further, station dogs wandering during the breeding season and dingoes entering towns has also been reported (Newsome 2001) and could pose another risk for rabies transmission between wild and domestic dogs.

Particular attention should also focus on dogs used in hunting. Hunting dogs have the potential to interact with wild dogs where they move out of sight of their handler for extended periods of time. In Australia, this is particularly relevant for dogs used in 'pig hunting.' Anecdotal reports have emerged of pig dogs being attacked by wild dogs during hunting expeditions. One hunter noted that when two of his dogs were holding a pig (in the early morning), there were 'three dingoes (sic) biting and attacking our dogs' (anon February 2012). Reports of wild dogs attacking and killing pet dogs have also been recorded in north-eastern NSW (P Fleming unpublished data 1984, G. Hart pers.

comm. 2013). Clearly, interactions between wild dogs and domestic dogs occur as evidenced by the high proportion of cross-breeds in much of Australia (Stephens 2011), but little is known about the frequency and extent of these interactions.

Research quantifying the interactions between wild dogs and domestic dogs will be critical in predicting the spread of rabies in Australia. Any such studies should not only focus on defining and estimating unsupervised contacts, but also quantifying working dog translocation events throughout Australia.

2.1.10 Management

2.1.10.1 Control of wild canids

A variety of control techniques are used to manage wild dog and fox populations in Australia. In most circumstances, an integrated approach using a combination of control options is recommended. Poisoning is the most cost-effective method of controlling wild canids, particularly for remote and inaccessible areas (Fleming *et al*. 2001). Compound 1080 (sodium fluroacetate) is the most commonly used chemical in wild dog baiting programs because it can be applied on a broad scale (e.g. through aerial baiting programs), is relatively cheap, biodegradable, target specific at the rates used for wild canids and can be used to control wild dogs, foxes and cats (Allen 2011). However, strict controls in the use of 1080 are enforced and its use is restricted in peri-urban regions because it is lethal to pet dogs.

Trapping is used in areas where poisoning is impractical or illegal (e.g. where there is a high risk of poisoning humans, pet dogs and other non-target species). However, setting of traps is labour intensive and requires training and experience to be effective and humane (Fleming *et al*. 2001). In addition, trapping provides the opportunity for members of the community to come into contact with target animals. Well-intentioned members of the public will attempt to release wild and domestic dogs from foothold traps (G. Ballard personal observation), providing another contact point for rabies transmission.

Although battues (the driving of game animals from cover to a stationary hunter) are sometimes used, shooting of wild dogs and foxes is usually undertaken to target specific individual animals by luring them within range with simulated howls or whistles (Fleming *et al*. 2006). Shooting is however, impractical on a broad scale and requires a high level of experience, skill and time investment. Exclusion fencing (see Figure 2-1), where wild dogs are physically excluded from an area remains popular in sheep production areas and at some human refuse disposal points. However, long perimeter fencing is expensive to establish and maintain, and on its own, does not control wild dogs already in the exclusion zone (Fleming *et al*. In press).

2.1.10.2 Domestic dog management

Within Australia, there are two broad areas of legislation relevant to companion animals; those related to their welfare and those related to their management. The legislative framework is developed by State governments and implemented by local government. There is no Commonwealth legislation relevant to the welfare or management of companion animals in Australia (Harlock Jackson Pty Ltd 2006).

Microchipping for individual identification of pet dogs is not mandatory in every Australian state and territory, while registration is compulsory throughout Australia except in the Northern Territory. Despite this, compliance is difficult to enforce and many dogs, including working dogs in NSW, likely remain unaccounted for.

Identifying the ratio of registered to unregistered dogs is important for accurately estimating dog densities and populations within local government areas and therefore, dog numbers in each state and territory. Quantifying abundance will improve the predictive capacity of rabies epidemiological models in Australia.

2.1.11 Monitoring dog bite incidents

Although only a proportion of rabies-infected dogs will show increased aggression (see ‘Hosts and clinical signs’), an increase in total population aggression may be an early indicator of a rabies outbreak. Further, rabies transmission would likely occur in Australia with current levels of dog bite incidences (e.g. in NSW; NSW Department of Premier and Cabinet 2012). Quantification of the current prevalence of dog bites to humans and other animals will provide a baseline for rabies preparedness planning. However, there is currently no comprehensive database for reporting dog bites in Australia (Australian Companion Animal Council 2007b). Information regarding dog attacks on humans is collected and recorded by Australia’s health systems (i.e. hospital records), while reports of dogs attacking other animals are generally kept by local government authorities (Australian Companion Animal Council 2007b). New South Wales is the only Australian state where it is mandatory for all dog attacks (incidents in which a dog rushes at, attacks, bites, harasses or chases a person or animal is classed as a dog attack, regardless of whether any injury is sustained, NSW Department of Premier and Cabinet 2012) to be reported, and reporting is required within 72 hours of notification of the incident.

Although current dog attack data are clearly imperfect, a number of studies have estimated the likely number of dog attacks per annum and have further attempted to describe risk factors associated with dog bites in Australia. Dendle and Looke (2008) estimated that 2% of Australians will be bitten by a dog each year. In a more localised study, Thompson (1997) estimated that dogs injure 6,500 people each year in the South Australian capital, Adelaide, with around 800 of those seeking hospital treatment (7.3 per 10,000 people per year). This was an order of magnitude greater than estimates of the national hospitalisation rate for dog attacks of 7.7 per 100,000 people in 1995 to 1996 (Ozanne-Smith *et al.* 2001) and between 2001 and 2003, Kreisfeld and Harrison (2005) estimated a hospitalisation rate of 11.3 per 100,000 people for treatment of dog-related injuries.

Data analysed in these studies were based on information from public hospitals, the Victorian Emergency Minimum Dataset and the National Injury Surveillance Unit, and does not include information about unreported dog bites and patients treated at private hospitals or by general practitioners. Indeed, most dog bites that occur in rural and remote communities are unlikely to be reported. Determining the true extent of dog bite related injuries will provide a more accurate assessment of the minimum risk of rabies infection in the event that rabies enters Australia. For example, in the United States where most domestic dogs are vaccinated against rabies, the risk of rabies infection after a bite from a dog (with no post-exposure prophylaxis) was estimated to be 0.00001 (i.e. 1 person develops rabies in 100,000 dog attacks) assuming a canine rabies prevalence of 0.1% (Vaidya *et al.* 2010).

Once the probability of rabies infection has been quantified, the costs associated with administration of post-exposure prophylaxis (PEP) treatment can be estimated. For example, during the 1987 rabies outbreak in Mexico, approximately 2.5% of city residents were bitten by a dog (Eng *et al.* 1993). Of those bitten, 60% were evaluated as requiring PEP treatment (bite from a known or suspect rabid dog) with 273 per 100,000 city residents administered PEP. With the direct cost of administering a full course of PEP estimated at US $2,500 (Vaidya *et al*. 2010), the Mexican outbreak cost an estimated US $682,500 per 100,000 citizens for PEP alone.

Although the collection of dog bite data cannot provide a precise forecast of rabies infection (prevalence) in humans should the disease enter Australia, it can indicate the potential size of the problem. With this information, it may be possible to estimate the minimum prophylaxis required and therefore the potential minimum costs to the Australian economy. Understanding the potential pre- and post-emptive response costs (i.e. large scale vaccination versus treatment) will assist in the determination of best management strategies should rabies breach Australian borders.

2.1.12 Predicting the spread using epidemiologic models

Models used to predict the introduction and spread of rabies range from simple systems of ordinary differential equations (e.g. Pech & Hone 1992) to extensive computational simulations (e.g. Panjeti & Real 2011). For any model utilised, a number of parameters need to be estimated. Parameters that are essential in predicting the spread of rabies include the ecology of the host species and the virus, environmental factors and human behaviour.

Of the epidemiological models currently available for use in rabies outbreaks, the majority are reactive to the outbreak (i.e. assessment of frontline movement and of the success or failure of control programs); or descriptive (e.g. Murray *et al.* 1986, Rosatte *et al*. 2006, Zinsstag *et al.* 2009). Models predicting the spread of rabies in countries like Australia, which are currently rabies free, are lacking. To develop such models, estimates are required for disease transmission factors including:

- the probability of rabies transmission after being bitten;
- the incubation period of the disease;
- duration of infective period;
- contact rates between susceptible and infected individuals; and
- host population characteristics (such as abundance or densities).

These parameters are required for disease spread models to be useful, for example, in determining the level of population control or vaccination that would be required to reduce the density of the susceptible host species to below the threshold required for disease establishment (Figure 2-2).

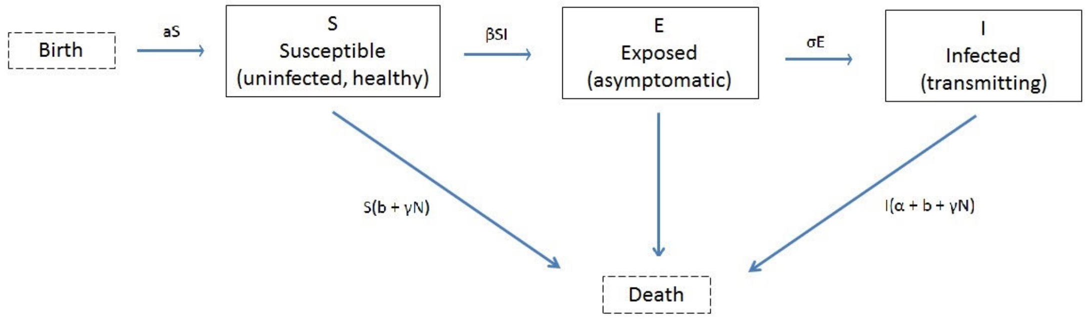


Figure 2-2 A simple susceptible-exposed-infectious-removed diagram for use in Australian rabies modelling

Note: symbols represent: susceptible hosts (S), exposed individuals (E), infectious individuals (I), birth rate (a), mean life expectancy (1/b), disease transmission factor (β), mortality rate of infectious individual (α + b). Source: Panjeti & Real (2011)

Hampson *et al*. (2009) estimated R_0 (the number of successful infections from an infectious individual during the infectious period) for rabies to be very low in rural Tanzania and throughout other rabies endemic countries ($1.1 < R_0 < 2$), indicating vaccination and therefore control, would be a viable option. Similar values for R_0 have been found elsewhere (Table 2-1). Parameters incorporated into the Hampson *et al*. (2009) model included information on mean bites per rabid dog, probability of rabies infection after being bitten by an infected dog and the timing and location of transmission events. Interestingly, it was found that there may not be a relationship between dog density and R_0 for rabies transmission, with further investigation required.

Hampson *et al*. (2009) used contact-tracing methods for individual dogs in their analyses, which may not be an effective method in an Australian context because of the extensive landscape and multiple hosts present. Further, Hampson *et al*. (2009) did not consider sylvatic rabies cycles; rather, they only assessed domestic dog rabies, where, unlike Australia, population numbers, dog bite incidences, contact rates and roaming behaviours are relatively well known.

More complex rabies modelling utilises ecological factors such as dog densities, habitat use and habitat carrying capacities to describe or predict how the disease front will behave (Zinsstag *et al*. 2009, Panjeti & Real 2011). These models have allowed researchers to understand how transmission barriers (i.e. culling and vaccination programs) can be designed and implemented to effectively control a rabies outbreak, but rely on unrealistic assumptions; that the population is homogenous throughout the landscape and rates of infection, births and deaths remain constant throughout an outbreak and are therefore limited in their accuracy in predicting the spread of rabies over a longer time (Shigesada & Kawasaki 1997).

Translocation of subclinically infected animals has been thought to be one of the major factors contributing to new outbreaks ahead of the disease front. As such, a number of models have also been developed that include a translocation transmission factor. For example, Smith *et al.* (2002) incorporated long-distance translocation into their raccoon rabies virus dispersal models as a low, constant rate of infection to simulate translocation of infected individuals by humans. This translocation would be far more important in any modelling of dog rabies spread as people often travel with their pet, hunting or working dogs.

As research into rabies epidemiology has progressed, it has become apparent that landscape heterogeneity plays an important role in the spatial spread of rabies. Finer scale spatial resolution data, such as habitat variability, population densities, abundance, behavioural characteristics and topographical features need to be incorporated into models to more accurately predict the spread of rabies, and therefore facilitate effective control strategies (Smith *et al*. 2002, Hampson *et al*. 2009). A number of complex models have been developed including agent-based simulation models (e.g. Hampson *et al*. 2009), interactive network models (e.g. Smith *et al*. 2002, Russell *et al.* 2006, Craft & Caillaud 2011), partial or fully stochastic models (e.g. Mjolsness *et al.* 2009, Jensen & Bachtrog 2011) and coupled stochastic susceptible-exposed-infectious-removed models (Duke-Sylvester *et al.* 2011, Panjeti & Real 2011).

More recently, the need to include natural barriers in rabies modelling (for example, mountain ranges, rivers and lakes) has been identified as these have been shown to alter the disease front and reduce the rate of spread in Europe (Holmala & Kauhala 2006). Smith *et al*. (2002) found river crossings slowed the spread of rabies (raccoon rabies variant) by a factor of 7 in Connecticut, north-eastern US. Through understanding the significance of natural barriers in Australia, it may be possible to better understand the spread of rabies and use these barriers in conjunction with manmade developments (such as vaccination barriers, baiting programs and exclusion fencing).

The implications of multispecies host susceptibility and understanding the ecosystem ecology of rabies has received little attention (Panjeti & Real 2011). In particular, rabies models reviewed here have been based on a single animal species. Models that incorporate the entire susceptible animal community are needed (Kauhala *et al.* 2006). To build such models, information on home range sizes, dispersal factors, densities and abundance, population statistics and inter- and intra-species contact rates is required. For example, Kauhala and Holmala (2006) sought to assess the risk of contact and contact rates among and between a guild of medium sized carnivores in south-east Finland, the raccoon dog (*Nyctereutes procyonoides*), red fox, European badger (*Meles meles*) and the domestic cat and found the risk of inter- and intra-species contact ranged from 0.07 to 0.88 per night.

2.1.13 Australian parameterisation

To develop appropriate and useful models for predicting the spread of rabies through an ecological community, an understanding of the parameters required for the model is necessary. In particular, characterising the behavioural and population dynamics of the different dog populations and how they interact is essential for predicting the spread of rabies in Australia. Key factors that need to be addressed include:

- dog population densities and abundance;
- dog population turnover rates;
- contact rates between susceptible individuals and populations;
- roaming behaviours, home range sizes and overlap;
- impacts of translocation events;
- effect of disease barriers;
- multi-species host interactions; and
- dog bite prevalence.

Since Australia does not currently have rabies, assumptions need to be made based on transmission factors in domestic dogs associated with its spread overseas (Table 2-1) and data commonly used in sylvatic rabies modelling (Table 2-2). Although these parameters can be applied in an Australian context in the first instance as proxies (or for contrast), transmission parameters from invasions in new endemic regions differ, so we must estimate Australian transmission parameters from locally measured contact rates.

Determining contact rates between dog populations and between dogs and humans is a fundamental aspect of rabies epidemiology and will play a critical role in understanding its spread in Australia. However, determining the number of times an individual dog comes into contact with another is difficult to measure, particularly in wild dogs that are crepuscular and often cryptic in their behaviour. Remote technologies – including GPS logging collars (e.g. Allen *et al*. 2013, Newsome *et al*. 2013) that take contemporaneous fixes, and proximity loggers that capture interactions between individual animals (e.g. between tuberculous badgers and cattle, Boehm *et al.* 2009) – have recently been developed and provide opportunities to investigate contacts that previously required visual observation of subject animal populations. Through improved understanding of wildlife-domestic animal interactions enabled by new technologies, management plans will be better informed to allow for targeted control actions, reducing the risk of disease transfer from wildlife to domestic animals and potentially, to humans.

Table 2-1 Range in values of parameters used in canine rabies modelling in rabies endemic countries. R_0 is the basic reproduction number of rabies – NC indicates studies where R_0 was not calculated or estimated.

Location	Dog population assessed	P dog rabies (risk)	Mean bites per rabid dog	Transmission rate	Transmission distance (km)	Rate of spread (km yr^{-1})	Incubation period (days)	Infectious period (days)	R_0	Reference
Java, Indonesia	free-roaming, domestic	0.00105* (~1 in 1000)							NC	Waltnertoews *et al.* 1990
Tanzania, Africa	free-roaming	0.49^	2.15		0.88 (range 0.83-0.92)		22.3	3.1 (range 2.9-3.4)	1.05	Hampson *et al.* 2009
Brazil	free-roaming, domestic					26.4			NC	Silva *et al*. 2004
Various	Urban dogs			$0.0085^{\sim}$			31.64	5.69	NC	Carroll *et al.* 2010
Chad, Africa	Urban dogs			$0.0807^{\#}$			29.26	5.67	1.01	Zinsstag *et al*. 2009
China	free-roaming, domestic	0.4^		$1.58x10^{-7\ \alpha}$			60.87		2	Zhang *et al.* 2011

* probability of an unvaccinated dog contracting rabies within a defined population

^ probability of an unvaccinated dog contracting rabies after being bitten by an infectious animal

$^{\sim}$ animal^{-1}

$^{\#}$ km^2 (dogs week)$^{-1}$

$^{\alpha}$ year^{-1}

Table 2-2 Range in values of parameters used in sylvatic rabies modelling in rabies endemic countries. R_0 is the basic reproduction number of rabies- NC indicates studies where R_0 was not calculated or estimated.

Location	**Species**	**Transmission rate**	**Rate of spread (km yr^{-1})**	**Incubation period (days)**	**Infectious period (days)**	**R_0**	**Reference**
Eastern USA	Raccoon (*Procyon lotor*)	0.04$^{\sim}$	40	22	12.5	1.6	Duke-Sylvester *et al.* 2011
Various	Fox (*Vulpes vulpes)*	0.1-0.4^	42	19		NC	David *et al.* 1982
Britain	European Badger (*Meles meles*)		9.3-54.3*	30	3	NC	Smith & Wilkinson 2002
Zimbabwe	Jackals (*Canis adustus and Canis mesomelas*)			20	5	NC	Rhodes *et al.* 1998
Europe	Fox (*Vulpes vulpes*)		80	28	5	NC	Murray *et al.* 1986
Various	Fox (*Vulpes vulpes*)	0.14$^{\#}$		24.5	7	NC	Eisinger *et al.* 2005
North America	Raccoon (*Procyon lotor*)	0.035$^{\#}$			7	NC	Rees *et al.* 2013

^ Probability of transmission varies depending on reproductive status of animal; highest values are for a vixen transmitting the virus to her cubs (0.4), lowest values are for dispersal of juveniles into new areas (0.1)

* Transmission rate depends largely on contact probabilities (i.e. density dependant) used in the simulation

$^{\sim}$ animal^{-1} day^{-1}

$^{\#}$ Probability of transmission

2.1.14 Research requirements

Before successfully modelling a disease outbreak, an understanding of the ecology of the host species and of the virus is required in a relevant context. Since rabies is not endemic in Australia, assumptions associated with its spread in other countries are required for modelling transmission. If Australia succumbs to a rabies outbreak, it will be possible and necessary to replace these assumptions with data collected in the field.

To parameterise rabies models for Australian contexts, research is required to reliably predict interactions among and between totally free-ranging wild dogs, wild dogs that are synanthropic, un-owned and unrestrained free-ranging domestic dogs, straying domestic dogs and restrained domestic dogs. Contacts between these different dog populations and humans and with other animals (including livestock, other pest species, pets and native fauna) also require parameterisation for useful models. Home range sizes, population abundances and densities also need quantification and mapping. These will provide insights into the potential for rabies to be transmitted from a sylvatic to urban cycle (or vice versa), identify areas of high risk of disease establishment and spread, and facilitate improved animal management, especially in high risk areas.

Models specifically targeted at Australia's high coastal urbanisation, unique ecosystems (which are predominated by marsupials and no large native predators but with widespread, abundant and often synathropic introduced mesopredators) and extensive agri-ecosystems are essential for predicting the likely spread of rabies through Australia. All dog and fox communities must be accounted for when designing control strategies for effective management of rabies once it enters Australia. Such an outbreak would not only impact Australian dog populations but will also affect human health, ecosystem function, agricultural production and ultimately, human association with, and social connection with 'man's best friend'. The potentially substantial social and economic costs of rabies outbreaks and suppression strategies also require investigation.

Even with knowledge from other countries, both from the developing and developed world experiences, Australia lacks sufficient data on its native and introduced fauna to reliably predict rabies epidemiology, undertake effective surveillance, or address rabies endemism. Learning from the recent Indonesian experience and recognising that each dog population likely represents different risk profiles for rabies susceptibility, transfer and persistence, we propose that an ecological database for dog populations exhibiting different behavioural and social structures and interactions be developed. Models of disease transmission for use in assigning cost-effective surveillance, stamping out an outbreak and planning vaccination programs for wildlife and domestic dogs, all require quantification of the behavioural and ecological parameters we have discussed. Only by using this information in disease spread models within a strategic management framework, will Australia improve its preparedness for controlling a rabies outbreak and its consequences.

2.1.15 Acknowledgements

We wish to thank the anonymous referees who provided valuable comments on the manuscript. Funding for this research was provided by the Department of Agriculture, Fisheries and Forestry's Wildlife and Exotic Disease Preparedness Program, 2012—2013. Jessica Sparkes is an Australian Postgraduate Award and UNE Apted scholar recipient, supervised by Dr Wendy Brown through the University of New England's School of Environmental and Rural Sciences. Salome Dürr received financial support from the Swiss National Foundation. Peter West provided the map in Figure 2-1.

Appendix 2-1: Literature review publication

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

STATEMENT OF ORIGINALITY

We, the PhD candidate and the candidate's Principal Supervisor, certify that the following text, figures and diagrams are the candidate's original work.

Type of work	**Page number/s**
Journal article and all encompassing information	5-50

Name of Candidate: Jessica Sparkes

Name/title of Principal Supervisor: Dr Wendy Brown

[redacted]

12 December 2015

Candidate

Date

[redacted]

12 December 2015

Principal Supervisor

Date

STATEMENT OF AUTHORS' CONTRIBUTION

We, the PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

	Author's Name	**% of contribution**
Candidate	Jessica Sparkes	Conception (60%) Data collection (100%) Manuscript development (60%)
Other Authors	Peter JS Fleming	Conception (30%) Manuscript development (15%)
	Guy Ballard	Conception (10%) Manuscript development (10%)
	Helen Scott-Orr	Manuscript development (5%)
	Salome Dürr	Manuscript development (5%)
	Michael P Ward	Manuscript development (5%)

Name of Candidate: Jessica Sparkes

Name/title of Principal Supervisor: Dr Wendy Brown

[redacted]

12 December 2015

Candidate

Date

[redacted]

12 December 2015

Principal Supervisor

Date

2.2 Social, conservation and economic implications of rabies in Australia

This Section has been written in the format of a scientific paper and has been published in the Australian Zoologist (Appendix 2-2) with the following citation:

Sparkes, J., Ballard, G., Fleming, P.J.S., Brown, W. (Online First 2014) Social, conservation and economic implications of rabies in Australia. *Australian Zoologist*. DOI: http://dx.doi.org/10.7882/AZ.2014.033

2.2.1 Abstract

Biophilia, our inherent love of living things, is a major driver of the modern conservation ethic worldwide. Australians are particularly fond of wildlife and consequently, our fauna are key to our national image. As a nation, we are known for our relatively carefree attitude towards some of the world's most dangerous animals, including venomous snakes and spiders, as well as sharks. This has arisen largely because we are familiar with these species, understand the actual level of risk they pose and have some idea of how to safely interact with them.

Unfortunately, the relationship between Australians and our wildlife could change significantly. Canine rabies, an infamous, fatal, viral zoonosis, is now less than 300 kilometers from the Australian mainland. We must face the possibility of a 'when', rather than 'if' scenario and begin to plan for rabies management on a continent where virtually the entire population is naïve.

Human and animal health would be affected. People, domestic animals and wildlife may die. Perhaps worse, in terms of scale, is the likely change in the Australian way of life, including the way we perceive, value and interact with wildlife, pets and livestock. Of course, rabies is endemic in many other countries and people continue to actively engage in conservation programs, but these people have had a long time to come to terms with the risk in their midst and many undergo prophylactic vaccination to enable them to work with wildlife.

Here, we discuss Australia's impending future with particular regard to how canine rabies could change our lives, the impacts it could have on wildlife conservation and the steps we must take to be prepared.

Keywords

Conservation, dingo, economic, human-wildlife dimensions, perceptions, rabies, domestic dog

2.2.2 Introduction

Human-dimensions researchers have documented Australians' affinity for wildlife. Surveys have found that Australians enjoy living with wildlife and value it highly (Miller 2003, FitzGibbon & Jones 2006, Russell *et al.* 2011, Wilks *et al.* 2013). However, these 'biophilic' attitudes (Wilson 1984) do not necessarily extend to 'pest' species, i.e. those which have a negative impact on humans, even when they are native (e.g. Fitzgibbon & Jones 2006, Dowle & Deane 2009).

It is rare that negative interactions between humans and wildlife culminate in human death, but when this does occur, media coverage and political agendas can escalate, with the potential to sway public perception of wildlife and negatively impact conservation efforts (Conover 2001, Evensen 2008, Decker *et al.* 2010, Degeling & Kerridge 2013). Zoonotic disease transmission is one way that wildlife can cause human death. When these tragic circumstances occur, conservation efforts can be threatened, and the human dimensions of wildlife management becomes particularly important (Decker *et al.* 2001).

2.2.3 Canine rabies

Canine rabies is a fatal, viral zoonosis which remains a significant issue for human health and wildlife management worldwide (Sterner & Smith 2006). There is no cure for rabies, although it is preventable by vaccination. Rabies is most commonly transmitted to susceptible hosts (any mammal) through the bite of an infected dog. This disease is now less than 300 kilometres from Australia's mainland (Sparkes *et al.* 2015), in the Tanimbar Islands and continues to spread eastwards through the Indonesian archipelago (Tenzin & Ward 2012, Putra *et al.* 2013) and potentially into Papua New Guinea. With more than 23 000 human movements between Papua New Guinea, the Torres Strait Islands and Cape York Peninsula each year (Brain 2013), it is possible that it is only a matter of time before Australia succumbs to a rabies outbreak (Sparkes *et al.* 2015).

2.2.4 Fear will change attitudes towards wildlife

Unfortunately, Australian communities do not sufficiently understand the implications of a rabies outbreak and its potential effects on wildlife, domestic animals and themselves. Australians' ignorance may quickly escalate to fear. Widespread disease in wildlife populations might encourage humans to view a broad range of wildlife as pests, rather than a resource worth conserving (Peterson *et al.* 2006), due to concern about their potential role as rabies vectors.

Canids and Chiropterans, particularly flying foxes (*Pteropus spp.*), are at risk of increased negative perceptions from humans, should rabies reach the Australian continent. Management of Australia's wild dogs (including dingoes *Canis lupus dingo*, domestic dogs *C.l. familiaris* and cross-breeds *C.l. dingo* X *C.l. familiaris*) is already complex due to their extensive distribution, impacts on agricultural production and dingoes' status as a native animal (Fleming *et al.* 2001, Fleming *et al.* In press). In some areas of public land, such as National Parks, conservation of dingoes is considered important, but on private land where wild dogs threaten agricultural production, landholders poison, trap and/or shoot them. Although many Australian's probably feel they are unlikely to encounter wild dogs, these animals also occur in peri-urban areas where they are often closely associated with humans (Allen *et al.* 2013, Newsome *et al.* 2013). This close proximity already causes some concern for health and safety (Tumaneng-Diete 2006) but with the potential introduction of canine rabies to Australia, the lines between conservation and control will become increasingly blurred. There is little doubt that the role wild dogs will play as vectors of rabies in Australia will contribute to the debate about management of wild dogs in the future.

Bats too, stand to suffer from Australian's ignorance with regard to canine rabies. Currently, many Australians seem to not adequately understand the risks associated with Australia's bat-borne zoonotic diseases, e.g. Hendra and the Australian Bat Lyssavirus (ABLV) (Degeling & Kerridge 2013, Hayes 2013). Education programs to allay fear and improve knowledge about the benefits of bats to ecosystem health are required to alter current perceptions; particularly of those communities in close proximity to bat colonies.

2.2.5 International experience

Until rabies reaches Australia, information about public attitudes toward this significant zoonotic disease can only be drawn from international experience.

A survey conducted in Munich, southern Germany assessed community members' fear and attitudes towards urban foxes (n=779) and found 35% of respondents were afraid of rabies, 75% felt foxes were a danger to people because they transmit disease and 65% wanted a marked reduction in the number of foxes in the community (Konig 2008). Similarly, Illinois residents were surveyed to determine their attitudes towards wildlife with 94% of respondents (n=805) indicating wildlife was important to them, but 57% were concerned about contracting diseases from wildlife (Mankin *et al.* 1999).

There is hope, however, that possible negative attitudes towards wildlife, in the face of newly arrived rabies, may be assuaged with time. Mankin *et al.* (1999) found that although the majority of respondents to a survey were concerned for their health, this did not appear to affect participation in non-consumptive forms of wildlife recreation activities. Similarly, although the risk of rabies to humans, domestic animals and wildlife was perceived to be high by community members, Hanisch-Kirkbride *et al.* (2013) found that respondents in the US were more concerned for the susceptibility of wildlife to disease than for humans or domestic animals.

2.2.6 Educating people about rabies

Even in countries where rabies is endemic, community members can lack vital knowledge on rabies transmission and prevention (Bingham *et al.* 2010, Dzikwi *et al.* 2012, Rumana *et al.* 2013). For example, in Texas, USA, 98% of respondents (n=922) to a household survey had heard of rabies, but only 59% knew that exposure to rabies without treatment could lead to death (Bingham *et al*. 2010). Similarly, Matibag *et al.* (2007) found that 90% of respondents (n=1570) knew that dogs were the most common reservoir of rabies in Sri Lanka, but only 79% knew rabies is fatal.

This lack of knowledge, combined with limited medical facilities in many regions (Warrell *et al.* 2007), contributes to the number of untreated rabies cases, with dire consequences. Annually, more than 55 000 people die from rabies (Knobel *et al.* 2005), with most of those deaths occurring in Asia and Africa (Warrell *et al*. 2007).

To reduce human deaths from rabies, education programs have been recommended in many countries (Vanak *et al.* 2007, Bingham *et al*. 2010, Burgos-Caceres 2011, Lapiz *et al.* 2012). In the Philippines, a rabies prevention and elimination project was initiated in 2007, including an educational component to raise awareness of the disease (Lapiz *et al*. 2012). As a direct result of the program, the number of dog-bite victims that sought medical attention after potential rabies exposure increased (Lapiz *et al*. 2012). Community education programs highlighting potential risks, methods to accurately identify infected individuals and preventative strategies could also be useful for rabies preparedness in Australia, particularly in northern Australia, where the risk of entry is highest.

2.2.7 Ecotourism

Beyond impacts on wildlife from shifts in public attitudes, if rabies enters Australia there is potential for significant impacts on the tourism industry. In 2012, ecotourism (including visiting National Parks, bush walking and visiting wildlife parks) contributed $4 billion to the Australian economy (Department of National Parks, Recreation, Sport and Racing 2013). Conservation of ecosystems, including native wildlife, are promoted and supported as a result of ecotourism, through financial support and education of tourists (Buckley 2010, Feck & Hamann 2013).

Potential interactions with Australian wildlife are a draw-card for many ecotourism operators (e.g. “touch and feel Australian wildlife”, “hold a koala”- Cleland Wildlife Park promotion: www.environment.sa.gov.au/clelandwildlife/Home). The Australian ecotourism hotspot; Fraser Island, attracts approximately 400,000 tourists annually (Ecosure 2012), with the majority of visitors expecting some form of interaction with dingoes (Burns & Howard 2003). Already, despite efforts from National Park rangers, negative interactions do occur between humans and dingoes and this has led to the destruction of these animals at tourist ‘hot spots’ (Environmental Protection Agency 2001). The destruction of dingoes in these circumstances has led to public outcry and negative media attention (Burns & Howard 2003).

In the advent of a rabies outbreak in Australia, initial management responses may involve the culling of wild dogs (including dingoes) and other mammals from infected areas, which may also result in negative media coverage. Further, ecotourism may decline as Australia loses its canine-rabies-free status and people become afraid of interactions with wild animals for fear of infection.

2.2.8 Domestic animals

Domestic dogs are known reservoirs for many important human and wildlife diseases including rabies and canine distemper (Cleaveland *et al.* 2000, Daszak *et al.* 2000, Vanak *et al*. 2007, Salb *et al.* 2008, Cleaveland *et al.* 2012). Prager *et al.* (2012) found that domestic dogs were the reservoir for rabies and likely played a critical role in the maintenance and transmission of the disease to native carnivores in Northern Kenya. Woodroffe *et al.* (2012) also found that wild dogs (*Lyacon pictus*) living in close proximity to domestic dogs were at greater risk of exposure to canine parvovirus, *Ehrlichia*, *Neospora* and rabies virus than those with limited contact. These results suggest that control and management of some important wildlife and human diseases should target domestic dogs rather than focus on native wildlife populations (Vanak *et al*. 2007, Bryan *et al.* 2011, Woodroffe *et al*. 2012) and this may also be the case in Australia.

The domestic dog population in Australia was estimated at 3.4 million in 2009, with 36% of Australian households owning a dog (Australian Companion Animal Council 2010). If rabies were to enter Australia, many of these dogs would need to be vaccinated to prevent the spread of rabies and protect domestic dogs, humans and wildlife against the disease. At an average cost of AUD$2.56 per dog (Kayali *et al.* 2006; 1 XOF = 0.00231 AUD, www.oanda.com, accessed 6 January 2014), and assuming maximum areal extent of the outbreak, annual domestic dog rabies vaccine in Australia could cost AUD$8.7 million, with these costs and the costs of vaccination being borne by Government under the current Emergency Animal Disease Response Agreement between the Australian Government and State and Territory Governments (Willis 2013).

An option proposed by Australian government authorities for the control of a rabies outbreak is to strengthen domestic animal management through ‘seizing, and detaining or destroying animals not properly controlled or vaccinated’ (Animal Health Australia 2011). Banks (1992) further recommended that animals wearing a tag (correctly licensed and vaccinated) should be kept in confinement for a fixed period of time, while animals not wearing correct identification should be euthanized when captured, dismissing any notion of potential rehoming through a rescue organisation. This strategy will likely be met with negative media attention and will impact rescue rates from pounds and the willingness of volunteers and community members to support rescue organisations. Rather than waiting for an Australian rabies outbreak as justification to strengthen domestic animal management, proactive management will reduce response times and improve chances of containing such an outbreak.

2.2.9 Oral rabies vaccination in wildlife

Although there has been great success in the control, and even eradication of rabies from countries in Europe and North America, considerable costs are associated with these outcomes (Freuling *et al.* 2013). The costs associated with oral rabies vaccination (ORV) of foxes (*Vulpes vulpes*) in European countries has ranged from AUD$379 101 to AUD$216 606 822 (1 € = 1.52478 AUD, www.oanda.com, accessed 11 February 2014), with the control of rabies taking between 5 and 26 years depending on the country involved (Freuling *et al*. 2013). Annual vaccination programs for wildlife and domestic animals remains an ongoing cost for many countries around the world.

Engagement of volunteers or community members may decrease the costs associated with some aspects of ORV programs, however the highest costs associated with an ORV program is that of bait manufacture (AUD$1.12 to 1.42 depending on bait type), with an estimated total cost of AUD$107 km^{-2} at a bait density of 66 km^{-2} for carnivores (Slate *et al.* 2005; 1 US = 1.11849 AUD, www.oanda.com, accessed 11 February 2014). Targeting gray foxes (*Urocyon cinereoargenteus*) and coyotes (*Canis latrans*) in Texas, USA, ORV campaigns were estimated to cost AUD$54 km^{-2} (Sterner *et al.* 2009).

Aerial baiting for the control of wild dogs occurs annually in parts of Western Australia (WA), Queensland, South Australia and New South Wales (NSW) at bait densities of 16 km^{-2} (NSW Environment Protection Authority 2010), while in parts of WA and NSW, baiting rates of up to 10 baits km^{-1} are used to control foxes. The national annual costs for such control campaigns are about $9.87m for wild dogs and $7.96m for foxes (from Gong *et al.* 2009). There have been no recent cost assessments of aerial baiting, but Thompson and Fleming (1991) found a strong relationship between the quantity of bait required and the overall cost of aerial baiting programs in north east NSW in 1988, where the mean cost of baiting was $4.21 kg^{-1} (current value Au$8.55 kg^{-1}, www.abs.gov.au/websitedbs/d3310114.nsf/home/consumer+price+index+inflation+calculator).

Based on the above estimate, a baiting density of 16km^{-2} and an average wild dog bait weight of 250 grams (NSW Environment Protection Authority 2010), annual aerial baiting campaigns in north-east NSW are estimated to cost $34 km^{-2}. This figure is comparable with costs associated with ORV campaigns undertaken in the US (Slate *et al*. 2005, Sterner *et al*. 2009). However, ORV campaigns are generally carried out twice per year (Freuling *et al*. 2013), targeting multiple canid species (Slate *et al*. 2005, Sterner *et al*. 2009) and similar would be expected for successful ORV in Australia, increasing annual costs above those already observed for the control of wild dogs and foxes.

2.2.10 Human costs

In addition to the vaccination of wildlife and domestic animals, significant costs are also associated with post-exposure-prophylaxis (PEP) of exposed humans to the disease. The direct costs of human PEP treatment has been estimated at between AUD$2 658 and $2 868 per exposed person in the US (Kreindel *et al.* 1998, Shwiff *et al.* 2007, Vaidya *et al.* 2010). As rabies is a Category 1 disease in Australia (Willis 2013), the costs associated with PEP treatment will likely fall with the Government's healthcare system.

2.2.11 Conclusion

Australia is unique in that it has never had endemic terrestrial rabies. Although other countries have learnt to live with rabies endemism, this has occurred over a long period of time. A new wildlife-borne disease in Australia is likely to cause fear in the short-term and may reasonably be expected to impact negatively on people's attitudes towards wildlife. Likely negative consequences will be felt in reduced support for conservation efforts, changes to the nature and frequency of human interactions with domestic animals and significant economic losses. Although culling of free-roaming dogs might be included in rabies control strategies, we are not recommending the broad-scale culling of wildlife. To reduce risks and associated costs to humans, domestic animals and wildlife of endemic rabies or a rabies outbreak, the current, relaxed attitude of many Australians towards domestic animal management would need to change. Achieving this important change will require strategic education programs to raise appropriate awareness of zoonosis prevention in the human population.

2.2.12 Acknowledgements

We acknowledge the financial support of the Wildlife and Exotic Disease Preparedness Program.

Appendix 2-2: Social implications of rabies publication

Sparkes, J., Ballard, G., Fleming, P.J.S., Brown, W. (Online First 2014) Social, conservation and economic implications of rabies in Australia. *Australian Zoologist*. DOI: http://dx.doi.org/10.7882/AZ.2014.033

STATEMENT OF ORIGINALITY

We, the PhD candidate and the candidate's Principal Supervisor, certify that the following text, figures and diagrams are the candidate's original work.

Type of work	**Page number/s**
Journal article and all encompassing information	53-68

Name of Candidate: Jessica Sparkes

Name/title of Principal Supervisor: Dr Wendy Brown

[redacted]

12 December 2015

Candidate

Date

[redacted]

12 December 2015

Principal Supervisor

Date

STATEMENT OF AUTHORS' CONTRIBUTION

We, the PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

	Author's Name	**% of contribution**
Candidate	Jessica Sparkes	Conception (60%) Analyses (90%) Manuscript development (70%)
Other Authors	Guy Ballard	Conception (40%) Manuscript development (10%)
	Peter JS Fleming	Analyses (10%) Manuscript development (10%)
	Wendy Brown	Manuscript development (10%)

Name of Candidate: Jessica Sparkes

Name/title of Principal Supervisor: Dr Wendy Brown

[redacted]

12 December 2015

Candidate Date

[redacted]

12 December 2015

Principal Supervisor Date

3 Domestic dog ownership and dog bite frequency in New South Wales

Parameters relating to the size of a susceptible population are fundamental to disease transmission models. As identified in Chapter 2, the owned proportion of the Australian domestic dog population is inadequately quantified, largely because registration regulations differ between States and because many dog owners fail to comply with registration and microchipping requirements.

In this chapter, I undertook a survey of residents in north-east New South Wales to quantify dog ownership and align current official records with true population estimates for domestic dogs. Understanding population densities and age structure of dog communities is a valuable first step in the event of a rabies outbreak, when reliable population estimates, recruitment rates and clearly defined movement behaviour will be essential to ensuring adequate control and/or vaccine coverage in an area.

Rabies transmission between characterised groups of Australian dogs is also likely dependent on the frequency and duration of direct interactions between them. Further, free-roaming domestic dogs may also provide a transmission pathway for rabies between sylvatic and urban rabies cycles. To estimate contact within and between groups requires measures of roaming behaviour. Hence, roaming behaviour was quantified to determine how far rabies could spread if it were to breach Australian borders.

Although rabies can alter dog behaviour, particularly by increasing aggressive and biting behaviour (Silva *et al.* 2004, Hampson *et al.* 2009), a contact rate involving biting is required for estimating potential rabies transmission to humans. As rabies is exotic to Australia and hence no measures of rabid-bite contacts are available, current reported dog attacks and biting rates provide a baseline which can be used as a minimum value. Unfortunately, dog bite reporting in Australia is inconsistent between states, dog attacks requiring medical treatment are so-called ‘reportable incidents’ in some jurisdictions, but no such requirements, or corresponding databases exist in others (Chapter 2). Hence, I further sought to derive independent estimates of the frequency of dog attacks and identify reasons for non-reporting.

3.1 Quantifying domestic dog ownership and dog bites in north-east New South Wales, Australia

This Chapter has been written in the format of a scientific paper and has been submitted to the Australian Journal of Veterinary Science with the following authorship:

J Sparkes[a,b,c,*], G Ballard[a,c,d], PJS Fleming[a,b,c] and WY Brown[a]

[a] School of Environmental and Rural Sciences, University of New England, Armidale, Australia, 2351

[b] Vertebrate Pest Research Unit, Biosecurity NSW, Orange, NSW, Australia, 2800

[c] Invasive Animals Cooperative Research Centre, Armidale, Australia, 2351

[d] Vertebrate Pest Research Unit, Biosecurity New South Wales, Armidale, Australia, 2351

[*] Corresponding author: Orange Agricultural Institute, Forest Rd, Orange, NSW, Australia, 2800; Phone: +61 2 6738 8501; email: jessica.sparkes@dpi.nsw.gov.au

3.1.1 Abstract

Context Despite the significant roles domestic dogs play in contemporary society, systems for recording dog numbers and monitoring dog attacks are limited and incomplete. Many of Australia's domestic dogs are unaccounted for, and the true burden of dog attacks on people is likely under-reported.

Objective To characterise ownership and roaming behaviour of owned dogs, determine frequency of dog attacks and identify reasons for non-compliance with companion animal legislation in New South Wales (NSW).

Methods 1,000 questionnaires were mailed to residents in north-eastern NSW. The survey comprised 33 multiple choice and open-ended questions, which collected information on domestic dog demographics and dog attacks on people and animals within the household.

Results A total of 180 responses were received, of which 64% owned at least one dog. Registration and microchipping was confirmed for 71% and 87% of dogs, respectively. In addition, 26% of the dog owners surveyed indicated their dog could wander away from the property (n=30). Dog attacks on humans and on other animals were reported but responses suggest just 14% of attacks on people and 19% of attacks on respondents' dogs were reported to authorities.

Conclusion Non-compliance to register and microchip owned domestic dogs, combined with failing to notify authorities of a dog's death, reduces the accuracy of population estimates, while under-reporting of dog attacks underestimates the impact on human and animal health. Despite risks associated with wandering animals, many respondents admitted their dog wanders outside the property boundaries.

Keywords
Disease, dog attack, free-roaming, human health, pet, questionnaire

Abbreviations
LGA Local Government Authority; NSW New South Wales

3.1.2 Introduction

Domestic dogs (*Canis familiaris*) have various important roles in Australian society as hunting partners, stock herders, law enforcement, assistance animals and as pets (Macpherson 2005). Based on registration and microchipping records, the domestic dog population within Australia was estimated at 3.41 million in 2009, with 2.9 million households owning a dog (Australian Companion Animal Council 2010). The State of New South Wales (NSW) has the largest human population and the most dogs with 1.8 million dogs owned (15 dogs per 100 people; Australian Companion Animal Council 2010, Office of Local Government 2014, Australian Bureau of Statistics 2015).

Currently, dog population estimates are based on official microchipping and registration records held by local government authorities (LGA). However, these records are dependent on reporting compliance of dog owners (NSW Government 2013) and are reliant on owners notifying local government of dog movements and deaths. Unfortunately, compliance is often difficult to enforce and is further confounded by an exemption from microchipping and registration for working farm dogs in NSW (Office of Local Government ND), presumably resulting in an underestimation of the owned dog population. However, as there is no incentive to notify local councils of dog deaths in NSW; where registration consists of lifetime registration rather than annual registration, mortality is also likely to be underreported, creating another source of bias in dog population estimates (Division of Local Government 2013). Understanding population densities and age structure of domestic dog communities is valuable in the event of zoonotic or contagious disease outbreaks (Sparkes *et al.* 2014, Sparkes *et al.* 2015). This is particularly relevant for exotic disease incursions such as canine rabies, where true population numbers, recruitment levels and defining movement behaviour are essential to ensuring adequate control and/or vaccine coverage in an area (Animal Health Australia 2011, Sparkes *et al*. 2015).

There are also potential risks to human health associated with free-roaming behaviour; where a domestic dog is allowed to wander unsupervised outside of its owner's property. These dogs can transmit diseases, cause motor vehicle accidents or attack people (Lunney *et al*. 2011). Domestic dog attacks, on both humans and other animals, are common and receive media attention across Australia (e.g. Doherty 2014, Killoran 2014). Despite this, no comprehensive database documents dog attacks (Australian Companion Animal Council 2007b). Data currently available is dispersed over various government agencies and remains incomplete and inconsistently reported across States and Territories (Australian Companion Animal Council 2007a). Information regarding dog attacks on humans is currently collected and recorded by Australia's health systems (i.e. hospital records), while reports of dogs attacking other animals are generally kept by LGAs (Australian Companion Animal Council 2007b). New South Wales is the only state in which councils are legally required to report all dog attacks to the State Government (NSW Department of Premier and Cabinet 2012).

Understanding how often, where and why dog attacks occur may be useful for reducing their frequency. Further, quantifying interactions (including dog attacks) between dogs and other animals is critical when predicting how diseases, such as rabies and canine distemper, and parasites, including *Echinococcus granulosus* (hydatid disease) and hookworms (*Ancylostoma caninum*) could spread (Murray & Penridge 1992, Kauhala & Holmala 2006, Sparkes *et al*. 2015).

Here, we aimed to collect data on domestic dog ownership and roaming behaviour in north-east NSW for domestic dogs. We further sought to derive independent estimates of the frequency of dog attacks and identify reasons for non-reporting.

3.1.3 Methodology

The study site incorporated communities within the North Coast Local Land Services region, which is in coastal north-east NSW (Figure 3-1). The region is diverse, encompassing urban developments, rural townships, small- to large-land holdings, tourist hotspots, State Forests and National Parks.

During September 2013, a self-administered questionnaire was mailed to a random sample (n=1,000), without replacement, of residents in the study area. Residents were selected for participation via a two-stage sampling design. We randomly selected communities (n=7) from the study region, ranging from Pottsville (28º39'S, 153º56'E) in the north to Moonee Beach (30º21'S, 153º15'E) in the south and west to Lismore (28º81S, 153º28E) (Figure 1), and subsequently, several streets within each community were randomly selected for questionnaire distribution. The population of the resultant surveyed region in 2013 was 343,393 people (Australian Bureau of Statistics 2014). The survey was promoted via media outlets, including newspapers and posters distributed in targeted communities to help achieve our targeted precision of 5-10% at 95% confidence level for binary responses about dog ownership, microchipping status and gender (i.e. 96-384 responses; Dillman 2000).

A covering letter, information sheet for participants and reply-paid envelope were included with each survey. The letter and information sheet outlined the purpose of the study, approximate time required to complete the survey and other information confirming anonymity of participants (See Appendix 3-1). The study was approved by the University of New England Human Research Ethics Committee (HE13-147).

The questionnaire consisted of three sections designed to collect quantitative information on dog ownership, dog characteristics and dog bites (See Appendix 3-2). Questions included 21 multiple choice, 11 short answer and 1 open-ended question. Data collected from the questionnaire were compared with local council registration and microchipping records for the relevant areas.

Chi-square tests were conducted in R (R Core Team 2013) to test for a relationship between the sex of the dog and neutering status and to determine whether the age of the dog affected its microchip status. The top six dog breeds attributed to attacking humans from the current survey were used to compare proportions of attacking dog breeds with official survey proportions for the same breed (Department of Local Government 2013). These [proportional] data were arc-sin transformed and a 2-sample z-test used to compare proportions of dog attacks attributed to specific breeds. Significance was set at $p < 0.05$.

3.1.4 Results

3.1.4.1 Survey response

In total, 180 surveys were completed and returned (18% response rate). As the survey was anonymous, no follow-up for unreturned surveys could be undertaken. Most responses were received from the Clarence Valley (including the towns Yamba, Grafton and Woombah) and Coffs Harbour Shire Council (including the towns Coffs Harbour, Glenreagh and Bucca) regions (n=59 and 57, respectively; Figure 3-1). The response rate achieved a sampling error of ±7.3% at 95% CI. As not all respondents answered every question, n indicates the total number of responses for a question.

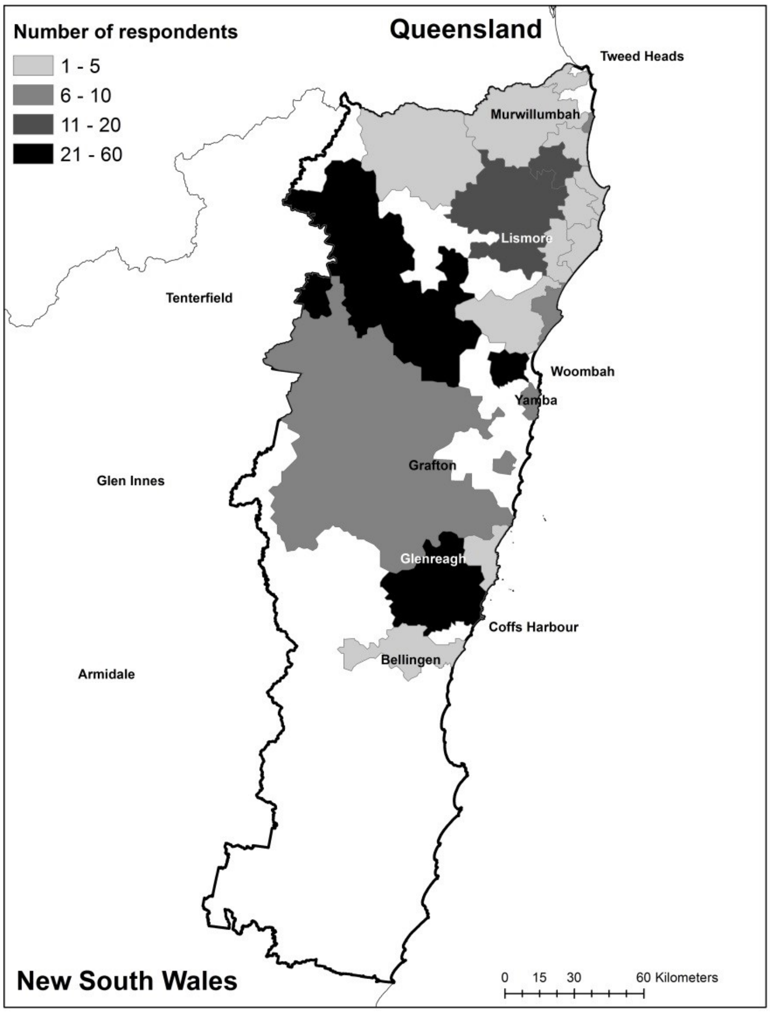


Figure 3-1 Location of survey respondents by postcode, North Coast Local Land Services region (bolded outline), north-east New South Wales, Australia

3.1.4.2 Dog demographics

Sixty four percent of respondents owned a dog (n=180), with most holding one or two dogs (66%, 26%, respectively), but up to a maximum of six dogs per household. The reported sex ratio of dogs was 56% female: 44% male, with 77.1% of all owned dogs being desexed (n=171 dogs). There was no relationship between sex and neutering status of dogs (χ^2=1.1, df=1, p=0.29). Despite compulsory registration and microchipping regulations in NSW, which came into effect in 1999 (NSW Government 2013), only 70.5% of dogs were registered and 87.1% microchipped at the time of the survey (September 2013). The median age of owned dogs included in the survey was 6 years (range: 3 weeks to 16 years); whereas older dogs comprised a large proportion of the population in official NSW records (Figure 3-2). No relationship was found between the age of the dog and its microchip status (χ^2=7.17, df=5, p=0.21). Based on survey data, predominant breeds in north-eastern NSW included working-type dogs such as the Border collie and Kelpie and small breeds such as Maltese terriers (Table 3-1).

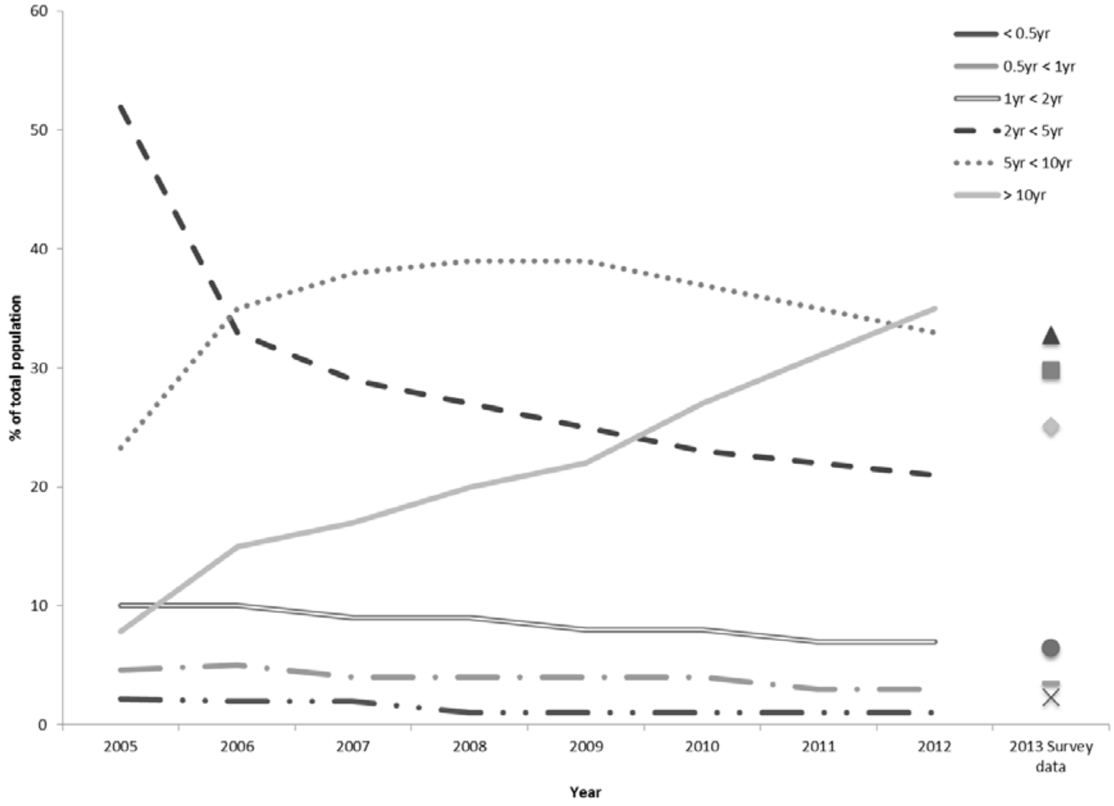


Figure 3-2 Age range of dogs from present survey (symbols) and Official NSW records^ (points) as a proportion of the population between 2005 and 2013

Symbols denote: ▲ 2 yr<5yr; ■5yr<10yr; ♦>10yr; ●1yr<2yr; —0.5yr>1yr; X<0.5yr

^ NSW Division of Local Government 2007, Division of Local Government 2011,2012,2013

3.1.4.3 Roaming behaviour

More than a quarter (26.1%) of 115 respondents stated their dog could roam away from the property. Frequency of roaming varied, with 36.7% wandering on a daily basis, 6.7% doing so weekly and 40% wandering only monthly or less frequently (n=34). Less than a fifth (16.7%) of respondents were unsure how often their dogs wandered. Most (79%) free-roaming behaviour was reported to last for a few minutes to an hour (n=33).

3.1.4.4 Dogs biting humans

Respondents frequently reported that members of their household had been bitten by dogs (31.7%, n=180). Ages of dog bite victims varied, with 6-10 year olds and 45-70 year old people receiving the greatest number of dog bites (32.4%, 22.1%, respectively; n=68). In 16 instances, the dog that bit the victim came from the household, while on 23 occasions, the dog was known to the victim but not from the same household. An unknown dog bit the victim on 19 occasions. Location of dog attacks included the victim’s home, the attacking dogs’ home and public places such as parks (28%, 37%, 35%, respectively; n=60). In 90% of cases, the dog bite broke the persons’ skin (n=57). Only 14% of respondents reported the attack to local authorities or medical practitioners (GPs and hospitals), which included one respondent whose skin had not been broken by the attack (n=56). Although most people said their dog had never bitten anyone, 5.8% of respondents said their dog had (n=121).

A total of 28 dog breeds were identified as biting a household member (n=69; Table 3-1). Of dog breeds identified, German Shepherd Dogs and Cattle Dogs were reported most frequently attacking people (n=10, 9 respectively). Survey data and official records did not differ with respect to the proportions of attacks attributed to particular breeds (z=0.75, p=0.2, n=6).

Table 3-1 Breed of dogs currently owned by respondents (n=171) and dog breed identified by respondents as involved in attacks on humans (n=69) and on resident dogs (n=52)

Dog Breed	Owned	Attacked human	Attacked pet dog
Airedale Terrier	1		
Akita			1
Australian Shepherd	2		
Australian Terrier		1	
Australian Terrier x	1		
Bichon	1		
Border collie	13	1	7
Border collie x	3	1	
Boxer	2		
Boxer x		1	
Bull terrier x	1		
Cattle dog	3	9	6
Cattle dog x	3	4	
Cavalier King Charles Spaniel	2		
Chihuahua x	2		
Corgi		2	
Dachshund	3		
Dalmatian	2		
Dingo x			1
Doberman		1	
English Sheepdog	1		
Fox terrier	4	2	
Fox terrier x	3	1	
German Shepherd	9	10	3
German Shepherd x			1
Golden Retriever	6		
Golden Retriever x	1		

Great Dane			1
Griffon	2	1	
Hungarian vizla	1		
Jack Russell	6	2	1
Jack Russell x	1		
Japanese Fighting Dog		1	
Kelpie	13	3	3
Kelpie x	7	2	
Labrador	5	2	1
Labrador x	9	1	1
Lhasa Apso	1		
Maltese	2		
Maltese x	13	1	
Maremma	1		
Mastiff x	4		
Pitbull		1	1
Pitbull x		1	
Pointer x			1
Poodle	4		
Poodle x	1		
Pug	2		
Pug x	1		
Ridgeback		1	1
Rottweiler	2	1	
Saluki	1		
Shepherd x	2		
Shetland sheepdog	3		
Shitzu x	1		
Spaniel	1	1	
Spitz	1		

Staffordshire Bull Terrier	9	2	7
Staffordshire Bull Terrier x	2	3	4
Tenterfield terrier	1		
Terrier	1	1	
Toy poodle		1	
Weimaraner			1
Whippet	1		
Unknown*	9	11	11

*Unknown- includes responses where the respondent could/did not identify a specific breed of dog, including general mixed breeds, large breeds, small breeds and unsure responses

3.1.4.5 Dogs biting other animals

When asked whether the resident dog had been bitten by another dog, 39.3% of respondents indicated they had (n=122). In most instances, the attacking dog was either known but not from that household or unknown (54.9%, 41.2%, respectively; n=51). Border Collies, Staffordshire Bull Terriers and Cattle Dogs were most frequently cited as the attacking dog breed (n=52; Table 3-1), with most attacks occurring in a public place (52%, n=50). Despite 71.4% of reported cases resulting in the dog's skin being broken, only 19% reported the attack to authorities or a local veterinarian (n=48). No attacks where the skin remained unbroken were reported to authorities. Reports of respondents' dogs attacking or biting other animal species were also common (20%, n=121) with a quarter (25.7%) of these attacks directed towards another domestic dog. Livestock (20%), pest animals (such as feral cats, rabbits and feral pigs; 15%) and native animals (including possums, wallabies and bandicoots; 35%) were also reported to have been attacked (n=40).

3.1.5 Discussion

Australia has one of the world's highest incidences of pet ownership (Australian Companion Animal Council 2010). Results from the present survey suggest that a much larger proportion of households own a dog compared with official records (64% present survey vs 36% official estimates). The differences observed between the present survey and official records may be a function of non-compliance with microchipping and registration laws.

This compliance issue has also been observed elsewhere. For example, microchip compliance amongst surveyed dog owners was 87%, while compliance varied regionally between 51 and 89% in Italy (Slater et al. 2008, Caminiti et al. 2014, Capello et al. 2015). Applying an 87% microchipping rate (derived from the present survey) to NSW's 1.81 million dogs that were registered as at 30 September 2014 (Office of Local Government 2014), the dog population would be expected to be closer to 2.1 million. However, confounding this estimate is the possibility that the NSW dog population is overestimated by the number of dogs that are not removed from the records when they die, as there is no incentive to notify authorities of pet deaths. This assumption is supported by two observations: first, the officially recorded dog population appears to be growing at a much faster rate than the human population (mean 7.1% vs 1.3% over the past 10 and 8 years, respectively; Australian Bureau of Statistics 2015, Figure 3-2). Second, over the past 8 years, official records indicate an apparent trend towards an aging dog population in NSW, while the proportion of young dogs remains relatively stable (Figure 3-2).

Assuming that our survey is representative and given its level of sampling error (7.3%), it is in general agreement with official records for dogs aged less than 2 years and between 5 and 10 years, but there is a major discrepancy in the 10 year and older category. Our findings suggest this age group comprises a much smaller proportion of the total population (25.1% present survey, 35% official records). Hence, accounting for the proportion reported microchipped in the present study and removing the apparent surplus of 'aged' dogs from the population (i.e. removal of 9.9% of the 10 year and older dogs), the true number of dogs within NSW should be expected to be 1.87 million. Although this number appears to be close to the current official record, the 2013 match is likely coincidental and given the identified errors in reporting, the accuracy of official records in future years should be questioned. In the absence of owners reporting pet deaths, a rule for maximum age or a ground-truthing exercise is needed to improve data quality.

Accurate estimates of population size and age structure of domestic dogs are valuable for informing animal management and are also a useful indicator of the general health of dogs at a population level (Jackman & Rowan 2007, Van Kesteren *et al*. 2013). Mean age of dog populations in Italy (4.8 years in central Italy; Slater *et al*. 2008 and 6.7 years in north-east Italy; Capello *et al*. 2015) are comparable to those of the present survey (6.1 years). In contrast, Kongkaew *et al*. (2004), Acosta-Jamett *et al*. (2010) and Van Kesteren *et al*. (2013) found low median ages (2 to 3 years) for dogs owned by survey respondents in Thailand, Chile and Kyrgyzstan, respectively. A low median age indicates a high population turnover and potentially limited veterinary care (Acosta-Jamett *et al*. 2010, Van Kesteren *et al*. 2013). Quantifying the rate of population turnover is also invaluable when devising vaccination campaigns to control the spread of transmissible diseases (Jackman & Rowan 2007, Van Kesteren *et al*. 2013, Sparkes *et al*. 2015).

Basic population demographics should be combined with other behavioural traits such as dog attacks and roaming behaviour to improve human and dog health, through minimising disease transmission potential, reducing accidents and improving general health and longevity of dogs. In NSW, allowing pets to roam unrestrained outside of the residential property is an infringement under the Companion Animals Act (NSW Government 2013). Despite this, thousands of straying dogs end up at local pounds every year (Pet Industry Association of Australia 2012). Our survey revealed that more than a quarter (26%) of dog-owning respondents allowed their dog/s to roam freely, which is similar to Chile (30%; Acosta-Jamett *et al*. 2010, Astorga *et al*. 2015) but greater than Italy (13%; Slater *et al*. 2008), and much lower than in developing countries such as Thailand and Guatemala (74 and 69%, respectively; Kongkaew *et al*. 2004, Pulczer *et al*. 2013).

Despite the opportunity for anonymity in this survey, one might expect that not all respondents would be aware, or willing to admit their dog regularly wanders. It is also worth noting, that the present survey targeted regional residential centres where the ability of dogs to roam may be greater compared with more densely populated cities. For example, Coman and Robinson (1989) found dogs living in the outer suburbs of Bendigo, Victoria were more likely to wander away from the home compared with inner city dogs. Nevertheless, if 26% of the NSW dog population is allowed to wander as the survey suggests, that would amount to over 480,000 domestic dogs roaming NSW streets and countryside unsupervised on a regular basis. The consequences of this behaviour appear evident: of the 5,650 dog attacks reported to NSW authorities during 2011/12, 62% occurred on public land with 47% of attacks on people resulting in some form of injury, ranging from minor injuries through to those requiring hospitalisation (n=3,329; Division of Local Government 2013).

However, not all dog attacks are reported, resulting in an underestimation of the true impact dog attacks have on society (Australian Companion Animal Council 2007ab, Sparkes *et al*. 2015). This is evidenced within the current study, where only 14% of attacks on people were reported to authorities. In contrast to official records (38%; Division of Local Government 2013), 65% of dog bites were reported to have occurred on private property in the current survey. The differences in proportions observed could be attributable to dog attacks occurring in the home being underreported; perhaps because owners, friends and relatives may be unwilling to make an official complaint on a known dog. Consequently, if our data pertain to other regions of NSW, then dog attacks are about seven times more common than officially reported (present reporting rate of 14%). However, the proportion of bites caused by roaming dogs is probably somewhat lower than official records, perhaps closer to 33% (the percentage of respondents attacked by a dog they did not know).

The proportion of attacks attributed to specific breeds did not differ between the present survey and official records (Thompson 1997, Division of Local Government 2013). It is worth noting that 18% of respondents were unable to identify the attacking dogs' breed but did provide generalisations on the type of dog. Because a large number of victims could not identify the attacking dog breed in both the questionnaire and from official records (18 and 17%, respectively; Division of Local Government 2013), identification of high risk breeds based on attack rates may not be reliable. Reliability of dog breed recognition by members of the community needs to be further investigated to ensure attack rates attributed to breed reflect the true proportions, rather than being an artefact of media coverage.

Attacks on other animals also appear to occur frequently. For example, between 2011 and 2012, 5,352 dog attacks on animals were reported to LGAs in NSW, with 78% of attacks resulting in an injury to the animal, ranging from minor injury through to death (Division of Local Government 2013). Similar to the reporting of dog attacks on humans, only 19% of attacks on the household dog were reported by respondents. Explanations for a lack of reporting included fear of retribution by the attacking dog's owner, that the attacking dog was a known dog or the family pet and no or only minor injury occurred to the attacked dog. In addition to attacks on domestic dogs, dogs have frequently been reported to harass, attack and even kill other animals such as livestock and native wildlife (Bulter *et al*. 2004, Hughes & Macdonald 2013, Office of Local Government 2014). These types of interactions can have an additional consequence of increasing the risk of contracting and transmitting parasites and diseases to humans, other pets and even other wildlife (Murray & Penridge 1992, Butler *et al*. 2004, Vanak & Gompper 2009). Reducing a dog's ability to roam could minimise these interactions and associated risks.

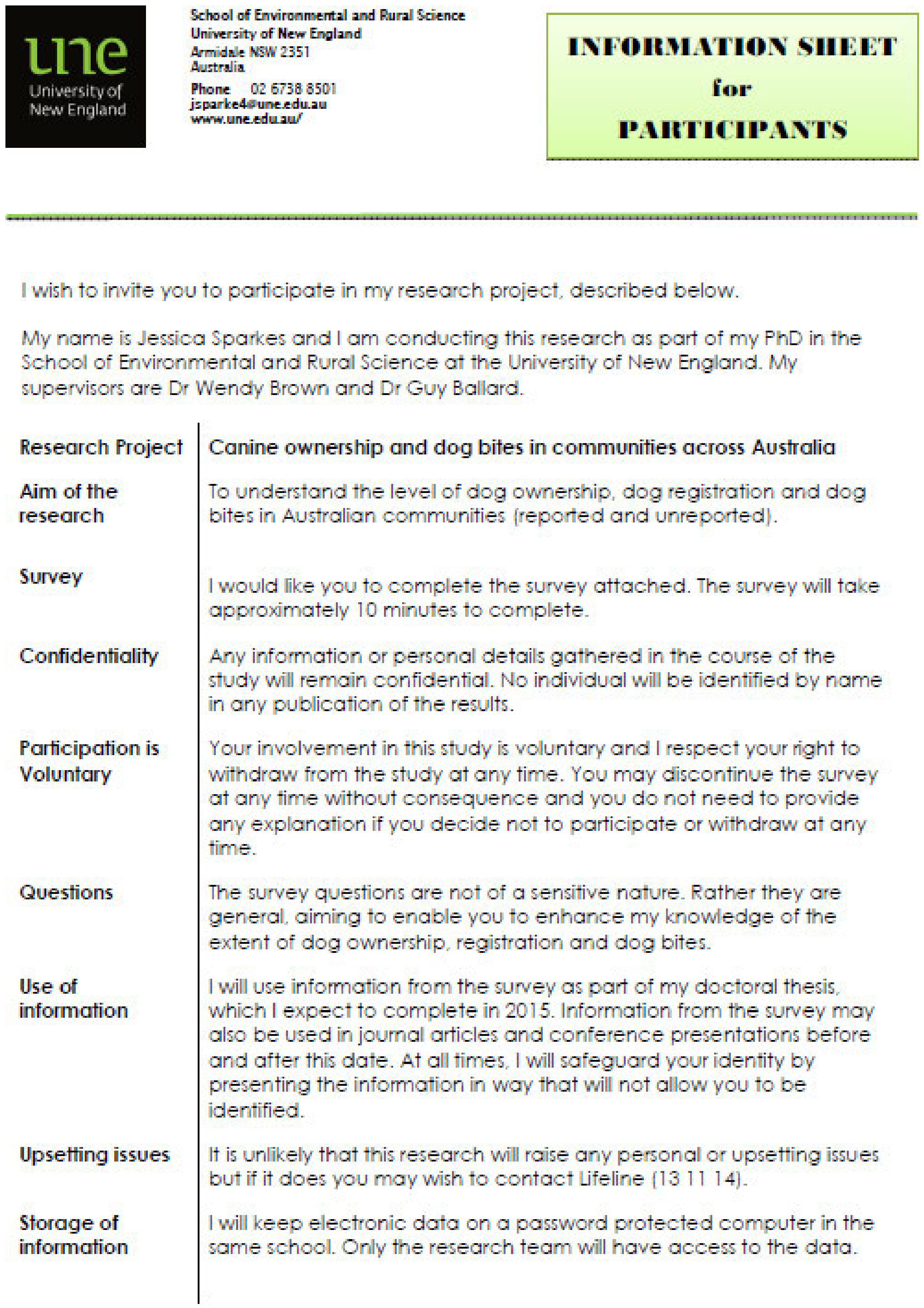
3.1.6 Conclusion

Our study provides quantitative data on dog ownership, roaming behaviour and dog attacks in north-east NSW, Australia. Documented non-compliance with domestic dog ownership regulations and underreporting of dog attacks on both humans and animals suggest a need to improve current reporting methods. Incentive schemes that encourage owners to report their ownership status on an annual basis may help to improve dog population estimates, which will assist in responding to a disease outbreak. At the very least, dogs that would have attained an unreasonable age should be automatically deleted from the records. Social awareness campaigns targeting the issue of free-roaming pet dogs and their potential impacts on humans and other animals may also help reduce the incidence of wandering behaviour and associated human and animal health impacts, such as dog attacks.

3.1.7 Acknowledgements

We wish to thank all survey participants for taking the time to provide valuable insights on dog ownership and attacks. Gerhard Körtner provided valuable comments on the drafting of this paper.

Appendix 3-1: Information sheet for participants



une
University of New England

School of Environmental and Rural Science
University of New England
Armidale NSW 2351
Australia
Phone 02 6738 8501
jsparke4@une.edu.au
www.une.edu.au/

INFORMATION SHEET
for
PARTICIPANTS

I wish to invite you to participate in my research project, described below.

My name is Jessica Sparkes and I am conducting this research as part of my PhD in the School of Environmental and Rural Science at the University of New England. My supervisors are Dr Wendy Brown and Dr Guy Ballard.

Research Project	**Canine ownership and dog bites in communities across Australia**
Aim of the research	To understand the level of dog ownership, dog registration and dog bites in Australian communities (reported and unreported).
Survey	I would like you to complete the survey attached. The survey will take approximately 10 minutes to complete.
Confidentiality	Any information or personal details gathered in the course of the study will remain confidential. No individual will be identified by name in any publication of the results.
Participation is Voluntary	Your involvement in this study is voluntary and I respect your right to withdraw from the study at any time. You may discontinue the survey at any time without consequence and you do not need to provide any explanation if you decide not to participate or withdraw at any time.
Questions	The survey questions are not of a sensitive nature. Rather they are general, aiming to enable you to enhance my knowledge of the extent of dog ownership, registration and dog bites.
Use of information	I will use information from the survey as part of my doctoral thesis, which I expect to complete in 2015. Information from the survey may also be used in journal articles and conference presentations before and after this date. At all times, I will safeguard your identity by presenting the information in way that will not allow you to be identified.
Upsetting issues	It is unlikely that this research will raise any personal or upsetting issues but if it does you may wish to contact Lifeline (13 11 14).
Storage of information	I will keep electronic data on a password protected computer in the same school. Only the research team will have access to the data.

Disposal of information	All the data collected in this research will be kept for a minimum of five years after successful submission of my thesis.
Approval	This project has been approved by the Human Research Ethics Committee of the University of New England (Approval No HE13-147, Valid to 11/07/2014).
Contact details	Feel free to contact me with any questions about this research by email at jsparke4@une.edu.au or by phone on 02 6738 8501. You may also contact my supervisors. My Principal supervisors name is Dr Wendy Brown and she can be contacted at wbrown@une.edu.au or 02 6773 5125 and my Co-supervisors name is Dr Guy Ballard and he can be contacted at gballar3@une.edu.au or 02 6738 8511.
Complaints	Should you have any complaints concerning the manner in which this research is conducted, please contact the Research Ethics Officer at: Research Services University of New England Armidale, NSW 2351 Tel: (02) 6773 3449 Fax: (02) 6773 3543 Email: ethics@une.edu.au
	Thank you for considering this request. regards, Jessica Sparkes

Appendix 3-2: Domestic dog ownership questionnaire

A brief survey about domestic dogs

This survey will take no more than 10 minutes to complete

All the information you provide will be treated confidentially

Dog ownership

Q1: Do you own a dog?

☐ No *Please go to Q7*

☐ Yes *Please go to Q2*

About your dogs

Q2: How many dogs do you own? ___________

Q3: Please complete the table for each dog you own

Dog	**Sex (M or F)**	**Desexed? (Y or N)**	**Age (years)**	**Breed?**	**Are they registered?**	**Are they microchipped?**
Example	Male		2	Labrador	No	Yes
Dog 1						
Dog 2						
Dog 3						
Dog 4						
Dog 5						

Q4: Are your dogs able to wander away from your property, unsupervised?

☐ Yes *Please go to Q5*

☐ No *Please go to Q7*

☐ I don't know *Please go to Q7*

Q5: How often would one or more of your dogs wander away from your property, unsupervised?

☐ Daily

☐ Weekly

☐ Monthly

☐ More than monthly

☐ I don't know

Q6: How long do these 'wanders' typically last?

☐ A few minutes to an hour

☐ More than an hour

☐ More than a day

☐ I don't know

Your experiences with domestic dogs

Q7: Has anyone living in your household been bitten by a dog?

☐ No *Please go to Q16*

☐ Yes Please go to Q8

Q8: How old was the person when they were bitten?

☐ 0-5 years

☐ 6-10 years

☐ 11-24 years

☐ 25-34 years

☐ 35-45 years

☐ 45-70 years

☐ 70 years +

Q9: When did this happen?

Year: ______________

Month:______________

Q10: Was the dog that bit the person

☐ From your household

☐ NOT from your household but known to the person who was bitten

☐ NOT from your household and unknown to the person who was bitten

Q11: What breed was the dog that bit the person? ______________________

Q12: Where did the incident occur?

☐ At your home

☐ At the dog's home (if it was not your dog)

☐ In a public place (e.g. street, park)

Q13: Did the dog bite cause the person's skin to be broken, at all?

☐ Yes

☐ No

Q14: Did you, or the person who was bitten, report the attack to authorities?

☐ Yes *Please go to Q15*

☐ No Why not: ____

Q15: To whom was the incident (dog bite) reported?

PLEASE TICK ALL THAT APPLY

☐ To the local council

☐ To the police

☐ To a general practitioner

☐ To the emergency department at the hospital

☐ Admitted to hospital

☐ Other: __________________________________

Q16: Has your dog ever bitten another person (*not you nor someone from your household*)?

☐ Yes *Please go to Q17*

☐ No *Please go to Q18*

☐ I don't own a dog *Please go to Q27*

Q17: Was the person:

☐ Family or friend visiting you

☐ A stranger to you

☐ An intruder

Q18: Has your dog/s ever been bitten by other dogs?

☐ Yes *Please go to Q19*

☐ No *Please go to Q25*

Q19: Was the dog that bit your dog/s

☐ From your household

☐ NOT from your household but known to you

☐ NOT from your household and unknown to you

Q20: What breed was the dog that bit your dog/s?_____________________

Q21: Where did the incident occur?

☐ At your home

☐ At the attacking dog's home (if it was not your dog)

☐ In a public place (e.g. street, park)

Q22: Did the dog bite cause your dog's skin to be broken, at all?

☐ Yes

☐ No

Q23: Did you report the attack to authorities?

☐ Yes *Please go to Q24*

☐ No Why not: ____

Q24: To whom was the incident (dog bite) reported?

PLEASE TICK ALL THAT APPLY

☐ To your veterinarian

☐ To the local council

☐ To the police

☐ Other: ______________________________

Q25: Has your dog/s ever bitten another animal (including wildlife but not including reptiles or birds)

☐	Yes	*Please go to Q26*
☐	No	*Please go to Q27*
☐	I don't know	*Please go to Q27*

Q26: What animal did your dog/s bite?

☐ Another dog

☐ A domestic pet (such as cats, rabbits, ferrets etc)

☐ Livestock (such as sheep, cattle, horses etc)

☐ Wild dog or dingo

☐ Kangaroo or wallaby

☐ Possum

☐ Other ___________________________________

Q27: What is your postcode? _____________

Q28: What town do you live in? ____________________

Q29: Are there any other comments you would like to add?

____

____

____

____

Thank you very much for your time.

Your responses will help to improve our understanding of domestic dog ownership.

STATEMENT OF ORIGINALITY

We, the PhD candidate and the candidate's Principal Supervisor, certify that the following text, figures and diagrams are the candidate's original work.

Type of work	Page number/s
Journal article and all encompassing information	72-92

Name of Candidate: Jessica Sparkes

Name/title of Principal Supervisor: Dr Wendy Brown

[redacted]

12 December 2015

Candidate

Date

[redacted]

12 December 2015

Principal Supervisor

Date

STATEMENT OF AUTHORS' CONTRIBUTION

We, the PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

	Author's Name	**% of contribution**
Candidate	Jessica Sparkes	Conception and design (80%) Data collection (100%) Analyses (100%) Manuscript development (70%)
Other Authors	Guy Ballard	Conception and design (15%) Manuscript development (20%)
	Peter J S Fleming	Conception and design (5%) Manuscript development (5%)
	Wendy Y Brown	Manuscript development (5%)

Name of Candidate: Jessica Sparkes

Name/title of Principal Supervisor: Dr Wendy Brown

[redacted]

12 December 2015

Candidate

Date

[redacted]

12 December 2015

Principal Supervisor

Date

4 Population dynamics and interactions among free-roaming domestic dogs

Free-roaming dogs are common worldwide, and play an important role in the maintenance of diseases that affect domestic pets and wildlife. Management of free-roaming dogs is difficult and often involves capture, treatment, neutering and release with the objective of reducing population growth and improving the overall health of the free-roaming dog population, as well as reducing the associated negative impacts on humans, other domestic pets and wildlife.

In Australia, free-roaming dogs are commonly associated with remote communities where dogs live and search for food around dwellings and community infrastructure (see ‘Chapter 2.1.7 Community dogs’).

Whereas Chapter 3 provided a general overview of dog ownership and free-roaming behaviour in eastern Australian communities, this Chapter focuses on dog population dynamics and sociality of one community of free-roaming domestic dogs in northern Australia. Dog population and social unit size, activity patterns and contact rates were quantified. Further, human interventions including neutering were assessed to determine if they affected dog interaction rates, which may have flow-on effects for the transmission of rabies.

4.1 Effects of sex and reproductive state on interactions between free-roaming domestic dogs

This Chapter has been written in the format of a scientific paper and has been published in PLoS ONE (Appendix 4-1) with the following citation:

Sparkes, J., Körtner, G., Ballard, G., Fleming, P.J.S., Brown, W.Y. (2014) Effects of sex and reproductive state on interactions between free-roaming domestic dogs. *PLoS ONE* **9**, e116053.

4.1.1 Abstract

Free-roaming dogs (*Canis familiaris*) are common worldwide, often maintaining diseases of domestic pets and wildlife. Management of these dogs is difficult and often involves capture, treatment, neutering and release. Information on the effects of sex and reproductive state on intraspecific contacts and disease transmission is currently lacking, but is vital to improving strategic management of their populations. We assessed the effects of sex and reproductive state on short-term activity patterns and contact rates of free-roaming dogs living in an Australian Indigenous community. Population, social group sizes and rates of contact were estimated from structured observations along walked transects. Simultaneously, GPS telemetry collars were used to track dogs' movements and to quantify the frequency of contacts between individual animals. We estimated that the community's dog population was 326±52, with only 9.8±2.5% confined to a house yard. Short-term activity ranges of dogs varied from 9.2 to 133.7 ha, with males ranging over significantly larger areas than females. Contacts between two or more dogs occurred frequently, with entire females and neutered males accumulating significantly more contacts than spayed females or entire males. This indicates that sex and reproductive status are potentially important to epidemiology, but the effect of these differential contact rates on disease transmission requires further investigation. The observed combination of unrestrained dogs and high contact rates suggest that contagious disease would likely spread rapidly through the population. Pro-active management of dog populations and targeted education programs could help reduce the risks associated with disease spread.

Keywords

activity patterns; canine; contact rate; desex; GPS; free-ranging; home range; Indigenous community; movement; tropical Australia

4.1.2 Introduction

Free-roaming dogs (*Canis familiaris*) occur in many parts of the world (Gompper 2014a), displaying a wide diversity of population sizes and social organisations, ranging from solitary individuals to members of large social groups (Boitani *et al*. 2007, Newsome *et al*. 2013, Majumder *et al*. 2014). The variation in sociality of these canids is often in response to population size and resource availability, including food, shelter and potential mates within an area (Cafazzo *et al*. 2010, Lisberg & Snowdon 2011, Pal 2011, Newsome *et al*. 2014). Management programs often involve capture, veterinary treatment and neutering, with the objective of reducing population growth and improving the overall health of the free-roaming dog population, associated humans, other domestic pets and wildlife (e.g. Jackman & Rowan 2007, Totton *et al*. 2010). However, information on the effect of sex and reproductive state (and hence neutering) on contact rates and movements is limited and appears to be location and context specific (Thomson 1992b, Vaniscotte *et al*. 2011, Van Kesteren *et al*. 2013).

In Australia, free-roaming dogs are commonly associated with remote communities where dogs live and search for food around dwellings and community infrastructure (Currie 1998, Newsome *et al*. 2013). In some remote Indigenous communities, dogs have cultural, spiritual and physical significance, which must be accounted for in dog management programs (Bourke 2009, Constable *et al*. 2010). However, these dogs also spread parasites and disease, such as sarcoptic mange (*Sarcoptes scabiei*), hookworm (*Ancylostoma caninum*), *Giardia duodenalis*, heartworm (*Dirofilaria immitis*), ticks (*Rhipicephalus sanguineus*) and fleas (Bradbury & Corlette 2006) to humans and wildlife (Meek 1999, Gompper 2014a). Neutering and veterinary care programs to limit dog population growth and reduce the incidence of both dog and human disease are underway in many of these communities (Hardaker 2012).

Despite the risk that these dogs pose to humans and other animals, population level studies are sparse (Meek 1999, Dürr & Ward 2014). In particular, key knowledge of the effects that sex and neutering programs have on movement behaviour and rates of contact between individual dogs is lacking. Understanding these factors is essential for determining the extent, appropriate timing and duration of dog health programs in these communities, while also providing essential parameters for endemic and epizootic disease modelling (Slater 2001, Bourke 2009, Sparkes *et al*. 2015).

Here, we quantified the dog population and social unit size, activity patterns and contact rates, and determined whether sex and neutering affected these parameters within a free-roaming dog population associated with an Aboriginal island community in northern Australia.

4.1.3 Method

4.1.3.1 Study site

The study was conducted in the Wurrumiyanga community (11.76ºS, 130.64ºE) on the south-east corner of Bathurst Island, within the Tiwi Islands group, Northern Territory, Australia. Bathurst Island spans an area of 169 300 ha, is tropical and mostly covered by tall eucalypt forests, interspersed with rainforest patches and mangroves. The average annual rainfall is 2 035mm; January is the wettest month and July the driest. Average maximum daytime temperature is 31.2ºC for the dry season, when the study was conducted (June/July) and 33.4ºC immediately prior to the wet season (Oct/Nov) (Bureau of Meteorology 2014). Mean minimum temperature for the same periods are 18.6 ºC and 23.7 ºC, respectively (Bureau of Meteorology 2014).

4.1.3.2 Population estimation

Over five consecutive days, sightings of all dogs, including known, collared and otherwise marked dogs were recorded by a team of two observers moving on foot along a pre-defined 5.5 km transect, covering 58% of the town's roadways, at 0700, 1200 and 1700 hrs ($N = 15$ transects). To aid identification, observers used a digital video camera to record all dogs observed on the transect. The number of dogs sighted, their confinement status and group sizes were also recorded. The Chapman estimator (Chapman 1951), which is unbiased for small recapture samples, was used to estimate the total dog population from repeated sightings of known marked dogs for each transect walk and the mean calculated from the 15 estimates.

4.1.3.3 Study animals for GPS tracking

Twenty dogs (2 entire females, 7 spayed females, 6 entire males and 5 neutered males) were recruited for Global Positioning Satellite (GPS) tracking by opportunistically asking community members to volunteer their pets (Plate 1 and 2). All study dogs were owned by residents but were unrestrained and allowed to roam freely about the community, which is normal for these animals. To record their movements and contacts, each dog was fitted with a Mobile Action (Taiwan) i-gotU GT-120 low-cost GPS-tracking device, mounted on an off-the-shelf dog collar (total weight 230 g). GPS-devices were programmed to record locations at 15 minute intervals. Data were downloaded upon retrieval of collars from the dogs.

The relatively short deployment period of the GPS collars (7 days) was deemed sufficient to provide areal context for observations along transect walks, but precluded calculation of traditional home ranges (Burt 1943). Therefore, the area encompassing the GPS fixes was termed an ‘activity range’ (AR), and pertained to the observational period only. The AR of each collared dog was calculated as a Minimum Convex Polygon (MCP; Kenward 1987). Based on the location data, the accumulated distance (adding all distances between each pair of successive data points) was calculated each day. Sex and reproductive effects for AR and accumulated distance were determined by running a 2-way ANOVA using R statistical software version 3.0.2 (R Core Team 2013).

Contacts between pairs of collared dogs were identified by searching through all GPS data sets for concurrent location fixes (±7.5 min) that were less than 20 m apart. Twenty meters was chosen as the contact threshold based on the effective accuracy of the GPS units. This decision was supported by observations along walked transects indicating that physical or close contact was likely to be elicited when two or more individuals sighted each other at this distance or shorter. The duration of contacts (an ‘event’) was calculated as the length of an uninterrupted string of contact records (i.e. number of contact records multiplied by 15 min). Subsequently, the contact data were searched for concurrent events involving two or more collared dogs to determine group size during a contact event. A 2-way ANOVA of dog sex (male, female) and reproductive state (neutered, entire) effects on contacts was conducted.

To determine if the number of recorded contacts for a pair of dogs were likely to be a result of random encounters of dogs moving within their AR, we simulated random encounters by using the original time and distance between subsequent location records but randomised direction of movement, constrained within the real AR for each dog. The average of 50 simulations was used to represent the number of chance encounters between a pair of dogs. As the AR of some dogs did not overlap, pairs with zero random encounters were removed from further analyses. Actual contacts for the remaining pairs were compared with simulated contacts and evaluated using a Welch's two sample *t*-test (Welch 1947). The whole procedure (both actual and simulated contacts), as well as the daily distance calculations and AR estimates were performed with programs written in Visual Basic 6.0 (Microsoft Corp.) by one of the authors (G.K). The programs enable the user to set parameter limitations that prevail in the dataset analysed (e.g. duration between successive fixes, altering distance threshold), ensuring application to a wide variety of datasets. Data are presented as mean ± 1 standard deviation; *N* = number of observations.

Research was conducted with approval from the UNE Animal Ethics Committee (AEC13-009). Fieldwork was carried out with permission from Tiwi Islands Shire Council.

4.1.4 Results

During transect walks, an average of 147±18 dogs were observed, with only 9.8±2.5% of dogs confined to a yard. Including the 20 GPS-collared dogs, 163 dogs were individually recognisable and all of these dogs were resighted during the transect walks. Subsequently, the community dog population was estimated at 326±52 (*N*=15), with an average of 1.1 dogs per household (21 dogs per 100 people; data based on Australian Bureau of Statistics 2013). This represents all dogs within the community, including owned free-roaming, confined and stray dogs greater than 6 weeks of age.

Consequently, the sample of dogs fitted with GPS collars (*N*=20) represented 6.1% of the population. Data were retrieved from 17 dogs (i.e. 5.2% of dog population); two collars were lost, while another became dysfunctional when bitten by a dog shortly after deployment. Solitary dogs were observed most often, with social groups ranging in size from 2 to 7 individuals. Size of social groups, determined from transect observations (*N*=1 423 groups observed), correlated strongly with those estimated for the GPS-collared dogs (transect walk = GPS data*0.76+3.48, r^2= 0.97, P<0.001; Figure 4-1). Overall, GPS-collared dog social groupings were smaller compared with transect observations because not all dogs were collared within the community.

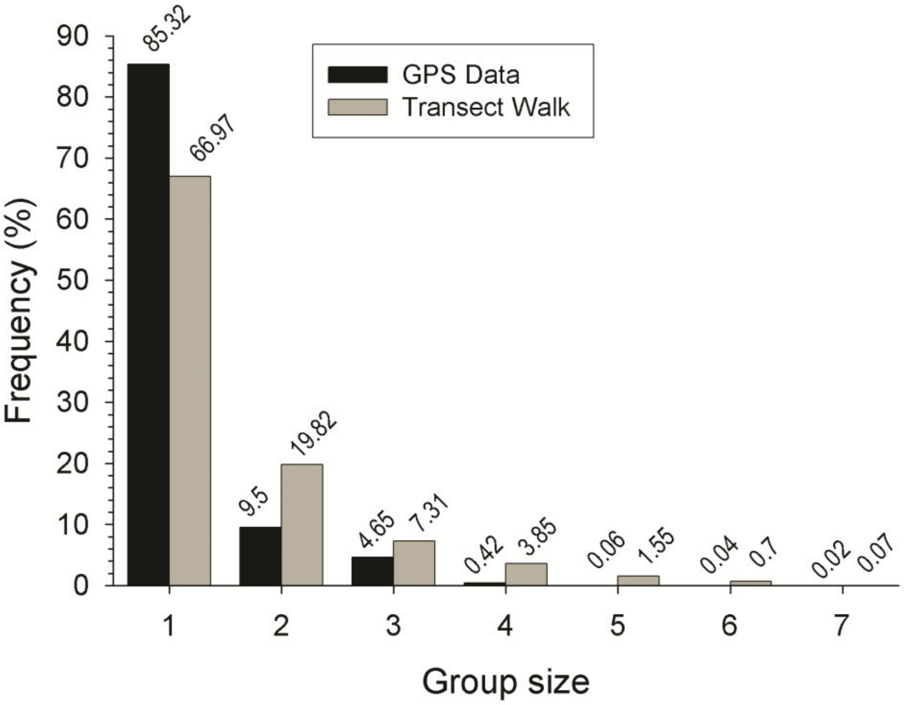


Figure 4-1 Comparison of social group sizes between GPS-collar and transect data

Overall, a total of 7 165 GPS fixes were recorded, with a GPS fix success rate of 73±14.4% (see Appendix 4-2 for an example of a GPS track). By chance, one GPS collar remained functional on the dog (#16) for 22 days, well beyond the calculated battery life of 7 days. This data set was used to compare its AR data with other shorter deployment durations. During the monitoring period, one dog undertook a long distance foray into the surrounding bush (17km). This foray was regarded as exploratory (*sensu* Harden 1985), falling outside the normal AR of the animal and was thus excluded from its AR and movement analyses.

The AR for collared dogs over the 7 days of deployment varied from 9.2 to 133.7 ha (mean AR=51.0±36.1; Table 4-1) and the mean daily distance travelled was 3 169±980 m (Table 4-1). The cumulative AR for Dog 16 over 21 days showed two marked plateaus (Figure 4-2), corresponding to a shift in its core area during the monitoring period. Despite this, the AR of this dog fell within the limits of other neutered male dogs with the shorter GPS deployment, indicating that short-term ARs were relatively stable and provided an appropriate timeframe for measuring contact rates.

Table 4-1 Activity range and distance travelled per day for free-ranging community dogs, northern Australia

Dog ID	Sex[#]	Activity Range (ha)	Distance (m/day)
9	FE	30.75	3 193
12	FE	68.6	3 798
1	FS	9.16	1 591
2	FS		
5	FS	37.47	3 514
14	FS	40.81	2 445
17	FS	18.12	2 012
18	FS	29.92	2 030
19	FS	18.56	2 399
4	ME	25.4	4 031
6	ME	14.97	2 364
7	ME	89.54	3 748
8	ME	76.5	4 168
15	ME		
20	ME	33.83	2 774
3	MN	88.34	4 446
10	MN	46.09	3 243
11	MN	133.69 (2293.09^)	5 182
13	MN		
16	MN	105.01	2 935

[#] FE: Female Entire; FS: Female Spayed; ME: Male Entire; MN: Male Neutered

^ Value incorporates foray undertaken during the study period

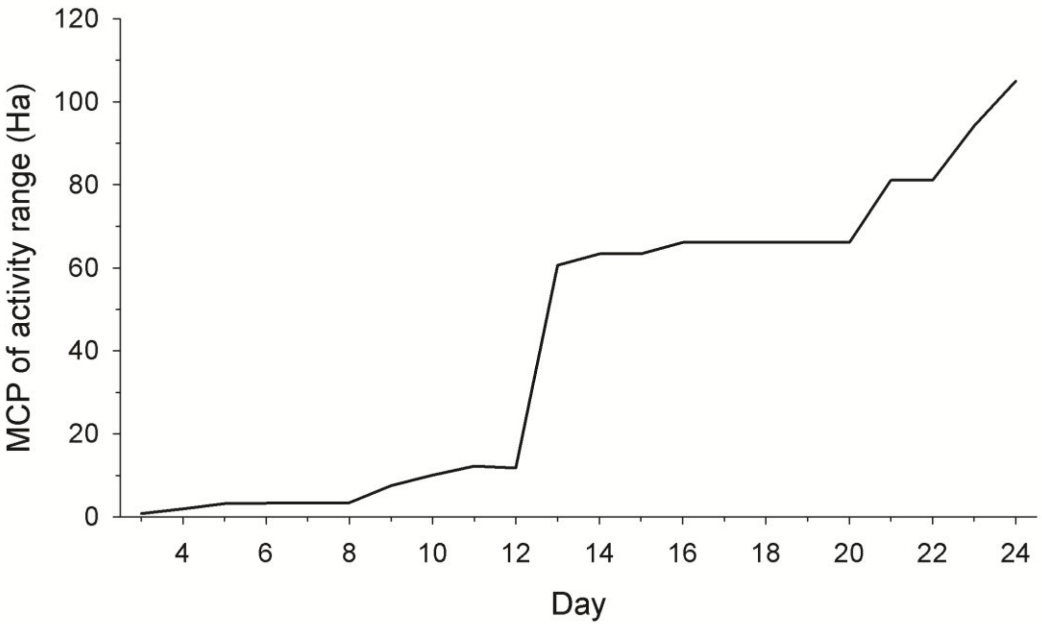


Figure 4-2 Cumulative activity range of Dog 16 (Minimum Convex Polygon (MCP) in 1 day increments) demonstrating abrupt changes in activity range

A 2-way ANOVA yielded a significant main effect for sex; male collared dogs utilised a larger area than females (mean AR = 68.15±40.17, N=9; 31.67±18.31, N=8, respectively), while there was no effect of reproductive state on AR (Table 4-2). However, the interaction effect was significant; indicating that neutered male dogs had significantly larger ARs than spayed female dogs (mean AR = 93.28±36.61, N=4; 25.67±12.38, N=6, respectively). Similarly, a significant main effect showed that overall, males travelled further each day compared with females (mean distance travelled = 3 654±901, N=9; 2 623±790, N=8, respectively, Table 4-2).

A total of 412 contacts, from 271 separate proximity events were recorded between pairs of collared dogs (mean: 5.24±5.30 contacts per dog per day; Figure 4-3). During the 7 days, 4 789 GPS fixes (85%) did not result in contact with another collared dog (i.e. a ‘solitary’ dog; Figure 4-1).

Table 4-2 Effect of sex (male, female) and reproductive state (entire, neutered) on activity range, accumulated distance moved and contacts (N = 17 dogs)

	F_1 value	Pr (>F)
Activity Range		
Sex effect	7.442	0.02
Reproductive state	1.477	0.25
Sex effect*Reproductive state	5.668	0.03
Accumulated Distance		
Sex effect	7.137	0.02
Reproductive state	0.132	0.72
Sex effect*Reproductive state	4.088	0.06
Contacts		
Sex effect	1.201	0.29
Reproductive state	0.060	0.81
Sex effect*Reproductive state	7.191	0.02
Number individuals contacted		
Sex effect	0.270	0.6
Reproductive state	0.001	0.98
Sex effect*Reproductive state	5.639	0.03

Depending on sex, neutering had the opposite effect on contacts, where neutered male and entire female dogs (mean contacts = 14.13±10.97, N=4; 16.17±10.84, N=2, respectively) had significantly more contacts with other collared dogs compared to spayed females and entire males (mean contacts = 2.35±3.09, N=6; 6.43±7.46, N=5, respectively, Table 4-2). There was no observable main effect of sex or reproductive state on contacts during the study period (Table 4-2). Event duration ranged from 15 minutes to 2.5 hours, with most events lasting 15 minutes (i.e. a single contact record).

Observed contact rates differed significantly from simulated contact rates for collared dogs (Welch t test: t_{113}=2.55, P=0.01). "Avoidance behaviour" (i.e. where the number of observed records was significantly less than those predicted from random encounters; <95% confidence interval) was recorded on 48 paired-collar instances, with the highest "avoidance" observed for dogs 07 and 17 (0 vs 2.24, 1 vs 3.14; actual vs simulated, respectively). In contrast, the number of recorded contacts was higher than the 95% confidence limit of the simulation for 37 pairs of dogs, while 30 pairs of collared dogs matched the simulation prediction.

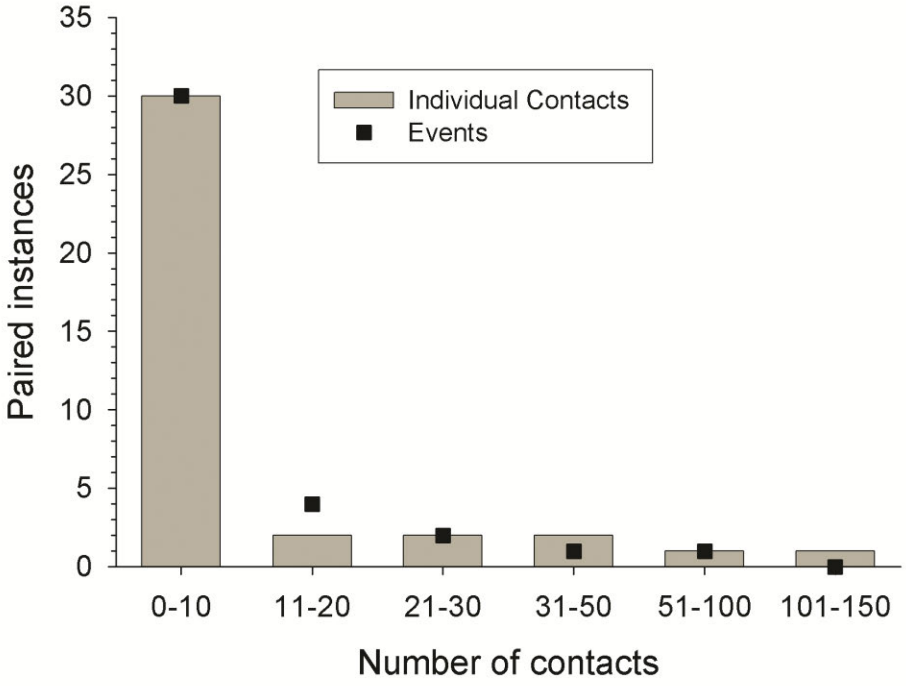


Figure 4-3 Number of individual contacts (columns) and proximity events (points) between paired GPS-collared dogs ≤20m apart

Group size of collared dogs ranged from 1 to 7 individuals, with most contacts occurring between two dogs only (Figure 4-1). The number of different collared dogs that an individual collared dog encountered during the study period ranged from 0 to 10 (mean individuals encountered=4±2.8, *N*=17). Similar to contact rates, there was no effect of sex or reproductive state on the number of dogs an individual came into contact with (Table 4-2). However, there was a significant interaction effect, where neutered male and female entire dogs (mean individuals contacted: 6.3±2.9, *N*=4; 7±1.4, *N*=2, respectively) contacted more dogs compared with male entire and female spayed dogs (mean individuals contacted: 3.6±3.4, *N*=5; 3.2±1.7, *N*=6; *P*=0.03, respectively; Table 4-2).

4.1.5 Discussion

Short-term activity ranges of the monitored free-roaming domestic dogs on Tiwi Islands were small relative to the reported home ranges of dingoes and other wild dogs from semi-arid and arid Australia (Thomson 1992b, Thomson & Marsack 1992, Newsome *et al*. 2013). Nevertheless, males still had significantly larger ARs than females, which is consistent with the pattern seen in longer studies of wild dogs (e.g. Thomson 1992b, Newsome *et al*. 2013). Contacts between individually collared dogs were frequent, but on average, entire female and neutered male dogs contacted significantly more dogs than spayed females and entire males respectively.

During the study period, dog ownership within the community was estimated at 1.1 dogs per household (21 dogs per 100 people), which is consistent with global estimates (1.1; Gompper 2014b) and only slightly higher than the Australia-wide estimate of 16 dogs per 100 people (Australian Companion Animal Council 2010). More importantly, very few dogs were confined. Community members' attitudes towards dog ownership and containment typically mean that their dogs are allowed to roam freely like any other member of the family (Hardaker 2012). Consequently, the probability of contacts occurring between dogs was high and groups of up to 7 individuals were observed. Similar to Rubin & Beck (1982), contact events (i.e. social groupings) were usually transitory aggregates, with the majority of events lasting less than 15 minutes. These transitory social groupings increase the probability of contacts occurring between a greater number of individuals, potentially increasing the rate of disease transmission.

However, as ARs of the study dogs were generally confined to the community boundaries, this would likely limit disease transmission to the community confines in the first instance. One dog did however, undertake a long distance foray towards the local rubbish tip. Interestingly, this dog was frequently observed within the town boundaries with its litter mate (#10) during transect walks, but the latter dog did not undertake a similar foray while collared. This was reflected in the high number of contacts between the pair but varying ARs and daily accumulated distances travelled even with the foray excluded (Table 4-1); with Dog 11 travelling further each day and over a larger area, suggesting the tendency of this dog to roam widely.

In a global context, Vaniscotte *et al*. (2011) estimated similar ARs to our study for free-roaming domestic dogs in Tibet (range 32.5–174.5 ha, *N*=78), while other studies have estimated much smaller home ranges, ranging from 2 to 10 ha for free-roaming domestic dogs in Australia, Indonesia and the USA (Fox *et al*. 1975, Rubin & Beck 1982, Berman & Dunbar 1983, Gunata 2011, Dürr & Ward 2014). Meek (1999) estimated much larger home ranges for free-roaming dogs from an Australian Indigenous community in coastal south-east New South Wales (range: 140–2 450 ha, *N*=10). Those dogs conducted regular forays into the surrounding bush and hence resemble the Tiwi Island Dog 11 estimate when including its foray (AR=2 293). The differences in ARs, home ranges and the propensity to undertake forays between studies may relate to methodological differences (e.g. duration of the monitoring period) and the size of the communities where studies were conducted. Resource availability; including food, shelter, companionship and barriers (natural or manmade) may have also affected effective ARs. Dogs living in resource rich areas tend to have smaller home ranges compared with resource poor areas, which reduce the need for the animal to travel greater distances to meet its biological and social requirements (Meek 1999, Boitani *et al*. 2007, Newsome *et al*. 2013, Newsome *et al*. 2014).

Some of the variability within the dog population was evidently related to sex and reproductive status. Collectively, male dogs travelled further each day and over a larger area than females. These findings are in agreement with Thomson (1992a) and Vaniscotte *et al*. (2011), but in contrast to Van Kesteren *et al*. (2013) and Dürr & Ward (2014), where no difference between male and female AR or distance traveled per day was found. At any rate, the larger area covered by males in the present study may increase their potential to spread diseases further through the community than females. For diseases that require physical contact (e.g. rabies, ringworm); contact between susceptible individuals would have greater significance for disease transmission. In the case of Tiwi Islands, an average of 5.24 contacts per collared dog per day was recorded and if extrapolated to the entire dog population, a contact rate of 101 per dog per day would be expected.

There were large variations in contacts for collared individuals, ranging from 0 to 24 contacts per day. Individual circumstances were important and some of the very high contact rates could be explained by cohabitation. For example, Dogs 10 and 11 were owned by the same household and recorded 105 contacts between the pair. In contrast, Dogs 08 and 12 came from a single household, but only recorded 42 contacts between the pair. As these dogs were not confined, individual dogs were allowed to express avoidance behaviour, even within a cohabitation environment.

In addition to obvious individual characteristics observed within the data, global trends for sociality were also evident. In contrast to AR and distance travelled, there was no significant difference in the number of contacts recorded between collared male and female dogs. However, there was a significant effect of reproductive state on contacts, with entire females and neutered males contacting more dogs than spayed females and entire males. Neutering has been found to disrupt sociality of dogs, removing the dominance hierarchy (Bradshaw *et al*. 2009), while also increasing activity in domestic dogs (Salmeri *et al*. 1991), creating more opportunities for contact with other dogs. Multiple-mate matings (Bradshaw *et al*. 2009, Cafazzo *et al*. 2010) and interactions with neutered dogs (i.e. lack of perceived competition for resources), may have resulted in the higher contacts recorded for entire females. As there is no clear breeding season on the Tiwi Islands; with dogs able to breed any time of year (S. Cutter, Pers. Comm.), confinement strategies tailored to the individual would need to be implemented to reduce these contacts. However, only two entire females were collared during the present study and further research is required to determine whether this effect is consistent at a population level. In contrast, dominance and territorial aggression was found to be more common in male dogs (Perez-Guisado & Munoz-Serrano 2009ab), which may result in fewer contacts due to avoidance behaviour exhibited by subordinate animals.

Our data describes short-term movements and provides the first quantitative assessment of contacts between free-roaming domestic dogs in northern Australia. This information is a critical precursor for modelling endemic and exotic diseases of community dogs, and devising appropriate control programs. Observed high contact rates, fidelity to home and the transitory nature of dog social groupings combined with a lack of confinement indicates the potential of a disease to spread rapidly through this and similar communities, with limited/delayed spread to the surrounding landscape. Spayed females did have significantly fewer contacts than entire females, suggesting that neutering programs targeted towards the female portion of the population would be beneficial in reducing contact rates and hence, opportunities for breeding as well as reducing the predicted rate of spread of contagious diseases.

4.1.6 Acknowledgements

We wish to thank the people of the Wurrumiyanga Community for participating in the study and staff and volunteers from Animal Management in Rural and Remote Indigenous Communities (AMRRIC) for their assistance throughout the project. Discussions with Michael Ward, Helen Scott-Orr, and Salome Dürr of University of Sydney Veterinary School, and Julia Hardaker and Jan Allen of AMRRIC assisted the project.

Appendix 4-1: Tiwi Islands collaring publication

Sparkes, J., Körtner, G., Ballard, G., Fleming, P.J.S., Brown, W.Y. (2014) Effects of sex and reproductive state on interactions between free-roaming domestic dogs. *PLoS ONE* **9**, e116053.

PLOS | ONE

RESEARCH ARTICLE

Effects of Sex and Reproductive State on Interactions between Free-Roaming Domestic Dogs

Jessica Sparkes[1,2,4]*, **Gerhard Körtner**[1,2,4], **Guy Ballard**[1,2,4],
Peter J. S. Fleming[1,3,4], **Wendy Y. Brown**[1]

1. School of Environmental and Rural Sciences, University of New England, Armidale, Australia, **2.** Vertebrate Pest Research Unit, Biosecurity New South Wales, Armidale, Australia, **3.** Vertebrate Pest Research Unit, Biosecurity New South Wales, Orange, Australia, **4.** Invasive Animals Cooperative Research Centre, Armidale, Australia

*jsparke4@une.edu.au

Citation: Sparkes J, Körtner G, Ballard G, Fleming PJS, Brown WY (2014) Effects of Sex and Reproductive State on Interactions between Free Roaming Domestic Dogs. PLoS ONE 9(12): e116053. doi:10.1371/journal.pone.0116053

Editor: Claire Wade, University of Sydney, Australia

Received: September 13, 2014

Accepted: December 3, 2014

Published: December 26, 2014

Data Availability: The authors confirm that, for approved reasons, some access restrictions apply to the data underlying the findings. Data ownership is shared with NSW Government. Data is stored in the NSW Department of Primary Industries formal record keeping system, TRIM (File Reference: V14/4334). Please contact Dr Peter Fleming (peter.fleming@dpi.nsw.gov.au) for access to data.

Funding: Jessica Sparkes is an Australian Postgraduate Award and UNE Apted scholar recipient. The authors acknowledge the financial support of the Wildlife and Exotic Disease Preparedness Program (www.daff.gov.au/animal plant health/emergency/wedpp). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

Abstract

Free-roaming dogs (*Canis familiaris*) are common worldwide, often maintaining diseases of domestic pets and wildlife. Management of these dogs is difficult and often involves capture, treatment, neutering and release. Information on the effects of sex and reproductive state on intraspecific contacts and disease transmission is currently lacking, but is vital to improving strategic management of their populations. We assessed the effects of sex and reproductive state on short-term activity patterns and contact rates of free-roaming dogs living in an Australian Indigenous community. Population, social group sizes and rates of contact were estimated from structured observations along walked transects. Simultaneously, GPS telemetry collars were used to track dogs' movements and to quantify the frequency of contacts between individual animals. We estimated that the community's dog population was 326 ± 52, with only $9.8 \pm 2.5\%$ confined to a house yard. Short-term activity ranges of dogs varied from 9.2 to 133.7 ha, with males ranging over significantly larger areas than females. Contacts between two or more dogs occurred frequently, with entire females and neutered males accumulating significantly more contacts than spayed females or entire males. This indicates that sex and reproductive status are potentially important to epidemiology, but the effect of these differential contact rates on disease transmission requires further investigation. The observed combination of unrestrained dogs and high contact rates suggest that contagious disease would likely spread rapidly through the population. Pro-active management of dog populations and targeted education programs could help reduce the risks associated with disease spread.

Introduction

Free-roaming dogs (*Canis familiaris*) occur in many parts of the world [1], displaying a wide diversity of population sizes and social organisations, ranging from solitary individuals to members of large social groups [2–4]. The variation in sociality of these canids is often in response to population size and resource availability, including food, shelter and potential mates within an area [5–8]. Management programs often involve capture, veterinary treatment and neutering, with the objective of reducing population growth and improving the overall health of the free-roaming dog population, associated humans, other domestic pets and wildlife (e.g. [9, 10]). However, information on the effect of sex and reproductive state (and hence neutering) on contact rates and movements is limited and appears to be location and context specific [11–13].

In Australia, free-roaming dogs are commonly associated with remote communities where dogs live and search for food around dwellings and community infrastructure [14, 15]. In some remote Indigenous communities, dogs have cultural, spiritual and physical significance, which must be accounted for in dog management programs [16, 17]. However, these dogs also spread parasites and disease, such as sarcoptic mange (*Sarcoptes scabiei*), hookworm (*Ancylostoma caninum*), *Giardia duodenalis*, heartworm (*Dirofilaria immitis*), ticks (*Rhipicephalus sanguineus*) and fleas [18] to humans and wildlife [19, 20]. Neutering and veterinary care programs to limit dog population growth and reduce the incidence of both dog and human disease are underway in many of these communities [21].

Despite the risk that these dogs pose to humans and other animals, population level studies are sparse [19, 22]. In particular, key knowledge of the effects that sex and neutering programs have on movement behaviour and rates of contact between individual dogs is lacking. Understanding these factors is essential for determining the extent, appropriate timing and duration of dog health programs in these communities, while also providing essential parameters for endemic and epizootic disease modelling [16, 23, 24].

Here, we quantified the dog population and social unit size, activity patterns and contact rates, and determined whether sex and neutering affected these parameters within a free-roaming dog population associated with an Aboriginal island community in northern Australia.

Method

Study site

The study was conducted in the Wurrumiyanga community (11.76°S, 130.64°E) on the south-east corner of Bathurst Island, within the Tiwi Islands group, Northern Territory, Australia. Bathurst Island spans an area of 169 300 ha, is tropical and mostly covered by tall eucalypt forests, interspersed with rainforest patches and mangroves. The average annual rainfall is 2 035mm; January is the wettest month and July the driest. Average maximum daytime temperature is

31.2℃ for the dry season, when the study was conducted (June/July) and 33.4℃ immediately prior to the wet season (Oct/Nov) [25]. Mean minimum temperature for the same periods are 18.6℃ and 23.7℃, respectively [25].

Population estimation

Over five consecutive days, sightings of all dogs, including known, collared and otherwise marked dogs were recorded by a team of two observers moving on foot along a pre-defined 5.5 km transect, covering 58% of the town's roadways, at 0700, 1200 and 1700 hrs ($N=15$ transects). To aid identification, observers used a digital video camera to record all dogs observed on the transect. The number of dogs sighted, their confinement status and group sizes were also recorded. The Chapman [26] estimator, which is unbiased for small recapture samples, was used to estimate the total dog population from repeated sightings of known marked dogs for each transect walk and the mean calculated from the 15 estimates.

Study animals for GPS tracking

Twenty dogs (2 entire females, 7 spayed females, 6 entire males and 5 neutered males) were recruited for Global Positioning Satellite (GPS) tracking by opportunistically asking community members to volunteer their pets. All study dogs were owned by residents but were unrestrained and allowed to roam freely about the community, which is normal for these animals. To record their movements and contacts, each dog was fitted with a Mobile Action (Taiwan) i-gotU GT-120 low-cost GPS-tracking device, mounted on an off-the-shelf dog collar (total weight 230 g). GPS-devices were programmed to record locations at 15 minute intervals. Data were downloaded upon retrieval of collars from the dogs.

The relatively short deployment period of the GPS collars (7 days) was deemed sufficient to provide areal context for observations along transect walks, but precluded calculation of traditional home ranges [27]. Therefore, the area encompassing the GPS fixes was termed an 'activity range' (AR), and pertained to the observational period only. The AR of each collared dog was calculated as a Minimum Convex Polygon (MCP; [28]). Based on the location data, the accumulated distance (adding all distances between each pair of successive data points) was calculated each day. Sex and reproductive effects for AR and accumulated distance were determined by running a 2-way ANOVA using R statistical software version 3.0.2 [29].

Contacts between pairs of collared dogs were identified by searching through all GPS data sets for concurrent location fixes ($\pm$7.5 min) that were less than 20 m apart. Twenty meters was chosen as the contact threshold based on the effective accuracy of the GPS units. This decision was supported by observations along walked transects indicating that physical or close contact was likely to be elicited when two or more individuals sighted each other at this distance or shorter. The duration of contacts (an 'event') was calculated as the length of an uninterrupted string of contact records (i.e. number of contact records multiplied by 15 min). Subsequently, the contact data were searched for concurrent events involving two or more collared dogs to determine group size during a contact event. A 2-way ANOVA of dog sex (male, female) and reproductive state (neutered, entire) effects on contacts was conducted.

To determine if the number of recorded contacts for a pair of dogs were likely to be a result of random encounters of dogs moving within their AR, we simulated random encounters by using the original time and distance between subsequent location records but randomised direction of movement, constrained within the real AR for each dog. The average of 50 simulations was used to represent the number of chance encounters between a pair of dogs. As the AR of some dogs did not overlap, pairs with zero random encounters were removed from further analyses. Actual contacts for the remaining pairs were compared with simulated contacts and evaluated using a Welch's two sample *t*-test [30]. The whole procedure (both actual and simulated contacts), as well as the daily distance calculations and AR estimates were performed with programs written in Visual Basic 6.0 (Microsoft Corp.) by one of the authors (G.K). The programs enable the user to set parameter limitations that prevail in the dataset analysed (e.g. duration between successive fixes, altering distance threshold), ensuring application to a wide variety of datasets. Data are presented as mean ±1 standard deviation; N= number of observations.

Research was conducted with approval from the UNE Animal Ethics Committee (AEC13-009). Fieldwork was carried out with permission from Tiwi Islands Shire Council.

Results

During transect walks, an average of 147±18 dogs were observed, with only 9.8±2.5% of dogs confined to a yard. Including the 20 GPS-collared dogs, 163 dogs were individually recognisable and all of these dogs were resighted during the transect walks. Subsequently, the community dog population was estimated at 326±52 (N=15), with an average of 1.1 dogs per household (21 dogs per 100 people; data based on [31]). This represents all dogs within the community, including owned free-roaming, confined and stray dogs greater than 6 weeks of age.

Consequently, the sample of dogs fitted with GPS collars (N=20) represented 6.1% of the population. Data were retrieved from 17 dogs (i.e. 5.2% of dog population); two collars were lost, while another became dysfunctional when bitten by a dog shortly after deployment. Solitary dogs were observed most often, with social groups ranging in size from 2 to 7 individuals. Size of social groups, determined from transect observations (N=1 423 groups observed), correlated strongly with those estimated for the GPS-collared dogs (transect walk = GPS data*0.76+3.48, r^2=0.97, $P<0.001$; Fig. 1). Overall, GPS-collared dog social

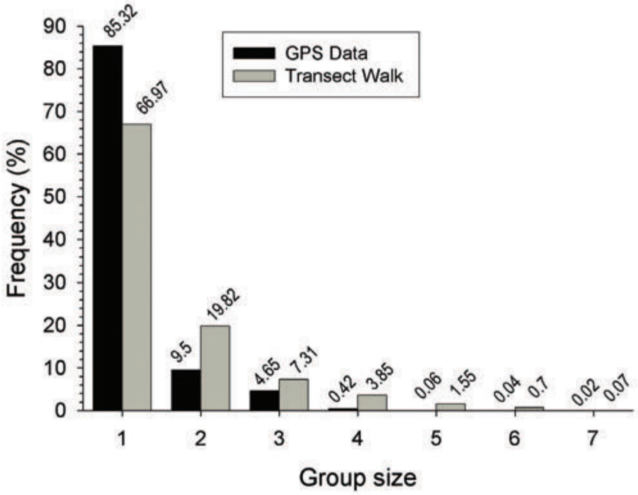


Fig. 1. Comparison of social group sizes between GPS-collar and transect data.

doi:10.1371/journal.pone.0116053.g001

groupings were smaller compared with transect observations because not all dogs were collared within the community.

Overall, a total of 7 165 GPS fixes were recorded, with a GPS fix success rate of 73±14.4%. By chance, one GPS collar remained functional on the dog (#16) for 22 days, well beyond the calculated battery life of 7 days. This data set was used to compare its AR data with other shorter deployment durations. During the monitoring period, one dog undertook a long distance foray into the surrounding bush (17 km). This foray was regarded as exploratory (*sensu* [32]), falling outside the normal AR of the animal and was thus excluded from its AR and movement analyses.

The AR for collared dogs over the 7 days of deployment varied from 9.2 to 133.7 ha (mean AR=51.0±36.1; Table 1) and the mean daily distance travelled was 3 169±980 m (Table 1). The cumulative AR for Dog 16 over 21 days showed two marked plateaus (Fig. 2), corresponding to a shift in its core area during the monitoring period. Despite this, the AR of this dog fell within the limits of other neutered male dogs with the shorter GPS deployment, indicating that short-term ARs were relatively stable and provided an appropriate timeframe for measuring contact rates.

A 2-way ANOVA yielded a significant main effect for sex; male collared dogs utilised a larger area than females (mean AR=68.15±40.17, N=9; 31.67±18.31, N=8, respectively), while there was no effect of reproductive state on AR (Table 2). However, the interaction effect was significant; indicating that neutered male dogs had significantly larger ARs than spayed female dogs (mean AR=93.28±36.61, N=4; 25.67±12.38, N=6, respectively). Similarly, a significant main effect showed that overall, males travelled further each day compared with females (mean distance travelled =3 654±901, N=9; 2 623±790, N=8, respectively, Table 2).

Table 1. Activity range and distance travelled per day for free ranging community dogs, northern Australia.

Dog ID	Sex[#]	Activity Range (ha)	Distance (m/day)
9	FE	30.75	3 193
12	FE	68.6	3 798
1	FS	9.16	1 591
2	FS		
5	FS	37.47	3 514
14	FS	40.81	2 445
17	FS	18.12	2 012
18	FS	29.92	2 030
19	FS	18.56	2 399
4	ME	25.4	4 031
6	ME	14.97	2 364
7	ME	89.54	3 748
8	ME	76.5	4 168
15	ME		
20	ME	33.83	2 774
3	MN	88.34	4 446
10	MN	46.09	3 243
11	MN	133.69 (2293.09[^])	5 182
13	MN		
16	MN	105.01	2 935

[#] FE: Female Entire; FS: Female Spayed; ME: Male Entire; MN: Male Neutered.

[^] Value incorporates foray undertaken during the study period.

doi:10.1371/journal.pone.0116053.t001

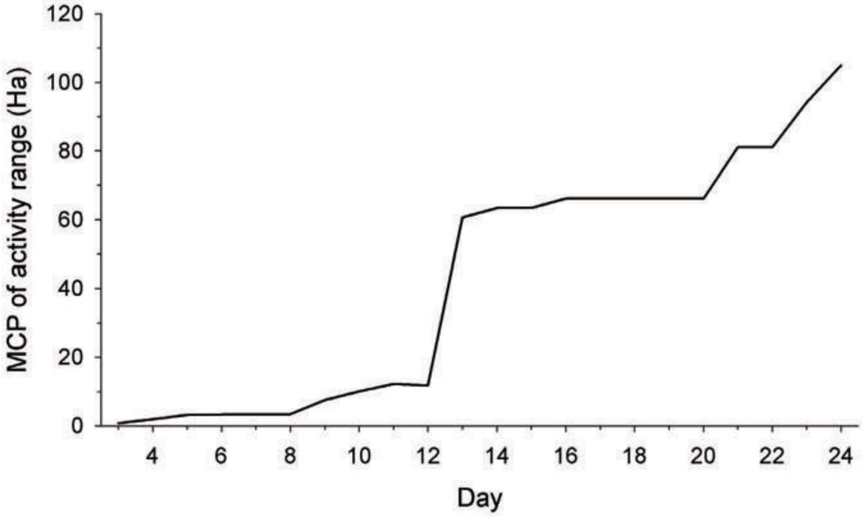


Fig. 2. Cumulative Activity Range of Dog 16 (Minimum Convex Polygon in 1 day increments) demonstrating abrupt changes in activity range.

doi:10.1371/journal.pone.0116053.g002

Table 2. Effect of sex (male, female) and reproductive state (entire, neutered) on activity range, accumulated distance moved and contacts (*N* 17 dogs).

	F_1 value	Pr (>F)
Activity Range		
Sex effect	7.442	0.02
Reproductive state	1.477	0.25
Sex effect*Reproductive state	5.668	0.03
Accumulated Distance		
Sex effect	7.137	0.02
Reproductive state	0.132	0.72
Sex effect*Reproductive state	4.088	0.06
Contacts		
Sex effect	1.201	0.29
Reproductive state	0.060	0.81
Sex effect*Reproductive state	7.191	0.02
Number individuals contacted		
Sex effect	0.270	0.6
Reproductive state	0.001	0.98
Sex effect*Reproductive state	5.639	0.03

doi:10.1371/journal.pone.0116053.t002

A total of 412 contacts, from 271 separate proximity events were recorded between pairs of collared dogs (mean: 5.24±5.30 contacts per dog per day; Fig. 3). During the 7 days, 4 789 GPS fixes (85%) did not result in contact with another collared dog (i.e. a 'solitary' dog; Fig. 1).

Depending on sex, neutering had the opposite effect on contacts, where neutered male and entire female dogs (mean contacts =14.13±10.97, N=4; 16.17±10.84, N=2, respectively) had significantly more contacts with other collared dogs compared to spayed females and entire males (mean contacts =2.35±3.09, N=6; 6.43±7.46, N=5, respectively, Table 2). There was no observable main effect of sex or reproductive state on contacts during the study period (Table 2). Event duration ranged from 15 minutes to 2.5 hours, with most events lasting 15 minutes (i.e. a single contact record).

Observed contact rates differed significantly from simulated contact rates for collared dogs (Welch t test: $t_{113}=2.55$, $P=0.01$). "Avoidance behaviour" (i.e. where the number of observed records was significantly less than those predicted from random encounters; <95% confidence interval) was recorded on 48 paired-collar instances, with the highest "avoidance" observed for dogs 07 and 17 (0 vs 2.24, 1 vs 3.14; actual vs simulated, respectively). In contrast, the number of recorded contacts was higher than the 95% confidence limit of the simulation for 37 pairs of dogs, while 30 pairs of collared dogs matched the simulation prediction.

Group size of collared dogs ranged from 1 to 7 individuals, with most contacts occurring between two dogs only (Fig. 1). The number of different collared dogs that an individual collared dog encountered during the study period ranged from 0 to 10 (mean individuals encountered =4±2.8, N=17). Similar to contact rates,

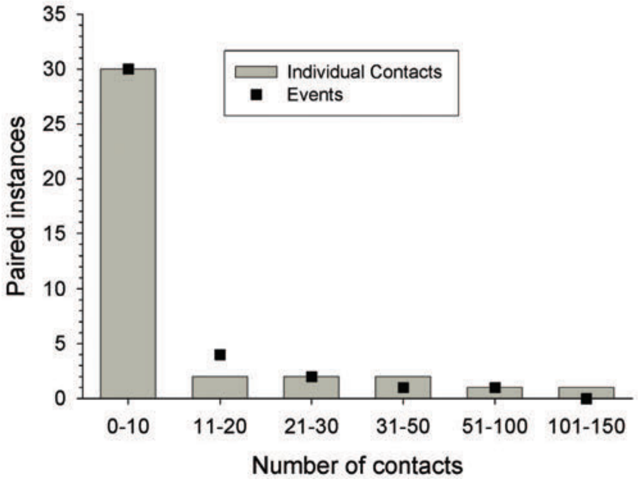


Fig. 3. Number of individual contacts (columns) and proximity events (points) between paired GPS-collared dogs ≤20 m apart.

doi:10.1371/journal.pone.0116053.g003

there was no effect of sex or reproductive state on the number of dogs an individual came into contact with (Table 2). However, there was a significant interaction effect, where neutered male and female entire dogs (mean individuals contacted: 6.3 ± 2.9, $N=4$; 7 ± 1.4, $N=2$, respectively) contacted more dogs compared with male entire and female spayed dogs (mean individuals contacted: 3.6 ± 3.4, $N=5$; 3.2 ± 1.7, $N=6$; $P=0.03$, respectively; Table 2).

Discussion

Short-term activity ranges of the monitored free-roaming domestic dogs on Tiwi Islands were small relative to the reported home ranges of dingoes and other wild dogs from semi-arid and arid Australia [3, 11, 33]. Nevertheless, males still had significantly larger ARs than females, which is consistent with the pattern seen in longer studies of wild dogs (e.g. [3, 11]). Contacts between individually collared dogs were frequent, but on average, entire female and neutered male dogs contacted significantly more dogs than spayed females and entire males respectively.

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These transitory social groupings increase the probability of contacts occurring between a greater number of individuals, potentially increasing the rate of disease transmission.

However, as ARs of the study dogs were generally confined to the community boundaries, this would likely limit disease transmission to the community confines in the first instance. One dog did however, undertake a long distance foray towards the local rubbish tip. Interestingly, this dog was frequently observed within the town boundaries with its litter mate (#10) during transect walks, but the latter dog did not undertake a similar foray while collared. This was reflected in the high number of contacts between the pair but varying ARs and daily accumulated distances travelled even with the foray excluded (Table 1); with Dog 11 travelling further each day and over a larger area, suggesting the tendency of this dog to roam widely.

In a global context, Vaniscotte et al. [12] estimated similar ARs to our study for free-roaming domestic dogs in Tibet (range 32.5–174.5 ha, $N=78$), while other studies have estimated much smaller home ranges, ranging from 2 to 10 ha for free-roaming domestic dogs in Australia, Indonesia and the USA [22, 35–38]. Meek [19] estimated much larger home ranges for free-roaming dogs from an Australian Indigenous community in coastal south-east New South Wales (range: 140–2 450 ha, $N=10$). Those dogs conducted regular forays into the surrounding bush and hence resemble the Tiwi Island Dog 11 estimate when including its foray (AR=2 293). The differences in ARs, home ranges and the propensity to undertake forays between studies may relate to methodological differences (e.g. duration of the monitoring period) and the size of the communities where studies were conducted. Resource availability; including food, shelter, companionship and barriers (natural or manmade) may have also affected effective ARs. Dogs living in resource rich areas tend to have smaller home ranges compared with resource poor areas, which reduce the need for the animal to travel greater distances to meet its biological and social requirements [2, 3, 8, 19].

Some of the variability within the dog population was evidently related to sex and reproductive status. Collectively, male dogs travelled further each day and over a larger area than females. These findings are in agreement with Thomson [11] and Vaniscotte et al. [12], but in contrast to Van Kesteren et al. [13] and Dürr and Ward [22], where no difference between male and female AR or distance traveled per day was found. At any rate, the larger area covered by males in the present study may increase their potential to spread diseases further through the community than females. For diseases that require physical contact (e.g. rabies, ringworm); contact between susceptible individuals would have greater significance for disease transmission. In the case of Tiwi Islands, an average of 5.24 contacts per collared dog per day was recorded and if extrapolated to the entire dog population, a contact rate of 101 per dog per day would be expected.

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We wish to thank the people of the Wurrumiyanga Community for participating in the study and staff and volunteers from Animal Management in Rural and Remote Indigenous Communities (AMRRIC) for their assistance throughout the project. Discussions with Michael Ward, Helen Scott-Orr, and Salome Dürr of University of Sydney Veterinary School, and Julia Hardaker and Jan Allen of AMRRIC assisted the project.

Author Contributions

Conceived and designed the experiments: JS GK GB. Performed the experiments: JS. Analyzed the data: JS GK PJSF. Contributed reagents/materials/analysis tools: GK. Wrote the paper: JS GK GB PJSF WYB. Designed the software used in analysis: GK.

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Appendix 4-2: Map of Dog 4’s movements, Bathurst Island, Northern Territory

Plate 1: Neutered male community dog with GPS collar (Dog 10), Bathurst Island, Northern Territory

Plate 2: Two GPS collared (Dogs 2 and 3) community dogs that were observed while undertaking a transect walk, Bathurst Island, Northern Territory

STATEMENT OF ORIGINALITY

We, the PhD candidate and the candidate's Principal Supervisor, certify that the following text, figures and diagrams are the candidate's original work.

Type of work	Page number/s
Journal article and all encompassing information	96-125

Name of Candidate: Jessica Sparkes

Name/title of Principal Supervisor: Dr Wendy Brown

[redacted]

12 December 2015

Candidate

Date

[redacted]

12 December 2015

Principal Supervisor

Date

STATEMENT OF AUTHORS' CONTRIBUTION

We, the PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

	Author's Name	% of contribution
Candidate	Jessica Sparkes	Conception and design (60%) Data collection (100%) Analyses (70%) Manuscript development (70%)
Other Authors	Gerhard Körtner	Conception and design (20%) Analyses (20%) Manuscript development (10%)
	Guy Ballard	Conception and design (10%) Analyses (5%) Manuscript development (7%)
	Peter JS Fleming	Conception and design (10%) Analyses (5%) Manuscript development (6%)
	Wendy Y Brown	Manuscript development (7%)

Name of Candidate: Jessica Sparkes

Name/title of Principal Supervisor: Dr Wendy Brown

[redacted]

12 December 2015

Candidate Date

[redacted]

12 December 2015

Principal Supervisor Date

5 Role of the working dog in disease spread

Globally, domestic dogs have been used for centuries to assist in hunting for game, in the herding and protection of livestock and to pull sleds. In Australia, dogs are still commonly used to hunt introduced pests and game animals and can be particularly useful for improving the success of hunting expeditions.

Despite the benefits of hunting with dogs, domestic dogs can also pose a risk to human and wildlife health through the transfer of zoonotic diseases, including rabies. Despite the associated risks to human and animal health, little research focusing on cooperative hunting with dogs has been undertaken in Australia. To address this knowledge gap, and provide additional parameters for rabies epidemiological modelling in Australia, the frequency and geographic distribution of hunting with domestic dogs in Australia was quantified using an online questionnaire. In addition, interactions between hunting parties and non-target wildlife that could contribute to the spread of rabies were documented.

Quantifying interactions between hunting dogs and wildlife will facilitate the development of risk profiles for disease transfer between wildlife, hunting dogs and humans. Armed with this information, we will be better prepared to deal with a rabies outbreak.

5.1 Cooperative hunting between humans and domestic dogs in eastern and northern Australia

This Chapter has been written in the format of a scientific paper and has been published in Wildlife Research (Appendix 5-1) with the following citation:

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

5.1.1 Abstract

Context: Dogs aid hunters in many parts of Australia. Because of close proximity, transfer of zoonotic disease between hunters, hunting dogs and wildlife can, and does, occur. Knowledge about cooperative hunting between humans and domestic dogs and interactions with wildlife in Australia is limited, but is necessary to improve zoonotic-risk mitigation strategies.

Aims: We aimed to describe the frequency and geographic distribution of hunting with dogs, and to document interactions between them and wildlife that could contribute to zoonosis transmission.

Methods: Australian hunters were invited via web-based hunting forums, hunting supply stores and government agency communications to complete an online questionnaire about their hunting activities.

Key results: Most of the 440 responding hunters resided on Australia's eastern coast. Pest animal management and recreation were their primary drivers for hunting with dogs. Most hunters used one or two dogs, and travelled ≥500 km to target feral pigs, rabbits, birds and deer. Almost a quarter of respondents (N=313) had lost a dog while hunting, but most (93%, N=61) were reportedly recovered within a few hours. Half the respondents indicated that they had encountered wild dogs while hunting, and reported a range of consequences from non-contact interactions through to attacks on the hunting dog or hunter.

Conclusions: Australian hunters frequently used dogs to assist in hunts of birds and introduced mammals, particularly where access was difficult because of rough terrain or thick vegetation. Interactions between hunters and non-target animals such as wild dogs were common, providing potential pathways for the spread of diseases. Furthermore, hunting expeditions >500 km from the point of residence occurred regularly, which could facilitate translocation of important zoonotic diseases between states and the creation of disparate foci of disease spread, even into highly populated areas.

Implications: Our improved understanding of hunting-dog use in Australia is essential to quantify the risk of disease transmission between wildlife and humans, identify transmission pathways and devise management plans to quash disease outbreaks. To promote rapid detection of exotic diseases, hunters should be encouraged to report unusual wildlife behaviour and interactions with their dogs.

Keywords

Contact, disease transmission, survey, wild dogs, wildlife, zoonosis

5.1.2 Introduction

Cooperative hunting between humans and dogs is a diverse activity that is conducted in many parts of the world for recreation and pest control, to facilitate the harvest of difficult prey and to assist in wildlife population management (White *et al.* 2003, Fiorello *et al.* 2006, Koster 2009, Godwin *et al.* 2013). Hunters often use purpose-bred dogs, including hounds, retrievers, pointers and gundogs, depending on the target species (White *et al.* 2003, Mecozzi & Guthery 2008). Dogs are particularly useful where other methods of hunting or pest control are ineffective because of rough or steep terrain and thick vegetative cover (e.g. Mowbray 2002, Parkes *et al.* 2002) and, generally assist by detecting, flushing, bailing, lugging and/or retrieving prey, to increase the probability of success (Godwin *et al.* 2013, Koster & Noss 2014). To minimise the risk of losing dogs, GPS-tracking collars are frequently used on hunts, particularly where dogs move out of sight of their owner.

Beyond their role in recreational hunting and hunting for food, cooperative hunting between humans and dogs is used when other forms of pest control are, or have become, ineffective (McIlroy & Saillard 1989, Caley & Ottley 1995). For example, hunting dogs have been integrated with other control techniques, such as trapping, aerial shooting and baiting, to successfully eradicate island populations of feral pigs (*Sus scrofa*; Parkes *et al.* 2010), goats (*Capra hircus*; Campbell *et al.* 2004), feral cats (*Felis catus*; Griffiths *et al.* 2015) and brushtail possums (*Trichosurus vulpecula*; Cowan 1992).

Despite the benefits of hunting with dogs, domestic dogs can also pose a risk to human and wildlife health through the transfer of zoonotic diseases (Vanak *et al.* 2007, Hughes & Macdonald 2013). Domestic dogs have been implicated in the transmission of diseases such as rabies (causative agent rabies virus, which is a *Lyssavirus*), canine distemper (which is caused by a *Morbillivirus*) and canine parvovirus disease, as well as parasites including *Neospora caninum* to carnivores such as wolves (*Canis lupus* and *Chrysocyon brachyurus*), foxes (*Cerdocyon thous* and *Pseudalopex gymnocercus*) and African wild dogs (*Lycaon pictus*) (Noss *et al.* 2003, Fiorello *et al.* 2006, Whiteman *et al.* 2008, Orozco *et al.* 2014). Because of the close proximity between humans, hunting dogs and feral pigs, hunters and dogs are particularly vulnerable to contracting brucellosis (causative agent *Brucella* spp., Zheludkov & Tsirelson 2010, Massey *et al.* 2011, Ridoutt *et al.* 2014). Although hunters have been surveyed to obtain serological samples for zoonoses testing in eastern Australia (Mason & Fleming 1999b), we do not currently understand the extent of contact between their hunting dogs and wildlife.

Non-target wildlife species such as wild dogs (including dingoes and other wild dogs (*Canis familaris*) and their cross-breeds) also have substantial zoonotic-disease transmission potential because they occur in almost all localities on mainland Australia (Fleming *et al.* 2014) and harbour many transmissible pathogens and parasites such as *Echinococcus granulosus* (hydatid disease), sarcoptic mange (*Sarcoptes scabiei*) and hookworms (*Ancylostoma caninum*) (Murray & Penridge 1992, Fleming *et al.* 2001). Anecdotal reports suggest that interactions between wild dogs and hunting parties occur in Australia (hunting and other online forums, http://bushwalk.com/forum/viewtopic.php?f=5&t=9224&start=90, February 2012), which could exacerbate the transmission of these diseases over greater distances, via human-mediated hunting movements (Choquenot *et al.* 1996).

Research has focused on general hunter activities and their contribution to the Australian economy and disease surveillance (Tisdell 1982, Hone & Pech 1990, Mason & Fleming 1998, Mason & Fleming 1999a). Despite the risks to human and animal health, little research focusing on cooperative hunting with dogs has been undertaken in Australia. Quantifying interactions between hunting dogs and wildlife will enable us to develop risk profiles for disease transfer between wildlife, dogs and humans. Armed with this information, we will be better able to deal with disease outbreaks in the future (Sparkes *et al.* 2015).

Here, we describe and quantify the use of hunting dogs by Australian hunters and their interactions with wild dogs on hunting trips, and assess the potential for zoonotic disease transmission.

5.1.3 Materials and methods

A self-administered questionnaire was developed to collect information from hunters about their experiences of cooperative hunting with dogs. We required a minimum of 384 responses to achieve a sampling error of ±5% at the 95% confidence level (Dillman 2000).

Participants were asked to complete eight multiple-choice, six short-answer and four open questions about aspects of cooperative hunting with domestic dogs (see Appendices 5-2 and 5-3).

The survey instrument was distributed via the SurveyMonkey website from September 2013 until January 2014. Following the findings of Finch *et al.* (2014) regarding substantial mistrust of the Government among Australian hunters, respondents could remain anonymous. Participation was invited via hunting forums, hunting shops and some State Government websites.

Responses to the questionnaire were tabulated in Excel. Descriptive statistics are presented for responses to each survey question (±SD where applicable). A two-sample test for equality of proportions was conducted in R (R Core Team 2013) to test for a relationship between the use of tracking collars and loss of hunting dogs. Both dogs lost and recovered, and lost without recovery were included within the analyses. Responses were removed where a clear link between use (or lack of use) of tracking collars and losing a dog could not be established. An ordered logistic regression to determine whether use of tracking collars affected time to dog recovery was also undertaken in R. Only dogs that were recovered after a period of time were included in the analyses. A P-value of <0.05 was considered significant for all analyses.

5.1.4 Results

We received 440 responses, with most (90%) returned within the first 60 days. On average, it took respondents 10.8 min (±9.8 min) to complete the survey. Although not all respondents answered every question, most did (79%, n=349). A small number of respondents (n=5) provided answers that indicated that they had clearly not participated in good faith. Consequently, they were removed from the dataset.

A majority of respondents lived and hunted in south-eastern Australia (Figure 5-1). Three respondents said they hunted in Tasmania. Maximum distance travelled to hunt varied from hunting on the respondents' property, up to 500 km or more on a hunting trip (Figure 5-2). Most respondents said they hunted on a weekly (53.1%) or monthly (40.4%) basis (N=340).

In total, 23% of respondents used guns and dogs, 17% hunted with dogs for pest-animal management and 13% used dogs only to track prey (N=248; Table 5-1). Hunting pigs with dogs was most common (52% of respondents), followed by birds (30%), deer (14%) and rabbits (14%; Table 5-1). Most hunters used only one or two dogs when hunting (25%, 40%, respectively; N=325) but some hunted with four or more dogs (11%).

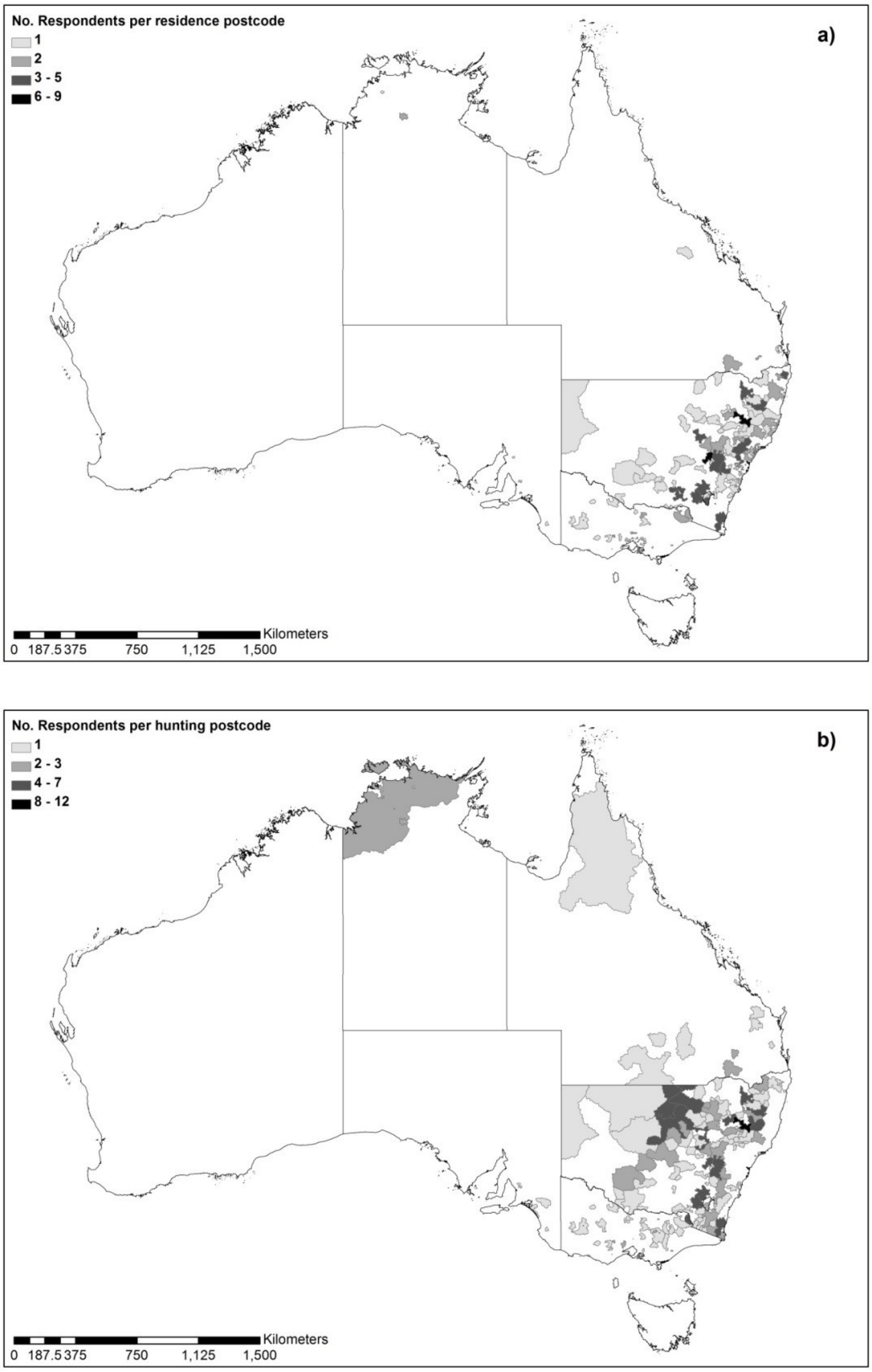

Figure 5-1 (a) Residence of respondents and (b) their hunting regions on the basis of postcode

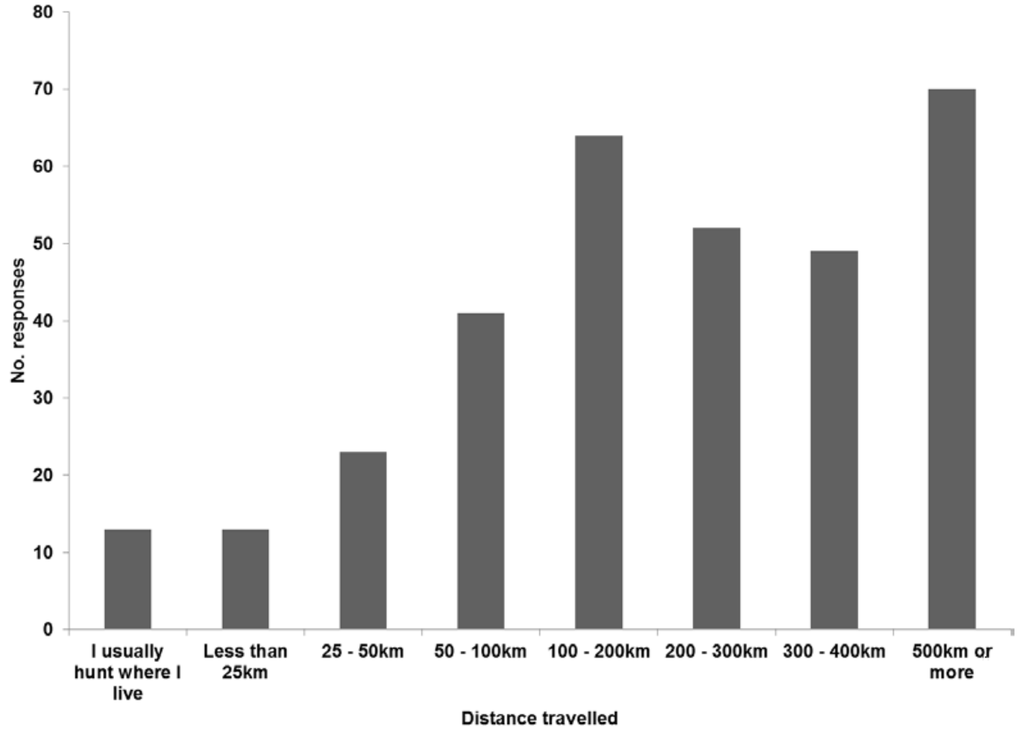

Figure 5-2 The maximum distance travelled by hunters to their hunting locations (N=325)

More than a fifth (22%) of respondents indicated that they had lost a dog while hunting (N=313); however, of those, 93% had recovered the animal. Of those found, most hunting dogs (62%) were recovered within 5h (N=61; Figure 5-3). Two thirds (67%) of respondents used GPS-tracking collars on their dogs (N=341). Many of these respondents said the use of tracking collars was essential in reducing the possibility of losing dogs when hunting. However, use of GPS-tracking collars was not associated with a decreased risk of losing dogs (χ^2 1.84, d.f.=1, P=0.17), nor did they have an impact on time to recovery (t=0.798, d.f.=56, P=0.43).

Table 5-1 Type of hunting undertaken with dogs and animals targeted^

Type of hunting	**% of respondents**
Firearms	23.4
Pest animal control	16.9
Tracking	13.3
Pointing	7.7
Retrieval	3.2
Recreation/competition	2.4
Animal targeted	
Pig	52.4
Bird	30.2
Deer	13.7
Rabbit	13.7
Fox	12.5
Goat	3.2
Cat	2.8
Small game	1.2
Waterfowl	1.2
Buffalo	0.8

^ Some respondents listed multiple hunting types and/or target animals, so percentages do not add up to 100

While hunting, 50% of respondents said that they had encountered wild dogs or dingoes (N=320). Details of these encounters suggested that the most common interaction involved one to four wild dogs (72%). Approximately half of the respondents (51%) said that they only heard or saw the wild dogs; 47% said they had shot one (N=158). In total, 5% of respondents had observed indirect aggression between their hunting dogs and the wild dogs (e.g. growling, chasing) with no direct contact, but 17% said wild dogs had attacked their hunting dogs. In total, 4% of hunters said they had been directly attacked by wild dogs. Some respondents listed multiple types of contact, so percentages did not add up to 100.

Whereas most respondents said that their dogs had never fought with another domestic dog while hunting, 8% reported that they had (N=318).

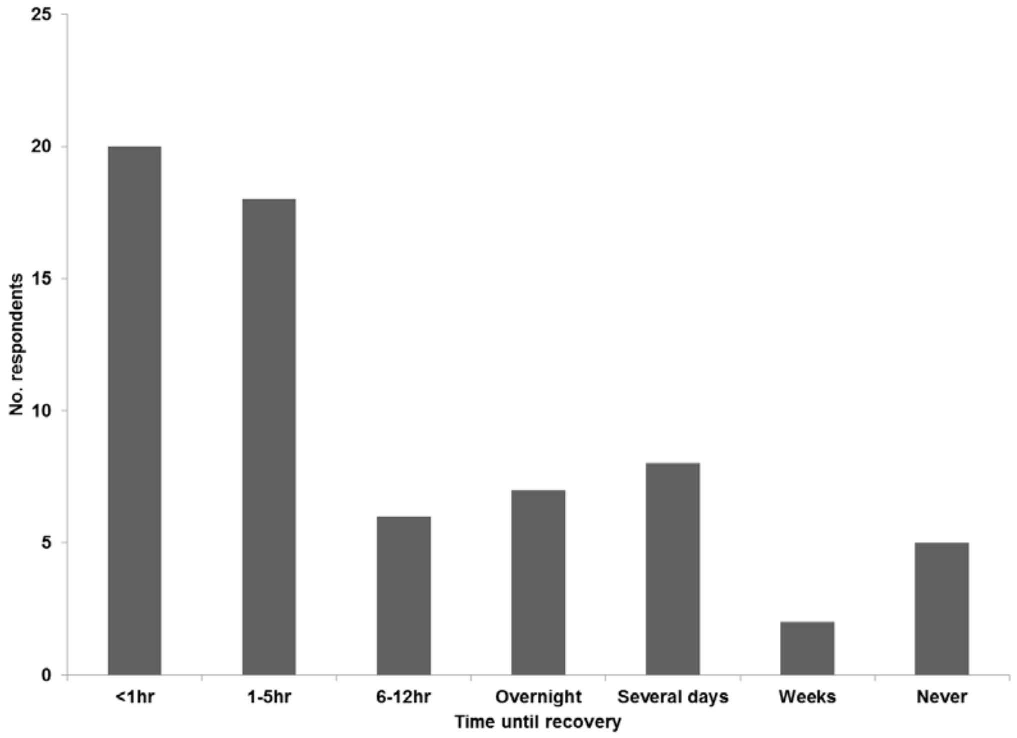

Figure 5-3 Time taken by hunters to recover hunting dogs after losing them (N=66)

5.1.5 Discussion

We found that hunting with dogs was an important pastime for many Australian hunters. Similar to previous international investigations, population management or pest-animal control, recreation and disease mitigation were cited as primary drivers of hunting with dogs (Milbourne 2003, Mecozzi & Guthery 2008, Brøseth & Pedersen 2010, Godwin *et al.* 2013). Although use of hunting dogs can improve take rates (Koster 2009), they can also create a link between wildlife and humans for the transmission of diseases. Minimising interaction time between susceptible hosts is vital in preventing the spread of important zoonotic diseases.

Humans undertaking cooperative hunting with dogs in eastern and northern Australia commonly used one or two dogs to hunt invasive or game species, which easily complies with relevant legal requirements (Game Management Authority 2014, www.dpi.nsw.gov.au/hunting/regulations#Hunting-with-dogs). The relatively small number of dogs reportedly used was comparable to that in other parts of the world where hunters pursue similar game species (e.g. Fiorello *et al.* 2006, Mecozzi & Guthery 2008, Scillitani *et al.* 2010). Although a smaller number of dogs may reduce the probability of disease transmission between dogs and between dogs and wildlife by minimising possible pairwise contacts, some hunting styles, such as pig hunting and chasing prey from dens, still result in physical contact between dogs and prey and, on occasion, non-target animals.

Furthermore, hunting dogs can operate unsupervised and out of sight for extended periods during the hunt and/or are lost either temporarily or permanently. Tracking collars are supposed to address the latter issue and are commonly employed throughout industrialised countries (Virginia Department of Game and Inland Fisheries 2008, Godwin *et al.* 2013), particularly since affordability has increased. Indeed, many respondents noted that the use of collars was essential for every hunting trip; however, the lack of a significant relationship between collar use and the likelihood of losing dogs, and the duration of time dogs spent lost, raises questions about the benefits of the technology. Many respondents noted failure of GPS units and/or receivers as the cause of losing dogs (e.g. thick scrub interfered with signal, dog moved out of range of receiver); however, it is also possible that hunters, feeling more confident about finding their collared animal, took more risks, letting their animals roam farther than they otherwise might with uncollared dogs. Further investigation seems warranted, given the requirement for tracking collar use in some jurisdictions (www.dpi.nsw.gov.au/hunting/regulations#Hunting-with-dogs).

Controlling and monitoring dogs during a hunt is of course not the only issue in preventing disease transmission. Hunting wildlife inevitably leads to close or physical contact between humans, hunting dogs and prey as well as non-target animals; these contacts entail the risk of disease transfer (Krebs *et al.* 1994, Fiorello *et al.* 2006). Of potential relevance to both dingo conservation, hunting-dog welfare and disease transmission, wild dogs were reportedly encountered frequently during hunting trips with hunting dogs. However, many zoonoses and parasites do not require direct contact between dogs and wildlife. Mere overlap in range can be sufficient for transmission and disease persistence (e.g. Woodroffe & Donnelly 2011, Jennett *et al.* 2013, Chen *et al.* 2014).

Although not currently in Australia, canine rabies is a disease worthy of further investigation, because it could result in significant human and animal casualties (both domestic and wildlife) and economic consequences for Australian communities (Sparkes *et al.* 2014a). Rabies has previously been thought to have moved from wild to domestic canids (i.e. from coyotes (*Canis latrans*) to hunting dogs) in Alabama, USA (Krebs *et al.* 1994). Consequently, in the USA and many European countries where rabies is endemic, the vaccination of hunting dogs and dogs entering the country has been compulsory for some time (e.g. Reinius 1988, South Carolina Legislative Services Agency 2002). That half of our respondents noted encounters with wild dogs, including dingoes, during hunting expeditions reinforces the potential for transfer of disease between hunting dogs and wild canids in the Australian context.

In Australia, swine brucellosis, caused by *Brucella suis*, is enzootic in feral pigs in Queensland and of significant public health concern, particularly for those involved in the handling and processing of infected animals (Mason & Fleming 1999ab, Massey *et al.* 2011). Recently, the disease has spread to northern New South Wales where cooperative hunting for feral pigs has been suspected as a possible reason for the transmission of swine brucellosis to hunting dogs (Ridoutt *et al.* 2014).

Importantly, although hunters pose a risk by linking susceptible populations (i.e. humans, hunting dogs and wildlife), particularly with large-scale movements (some over 500 km), they also pose an opportunity for detecting and reporting zoonotic disease. In northern Australia, where rabies is most likely to enter, or eastern Australia, where it will conceivably spread rapidly (Sparkes *et al.* 2015), hunters could be used as reporting agents for unusual animal behaviour or encouraged and trained to safely collect samples from suspect animals (McIlroy & Saillard 1989, Hone & Pech 1990, Mason & Fleming 1999a, Sparkes *et al.* 2015). Compulsory vaccination of hunting dogs, as enforced overseas, combined with movement restrictions, may be required to mitigate the probability of disease spread in the advent of an exotic disease outbreak.

Cooperative hunting between dogs and humans is a popular activity for many Australians. Hunting trips in excess of 500 km, where hunters take one or two purpose-bred dogs, are common. Frequent interactions with target species and non-target animals, including wild dogs, may pose challenges for minimising the spread of diseases, such as endemic brucellosis and exotic rabies. However, because of the remote locations traversed, hunters may be a valuable resource for identifying initial exotic disease outbreaks and should be encouraged to report unusual wildlife behaviour to promote rapid detection of diseases.

5.1.6 Acknowledgements

We thank proprietors of hunting shops who served as distribution points, and all survey respondents for taking the time to provide invaluable insights into the activities surrounding hunting with dogs in Australia. Gerhard Körtner and Wendy Brown made valuable comments on the draft of this paper. Remy van de Ven provided statistical support. Jessica Sparkes is an Australian Postgraduate Award scholar recipient.

Appendix 5-1: Hunting with dogs publication

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

CSIRO PUBLISHING
Wildlife Research, 2016, **43**, 20 26
http://dx.doi.org/10.1071/WR15028

Cooperative hunting between humans and domestic dogs in eastern and northern Australia

Jessica Sparkes[A,B,C,E], *Guy Ballard*[A,C,D] *and Peter J. S. Fleming*[A,B,C]

[A]School of Environmental and Rural Sciences, PO Box U86, University of New England, Armidale, NSW 2351, Australia.
[B]Vertebrate Pest Research Unit, Biosecurity NSW, Orange, NSW 2800, Australia.
[C]Invasive Animals Cooperative Research Centre, Armidale, NSW 2350, Australia.
[D]Vertebrate Pest Research Unit, Biosecurity NSW, Armidale, NSW 2350, Australia.
[E]Corresponding author. Email: Jessica.sparkes@dpi.nsw.gov.au

Abstract

Context. Dogs aid hunters in many parts of Australia. Because of close proximity, transfer of zoonotic disease between hunters, hunting dogs and wildlife can, and does, occur. Knowledge about cooperative hunting between humans and domestic dogs and interactions with wildlife in Australia is limited, but is necessary to improve zoonotic risk mitigation strategies.

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Methods. Australian hunters were invited via web based hunting forums, hunting supply stores and government agency communications to complete an online questionnaire about their hunting activities.

Key results. Most of the 440 responding hunters resided on Australia's eastern coast. Pest animal management and recreation were their primary drivers for hunting with dogs. Most hunters used one or two dogs, and travelled $\geq$500 km to target feral pigs, rabbits, birds and deer. Almost a quarter of respondents ($N = 313$) had lost a dog while hunting, but most (93%, $N = 61$) were reportedly recovered within a few hours. Half the respondents indicated that they had encountered wild dogs while hunting, and reported a range of consequences from non contact interactions through to attacks on the hunting dog or hunter.

Conclusions. Australian hunters frequently used dogs to assist in hunts of birds and introduced mammals, particularly where access was difficult because of rough terrain or thick vegetation. Interactions between hunters and non target animals such as wild dogs were common, providing potential pathways for the spread of diseases. Furthermore, hunting expeditions >500 km from the point of residence occurred regularly, which could facilitate translocation of important zoonotic diseases between states and the creation of disparate foci of disease spread, even into highly populated areas.

Implications. Our improved understanding of hunting dog use in Australia is essential to quantify the risk of disease transmission between wildlife and humans, identify transmission pathways and devise management plans to quash disease outbreaks. To promote rapid detection of exotic diseases, hunters should be encouraged to report unusual wildlife behaviour and interactions with their dogs.

Additional keywords: contact, disease transmission, survey, wild dogs, wildlife, zoonosis.

Received 5 February 2015, accepted 12 December 2015, published online 30 March 2016

Introduction

Cooperative hunting between humans and dogs is a diverse activity that is conducted in many parts of the world for recreation and pest control, to facilitate the harvest of difficult prey and to assist in wildlife population management (White *et al*. 2003; Fiorello *et al*. 2006; Koster 2009; Godwin *et al*. 2013). Hunters often use purpose bred dogs, including hounds, retrievers, pointers and gundogs, depending on the target species (White *et al*. 2003; Mecozzi and Guthery 2008). Dogs are particularly useful where other methods of hunting or pest control are ineffective because of rough or steep terrain and thick vegetative cover (e.g. Mowbray 2002; Parkes *et al*. 2002) and, generally, assist by detecting, flushing, bailing, lugging and/or retrieving prey, to increase the probability of success (Godwin *et al*. 2013; Koster and Noss 2014). To minimise the risk of losing dogs, GPS tracking collars are frequently used on hunts, particularly where dogs move out of sight of their owner.

Beyond their role in recreational hunting and hunting for food, cooperative hunting between humans and dogs is used when other forms of pest control are, or have become, ineffective (Mcilroy and Saillard 1989; Caley and Ottley 1995). For example, hunting dogs have been integrated with other control techniques, such as trapping, aerial shooting and baiting, to successfully eradicate island populations of feral pigs (*Sus scrofa*; Parkes *et al*. 2010), goats (*Capra hircus*; Campbell *et al*. 2004), feral cats (*Felis catus*; Griffiths *et al*. 2015) and brushtail possums (*Trichosurus vulpecula*; Cowan 1992).

Despite the benefits of hunting with dogs, domestic dogs can also pose a risk to human and wildlife health through the transfer of zoonotic diseases (Vanak *et al*. 2007; Hughes and Macdonald 2013). Domestic dogs have been implicated in the transmission of diseases such as rabies (causative agent rabies virus, which is a *Lyssavirus*), canine distemper (which is caused by a *Morbillivirus*) and canine parvovirus disease, as well as parasites including *Neospora caninum* to carnivores such as wolves (*Canis lupus* and *Chrysocyon brachyurus*), foxes (*Cerdocyon thous* and *Pseudalopex gymnocercus*) and African wild dogs (*Lycaon pictus*) (Noss *et al*. 2003; Fiorello *et al*. 2006; Whiteman *et al*. 2008; Orozco *et al*. 2014). Because of the close proximity between humans, hunting dogs and feral pigs, hunters and dogs are particularly vulnerable to contracting brucellosis (causative agent *Brucella* spp., Zheludkov and Tsirelson 2010; Massey *et al*. 2011; Ridoutt *et al*. 2014). Although hunters have been surveyed to obtain serological samples for zoonoses testing in eastern Australia (Mason and Fleming 1999*b*), we do not currently understand the extent of contact between their hunting dogs and wildlife.

Non target wildlife species such as wild dogs (including dingoes and other wild dogs (*Canis familaris*) and their cross breeds) also have substantial zoonotic disease transmission potential because they occur in almost all localities on mainland Australia (Fleming *et al*. 2014) and harbour many transmissible pathogens and parasites such as *Echinococcus granulosus* (hydatid disease), sarcoptic mange (*Sarcoptes scabiei*) and hookworms (*Ancylostoma caninum*) (Murray and Penridge 1992; Fleming *et al*. 2001). Anecdotal reports suggest that interactions between wild dogs and hunting parties occur in Australia (hunting and other online forums, http://bushwalk.com/forum/viewtopic.php?f=5&t=9224&start=90, February 2012), which could exacerbate the transmission of these diseases over greater distances, via human mediated hunting movements (Choquenot *et al*. 1996).

Research has focused on general hunter activities and their contribution to the Australian economy and disease surveillance (Tisdell 1982; Hone and Pech 1990; Mason and Fleming 1998; Mason and Fleming 1999*a*). Despite the risks to human and animal health, little research focusing on cooperative hunting with dogs has been undertaken in Australia. Quantifying interactions between hunting dogs and wildlife will enable us to develop risk profiles for disease transfer between wildlife, dogs and humans. Armed with this information, we will be better able to deal with disease outbreaks in the future (Sparkes *et al*. 2015).

Here, we describe and quantify the use of hunting dogs by Australian hunters and their interactions with wild dogs on hunting trips, and assess the potential for zoonotic disease transmission.

Materials and methods

A self administered questionnaire was developed to collect information from hunters about their experiences of cooperative hunting with dogs. We required a minimum of 384 responses to achieve a sampling error of ± 5% at the 95% confidence level (Dillman 2000).

Participants were asked to complete eight multiple choice, six short answer and four open questions about aspects of cooperative hunting with domestic dogs (see Supplementary material for this paper).

The survey instrument was distributed via the SurveyMonkey website from September 2013 until January 2014. Following the findings of Finch *et al*. (2014) regarding substantial mistrust of the Government among Australian hunters, respondents could remain anonymous. Participation was invited via hunting forums, hunting shops and some State Government websites.

Responses to the questionnaire were tabulated in Excel. Descriptive statistics are presented for responses to each survey question (± s.d., where applicable). A two sample test for equality of proportions was conducted in R (R Core Team 2013) to test for a relationship between the use of tracking collars and loss of hunting dogs. Both dogs lost and recovered, and lost without recovery were included within the analyses. Responses were removed where a clear link between use (or lack of use) of tracking collars and losing a dog could not be established. An ordered logistic regression to determine whether use of tracking collars affected time to dog recovery was also undertaken in R. Only dogs that were recovered after a period of time were included in the analyses. A P value of <0.05 was considered significant for all analyses.

Results

We received 440 responses, with most (90%) returned within the first 60 days. On average, it took respondents 10.8 min (± 9.8 min) to complete the survey. Although not all respondents answered every question, most did (79%, $n = 349$). A small number of respondents ($n = 5$) provided answers that indicated that they had clearly not participated in good faith. Consequently, they were removed from the dataset.

A majority of respondents lived and hunted in south eastern Australia (Fig. 1). Three respondents said they hunted in Tasmania. Maximum distance travelled to hunt varied from hunting on the respondents' property, up to 500 km or more on a hunting trip (Fig. 2). Most respondents said they hunted on a weekly (53.1%) or monthly (40.4%) basis ($N = 340$).

In total, 23% of respondents used guns and dogs, 17% hunted with dogs for pest animal management and 13% used dogs only to track prey ($N = 248$; Table 1). Hunting pigs with dogs was most common (52% of respondents), followed by birds (30%), deer (14%) and rabbits (14%; Table 1). Most hunters used only one or two dogs when hunting (25%, 40%, respectively; $N = 325$) but some hunted with four or more dogs (11%).

More than a fifth (22%) of respondents indicated that they had lost a dog while hunting ($N = 313$); however, of those, 93% had recovered the animal. Of those found, most hunting dogs (62%) were recovered within 5 h ($N = 61$; Fig. 3). Two thirds

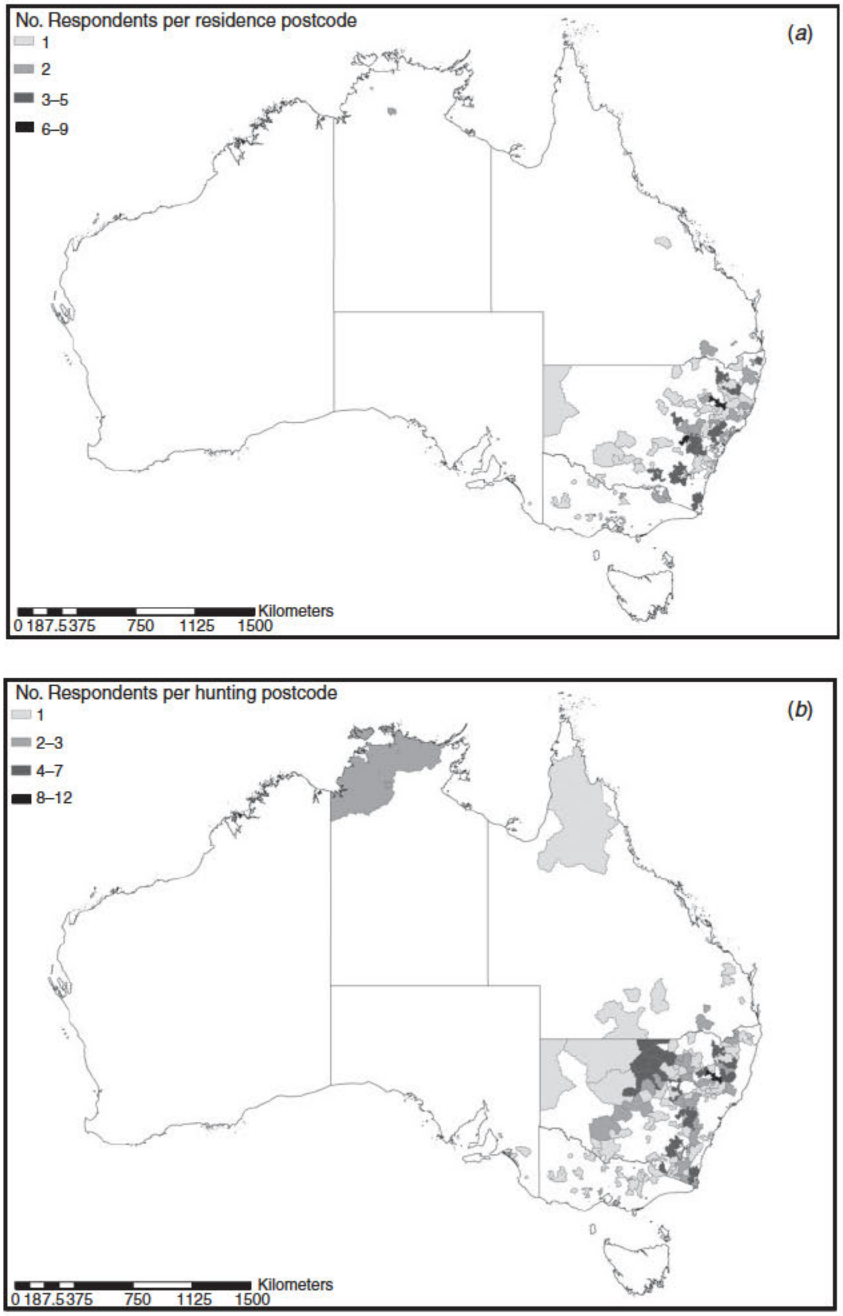

Fig. 1. (*a*) Residence of respondents and (*b*) their hunting regions on the basis of postcode.

(67%) of respondents used GPS tracking collars on their dogs ($N = 341$). Many of these respondents said the use of tracking collars was essential in reducing the possibility of losing dogs when hunting. However, use of GPS tracking collars was not associated with a decreased risk of losing dogs ($\chi^2 = 1.84$, d.f. = 1, $P = 0.17$), nor did they have an impact on time to recovery ($t = 0.798$, d.f. = 56, $P = 0.43$).

While hunting, 50% of respondents said that they had encountered wild dogs or dingoes ($N = 320$). Details of these encounters suggested that the most common interaction involved one to four wild dogs (72%). Approximately half of the respondents (51%) said that they only heard or saw the wild dogs; 47% said they had shot one ($N = 158$). In total, 5% of respondents had observed indirect aggression between their hunting dogs and the wild dogs (e.g. growling, chasing) with no direct contact, but 17% said wild dogs had attacked their hunting dogs. In total, 4% of hunters said they had been directly attacked by wild dogs. Some respondents listed multiple types of contact, so percentages did not add up to 100.

Whereas most respondents said that their dogs had never fought with another domestic dog while hunting, 8% reported that they had ($N = 318$).

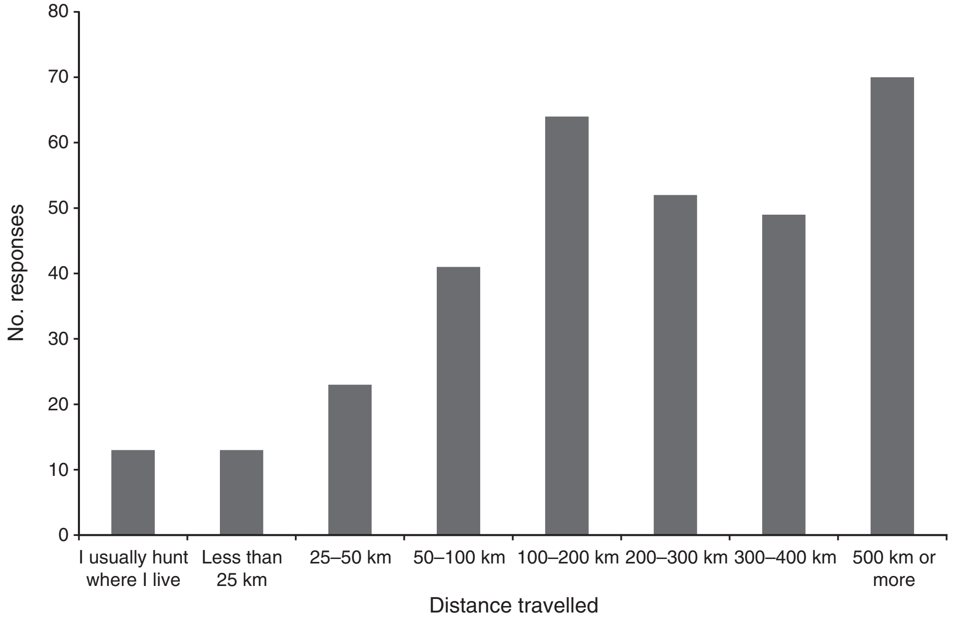

Fig. 2. The maximum distance travelled by hunters to their hunting locations (*N* 325).

Table 1. Type of hunting undertaken with dogs and animals targeted
Some respondents listed multiple hunting types and/or target animals, so percentages do not add up to 100

Parameter	% of respondents
Type of hunting	
Firearms	23.4
Pest animal control	16.9
Tracking	13.3
Pointing	7.7
Retrieval	3.2
Recreation or competition	2.4
Animal targeted	
Pig	52.4
Bird	30.2
Deer	13.7
Rabbit	13.7
Fox	12.5
Goat	3.2
Cat	2.8
Small game	1.2
Waterfowl	1.2
Buffalo	0.8

Discussion

We found that hunting with dogs was an important pastime for many Australian hunters. Similar to previous international investigations, population management or pest animal control, recreation and disease mitigation were cited as primary drivers of hunting with dogs (Milbourne 2003; Mecozzi and Guthery 2008; Brøseth and Pedersen 2010; Godwin *et al*. 2013). Although use of hunting dogs can improve take rates (Koster 2009), they can also create a link between wildlife and humans for the transmission of diseases. Minimising interaction time between susceptible hosts is vital in preventing the spread of important zoonotic diseases.

Humans undertaking cooperative hunting with dogs in eastern and northern Australia commonly used one or two dogs to hunt invasive or game species, which easily complies with relevant legal requirements (Game Management Authority 2014; www.dpi.nsw.gov.au/hunting/regulations#Hunting with dogs). The relatively small number of dogs reportedly used was comparable to that in other parts of the world where hunters pursue similar game species (e.g. Fiorello *et al*. 2006; Mecozzi and Guthery 2008; Scillitani *et al*. 2010). Although a smaller number of dogs may reduce the probability of disease transmission between dogs and between dogs and wildlife by minimising possible pairwise contacts, some hunting styles, such as pig hunting and chasing prey from dens, still result in physical contact between dogs and prey and, on occasion, non target animals.

Furthermore, hunting dogs can operate unsupervised and out of sight for extended periods during the hunt and/or are lost either temporarily or permanently. Tracking collars are supposed to address the latter issue and are commonly employed throughout industrialised countries (Virginia Department of Game and Inland Fisheries 2008; Godwin *et al*. 2013), particularly since affordability has increased. Indeed, many respondents noted that the use of collars was essential for every hunting trip; however, the lack of a significant relationship between collar use and the likelihood of losing dogs, and the duration of time dogs spent lost, raises questions about the benefits of the technology. Many respondents noted failure of GPS units and/or receivers as the cause of losing dogs (e.g. thick scrub interfered with signal, dog moved out of range of receiver); however, it is also possible that hunters, feeling more confident about finding their collared animal, took more risks, letting their animals roam farther than they otherwise might with uncollared dogs. Further investigation seems warranted,

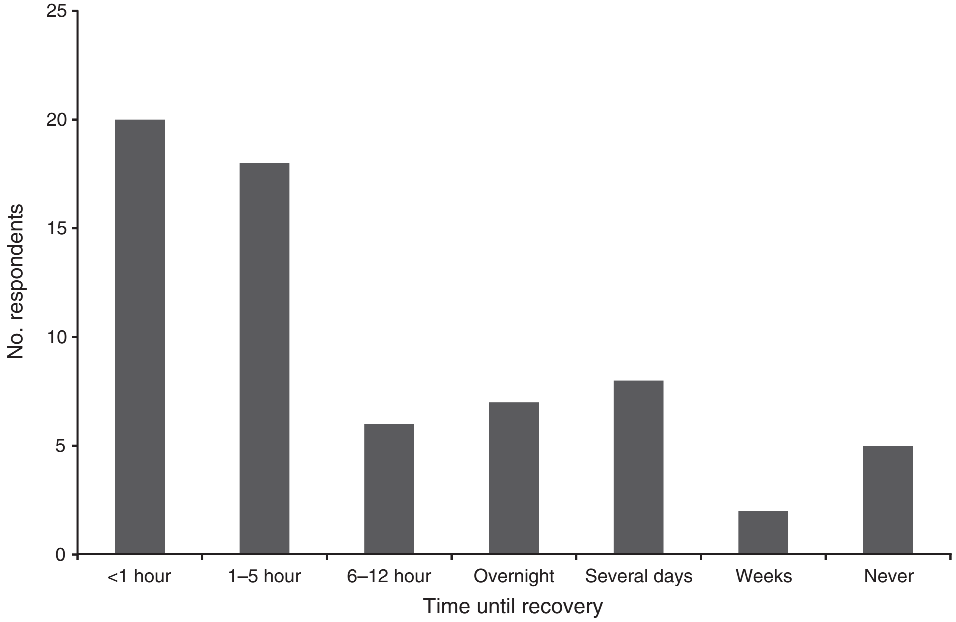

Fig. 3. Time taken by hunters to recover hunting dogs after losing them (N 66).

given the requirement for tracking collar use in some jurisdictions (www.dpi.nsw.gov.au/hunting/regulations#Hunting with dogs).

Controlling and monitoring dogs during a hunt is of course not the only issue in preventing disease transmission. Hunting wildlife inevitably leads to close or physical contact between humans, hunting dogs and prey as well as non target animals; these contacts entail the risk of disease transfer (Krebs *et al.* 1994; Fiorello *et al.* 2006). Of potential relevance to both dingo conservation, hunting dog welfare and disease transmission, wild dogs were reportedly encountered frequently during hunting trips with hunting dogs. However, many zoonoses and parasites do not require direct contact between dogs and wildlife. Mere overlap in range can be sufficient for transmission and disease persistence (e.g. Woodroffe and Donnelly 2011; Jennett *et al.* 2013; Chen *et al.* 2014).

Although not currently in Australia, canine rabies is a disease worthy of further investigation, because it could result in significant human and animal casualties (both domestic and wildlife) and economic consequences for Australian communities (Sparkes *et al.* 2014). Rabies has previously been thought to have moved from wild to domestic canids (i.e. from coyotes (*Canis latrans*) to hunting dogs) in Alabama, USA (Krebs *et al.* 1994). Consequently, in the USA and many European countries where rabies is endemic, the vaccination of hunting dogs and dogs entering the country has been compulsory for some time (e.g. Reinius 1988; South Carolina Legislative Services Agency 2002). That half of our respondents noted encounters with wild dogs, including dingoes, during hunting expeditions reinforces the potential for transfer of disease between hunting dogs and wild canids in the Australian context.

In Australia, swine brucellosis, caused by *Brucella suis*, is enzootic in feral pigs in Queensland and of significant public health concern, particularly for those involved in the handling and processing of infected animals (Mason and Fleming 1999*a*, 1999*b*; Massey *et al.* 2011). Recently, the disease has spread to northern New South Wales where cooperative hunting for feral pigs has been suspected as a possible reason for the transmission of swine brucellosis to hunting dogs (Ridoutt *et al.* 2014).

Importantly, although hunters pose a risk by linking susceptible populations (i.e. humans, hunting dogs and wildlife), particularly with large scale movements (some over 500 km), they also pose an opportunity for detecting and reporting zoonotic disease. In northern Australia, where rabies is most likely to enter, or eastern Australia, where it will conceivably spread rapidly (Sparkes *et al.* 2015), hunters could be used as reporting agents for unusual animal behaviour or encouraged and trained to safely collect samples from suspect animals (Mcilroy and Saillard 1989; Hone and Pech 1990; Mason and Fleming 1999*a*; Sparkes *et al.* 2015). Compulsory vaccination of hunting dogs, as enforced overseas, combined with movement restrictions, may be required to mitigate the probability of disease spread in the advent of an exotic disease outbreak.

Cooperative hunting between dogs and humans is a popular activity for many Australians. Hunting trips in excess of 500 km, where hunters take one or two purpose bred dogs, are common. Frequent interactions with target species and non target animals, including wild dogs, may pose challenges for minimising the spread of diseases, such as endemic brucellosis and exotic rabies. However, because of the remote locations traversed, hunters may be a valuable resource for identifying initial exotic disease outbreaks and should be encouraged to report unusual wildlife behaviour to promote rapid detection of diseases.

Acknowledgements

We thank proprietors of hunting shops who served as distribution points, and all survey respondents for taking the time to provide invaluable insights into the activities surrounding hunting with dogs in Australia. Gerhard Körtner and Wendy Brown made valuable comments on the draft of this paper. Remy van de Ven provided statistical support. Jessica Sparkes is an Australian Postgraduate Award scholar recipient.

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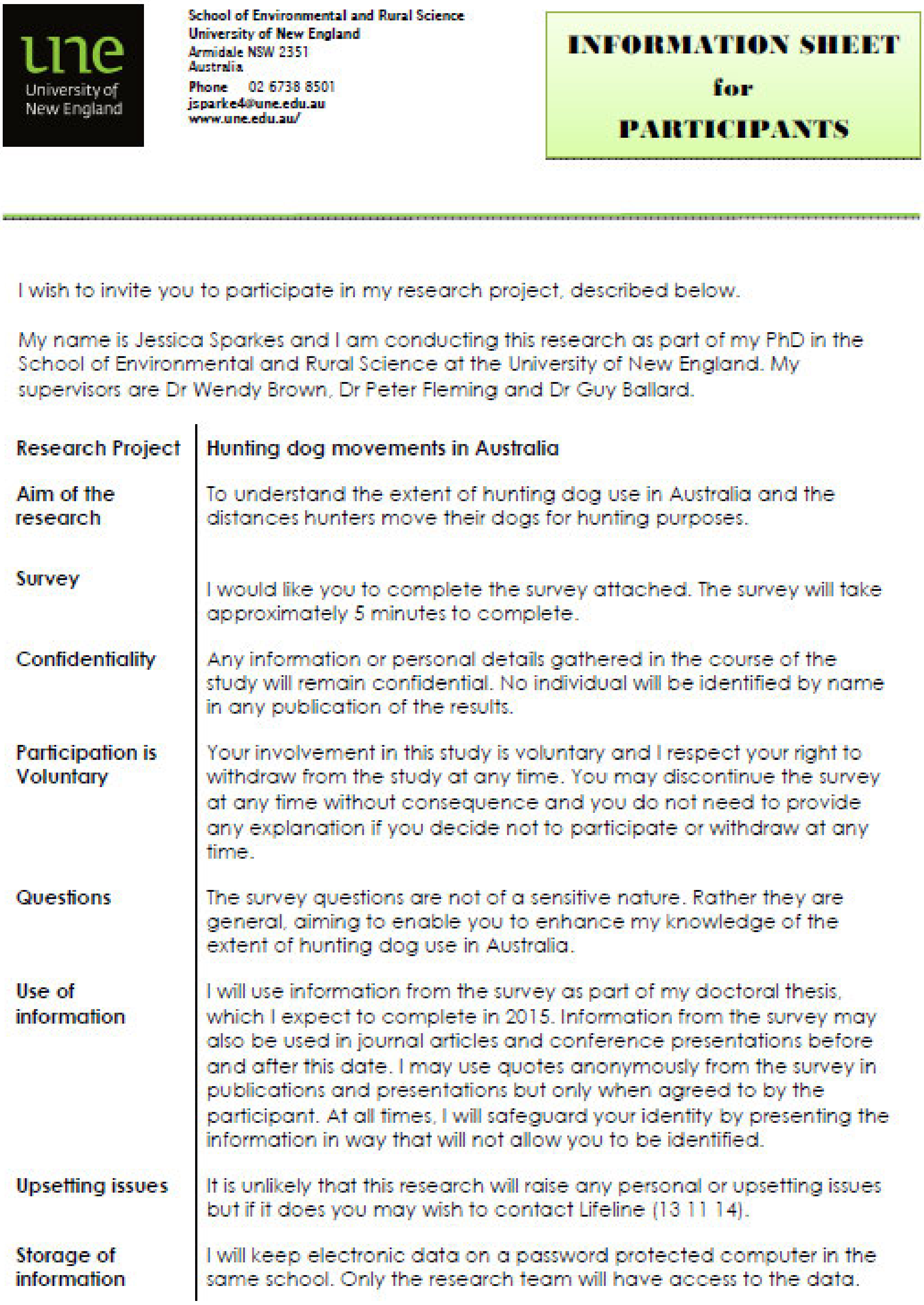
Appendix 5-2: Information sheet for participants



une
University of New England

School of Environmental and Rural Science
University of New England
Armidale NSW 2351
Australia
Phone 02 6738 8501
jsparke4@une.edu.au
www.une.edu.au/

INFORMATION SHEET for PARTICIPANTS

I wish to invite you to participate in my research project, described below.

My name is Jessica Sparkes and I am conducting this research as part of my PhD in the School of Environmental and Rural Science at the University of New England. My supervisors are Dr Wendy Brown, Dr Peter Fleming and Dr Guy Ballard.

Research Project	**Hunting dog movements in Australia**
Aim of the research	To understand the extent of hunting dog use in Australia and the distances hunters move their dogs for hunting purposes.
Survey	I would like you to complete the survey attached. The survey will take approximately 5 minutes to complete.
Confidentiality	Any information or personal details gathered in the course of the study will remain confidential. No individual will be identified by name in any publication of the results.
Participation is Voluntary	Your involvement in this study is voluntary and I respect your right to withdraw from the study at any time. You may discontinue the survey at any time without consequence and you do not need to provide any explanation if you decide not to participate or withdraw at any time.
Questions	The survey questions are not of a sensitive nature. Rather they are general, aiming to enable you to enhance my knowledge of the extent of hunting dog use in Australia.
Use of information	I will use information from the survey as part of my doctoral thesis, which I expect to complete in 2015. Information from the survey may also be used in journal articles and conference presentations before and after this date. I may use quotes anonymously from the survey in publications and presentations but only when agreed to by the participant. At all times, I will safeguard your identity by presenting the information in way that will not allow you to be identified.
Upsetting issues	It is unlikely that this research will raise any personal or upsetting issues but if it does you may wish to contact Lifeline (13 11 14).
Storage of information	I will keep electronic data on a password protected computer in the same school. Only the research team will have access to the data.

Disposal of information	All the data collected in this research will be kept for a minimum of five years after successful submission of my thesis.
Approval	This project has been approved by the Human Research Ethics Committee of the University of New England (Approval No HE13-146, Valid to 11/07/2014).
Contact details	Feel free to contact me with any questions about this research by email at jsparke4@une.edu.au or by phone on 02 6738 8501. You may also contact my supervisors. My Principal supervisors name is Dr Wendy Brown and she can be contacted at wbrown@une.edu.au or 02 6773 5125. My Co-supervisors names are Dr Peter Fleming and Dr Guy Ballard and they can be contacted at peter.fleming@dpi.nsw.gov.au or 02 6391 3806 or gballar3@une.edu.au or 02 6738 8511.
Complaints	Should you have any complaints concerning the manner in which this research is conducted, please contact the Research Ethics Officer at: Research Services University of New England Armidale, NSW 2351 Tel: (02) 6773 3449 Fax: (02) 6773 3543 Email: ethics@une.edu.au

Thank you for considering this request.

regards,

Jessica Sparkes

Appendix 5-3: Hunting with dogs questionnaire

Hunting with dogs

This survey is for people who hunt with dogs.
It will take no more than 5 minutes to complete.
All of the information you provide will be treated confidentially.

Q1: Do you give consent to be quoted anonymously in any publication or presentation as a result of this research?

No ☐ Yes ☐

Q2: What type/style of hunting do you participate in? ___________________

Q3: Do you use GPS collars to track your dogs, when hunting?

No ☐ Yes ☐

Q4: How many dogs do you usually hunt with?

a. 1 ☐
b. 2 ☐
c. 3 ☐
d. 4 or more ☐

Q5: How often do you hunt, with dogs?

a. Daily ☐
b. Weekly ☐
c. Monthly ☐
d. Less than once a year ☐
e. Once a year ☐

Q6: On average, how far from home do you travel to go hunting with dogs?

a. I usually hunt where I live ☐
b. Less than 25km ☐
c. 25 – 50km ☐
d. 50 – 100km ☐
e. 100 - 200km ☐
f. 200 – 300km ☐
g. 300 – 400km ☐
h. 500km or more ☐

Q7: What Postcode do you usually hunt in? _________

Q8: What town do you usually hunt in? _________________________

Q9: Have you ever encountered wild dogs / dingoes while hunting with your own dogs?

- a. No ☐
- b. Yes ☐
  - i. Number of wild dogs involved: ________________
  - ii. Extent of contact (e.g. shot/killed wild dog, hunting dog attacked, person attacked

Q10: Have your hunting dogs ever fought with other hunting dogs, while you were hunting?

- a. No ☐
- b. Yes ☐

Q11: Have you ever lost (couldn't find) one of your dogs while out hunting?

- a. No ☐
- b. Yes ☐
  - i. How did it happen?
  - ii. Did you recover the dog and after how long?

Q12: We'd appreciate it if you would let us know your postcode please:

____

Q13: We'd appreciate it if you would let us know the town you live in please:

____

Q14: Please write any additional comments you would like to make, about hunting with dogs, here:

Thank you very much for your time.

Your responses will help to improve our understanding of recreational hunting with dogs.

STATEMENT OF ORIGINALITY

We, the PhD candidate and the candidate's Principal Supervisor, certify that the following text, figures and diagrams are the candidate's original work.

Type of work	**Page number/s**
Journal article and all encompassing information	129-152

Name of Candidate: Jessica Sparkes

Name/title of Principal Supervisor: Dr Wendy Brown

[redacted] 12 December 2015

Candidate Date

[redacted] 12 December 2015

Principal Supervisor Date

STATEMENT OF AUTHORS' CONTRIBUTION

We, the PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

	Author's Name	**% of contribution**
Candidate	Jessica Sparkes	Conception and design (75%) Data collection (100%) Analyses (90%) Manuscript development (80%)
Other Authors	Guy Ballard	Conception and design (20%) Analyses (10%) Manuscript development (10%)
	Peter JS Fleming	Conception and design (5%) Manuscript development (10%)

Name of Candidate: Jessica Sparkes

Name/title of Principal Supervisor: Dr Wendy Brown

[redacted]

12 December 2015

Candidate Date

[redacted]

12 December 2015

Principal Supervisor Date

6 Interactions within and between wild and free-roaming domestic dog populations

Domestic dogs are prominent worldwide, often residing in close proximity to humans. As discussed in previous chapters, dogs (including dingoes, domestic dogs and their crossbreeds) can be found throughout the Australian landscape. Based primarily on their degree of association with humans, dogs can be broadly divided into three groups: wild, free-roaming domestic and restrained domestic dogs. All these dogs have the potential to transmit rabies to other domestic animals, humans and wildlife, but despite this, researchers have rarely sought to quantify their interactions. Consequently, the probability of disease transfer among dog groups and to people and livestock is poorly understood.

In this study, I used camera traps to quantify interactions within and between sympatric wild and domestic dog populations. As the largest numbers of Australian dogs (wild and domestic) reside along the eastern seaboard (West 2008, Australian Companion Animal Council 2010), camera monitoring stations were positioned on roads and tracks in north-east New South Wales. Images captured by the cameras were used to quantify temporal activity patterns and estimate abundance and contact rates for domestic and wild dogs. Implications of these results for rabies transmission are also discussed.

6.1 Contact rates of wild-living and domestic dog populations in Australia: a new approach

This Chapter has been written in the format of a scientific paper and has been submitted to Oecologia with the following authorship:

Jessica Sparkes[a,b,d,f], Guy Ballard[a,c,d], Peter J.S. Fleming[a,b,d], Remy van de Ven[e] and Gerhard Körtner[a,c,d]

[a] School of Environmental and Rural Science, University of New England, Armidale, NSW, 2351, Australia

[b] Vertebrate Pest Research Unit, Biosecurity NSW, Orange, NSW, 2800, Australia

[c] Vertebrate Pest Research Unit, Biosecurity NSW, Armidale, NSW, 2351, Australia

[d] Invasive Animals Cooperative Research Centre, Armidale, NSW, 2351, Australia

[e] Biometrics and Research Business Unit, NSW Department of Primary Industries, Orange, NSW, 2800, Australia

[f] Corresponding author:

Email: Jessica.sparkes@dpi.nsw.gov.au

Ph: +61 2 6391 3100

Fax: +61 2 6391 3972

Address: Locked Bag 6006, Orange, NSW, Australia, 2800

6.1.1 Abstract

Dogs (*Canis familiaris*) can transmit pathogens to other domestic animals, humans and wildlife. Both domestic and wild-living dogs are ubiquitous within mainland Australian landscapes, but their interactions are mostly unquantified. Consequently, the probability of pathogen transfer among wild-living and domestic dogs is unknown.

To address this knowledge deficit, we established 65 camera trap stations, deployed for 26,151 camera trap nights, to quantify domestic and wild-living dog activity during two years across eight sites in north-east New South Wales, Australia.

Wild-living dogs were detected on camera traps at all sites, and domestic dogs recorded at all but one. No contacts between domestic and wild-living dogs were recorded, and limited temporal overlap in activity was observed (32%); domestic dogs were predominantly active during the day and wild-living dogs mainly during the night.

Contact rates between wild-living and between domestic dogs respectively varied between sites and over time (range: 0.003–0.56 contacts per camera trap night). Contact amongst wild-living dogs occurred mainly within social groupings, and peaked when young were present. However, pup emergence occurred throughout the year within and between sites and consequently, no overall annual cycle in contact rates could be established.

Due to infrequent interactions between domestic and wild-living dogs, there are likely limited opportunities for pathogen transmission that require direct contact. In contrast, extensive spatial overlap of wild-living and domestic dogs could facilitate the spread of pathogens that do not require direct contact, some of which may be important zoonoses.

Keywords

Camera trap, dingo, disease, epidemiological modeling, interaction

6.1.2 Introduction

On the Australian mainland, dogs (*Canis familiaris*; which includes Australian dingoes and other wild-living dogs, domestic dogs and their hybrids) occur throughout the landscape. Based primarily on varying levels of association with humans and their ability to roam, Australia's dog population can be subdivided into three groups: wild (un-owned with limited- to no- interaction with humans and always free to roam), free-roaming domestic (owner but allowed to roam freely at some point) and restrained domestic (owned with their movement restricted) dogs (Dürr & Ward 2014, Gompper 2014, Sparkes *et al*. 2014b, Sparkes *et al*. 2015). All dogs, unless vaccinated, have the potential to transmit infectious pathogens to other domestic animals, humans and wildlife (Fleming *et al*. 2001, Macpherson 2005, Woodroffe & Donnelly 2011).

Disease spill over into wildlife populations, such as wild-living dogs, can make pathogen management efforts (e.g. vaccination) more difficult. There is usually limited and infrequent contact between humans and wildlife, but wildlife can provide additional host reservoirs and can potentially accelerate disease spread nevertheless (Gortazar *et al*. 2007, Miller *et al*. 2013, Dohna *et al*. 2014). Because Australia's wild dog population is large and has great spatial extent (West 2008, Fleming *et al*. 2014), there is potential for them to act as a reservoir for endemic pathogens (e.g. canine distemper virus, Norris *et al.* 2006) and non-endemic pathogens (e.g. rabies virus, Sparkes *et al.* 2015). Wild dogs then have the potential to transmit these pathogens to other domestic animals and wildlife and to humans.

Appropriate planning to prevent the introduction and establishment of non-endemic pathogens, such as the rabies virus in Australia, requires prevention against incursions, plus preparedness in case prevention fails. Both require that disease managers can predict how the virus would spread within and among free-roaming dog populations. The epidemiological models (e.g. Townsend *et al.* 2013, Cummings & Lessler 2014, Dürr & Ward 2015) necessary for this depend upon parameters that include contact rates within and between dog populations.

Contact between susceptible individuals plays a critical role in the transmission of rabies (Krebs *et al.* 1994, Vanak *et al.* 2007, Woodroffe & Donnelly 2011). Domestic dogs have greater contact with humans than do wild-living dogs, hence may pose a greater rabies transmission risk to humans. However, animals that are unrestrained, as are wild and free-roaming domestic dogs, have the potential to spread disease over large areas, increasing rate of spread and enlarging the area required for containment and/or control (Lunney *et al.* 2011). Despite significant attention afforded to free-roaming domestic and wild dogs (e.g. Doherty 2014, Jones 2014, Killoran 2014) and their impacts on human health, the risk they pose for pathogen transmission in Australia is largely unassessed (Coman & Robinson 1989, Dürr & Ward 2014, Sparkes *et al.* 2014b).

Interactions at the wild-domestic dog interface provide opportunity for disease maintenance and spread, particularly in Australia where wild dogs enter urban areas (e.g. Allen *et al.* 2013). Although there are anecdotal reports of wild and domestic dogs interacting (e.g. Allen 2010, Sparkes *et al.* 2016), the regularity of such contact between these groups has not been quantified. Technological advances, such as the advent of proximity loggers, GPS telemetry and camera traps, have made assessing the probability of such interactions increasingly feasible (Courtenay *et al.* 2001, Kauhala & Holmala 2006, Böhm *et al.* 2009). Camera traps in particular, have become increasingly popular as a monitoring tool (Meek *et al.* 2015), especially for cryptic and crepuscular species (e.g. Kelly & Holub 2008, Si *et al.* 2014, Burton *et al.* 2015) like wild dogs (Thomson 1992ab). For epidemiological investigations, appropriately used camera traps can permit detection and individual identification of a range of species (Swann *et al*. 2004, Sarmento *et al*. 2009, Bengsen *et al*. 2011). Information collected at the individual level can be used to estimate density of target species and to improve understanding of sociality, thereby informing managers about likely patterns of disease spread (Rowcliffe *et al*. 2014, Swann & Perkins 2014).

In this study, we used camera traps to quantify within and between group contact rates for wild-living and domestic dogs in north-east New South Wales, Australia.

6.1.3 Methods

6.1.3.1 Study area

North-east New South Wales (NSW) is a mosaic of human settlement, agricultural areas, State Forests and National Parks. Vegetation includes subtropical rainforests, wet and dry sclerophyll forests, heath, wetlands, hardwood plantations and open farmland, with the latter predominantly used for cattle grazing. Steep slopes and ridges bound the region to the west, whilst lowland swamps, mangroves and beaches define its eastern edge.

Monitoring stations were established at eight sites progressively from May 2013, in the region between the Queensland-NSW border in the north and Coffs Harbour in the south (Figure 6-1). The distance between consecutive sites ranged from 18 km to 59 km. Each site included a mixture of private and public (e.g. National Park and State Forest) managed land and had between five and seven camera monitoring stations, except South Bundjalung which had 26 (Figure 6-1; Table 6-1). Due to budgetary constraints, South Bundjalung was the longest monitored site and was used to contrast the smaller sampling efforts of the other seven sites.

6.1.3.2 Monitoring stations

Each monitoring station comprised a Reconyx HC600 Hyperfire camera trap placed in a purpose-built housing and post (after Meek *et al*. 2013). The station was positioned close to an established track such that the lens of the camera was approximately 60 cm above the level of the road surface and angled 22.5° towards the centre of the road (*sensu* Ballard *et al*. 2014). From a random starting point, camera traps were placed at least 1 km apart along formed roads and trails, targeting areas used by dogs and other wildlife (including intersections and ridges). The camera traps were triggered by activation of in-built passive infrared detectors, with each trap programmed to take 10 pictures per trigger with no delay between trigger events. The number of days each camera was active and able to be triggered was recorded as camera trap nights (CTN). The number of monitoring stations and CTN varied between sites, primarily due to theft of camera traps, the area monitored and funding restrictions.

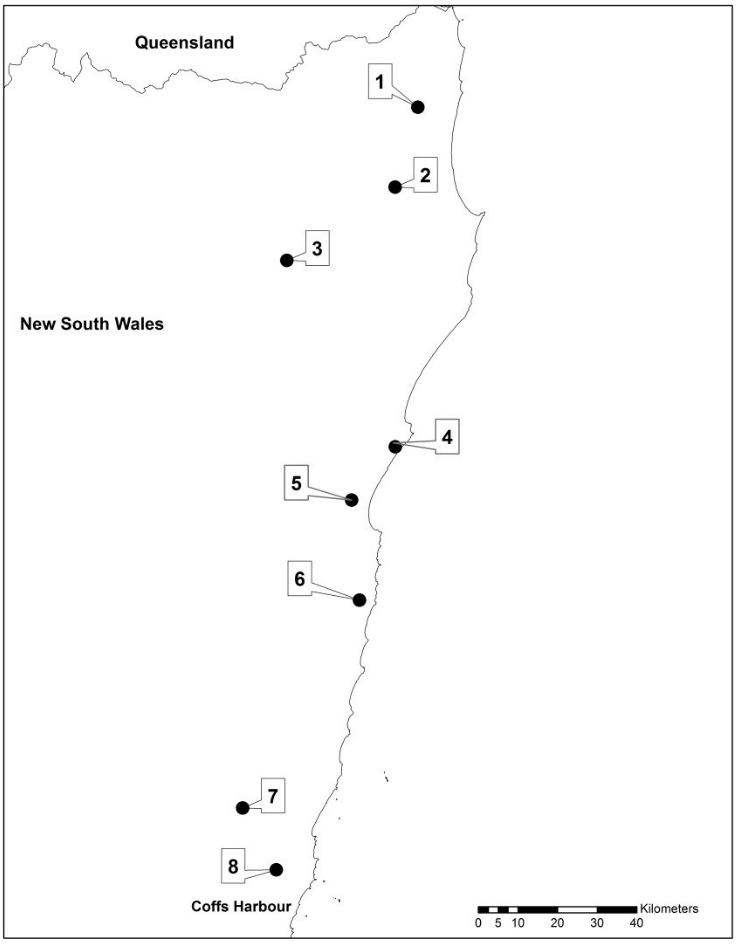


Figure 6-1 Location of field sites for camera trap monitoring in north-east New South Wales

From north to south: (1) Mooball, (2) Goonengerry, (3) Muckleewee, (4) North Bundjalung, (5) South Bundjalung, (6) Yuraygir, (7) North Sherwood and (8) Conglomerate

6.1.3.3 Metadata

Using 'ExifPro' software (Kowalski & Kowalski 2013), files containing images of dogs were manually assigned a metadata tag of 'dog' and then additionally tagged to either wild dogs, supervised domestic dogs or unsupervised domestic dogs. Dogs were assigned to each group based on phenotypic characteristics (i.e. breed, build and body condition), whether they were in the presence of a human or wearing a collar (see Plates 3-8 for examples of dogs assigned each group). Dog images were further assigned to individual animals, based on phenotypic characteristics (including sex, reproductive status, life stage, coat colouration, build and injuries). A reference library of images for each individual dog was developed using distinctive combinations of these characteristics. Where an image of a dog was unable to be readily identified as a particular, known individual (e.g. due to poor image quality, such as occurs when a dog passes by a camera too quickly), the file was assigned a tag of ‘unsure’. All metadata were subsequently extracted from camera trap images and tabularized using ‘EXIFTOOL’ (Harvey 2015), via a user interface developed by one of the authors (GK).

6.1.3.4 Temporal activity, and contact rate and event definition

Temporal activity of domestic (with and without humans present) and wild dogs, based on the time stamp of the images, was analysed for all sites using the package *overlap* (Ridout & Linkie 2009) under R (R Core Team 2015).

Measures of contact were based on individuals’ relative proximity in space and time. From direct observations of wild and unrestrained domestic dogs undertaken prior to the study, a distance threshold of 50 m was established to delimit contact occurring between individuals, i.e. two or more dogs closer than 50 m were deemed to have come into close proximity sufficient for visual, social or physical contact to occur, whereas animals further apart were classified as independent events. Therefore, mean velocity of dog movements along trails was calculated in order to determine a temporal threshold associated with a separation of at least 50 m between animals. As all images were date and time stamped, velocity was calculated by measuring the time it took for individual dogs to pass consecutive, georeferenced camera stations. To quantify velocity of travel along trails, we randomly selected a sample of individual wild dogs from a randomly selected subset of six social groups across sites, only using those recordings where dogs passed consecutive cameras. Using the 50 m distance threshold for contact between dogs and the mean velocity of wild dogs (see Results), we defined an event as a series of consecutive dog images from the same camera taken within a minute from each other. Where dogs were observed resting or lying down in front of a camera for periods longer than one minute, that sequence of images was also considered a single event.

Group size (number of individual dogs observed) per event was quantified to determine the number of pairwise contacts. Contact rates for each site were subsequently calculated based on the number of contacts per CTN per site.

To identify the presence of any factors influencing contact rates at each site, observations were further broken down into contacts for each month for all further analyses. For these contact rates, all images of dogs were included, regardless of whether specific individuals could be identified.

6.1.3.5 Site effects on wild dog contacts

Analysis of observed monthly contacts amongst wild dogs at sites was undertaken using a mixed effects log-linear model analysis with a Poisson (possibly over-dispersed) distribution. Fixed effect covariates included in the model, on the log scale for each site x month were: the number of wild dogs minus 1; number of cameras; average number of trap nights per site per month; and the area monitored (minimum convex polygon encompassing active cameras). ‘Site’ itself was included in the model as a random effect, thus incorporating a correlation for monthly results from the same site. Monthly data at sites with zero or only one dog present (and therefore no contact observed) were excluded from the analysis. The model was fitted to the observed data using the package *asreml* (Butler 2009) under R (R Core Team 2015).

6.1.3.6 Seasonality of interactions

The average number of events, dog group size and (pairwise) contacts were calculated separately for wild and domestic dogs, per CTN for each Site by Month. These averages were square-root transformed to homogenise variation. The longitudinal model fitted included an overall spline trend with Time (months since May 2013) as well as deviation from average trend with Time for each Site, also modeled using splines. Independent random effects in the model were effects associated with Year (2013, 2014, 2015); Month (Jan, Feb,…, Dec); Year x Month; Site x Year; and Site x Month.

The residuals (random errors) in the model were modeled with variance inversely proportional to the number of CTNs. Each model was then examined to test if there were significant trends with Time averaged over Sites. Effects associated with Month; Year x Month; and/or spline Time were tested for significance.

6.1.3.7 Interactions between individual dogs

Contact rates between two individual animals were derived by dividing the number of events by the number of days both animals were detected at a site (regardless of whether an interaction occurred; i.e. concurrent detection days). A contact matrix of all dogs at each site was then used to determine the number of different dogs an individual dog came into contact with, excluding pups too young for individual identification and 'unsure' images. Where possible, contacts were then interpreted in the context of social groupings (i.e. individuals observed together) and the relationships between pairs of dogs (i.e. known pairings, observing adults with young and using DNA from animals trapped in a concurrent project). A Tukey pair-wise comparison was used to detect whether a relationship type (parent-offspring, littermates, mating pair, siblings (not littermates), grandparent-grandchild and unknown relationships) influenced contact rates.

Unless indicated otherwise, data are presented as the mean ± 1SD and a P-value < 0.05 was considered significant.

6.1.4 Results

In total, 164,116 images of putative wild dogs and 12,332 images of putative domestic dogs were recorded from 26,151 camera trap nights (Appendix 6-1; See Plates 3-8 for example images). Dogs could be identified to the individual level most of the time (14.7 ±11.0% of wild and 0.3 ±0.8% of domestic dog events were unable to be individually identified across sites). Unsupervised free-roaming domestic dogs comprised 36% of domestic dog events. The number of individual wild dogs identified at a site ranged from 6 to 27, while domestic dog numbers ranged from 0 to 26 individuals (Table 6-1). Eight randomly selected wild dogs from six identified social groupings yielded 4,579 useable records to quantify velocity of travel. From these records, mean velocity along trails was 3.9 (±0.6) km h^{-1}.

Table 6-1 Number of camera monitoring stations, wild and domestic dogs and camera trap nights (CTN), and area monitored

Site	No. camera stations	No. individuals		CTN	Monitored area
		Wild	Domestic		(km^2)
1	5	12	4	643	5.2
2	7	8	10	1,046	3.1
3	5	19	11	995	6.5
4	6	6	0	2,779	7.7
5	26	24	26	15,567	37.3
6	5	21	18	1,940	14.2
7	5	21	1	1,844	1.8
8	6	27	15	1,337	1.4

The number of events per individual wild dog ranged from one (i.e. an apparently transient visit) through to more than 2,500 events (i.e. a dog consistently occupying a monitored site). In contrast, domestic dog events per individual were much lower, ranging from 1 to 236 events per individual. The mean number of events per dog varied across sites, ranging from 9±8 to 520±839 for wild and 3±3 to 27±74 for domestic dogs. Images of the same wild dog were not captured at more than one site (implying independence between sites), but images of an individually recognisable domestic dog were captured at two neighbouring sites. The domestic dog of interest was predominantly observed at Site 5 and on a single occasion at Site 6, which was assumed a human-mediated, short-term translocation event as it was also observed on-lead with a human at this site.

6.1.4.1 Temporal activity

Domestic dogs were most active between 0700 and 1700 hrs. The degree of temporal activity overlap was high for supervised and unsupervised free-roaming domestic dogs (overlap: 0.87 with 95% CI (0.81, 0.92)). Consequently, the two groups were pooled for all further analyses. In contrast to domestic dogs, wild dog activity peaked at 2300 hrs and was generally high during nocturnal hours, resulting in low temporal activity overlap between the two dog groups (overlap: 0.32 with 95% CI (0.3, 0.35), Figure 6-2).

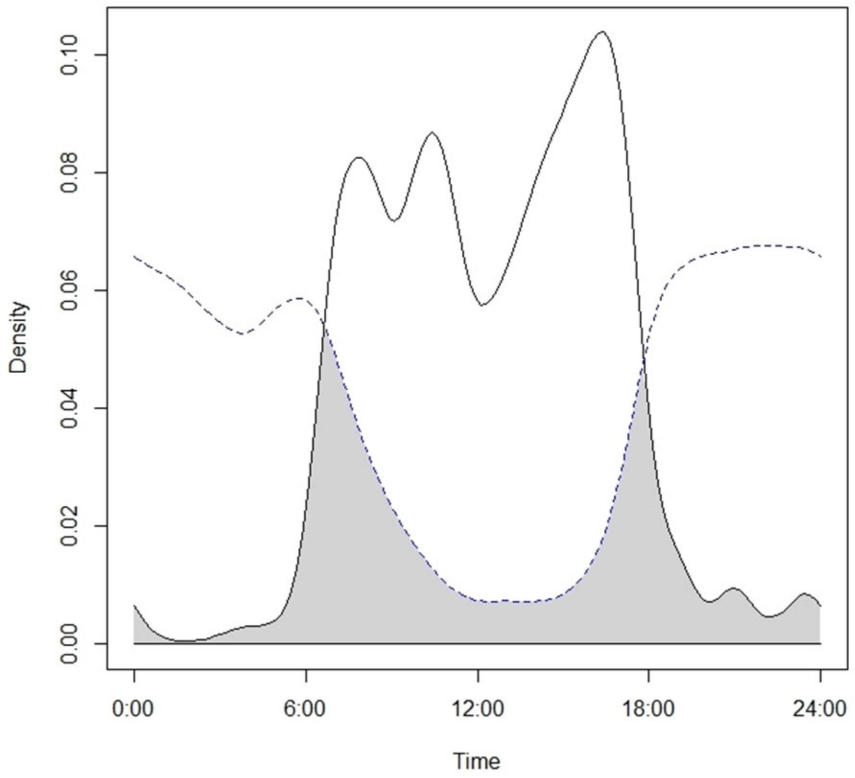


Figure 6-2 Temporal activity of domestic (solid) and wild (dashed) dogs. The grey shaded area between lines indicates the degree of overlap (0.32)

No contacts were recorded between wild and domestic dogs. However, on three occasions, domestic and wild dogs were captured at the same monitoring station less than half an hour apart. Each of these events occurred during daylight hours (between 0630 and 1600 hrs).

6.1.4.2 Group size

Group size of wild dogs ranged from 1 to 7 individuals (mean: 1.7 ±1.0), with solitary dogs most frequently observed across all sites (44-81% of events across sites involved solitary wild dogs). Domestic dog group size ranged from 1 to 5 individuals (mean: 1.4 ±0.6). Similar to wild dogs, solitary individuals were most commonly observed across sites, except for Site 5 where pairs of domestic dogs were most common.

6.1.4.3 Contact rates and site effects

For wild dogs, contact rates per CTN were highly variable across sites, ranging from 0.02 to 0.56 contacts (mean: 0.2 ±0.2). Domestic dog contact rates were generally much lower, ranging from 0.003 to 0.075 contacts per CTN (mean: 0.016 ±0.025).

Sampling effort (i.e. number of cameras, average number of CTN per month and area monitored (MCP)) had a significant effect on the number of contacts recorded (Wald test: logCams $F_{1,10}$=6.63, P = 0.03, logAvCTN $F_{1,108}$=9.22, P = <0.01, logMCP $F_{1,7}$ = 5.20, P = 0.05), while no significant effect of number of dogs per site was found (Wald test: logDogsM1 $F_{1,96}$ = 0.94, P = 0.34). Subsequently, the number of dogs at a site was removed, with the estimated model for number of contacts for an average site being:

$$E(\text{Contacts}) = \exp(-3.91) \times \text{Cams}^{1.02} \times (\text{CTN/Cams})^{1.31} \times \text{MCP}^{0.59}$$

6.1.4.4 Seasonality of interactions

For wild dogs across sites, no significant trend with Time (spline time), nor effects for Month or Year x Month were observed for average number of dogs per CTN or average dog group size. In contrast, these two traits differed across Time (Year x Months) for domestic dogs when averaged over sites, though the differences were not consistent across months within a year, nor were they smooth over time (range: 0.00-0.20 for the average number of events and 0.00-0.24 for group size of domestic dogs per CTN across Time). Significant differences in the number of contacts between dogs across time were observed for both wild and domestic dogs, but these differences were not consistent across months within a year or between years (Figure 6-3).

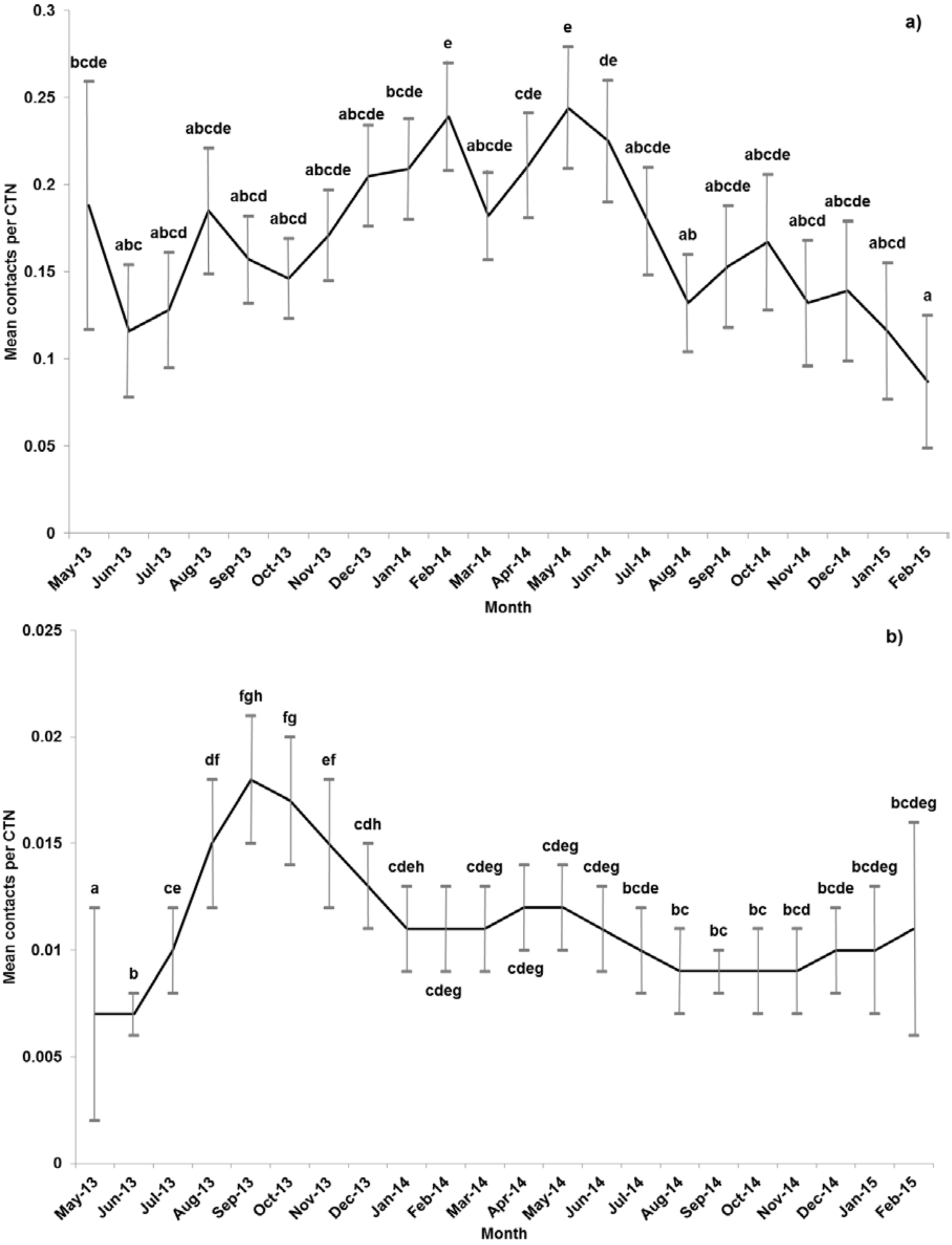


Figure 6-3 Across site average (±SD) number of wild (a) and domestic (b) dog contacts per camera trap night (CTN) by month

Averages without a letter in common differ significantly ($P < 0.05$)

6.1.4.5 Interactions between individuals

Interactions between individual wild dogs were relatively complex, compared to those between domestic animals. The number of dogs an individual dog contacted during the monitoring period varied across sites and between dog types (mean: 2.1 ±2.1, 0.9 ±1.0 wild and domestic dogs contacted, respectively; Table 6-2). At all sites, some wild and domestic dogs were never observed in the company of another dog (Table 6-2). Within sites, some dogs were separated in time (i.e. not detected on the transect concurrently) whilst others were separated in space (i.e. detected on the transect concurrently, but in different locations).

Table 6-2 Range and mean number of wild and domestic dogs contacted at each site

	Wild		Domestic	
Site	Range	Mean (±SD)	Range	Mean (±SD)
1	0-4	2.4 (±1.71)	0-2	1.5 (±1.0)
2	0-1	0.7 (±0.52)	0-1	0.4 (±0.5)
3	0-2	0.9 (±0.86)	0-1	0.5 (±0.5)
4	0-3	2 (±1.55)		
5	0-11	4.3 (±3.18)	0-2	0.7 (±0.6)
6	0-3	1.7 (±1.33)	0-4	1.1 (±1.1)
7	0-4	2 (±1.46)		
8	0-4	1.5 (±1.26)	0-4	1.6 (±1.5)

Interactions between two individual dogs varied across dog type, with 0 contacts followed by 0.51–1 contacts per concurrent detection day most common for wild dogs, while 0.51–1 contacts were most common for domestic dogs (Figure 6-4).

The number of contacts per detection day between individual wild dogs varied according to their apparent relationship. Contacts between parents and offspring (i.e. known to be from the same social group) were significantly greater than contacts between unknown-relationship paired dogs (P = 0.01; Table 6-3). Contact between littermates were also greater than contacts between paired dogs with an unknown relationship (P = 0.06; Table 6-3).

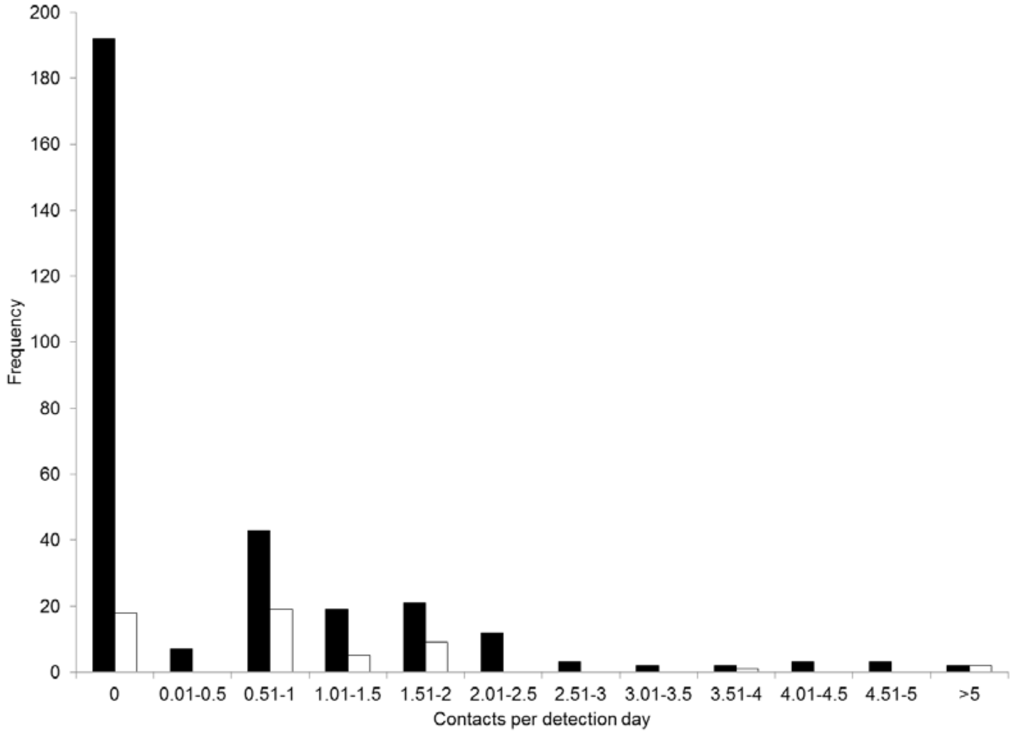


Figure 6-4 Frequency of the number of contacts between paired individuals per concurrent detection day for wild (filled) and domestic (no fill) dogs across sites

Table 6-3 Range and mean number of average daily contacts between two individual wild dogs for identified relationships

Type of relationship	Range	[N=117].	Mean (±SD)
Grandparent-Grandchild		[1]	0.67
Litter Mates	0.83-5.00	[16]	1.98 (±1.19)
Mates	0.50-4.72	[14]	1.72 (±1.15)
Parent-Offspring	0.38-5.33	[44]	1.88 (±1.33)
Siblings^	2.17-2.80	[4]	2.42 (±0.29)
Unknown	0.01-2.10	[38]	1.12 (±0.55)

^ not litter mates

6.1.5 Discussion

Our novel application of camera traps successfully quantified interactions of wild-living and domestic dogs. Contacts between the wild dogs occurred mainly within their social group (i.e. contacts between littermates, parents and offspring and mate pairs), but also infrequently between groups. Importantly, the number of contacts recorded was not affected by an increase in dog density, suggesting that contact between dogs is frequency- (i.e. rate of contact) rather than density-dependent (Begon *et al*. 2002). Wild and domestic dogs were found at the same sites, despite prohibition of domestic dogs in conservation areas that comprised a large proportion of sites. However, there was little temporal overlap between wild and domestic dogs, with no direct contacts recorded between these two groups. The lack of observed contacts between wild and domestic dogs suggests that opportunities for pathogen transmission between these dog types may be rare, and therefore the probability of rabies virus transmission from wild to domestic dogs and then domestic dogs to humans may be low. However, the behavioural changes observed in rabid dogs (Hampson *et al*. 2009) could result in greater contact between wild and domestic dogs than we observed with healthy animals. In contrast, due to relatively high interactions rates within dog types, rabies virus transmission could occur rapidly within each of the dog groups, should rabies be introduced into one of the populations.

In contrast to African Wild Dogs (*Lycaon pictus*) that avoided human settlements (Woodroffe & Donnelly 2011), Australian wild dogs often reside within close proximity to humans (Claridge *et al*. 2009, Allen *et al*. 2013, present study). As such, the risk of spreading non-contact dependent pathogens such as hydatids (Brown & Copeman 2003, Jenkins 2006), *Neospora caninum* (King *et al*. 2010) and parvo virus (Woodroffe *et al*. 2012) between dog groups should be high. While this notion is supported by recent research that suggests wild dogs act as the reservoir of canine-borne pathogens such as hydatids and *N. caninum* in Australia (Jenkins *et al*. 2008, King *et al*. 2011), consideration should also be given for the transmission of diseases from domestic to wild dogs and other wildlife (i.e. domestic dog as the disease reservoir).

The roaming behaviour of domestic dogs has rarely been documented in Australia (Coman & Robinson 1989, Meek 1999, Dürr & Ward 2014, Sparkes *et al*. 2014b), and this is the first study to assess their risk of contact with wild-living dogs. Because unsupervised free-roaming domestic dogs displayed the same diel activity profile as their supervised counterparts, thereby avoiding much temporal overlap with wild dogs, free-roaming behaviour, despite the undesirable impact on wildlife, livestock and humans, might not overly heighten the risk of spreading directly transmissible pathogens, such as rabies. However, because camera traps monitor a single small area and require passage of animals in front of the camera, infrequent interactions between wild and domestic dogs may have gone undetected within the present study. Indeed, spill over of disease from wildlife to domestic animals through direct or indirect contact has been reported elsewhere (Grainger & Jenkins 1996, Steinel et al. 2001, Vercauteren *et al*. 2007, Jenkins *et al*. 2008). To maximise detection of these apparently infrequent interactions, alternative methods, including use of genetic analyses, proximity loggers and GPS telemetry could be employed. However, unless all individual wild and domestic dogs in an area have been tagged, these methods also can only provide an index for contact rates. A mix of camera traps and individual tracking might provide the best obtainable measure for rates of contact between individuals.

Should rabies enter the Australian wild dog population, it could be expected that the disease will spread rapidly within a social group where contacts were most frequently observed (i.e. between parents and offspring, between littermates and between mate pairs; see also Thomson *et al*. 1992a). However, while contact rates were observed to peak when young were present (i.e. contact between parents and offspring and between littermates; see Table 6-3), at least in north-east NSW where the present study was conducted, no seasonal risk profile for pathogen transmission could be established, as the time of pup emeregence varied both across and within monitored sites. This finding contrasts with previous suggestions of relatively focussed breeding seasons within dingo populations elsewhere (Jones & Stevens 1988, Catling *et al*. 1992, Thomson 1992a). Hence, control programs where wild dogs are targeted at the same time annually may not be the optimal strategy for regions such as north-east NSW. Rather, managers should take into consideration pup emergence and social structure when developing control programs; particularly when dealing with directly transmissible pathogens such as the rabies virus.

Heterogeneity of individuals within and across populations (e.g. due to social hierarchy and/or the territorial nature of the individual; Pitt *et al*. 2003, Böhm *et al*. 2009) might also explain the observed lack of density dependency for contact rates. For example, despite having the highest wild dog density, Site 8 recorded one of the lowest contact rates per CTN; perhaps a function of few observed pups and small group sizes (1–3 individuals per group). Similarly, more domestic dogs at a site did not result in higher contact rates and this finding for dogs is consistent with those for a number of other species, where an increase in animal density does not exert a proportional increase in contact rates (Ji *et al*. 2005, Kauhala & Holmala 2006, Porphyre *et al*. 2011, Morters *et al*. 2013). These results highlight heterogeneity of social contact among individuals, with some having the potential to act as major contact points for the spread of disease through populations (Courtenay *et al*. 2001, Pitt *et al*. 2003, Porphyre *et al*. 2008, 2011, Böhm *et al*. 2009). In light of this, frequency-dependent transmission (i.e. rate of contact) for diseases such as rabies should be given greater consideration. This would be a departure from traditional assumptions of density-dependent transmission (Panjeti & Real 2011) and more aligned with the probabilstic rabies model of Townsend *et al.* (2013).

Our study and previous work also found infrequent interactions between wild dogs of unknown relationships (i.e. likely unrelated individuals), which would likely constrain onward transmission of directly transmissible pathogens between social groups (Thomson 1992b, Woodroffe & Donnelly 2011, Woodroffe *et al*. 2012). However, individuals with high social connectivity are likely to breach this barrier eventually and, considering the spatial overlap documented here, infrequent contacts between social groups could prove the most important forms of contact for disease spread. These wild individuals have the greatest potential for broad geographic spread of disease. Likewise, a few domestic dogs could be most important in disease spread between communities (Dürr & Ward 2014, Sparkes *et al*. 2014). For example, Sparkes et al. (2014) found that some free-roaming domestic dogs in northern Australia contacted more dogs than others (Range: 0-10 dogs contacted), suggesting that socially connected dogs may pose a greater risk for pathogen transmission than less sociable individuals. Similarly, Dürr & Ward (2014) found most free-roaming domestic dogs in northern Australian indigenous communities remained in close proximity to the owners' house (50% isopleth median core Home Range = 0.2-0.4 ha), while some individual dogs roamed much further (40-104 ha). The authors hypothesised that far roaming dogs may play a greater role in pathogen transmission in these environments. In this context, the effects of lethal control programs for dogs in response to a rabies outbreak should be reviewed, as it generally involves indiscriminant dog removal (i.e. lack of target specificity for perceived high risk individuals) and has the potential to disrupt social structures within the population, potentially increasing contact rates within and between groups, thereby increasing disease spread (Morters *et al*. 2013). Alternative analyses and comparisons across sites would be beneficial to further explore interactions at the individual and community level.

Quantifying wildlife contact patterns has previously been difficult; particularly where direct observations are impractical due to the cryptic or nocturnal nature of the target species and in rugged terrain and dense vegetation. Here, we deployed camera traps across multiple sites in north-east NSW to quantify interactions between and within wild and domestic dog groups. This study represents the first use of this technology for a wildlife-domestic system. Although camera traps cannot capture all contacts within the landscape, they provide a probability index for contacts between individual animals. This approach takes into account the variable nature of contacts between social animals and will strengthen epidemiological models, improve prediction capabilities and maximise the potential to implement effective control strategies.

6.1.6 Ethical approval

Research was conducted with approval from the UNE Animal Ethics Committee (AEC13-007) and under National Parks & Wildlife Services scientific licence SL101145. All applicable institutional and/or national guidelines for the care and use of animals were followed.

6.1.7 Acknowledgements

We thank the anonymous referees who provided valuable comments on the manuscript. Funding for this research was provided by the Northern Rivers Regional Organisation of Councils and the Department of Agriculture, Fisheries and Forestry’s Wildlife and Exotic Disease Preparedness Program, 2012—2013. J.S is an Australian Postgraduate Award and UNE Apted scholar recipient, supervised by Dr Wendy Brown through the University of New England’s School of Environmental and Rural Science. We also thank all private landholders for allowing camera monitoring stations to be erected on their properties.

Appendix 6-1: Total images and number of images for each animal photographed per site, north-east New South Wales

	Site^							
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Total Images	8480	55642	98225	86909	505408	153110	39770	40669
Bandicoot	90	60	310	30	890	150	670	340
Bird	30	150	200	510	1400	1950	230	258
Brush tail possum	30	20	190	0	340	0	110	1340
Cat	0	230	20	1040	7170	210	1700	1591
Cow	0	0	25880	0	0	76197	3440	5116
Domestic dog	170	3270	290	0	3762	670	10	4160
Dog	2340	680	2631	7220	131967	8940	6670	3668
Researcher	840	1952	2419	2949	76416	2141	10438	2772
Echidna	0	0	60	90	300	80	20	70
Eastern grey kangaroo	0	0	0	620	23260	1510	2070	100
Emu	0	0	0	0	0	6370	0	0
Fox	90	510	1030	710	1680	880	5140	929
Goanna	90	20	50	70	1310	0	80	140
Hare	0	0	0	100	450	150	0	10
Horse	420	940	140	0	2827	40	0	300
Human	1540	11060	3910	5530	28498	6120	210	2473
Insect	0	0	0	0	30	410	0	0
Koala	10	0	0	0	40	0	0	0
Lizard	0	0	0	0	0	10	0	0
Lyrebird	0	30	0	0	0	0	0	180
Macropod	20	80	490	50	1540	110	530	1260
Motorbike	480	720	17760	870	7797	2450	1243	2579
NIL	520	20552	4690	22173	130320	12396	2250	7042

Pademelon	20	30	10	0	40	0	0	0
Peacock	0	0	470	0	0	0	0	0
Pig	0	0	0	40	4760	960	0	0
Potoroo	0	10	10	0	260	0	10	0
Red-necked pademelon	0	0	3910	0	0	0	0	0
Ring tail possum	0	0	0	0	20	0	0	0
Red neck wallaby	0	0	1520	0	4080	0	1260	960
Snake	0	0	0	0	80	0	0	0
Spider	0	0	0	30	10	0	0	0
Spotted tail quoll	0	0	0	0	0	0	10	0
Swamp wallaby	150	410	1270	21680	19827	670	2140	1140
Brush turkey	1750	760	1550	250	70	0	20	570
Unknown	81	190	750	370	1290	230	450	392
Vehicle	190	18908	24610	23430	61089	34770	2548	6001
Wedge tail eagle	80	0	0	0	0	0	20	250

^ (1) Mooball, (2) Goonengerry, (3) Muckleewee, (4) North Bundjalung, (5) South Bundjalung, (6) Yuraygir, (7) North Sherwood and (8) Conglomerate

Plate 3: Solitary wild dog, South Bundjalung National Park, New South Wales

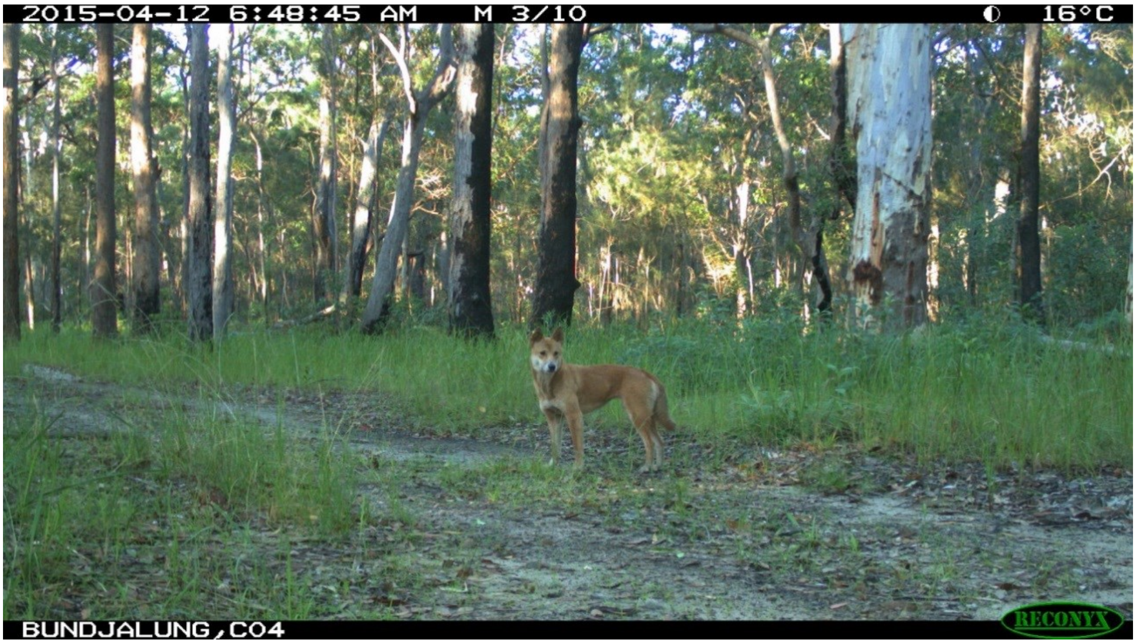


Plate 4: Wild dog mate pair, South Bundjalung National Park, New South Wales

Plate 5: Female wild dog with pups, private property, Muckleewee, New South Wales

Plate 6: Restrained domestic dogs, Bundjalung National Park, New South Wales


[redacted]

Plate 7: Free-roaming domestic dogs, Mooball National Park, New South Wales

Plate 8: Solitary free-roaming domestic dog, private property, Conglomerate, New South Wales

STATEMENT OF ORIGINALITY

We, the PhD candidate and the candidate's Principal Supervisor, certify that the following text, figures and diagrams are the candidate's original work.

Type of work	Page number/s
Journal article and all encompassing information	156-178

Name of Candidate: Jessica Sparkes

Name/title of Principal Supervisor: Dr Wendy Brown

[redacted]

12 December 2015

Candidate

Date

[redacted]

12 December 2015

Principal Supervisor

Date

STATEMENT OF AUTHORS' CONTRIBUTION

We, the PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

	Author's Name	**% of contribution**
Candidate	Jessica Sparkes	Conception and design (70%) Data collection (90%) Analyses (60%) Manuscript development (75%)
Other Authors	Guy Ballard	Conception and design (15%) Data collection (5%) Manuscript development (7%)
	Peter JS Fleming	Conception and design (15%) Data collection (5%) Manuscript development (5%)
	Remy van de Ven	Analyses (40%) Manuscript development (5%)
	Gerhard Körtner	Manuscript development (8%)

Name of Candidate: Jessica Sparkes

Name/title of Principal Supervisor: Dr Wendy Brown

[redacted]

12 December 2015

Candidate

Date

[redacted]

12 December 2015

Principal Supervisor

Date

7 Modelling rabies spread in Australia

7.1 Introduction

Once rabies enters Australia, its spread will likely be complex, involving different ‘groups’ or ‘classifications’ of dogs. These dogs range on the spectrum from domesticated pet dogs that are completely reliant on humans through to wild dogs (including dingoes) that do not rely on humans for resources such as food and shelter (Chapters 2-6). Although the same species, due to differences in behaviour, their association with humans and population characteristics observed for these dog groups (see Coman & Robinson 1989, Meek 1999, Fleming *et al*. 2001, Claridge *et al*. 2009, Allen *et al*. 2013, Dürr & Ward 2014, Sparkes *et al*. 2014b for examples), it is essential to break down the *Canis lupis* specie into a number of sub-types to allow for targeted modelling of disease spread and identification of the types of dogs most at risk of contracting and spreading rabies in Australia.

7.1.1 Dog types based on rabies transmission risk

In this Chapter, I draw on data presented earlier in this thesis and the wider literature to provide parameter estimates for rabies modelling. Here, Australia’s dog population has been loosely divided into four categories; domestic restrained, working, domestic free-roaming owned and wild dogs. Despite these classifications, it is important to note that the categories exist on a continuum, with individual dogs able to move between categories at any stage in their lives.

Developing a conceptual framework for rabies spread is an important first step for understanding how these different types of dog interact and identifying the potential for disease spread through communities. As the different dog types reside in similar locations, an understanding of how these dogs interact is important for rabies modelling. Further, ranking interactions based on the most important factors for disease maintenance and transmission will aid the development of appropriate control strategies which are feasible for each dog type. Figure 7-1 highlights the potential interactions within and between the different dog groups and the risk profile associated with each. The sections below describe and quantify parameters associated with rabies transmission within and between dog types.

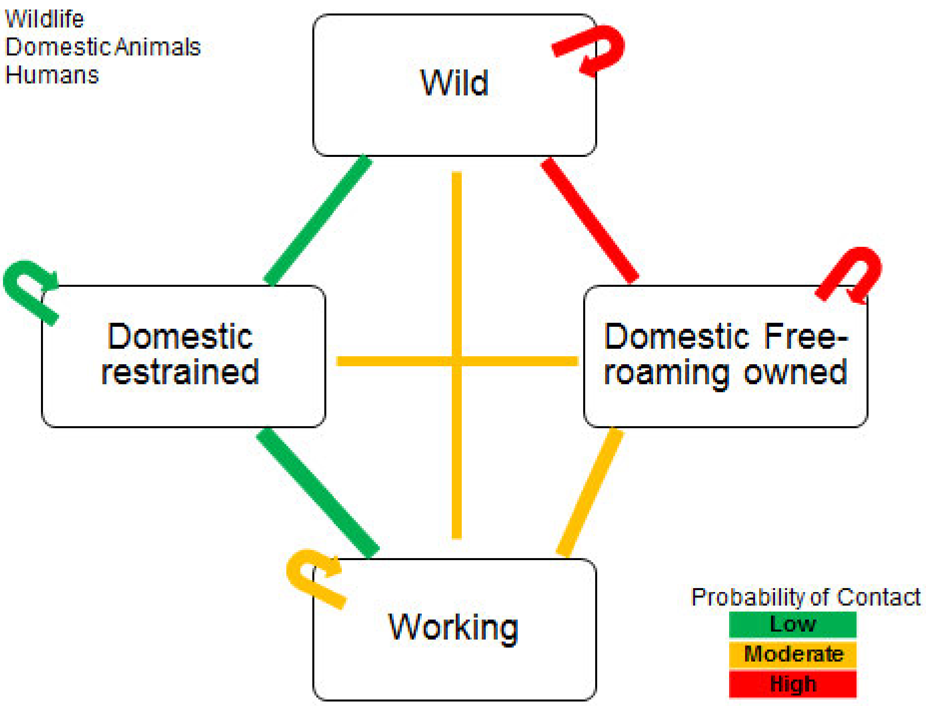


Figure 7-1 Conceptual model for probability of contact between different dog groups in Australia

7.1.2 Domestic restrained

Domestic dogs that are restrained in some manner (such as through fencing or tethering) are unlikely to encounter other dogs without human supervision. The risk of disease transfer between these restrained dogs is therefore low. However, there are many anecdotal reports of restrained dogs being attacked and/or killed by wild dogs (D. Chamberlain, Team Leader, Invasive Species & Plant Health, North Coast Local Land Services, pers. com. 2015), particularly in coastal regions where both wild and domestic dog numbers are high (West 2008, Australian Companion Animal Council 2010).

Although not critical for epidemiological modelling, quantifying the total number of domestic dogs and understanding human-mediated movements of these dogs across Australia is important for estimating the number of vaccines required if rabies were to breach Australian borders. Drawing on Chapter 3 and the wider literature, the north-east NSW restrained domestic dog population was estimated at 0.34 million, with an annual population growth rate of 0.3% (Table 7-1). With an estimated 1.5 dogs owned per dog-owning household (Chapter 3), a contact rate of 1 (continual contact) between restrained dogs would be expected (Table 7-1).

If rabies were to enter Australia, restrained domestic dogs are likely to be highly accessible for monitoring and implementation of vaccination programs. As such, it is reasonable to assume that this dog type would provide the lowest risk for rabies maintenance and spread and transmission to humans.

Table 7-1 Model parameters for domestic restrained dogs in north-east New South Wales

Parameter^	Value	Reference
Population	**0.34 million**	
Area	76,275 km^2	3 LLS boundaries: Hunter, North Coast and Northern Tablelands, excluding National Parks and State Forests
North-east NSW domestic dog population	0.46 million	Office of Local Government, 2015
% domestic dogs restrained	74%	Chapter 3
Births#	**56,609**	
Population estimate	0.34 million	
% female and entire	10.84%	Chapter 3
Litters per entire female	0.51	Di Nardo *et al*. 2007
Pups per litter	3	Di Nardo *et al*. 2007
Deaths#	**55,588**	
Population estimate	0.34 million	
P of mortality for each age	Varies per age class Range: 0.02 - 1	Di Nardo *et al*. 2007
Mean age at death	13 years	Michell 1999, Di Nardo *et al*. 2007
% dogs in each age class	varied	Chapter 3
Contact rate	**1 (continual) contact/household/day**	
Mean number of dogs owned	1.5 ±0.87	Chapter 3

^ Bolded parameters are derived from non-bolded parameters listed below each value, hence no reference is provided for that row

annual value

7.1.3 Working dogs

Working dogs used for stock herding, livestock protection and hunting can be free-roaming while working but normally restrained at other times. When working, there is potential for such dogs to contact other dogs. As most stock-working and guardian dogs working a particular property or area would likely be owned by a single family/owner, so could be treated as a single unit when considering rabies spread. However, in practice, contractors (e.g. for shearing and mustering) can take their dogs onto a number of different properties in a relatively short period of time. In these instances, it is likely that different dog units could contact one another, with the potential to spread rabies between properties. However, most dogs in this situation are under constant supervision and would likely not constitute a significant threat for rabies spread.

Livestock guardian dogs are becoming increasingly popular as an alternative, non-lethal method to reduce the negative impacts of wild dogs and foxes on livestock production (van Bommel 2010). However, limited studies have sought to quantify interactions between these and wild dogs. In Queensland, Allen (2010) found GPS collared maremma guardian dogs and wild dogs overlapped spatially and temporally, suggesting potential for physical interactions. Anecdotal reports also suggest that interactions between these dog types occur. For example, guardian dogs have both reportedly been killed by wild dogs, and chase wild dogs away from livestock such as cattle, sheep and poultry (Neales 2013, P. Meek twitter 16 June 2015). Further research is required to quantify interactions between guardian and wild dogs in a range of situations to improve preparedness for a rabies incursion in Australia.

Hunting dogs are frequently used by recreational hunters to locate, hold and retrieve game. Interactions between hunting dogs when on hunting trips occur, particularly when ‘mates’ come together to hunt and each brings a dog/s with them. The interaction between these dogs can escalate to dog fights, particularly when dogs are sorting out pack dominance (Chapter 5). As hunters can travel in excess of 500km in a single trip (Figure 5-2), interactions between hunting dogs and the potential for dog fights is important for the translocation of rabies over long distances. In addition, as highlighted in Chapter 5, interactions between hunting parties and wild dogs occur frequently, with half of all survey respondents stating they had encountered wild dogs while hunting (N = 320).

Because hunting dogs are generally restrained when not actively hunting, it would be unlikely that these dogs would contribute greatly to an epidemic. However, hunting dogs may be at greater risk of rabies infection from interactions with wild dogs, creating a transmission pathway between sylvatic and urban rabies cycles, where humans may be unexpectedly exposed. With a mean of 0.1 hunts occurring with dogs per hunter per day, and long distances traversed in a single hunting trip, hunting dogs have the potential to create disparate foci for rabies spread, which could result in the requirement for increased control efforts over a larger area (Table 7-2).

Table 7-2 Model parameters for hunting dogs, Australia

Parameter^	Value	Reference
Population	**465,647**	
Number of hunters	700,000	Finch *et al.* 2014
% hunters use dogs	30.1%	Baxter *et al.* 2012
Mean dogs per hunter	2.21±0.94	Chapter 5
Births*	**77,228**	
Population estimate	0.47 million	
% female and entire	10.84%	Chapter 3
Litters per entire female	0.51	Di Nardo *et al.* 2007
Pups per litter	3	Di Nardo *et al.* 2007
Deaths*	**75,860**	
Population estimate	0.47 million	
P of mortality for each age	Varies per age class Range: 0.02 - 1	Di Nardo *et al.* 2007
Mean age at death	11 years	Michell 1999
% dogs in each age class	varied	Chapter 3
Contact rate	**1.8 contacts/trip**	
Mean dogs used	2.21±0.94	Chapter 5
Human mediated excursions	**0.113 ± 0.149 hunts/hunter/day**	**Chapter 5**

^ Bolded parameters are derived from non-bolded parameters listed below each value, hence no reference is provided for that row

\# Double counted in domestic and hunting dogs

* annual value

7.1.4 Domestic free-roaming owned

Owned domestic dogs that are allowed to roam freely occur in many parts of Australia, including in Indigenous communities, peri-urban areas (such as hobby farms) and in urban and rural communities. In many instances, fencing is absent, or insufficient, preventing effective containment (e.g. Sparkes *et al*. 2014b). However, cultural influences also preclude restraint of some domestic dogs on occasion (Smith & Litchfield 2009). For example, some residents moving from cities to peri-urban areas feel their dogs should not be restrained because there is more land and they should be allowed to express their 'natural' behaviours (J. Sparkes pers. obs.). However, these dogs can become menacing for local wildlife and also have the potential to cause car accidents, be injured or killed (through encounters with wildlife including snakes and wild dogs, car accidents, dog fights or getting lost) and are likely to contract and increase the spread of zoonotic diseases over greater distances (Woodroffe *et al*. 2012, Schlacher *et al*. 2015).

The risk of contact between these owned free-roaming dogs is high for localised areas, with risk of infection great for single communities or areas (Dürr & Ward 2014, Sparkes *et al*. 2014b). However, because these dogs are generally associated with a single household, distances travelled compared with wild dogs will likely be reduced, restricting the spatial spread of rabies.

During my research, I assessed two free-roaming domestic dog populations: Tiwi Islands, Northern Territory (Chapter 4) and north-east New South Wales (NSW) (Chapters 3 and 6). These populations were chosen based on the identified high risk areas for rabies incursion into Australia (Tiwi Islands) and where the highest densities of dogs (both owned domestic and wild dogs) reside (along the eastern seaboard) (West 2008, Australian Companion Animal Council 2010, Cookson *et al*. 2012).

7.1.4.1 Population 1: Tiwi Islands

Via mark-recapture along transects, I estimated the Wurrumiyanga dog population to comprise 326 dogs, with 1.1 dogs owned per household (Chapter 4). Although dog ownership per household was similar to global domestic dog ownership estimates (Gompper 2014), 90.2% of dogs were free-to-roam. The large number of free-roaming dogs observed within the community resulted in high contact rates between dogs (Table 7-3) and a very high risk of rabies transmission through the community.

Population turnover was high, due to limited availability of veterinary care and the free-roaming nature of the dogs (Chapter 4). That is similar to situations elsewhere, such as in Indonesia, India and Chile (Reece *et al*. 2008, Acosta-Jamett *et al*. 2010, Morters *et al*. 2014). Although there were some reports of human-mediated dog movement between the Tiwi Islands and mainland Australia, for the purpose of this analysis it was assumed to be a closed population, because the frequency of these trips was considered lower than that required for disease progression per year (Table 7-3).

7.1.4.2 Population 2: north-east New South Wales

Free-roaming domestic dogs are common in urban and peri-urban Australia (Chapters 3 and 6, Coman & Robinson 1989, Meek 1999). In north-east NSW, the free-roaming domestic dog population was estimated at 0.12 million (Table 7-4). Similar to restrained domestic dogs, a population growth rate of 0.3% was estimated for this region (Table 7-4). Due to the relatively small activity range per day (0.26 km^2; Table 7-4) and a tendency of dogs to be tied to a single household, estimated contact rates for this group were small, ranging from 0.001 to 0.02 contacts per dog per day, with limited impact on disease transmission over a large scale. Although not discussed here, consideration should also be given to human mediated translocation of asymptomatic dogs ahead of a disease front, as this may create localised rabies outbreaks outside the main infected area.

Table 7-3 Model parameters for free-roaming dogs, Tiwi Islands, Australia

Parameter^	Value	Reference
Population	**326±52**	**Chapter 4**
Births#	**235**	
Population estimate	326	Chapter 4
% female and entire	26.32%	J. Sparkes unpub. data, N = 95
Litters per entire female	0.52	Reece *et al*. 2008, Acosta-Jamett *et al*. 2010, Gsell *et al*. 2012
Pups per litter	5.31	Reece *et al*. 2008, Acosta-Jamett *et al*. 2010, Gsell *et al*. 2012, Morters *et al*. 2014
Deaths#	**230**	
Population estimate	326	Chapter 4
P of mortality for <1yr old	0.48	Reece *et al*. 2008, Morters *et al*. 2014
P of mortality for adults	0.36	Reece *et al*. 2008, Morters *et al*. 2014
Contact rate	**5.24±5.30 contacts/dog/day**	**Chapter 4**
Human mediated excursions	**0**	**Assume no excursions—Island population**

^ Bolded parameters are derived from non-bolded parameters listed below each value, hence no reference is provided for that row

annual value

Table 7-4 Model parameters for free-roaming domestic dogs in north-east New South Wales

Parameter^	Value	Reference
Population	**0.12 million**	
Area	76,275 km^2	3 LLS boundaries: Hunter, North Coast and Northern Tablelands, excluding National Parks and State Forests
North-east NSW domestic dog population	0.46 million	Office of Local Government 2015
% domestic dogs free-to-roam	26%	Chapter 3
Births#	**19,890**	
Population estimate	0.12 million	
% female and entire	10.84%	Chapter 3
Litters per entire female	0.51	Di Nardo *et al*. 2007
Pups per litter	3	Di Nardo *et al*. 2007
Deaths#	**19,531**	
Population estimate	0.12 million	
P of mortality for each age	Varies per age class Range: 0.02 - 1	Di Nardo *et al*. 2007
Mean age at death	11 years	Michell 1999
% dogs in each age class	varied	Chapter 3
Contact rate	**0.004 contacts/dog/day** **Range: 0.001-0.02**	
Contacts/CTN	0.016 ±0.025 Range: 0.003-0.075	Chapter 6
Daily activity range	0.26 ± 1.88km^2	Sparkes, Körtner, Ballard *et al*. unpub. data, N = 892 days, 21 dogs

^ Bolded parameters are derived from non-bolded parameters listed below each value, hence no reference is provided for that row; # annual value

7.1.5 Wild dogs

Wild dogs (including feral domestic dogs, dingoes and their crossbreeds) are a prominent feature throughout mainland Australia. They have both conservation value (in the case of pure dingoes) and are also targeted for control, due to negative impacts on livestock (including disease transfer and injuring and killing livestock; Chapters 2 and 6). Despite continued/sustained control efforts, wild dogs are found in almost all localities across Australia (West *et al*. 2012). Understanding how these dogs interact and utilise their environment is important, not only for controlling wild dog populations, but also for predicting the spread of rabies.

Through the use of data collected in Chapter 6 and the wider literature, the north-east NSW wild dog population was estimated at 8,701 dogs, with an annual population growth rate of 2.8% (Table 7-5). Due to high dog densities along the coast and large daily activity ranges of wild dogs (3.56 km^2; Table 7-5), contact rates were high, compared with free-roaming domestic dogs (range: 0.07–1.99 contacts per dog per day; Table 7-5). Although contact was associated with whelping and young emergence (Chapter 6), no seasonal pattern in contact rates was observed because litters were born throughout the year. Hence, targeting one particular season or time period for rabies management, would be unlikely to elicit a reduction in rabies transmission dynamics for the populations studied.

Table 7-5 Model parameters for wild dogs in north-east New South Wales

Parameter^	Value	Reference
Population	**8,701**	
Wild dog density	0.31±0.53 dogs km^{-2}	Chapter 6, McIlroy *et al*. 1986, Thomson 1992b, Corbett 2001, Fleming *et al*. 2001
North-east NSW State Forest and National Parks area	28,259km^{2}	National Park and State Forest area within 3 LLS boundaries: Hunter, North Coast and Northern Tablelands
Births#	**11,281**	
Population	8,701	
% female	46%	J. Sparkes unpub. camera data, N = 44
Proportion of females sexually mature (across all ages)	0.70	Jones & Stevens 1988
Litters per female	0.79	Thomson *et al*. 1992a
Pups per litter	5.1	Thomson *et al*. 1992a, Corbett 2001, Fleming *et al*. 2001
Deaths#	**11,038**	
Population estimate	8,701	
P of mortality for <1yr old	0.67±0.02	J. Sparkes unpub. camera data, N = 11, Corbett 2001
P of mortality for adults	0.40±0.34	J. Sparkes unpub. collar data, N = 11, McIlroy *et al*. 1986, Thomson *et al*. 1992a
Contact rate	**0.71** **Range: 0.07-1.99**	
Contacts/CTN	0.2 ±0.2 Range: 0.02-0.56	Chapter 6
Daily activity range	3.56 ± 4.98km^{2}	Ballard, Sparkes, Meek *et al*. unpub. data, N = 4041 days, 23 dogs

^ Bolded parameters are derived from non-bolded parameters listed below each value, hence no reference is provided for that row; # annual rate

7.1.6 Between-group rabies transmission

From the conceptual model in Figure 7-1 and parameters highlighted above, the highest risk of disease transfer between the different groups of dogs would likely originate from interactions with wild dogs. Table 7-6 provides parameter estimates for interactions between wild and free-roaming domestic and hunting dogs.

Reports of interactions between pet dogs and wild dogs are frequent (D. Chamberlain, Team Leader, Invasive Species & Plant Health, North Coast Local Land Services, pers. com. 2015), particularly in peri-urban environments where there are large numbers of both free-roaming domestic dogs and wild dogs. In a peri-urban area of north-east NSW, one local landholder described seeing his two free-roaming domestic dogs travel through the paddock, approximately 200 metres from his house, to interact with three wild dogs (Jock Cunningham, pers. com. 2014). This interaction resulted in one of the domestic dogs receiving bite wounds to the hind legs and rump. Although interactions between wild and domestic dogs in north-east NSW were considered low (0.0012 contacts per dog per day; Table 7-6), this transmission pathway is likely to be a key link between urban and sylvatic rabies cycles and should be given high priority for rabies management during an outbreak.

Table 7-6 Between-group contact rates for hunting, wild and free-roaming domestic dogs

Parameter^	Value	Reference
Hunting—wild	**0.057 wild dog encounters per hunter per day**	Chapter 5
Free-roaming domestic—wild	**0.00012 contacts/dog/day**	
Non-violent contact	0.000115 contacts/dog/day~	Chapter 6
Attacks (injured and death)	19.35 attacks pa	Local Land Services domestic dog reported attacks, north-east NSW
North coast LLS area free-roaming dog population	42,182	Office of Local Government 2015, LLS north coast regional area

^ Bolded parameters are derived from non-bolded parameters listed below each value, hence no reference is provided for that row

~Based on ‘interactions’ between wild and domestic dogs <0.5hrs

In contrast to wild dogs, interactions between working dogs and restrained domestic dogs would be limited, unless they reside at the same location. Because of the limited opportunity for contact, the risk of infection between these groups of dogs at a large scale is low.

Although not discussed here, consideration should also be given to how these different dog types interact with other animals, as rabies can infect any mammal. In particular, focus should be given to the potential spread of rabies into foxes and feral cats as they are numerous across Australia (West 2008) and, as seen elsewhere, have the potential to become infected and transmit the disease (Fogelman *et al*. 1993, Holmala & Kauhala 2006, Dyer *et al*. 2014).

7.2 Transmission dynamics

As discussed in Chapter 2, models used to predict the introduction and spread of rabies can range from simple systems of ordinary differential equations (e.g. state-transition models) to extensive computational simulations (e.g. multi-patch stochastic models) (McCormack & Allen 2007, Panjeti & Real 2011, Zhang *et al*. 2011). For any model utilised, virus ecology parameters need to be identified and defined. Table 7-7 highlights important disease parameters for use in rabies modelling.

Table 7-7 Table of rabies-specific parameters

Parameter	Value	Reference
P dog rabies (risk)^	0.45	Hampson *et al.* 2009, Zhang *et al.* 2011
Mean bites per rabid dog	2.15	Hampson *et al.* 2009
Transmission rate	0.0085 per animal	Carroll *et al.* 2010
Latent period	22.3 days 95% CI: 20.0-25.0	Hampson *et al.* 2009
Infectious period	4.8 days Range: 2.9-5.7	Hampson *et al.* 2009, Zinsstag *et al.* 2009, Carroll *et al.* 2010
Death rate	1 (all infected dogs die)	Dürr & Ward 2015

^ Probability of an unvaccinated dog contracting rabies after being bitten by an infectious animal

7.3 Control options

Probability of (successful) intervention will likely change based on dog type. For example, rabies has been virtually eliminated in domestic dogs in North America and parts of Europe (Müller *et al*. 2012, Dyer *et al*. 2014). In contrast, rabies vaccination and control programs to contain wildlife rabies outbreaks continue at high cost in many countries (Sterner & Smith 2006, Freuling *et al*. 2013). These differences are likely due to lower accessibility of wildlife for vaccination/control programs and proximity to, and interactions with, humans. A similar situation would be expected in Australia if rabies were to enter the wild dog population.

In the following section, I developed state-transition (SEIR compartmental) models to demonstrate how data collected throughout my thesis can be used to model rabies spread through different dog communities in Australia. I further sought to identify the most effective management strategies to deploy in the event of a rabies outbreak.

7.4 Rabies disease dynamics in naïve dog populations in Australia

This Chapter has been written in the format of a scientific paper and has been submitted to Preventive Veterinary Medicine with the following authorship:

Jessica Sparkes[a,b,c,e], Steven McLeod[b], Guy Ballard[a,d,c], Peter J S Fleming[a,b,c], Gerhard Körtner[a,c,d] and Wendy Y Brown[a]

[a] School of Environmental and Rural Science, University of New England, Armidale, NSW, 2351, Australia

[b] Vertebrate Pest Research Unit, Biosecurity NSW, Orange, NSW, 2800, Australia

[c] Invasive Animals Cooperative Research Centre, Armidale, NSW, 2351, Australia

[d] Vertebrate Pest Research Unit, Biosecurity NSW, Armidale, NSW, 2351, Australia

[e] Corresponding author:

Email: jessica.sparkes@dpi.nsw.gov.au

Ph: +61 2 6391 3100

Fax: +61 2 6391 3972

Address: 1447 Forest Rd, Orange, NSW, Australia, 2800

7.4.1 Abstract

Currently, Australia is free from terrestrial rabies but an incursion from nearby Indonesia, where the virus is endemic, is a feasible threat. Here, we aimed to determine whether the response to a simulated rabies incursion would vary between three extant Australian dog populations; free-roaming domestic dogs from a remote Indigenous community in northern Australia, and free-roaming domestic and wild dogs in peri-urban areas of north-east New South Wales. We further sought to predict how different management strategies impacted disease dynamics in these populations.

We used simple stochastic state-transmission models and dog demographic and contact rate data from the three dog populations to simulate rabies spread, and used global and local sensitivity analyses to determine effects of model variables. To identify the most effective control options, dog removal and vaccination strategies were also simulated.

Responses to simulated rabies incursions varied between the dog populations. Free-roaming domestic dogs from north-east New South Wales exhibited the lowest risk for rabies maintenance and spread. Due to low containment and high contact rates, rabies progressed rapidly through free-roaming dogs from Indigenous communities in northern Australia. In contrast, rabies remained at relatively low levels within the north-east New South Wales wild dog population for over a year prior to an epidemic. Across all scenarios, sensitivity analyses revealed that contact rates and the probability of transmission were the most important drivers of the number of infectious individuals within a population. The number of infectious individuals was less sensitive to birth and death rates across all populations. Removal of dogs as a control strategy was not effective for any population modelled, while vaccination rates in excess of 70% of the population resulted in significant reductions in disease progression.

The variability in response between these distinct dog groups to a rabies incursion, suggests that a blanket approach to management would not be effective or feasible to control rabies in Australia. Control strategies that take into account the different population and behavioural characteristics of these dog groups will maximise the likelihood of effective and efficient rabies control in Australia.

7.4.2 Highlights

- Rabies transmission in three extant Australian dog populations was modelled with stochastic state-transmission models
- Disease progression was rapid in free-roaming dogs within Indigenous communities
- Low contact rates amongst free-roaming domestic dogs in NSW inhibited rabies spread
- Rabies spread in wild dogs was prolonged; an epidemic peaked 1 year post incursion
- High vaccination rates with limited dog removal proved the best control option

Keywords

Canis familiaris, dingo, disease modelling, free-ranging, SEIR, state-transition

7.4.3 Introduction

Terrestrial rabies, a preventable viral zoonosis, is responsible approximately 59,000 deaths annually (Hampson *et al.* 2015). In developing continents such as Africa and Asia, rabies virus is usually transmitted to humans in saliva via the bite of an infected dog (*Canis familiaris*) (Warrell & Warrell 2004). Although rabies is not currently in Australia, an incursion of a canine rabies biotype from Indonesia, where recent outbreaks have occurred in humans and domestic dogs (Tenzin & Ward 2012) is a realistic and imminent threat (Murray *et al.* 2012). Because current Australian policies prevent prophylactic vaccination of animals against rabies (Animal Health Australia 2011), all Australian dogs will be susceptible to rabies virus infection.

Most available models of rabies spread tend to simulate control strategies that have not yet been applied to rabies virus affected regions (e.g. Zinsstag *et al*. 2009, Brunker *et al*. 2012, Zhang *et al*. 2012). Because Australia has never had endemic rabies (there has likely only been one incursion, in 1867 (Pullar & McIntosh 1954) and the disease did not persist), model outputs from rabies endemic regions may not be representative of an Australian rabies outbreak scenario. Consequently, it is imperative that Australia develop models using local dog behavioural and population dynamic parameters, in conjunction with known rabies epidemiological parameters, to aid preparation for a terrestrial rabies outbreak (Sparkes *et al*. 2015).

As well as being free of rabies, Australia differs to other countries in the assemblage of functional categories of dogs present. Australia's dogs can be separated into three groups or populations based on the extent and type of association with humans and their ability to roam: a) restrained domestic dogs, that rely solely on humans for food and shelter; b) free-roaming domestic dogs, that are owned but allowed to roam freely at some point; and c) wild dogs, including dingoes, that are not reliant on humans for resources and always free to roam. Although classified into distinct categories here, these dog functional groups exist along a continuum and individuals from the functional groups interact (e.g. Dürr & Ward 2014; Sparkes *et al*. 2014). Although wild dogs are very seldom tamed and restrained, some of the other dogs may move between different groups during their life (e.g. usually restrained dogs escaping through an open gate, working dogs being retired or restrained when not working, hunting dogs being restrained except when hunting). Previous research (e.g. Coman & Robinson 1989, Meek 1999, Claridge *et al*. 2009, Allen *et al*. 2013, Dürr & Ward 2014) reinforces behavioural differences between these functional groups, hence, it is reasonable to expect each may respond differently to a rabies incursion.

Although Dürr & Ward (2015) recently modelled rabies spread from data collected in two remote regions of northern Australia, only one of the three dog groups identified here, i.e. community free-roaming dogs, was assessed. To our knowledge, no studies have attempted to model a rabies incursion in more than one of these functional groups. The differences between Australian dog groups makes it imperative that an explicit understanding of their likely responses to a rabies incursion is established, to ensure targeted and effective control strategies that encompass behavioural differences between the functional groups. It should also be noted that while rabies can infect any mammal, there are several variants of the virus, and the arrival of the canine rabies biotype into Australia is the most likely scenario, rendering the spill over of rabies into other species such as the European Red Fox (*Vulpes vulpes*), a side issue (Sparkes *et al.* 2015).

In Australia's national rabies preparedness strategy, the rabies AUSVETPLAN, control strategies hinge on vaccination and dog removal (Animal Health Australia 2011). These strategies are based on models and experiences from rabies endemic countries (e.g. Shwiff *et al*. 2008, Hampson *et al*. 2009, Morters *et al*. 2013). Although it has sometimes failed (Tenzin & Ward 2012), vaccination has generally been more successful in controlling rabies, than dog culling programs (Rupprecht *et al*. 1995, Morters *et al*. 2013). Culling for rabies mitigation purposes usually targets dogs suspected to be infected and is not typically applied as a prophylactic, or as a reactive management action to control rabies. However, culling is commonly undertaken in Australia to reduce populations of wild dogs to protect livestock from predation (e.g. Fleming *et al*. 2001; Allen *et al*. 2014, Fleming *et al.* 2014). Hence, Australia's range of rabies control strategies among wild dogs would likely include the removal of suspected infected individuals, population reduction and oral vaccination (Animal Health Australia 2011) or combinations of these. Although Dürr & Ward (2015) found culling of detected rabid dogs was likely an unsuccessful strategy for rabies extinction in Australia, they did not model proportional removals of susceptible individuals, nor population reductions.

Here, we developed simple models to describe the temporal response of dogs to a rabies incursion in Australia. We used two realistic incursion scenarios and sought to identify optimal management strategies for each scenario. Rather than treating all dogs homogenously, we modelled responses for three different dog populations: a) free-roaming domestic dogs from a remote Indigenous community; b) free-roaming domestic dogs from peri-urban areas; and c) wild dogs.

7.4.4 Scenarios

The most likely incursion scenario, for Australia, would be the importation of an asymptomatic (latently infected) dog from a neighbouring island, as occurred in the 2008 rabies outbreak in Bali, Indonesia (Clifton 2010). In Australia's case, a dog infected with rabies would likely originate from Indonesia.

Here, we propose two scenarios, a rabies incursion into 1) free-roaming domestic dogs within a remote Australian Indigenous community in northern Australia and 2) a peri-urban free-roaming domestic and wild dog population in north-east New South Wales (NSW). Parts of mainland northern Australia lie less than 300km from rabies-endemic regions of Indonesia (Tenzin & Ward 2012), while the largest human and dog populations are located in eastern NSW (West 2008, Australian Companion Animal Council 2010, Australian Bureau of Statistics 2014). Therefore, these regions are likely at the highest risk areas for rabies introduction and spread, and are the focus of our scenarios.

7.4.4.1 Scenario 1- Incursion into a remote Indigenous community, northern Australia

A dog– infected with rabies but prior to the onset of clinical signs– is introduced into a remote Australian Indigenous community, via an Indonesian fishing boat (*sensu* Sparkes *et al*. 2015). Within a few days, the dog shows clinical signs of rabies and is abandoned or lost nearby or within the community. As in many northern Australian Indigenous communities, free-roaming dogs are common, with 90.2% of the dog population free-to-roam (Sparkes *et al*. 2014b), and the infected dog interacts with these community dogs. Due to the altered behaviour of the infected dog (Hampson *et al.* 2009) and because dogs are territorial (Perez-Guisado & Munoz-Serrano 2009b), aggressive interactions result between local dogs and the infectious intruder. Consequently, rabies is transmitted to resident community dogs, which soon begin to die.

Due to a lack of rabies awareness within the community, time to detect the initial rabies outbreak is prolonged (Dürr & Ward 2015). Absence of veterinary facilities within the community further confounds detection. Following an increase in dogs biting humans, local medical staff seek assistance. An itinerant veterinary officer performs a necropsy on a symptomatic dog and sends samples to the Australian Animal Health Laboratory in Victoria, for testing. The rabies virus is positively identified and the Australian veterinary emergency plan for a rabies incursion (AUSVETPLAN) is triggered (Animal Health Australia 2011).

7.4.4.2 Scenario 2- Incursion into north-east New South Wales

A dog– infected with rabies but prior to the onset of clinical signs– is illegally brought to the port of Ballina, north-east NSW from Indonesia on a vessel (e.g. yacht or fishing boat; Sparkes *et al*. 2015). Within a few days, the dog shows clinical signs of rabies and is abandoned or lost nearby or within the community. North-east NSW becomes the focus of the rabies epidemic for Scenario 2. The infected dog roams through private, peri-urban properties and public land (e.g. National Parks and State Forests), where it encounters other free-roaming domestic and wild dogs in the region. Some encounters result in aggressive confrontations and the dog is killed by wild dogs. The virus is transmitted to local wild dogs and free-roaming domestic dogs. As per Scenario 1, aggression towards humans results in the identification of rabies and the Australian veterinary emergency plan for a rabies incursion (AUSVETPLAN) is triggered (Animal Health Australia 2011).

7.4.5 Methods

Three populations of dogs were considered in this study; free-roaming Island community dogs, peri-urban free-roaming domestic dogs and wild dogs. Using state-transition models, each dog population was classified into four subclasses: susceptible (S), exposed (E), infectious (I) and removed or immune (R). Figure 7-2 describes the flow of dogs between states. For dog population i, B_i describes the annual birth rate, with births remaining constant throughout the year, σ_i denotes the inverse of the incubation period, α_i represents the disease death rate, d_i is the natural death rate, $cull_i$ the routine culling practices (for wild dogs only) and β_i describes the transmission of rabies by interactions between infectious and susceptible dogs, where:

β_i = contact rate*Probability of rabies virus transmission

The model was solved using a daily time step, with all populations considered to be closed (See Appendix 7-1 for parameter estimates).

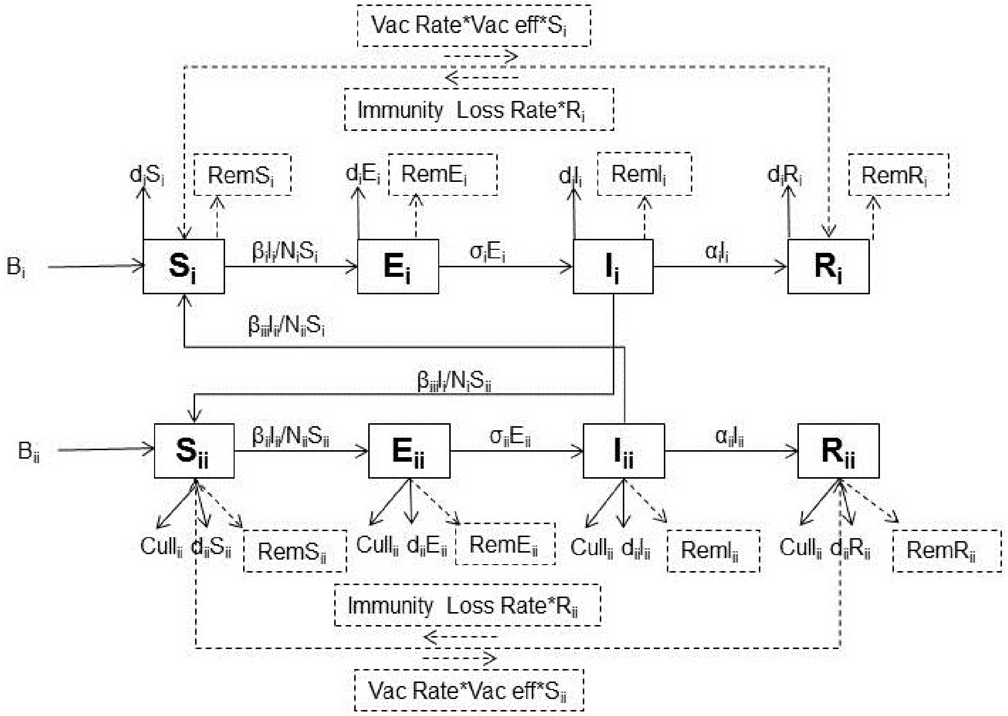


Figure 7-2 Transition model diagram of rabies within and between dog populations. S_i, E_i, I_i and R_i represent susceptible, exposed, infectious and removed or immune (i.e. vaccinated) dogs, respectively. The dashed lines indicate movement of individuals between states only when control is implemented.

The state-transition models were solved in R (R Core Team 2015) using the *Desolve* (Soetaert *et al.* 2010) and *MC2D* packages (Pouillot & Delignette-Muller 2010). A single host model was used for scenarios one and two, while a multi-host model was also used for scenario two. For both scenarios, a single infected dog entering the population was considered the source of infection.

Model 1:

For the single host models, three ordinary differential equations were used:

$$\frac{dS_i}{dt} = (B_i - d_i) * S_i - \beta_i * \frac{I_i}{N_i} * S_i - cull_i * S_i \qquad \text{Eq. 1}$$

$$\frac{dE_i}{dt} = \beta_i * \frac{I_i}{N_i} * S_i - (\sigma_i + d_i) * E_i - cull_i * E_i \qquad \text{Eq. 2}$$

$$\frac{dI_i i}{dt} = \sigma_i * \mathrm{E}_i - (\alpha_i + \mathrm{d}_i) * \mathrm{I}_i - \mathrm{cull}_i * \mathrm{I}_i \qquad \text{Eq. 3}$$

Model 2:

For the multi-host transition model used in scenario two, an additional set of parameters were included to take account of transmission between dog groups:

$$\frac{dS_1}{dt} = (B_1 - d_1) * S_1 - \beta_1 * \frac{I_1}{N_1} * S_1 - \beta_3 * \frac{I_2}{N_2} * S_1 \qquad \text{Eq. 4}$$

$$\frac{dE_1}{dt} = \beta_1 * \frac{I_1}{N_1} * S_1 + \beta_3 * \frac{I_2}{N_2} * S_1 - (\sigma_1 + d_1) * E_1 \qquad \text{Eq. 5}$$

$$\frac{dI_1}{dt} = \sigma_1 * E_1 - (\alpha_1 + d_1) * I_1 \qquad \text{Eq.6}$$

$$\frac{dS_2}{dt} = (B_2 - d_2) * S_2 - \beta_2 * \frac{I_2}{N_2} * S_2 - \beta_3 * \frac{I_1}{N_1} * S_2 - \text{cull}_2 * S_2 \qquad \text{Eq. 7}$$

$$\frac{dE_2}{dt} = \beta_2 * \frac{I_2}{N_2} * S_2 + \beta_3 * \frac{I_1}{N_1} * S_2 - (\sigma_2 + d_2) * E_2 - \text{cull}_2 * E_2 \qquad \text{Eq. 8}$$

$$\frac{dI_2}{dt} = \sigma_2 * E_2 - (\alpha_2 + d_2) * I_2 - \text{cull}_2 * I_2 \qquad \text{Eq. 9}$$

where S_1, E_1 and I_1, are susceptible, exposed and infectious free-roaming domestic dogs and S_2, E_2 and I_2 are susceptible, exposed and infectious wild dogs and β_3 is the transmission coefficient between dog groups. Two simulations were run for this model, where the initial infected dog originated from a wild or domestic dog, respectively. In both models, an infected dog was introduced at day one, with all simulations run for 800 days.

Global and local sensitivity analyses were undertaken in R using the FME package (Soetaert & Petzoldt 2010) for each of three dog populations (using Model 1). The sensitivity of the model's state variables (S, E, I and N) to the parameters σ, α, contact rate and probability of transmission were examined using a global sensitivity analyses. For this analyses, all parameters were varied simultaneously over their entire feasible space (i.e. the maximum and minimum values specified; see Appendix 7-2), using a sampling based approach (n=100 model repetitions). For the local sensitivity analyses, parameters (σ, α, contact rate, probability of transmission, birth and death rates and, for wild dogs only, culling rate) were varied one at a time by a small amount around a fixed point (see Appendix 7-2).

7.4.5.1 Control strategies

After running the simulations described above, control via vaccination and dog removal, were applied to the dog populations where rabies was sustained (See Appendix 7-3 for model). In Scenario one, rabies was detected early and control initiated at day 14. For Scenario two, time to initial response was considered much longer due to reduced human contact with wild dogs and lower likelihood of detection, and commenced at day 200. Vaccination (Vac) and/or removal (Rem) rates of 0, 0.1, 0.3, 0.5, 0.7, 0.9 and 1 of the dog population were applied to the model over a period of 7 days in the northern Australian free-roaming dog population and for 30 days for the north-east NSW wild dog population, with control periods initiated annually. Rates were chosen based on the ability to access dogs and published data on removal (Fleming 1996, Fleming & Ballard 2014) and rabies vaccination success rates (World Health Organisation 2005, Tenzin & Ward 2012). The free-roaming northern Australian community dog control simulations were run for 300 days, while the wild dog simulations were run for 800 days.

Due to large variation reported for contact rates in wild and free-roaming dog populations, these model parameters for the control simulations were defined as either beta-pert distributions (minimum, mode, maximum), uniform distributions (minimum, maximum) or fixed values (see Appendix 7-1 for parameter estimates). Each simulation was repeated 1,000 times and the mean number of infected individuals per day of the simulation was calculated to compare control efficacy. Data for infected individuals per day are presented as mean (±SD). Results of vaccination- and removal-only simulations were compared using a Welch's two sample paired *t*-test (Welch 1947).

7.4.6 Results

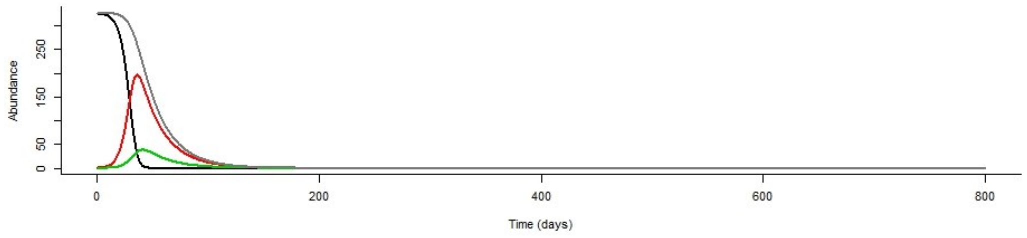
7.4.6.1 Single host, no control

For Scenario one, rabies progressed rapidly through the free-roaming community dogs, with a peak in exposed individuals at day 36 (Figure 7-3a). By day 127, the number of infected individuals in the population fell below one. Without intervention, rabies caused the dog population to collapse, with no dogs surviving. At the broadest contact rates estimated by Sparkes et al. 2014, global sensitivity results were overwhelmed by the variance in contact rates (See Appendix 7-2). Subsequently, a narrower range of contact rates (3.0-7.0 contacts per dog per day) was used. Local sensitivity analysis revealed that the number of infectious (I) individuals was most sensitive to σ, contact rate and probability of transmission, followed by α and birth and death rates (See Appendix 7-2).

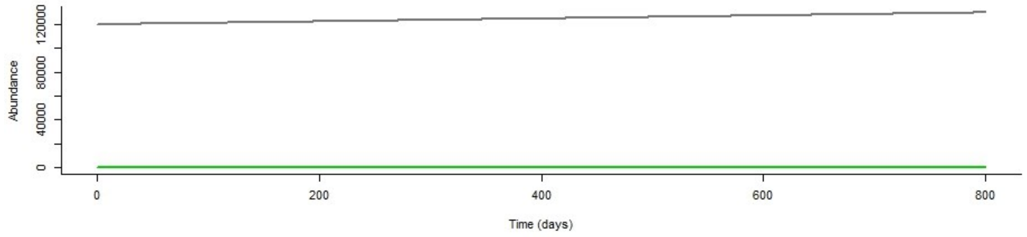
In contrast to Scenario one, the free-roaming domestic dogs in Scenario two were relatively unaffected by a single rabid dog incursion (Figure 7-3b), likely due to limited contact between susceptible individuals. Global and local sensitivity analyses indicated that the number of infectious free-roaming domestic dogs in north-east NSW were most sensitive to α, σ, contact rates and the probability of transmission (See Appendix 7-2).

In the north-east NSW scenario for wild dogs (Figure 7-3c), the lag phase prior to an epidemic was drawn out, with the number of infected individuals peaking at day 565. By day 781, the number of infected individuals fell below one. Without intervention, the wild dog population collapsed, with only two dogs surviving at day 800. Within the wild dog scenario modelled, α, contact rates and the probability of transmission were all equally important in rabies transmission (See Appendix 7-2). The number of infectious individuals was much less sensitive to σ, birth and death rates, while sensitivity to the culling rate of wild dogs was low.

a) Tiwi Islands



b) Free roaming domestic



c) Wild

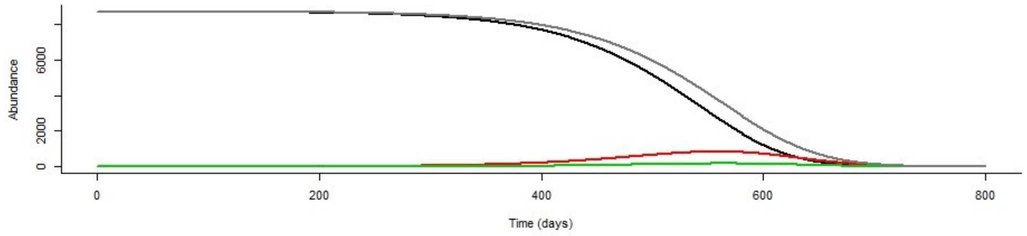


Figure 7-3 Rabies progression in a single dog category without intervention for a) free-roaming community dogs, Tiwi Islands, remote northern Australia, b) peri-urban north-east New South Wales free-roaming domestic dogs and c) peri-urban north-east New South Wales wild dogs. Lines represent total population (grey), susceptible (black), exposed (red) and infectious (green) individuals. Time is in days.

7.4.6.2 Multi-host model, no control

For the multi-host model, contact between free-roaming domestic and wild dogs did not facilitate rabies transfer between reservoir dog groups. However, due to the low contact rates recorded between these dog groups, wild dogs may be an infrequent source of rabies spillover from sylvatic to urban cycles. This would be particularly important during the peak of the epidemic (in the second year of disease progression), where the risk of domestic dogs contacting an infective wild dog would be greater compared with the early or late phase of disease dynamics (Figure 7-3).

7.4.6.3 Single host, with control

The results of Models 1 and 2 indicate that in free-roaming domestic dogs in north-east NSW, it is unlikely that a single infected individual will cause a rabies epizootic. As such, control simulations were carried out for northern Australian free-roaming domestic and north-east NSW wild dogs only.

Scenario 1: Free-roaming domestic dogs, northern Australia

Increasing the proportion of dogs vaccinated or removed within the community reduced the mean number of infected individuals, slowing rabies progression (Figures 7-4 and 7-5). Vaccination alone provided significantly better reductions in mean infected individuals at all vaccination and removal levels (Welch t test: t_5=-4.56, P = 0.006) compared with dog removal alone (Figure 7-4). However, the variation observed amongst simulation runs revealed vaccination alone resulted in increased uncertainty compared with dog removal (i.e. larger standard deviation was observed for vaccination versus dog removal). Despite this, vaccination of free-roaming domestic dogs remained the most effective control strategy.

When used in combination, medium to high vaccination and removal rates (≥50%) reduced mean infected individuals to less than 1 per day (Figure 7-6). However, increasing vaccination and removal rates above 0.7 did not greatly reduce the mean number of infected individuals compared with rates of cf. 50-70% (Figure 7-6). In contrast, low vaccination rates and high removal rates resulted in an increase in mean infected individuals within the population (Figure 7-6).

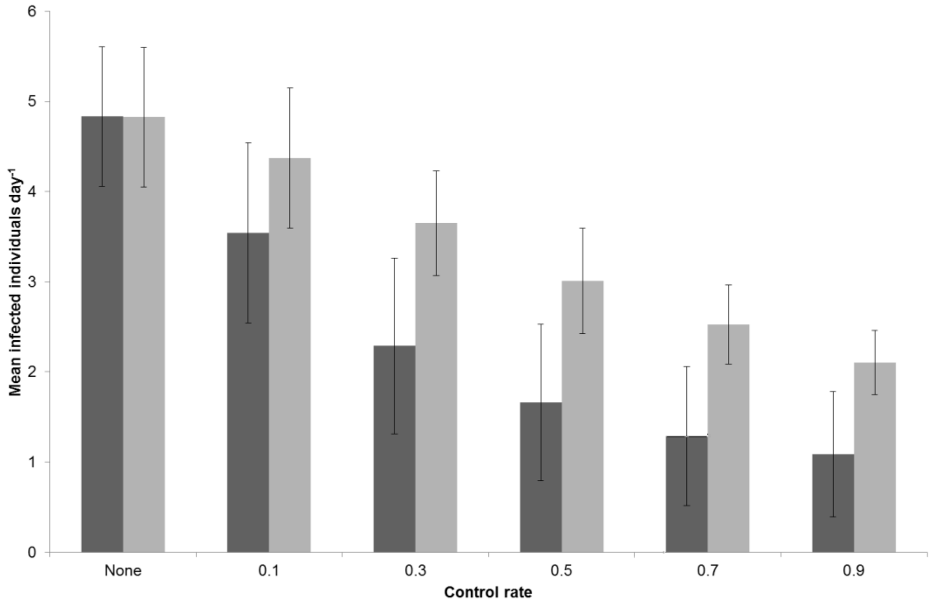


Figure 7-4 Mean infected individuals per day (±SD) with 0, 0.1, 0.3, 0.5, 0.7 and 0.9 of the free-roaming remote northern Australian community dog population vaccinated (dark) or subject to removal (light), based on 1,000 simulation runs per control option.

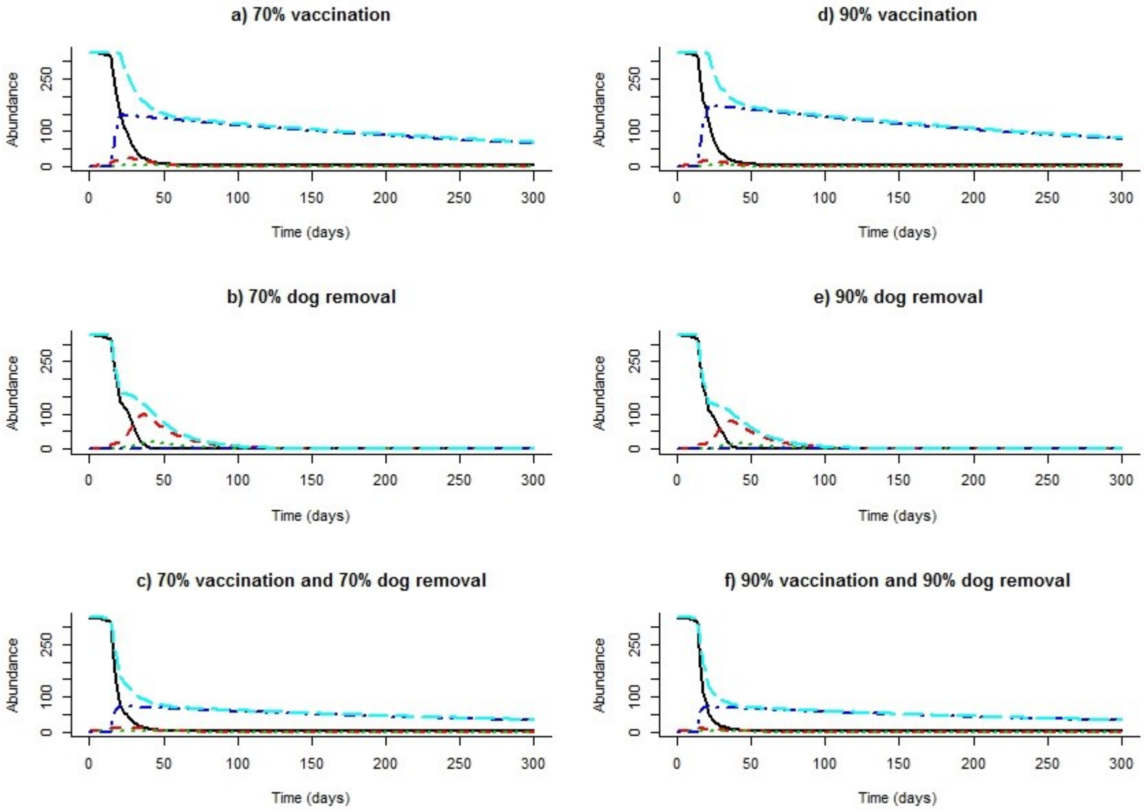


Figure 7-5 Example simulation runs for 0.7 (left column) and 0.9 (right column) of the Tiwi Islands free-roaming domestic dog population vaccinated (a), (d), removed (b) (e) and combined vaccinated and removed (c), (f), with a contact rate of 5.24 contacts per dog per day. Lines represent total population (light blue longdash), susceptible (black solid), removed (immune) (blue dotdash), exposed (red dashed) and infectious (green dotted) individuals and time is in days.

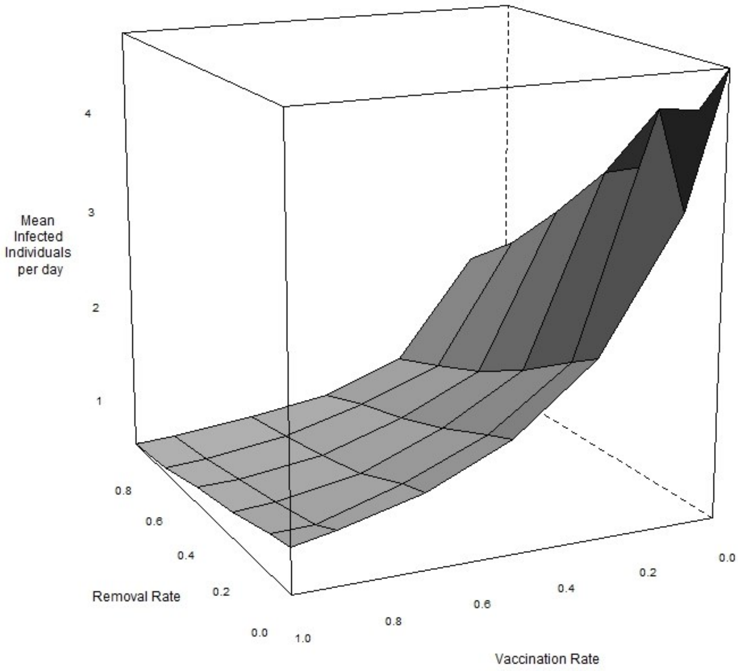


Figure 7-6 Response surface showing the interaction between vaccination and removal rates expressed as mean infected remote community dog individuals per day, northern Australia, based on 1,000 simulation runs per control combination. Light to dark shading depicts fewer to greater numbers of infected individuals.

Scenario 2: Wild dogs, north-east New South Wales

Increasing the proportion of dogs vaccinated, or the proportion removed from the population reduced the mean number of infected individuals (Figures 7-7 and 7-8). However, the rate at which the mean number of infected individuals per day decreased, slowed when 70% of the population was either vaccinated or removed. In contrast to Scenario 1, there was no difference between vaccination and removal strategies when undertaken in isolation (Welch t test: t_9=1.26, P = 0.24; Figure 7-7). However, due to large variation observed around the mean number of infected individuals per simulation run (Figure 7-7), the outcome from wild dog rabies control strategies was less predictable compared with control strategies implemented for free-roaming community dogs.

A combination of vaccination and removal provided a positive multiplicative effect on the mean number of infected individuals when removal rates exceeded vaccination rates

(Figure 7-9). However, increasing vaccination rates above 0.7 and removal rates above 0.5 did not greatly reduce the mean number of infected individuals per day (Figures 7-8 and 7-9).

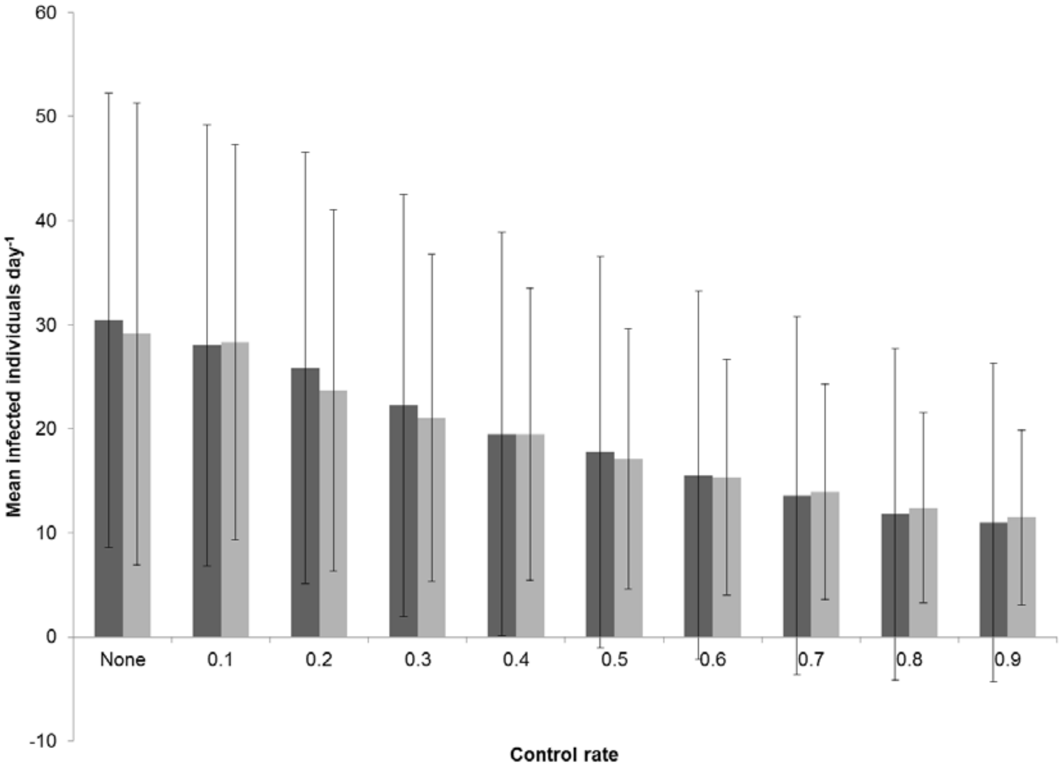


Figure 7-7 Mean infected individuals (±SD) per day with 0, 0.1, 0.3, 0.5, 0.7 and 0.9 of the peri-urban north-east New South Wales wild dog population vaccinated (dark) or subject to removal (light), based on 1,000 simulation runs per control option.

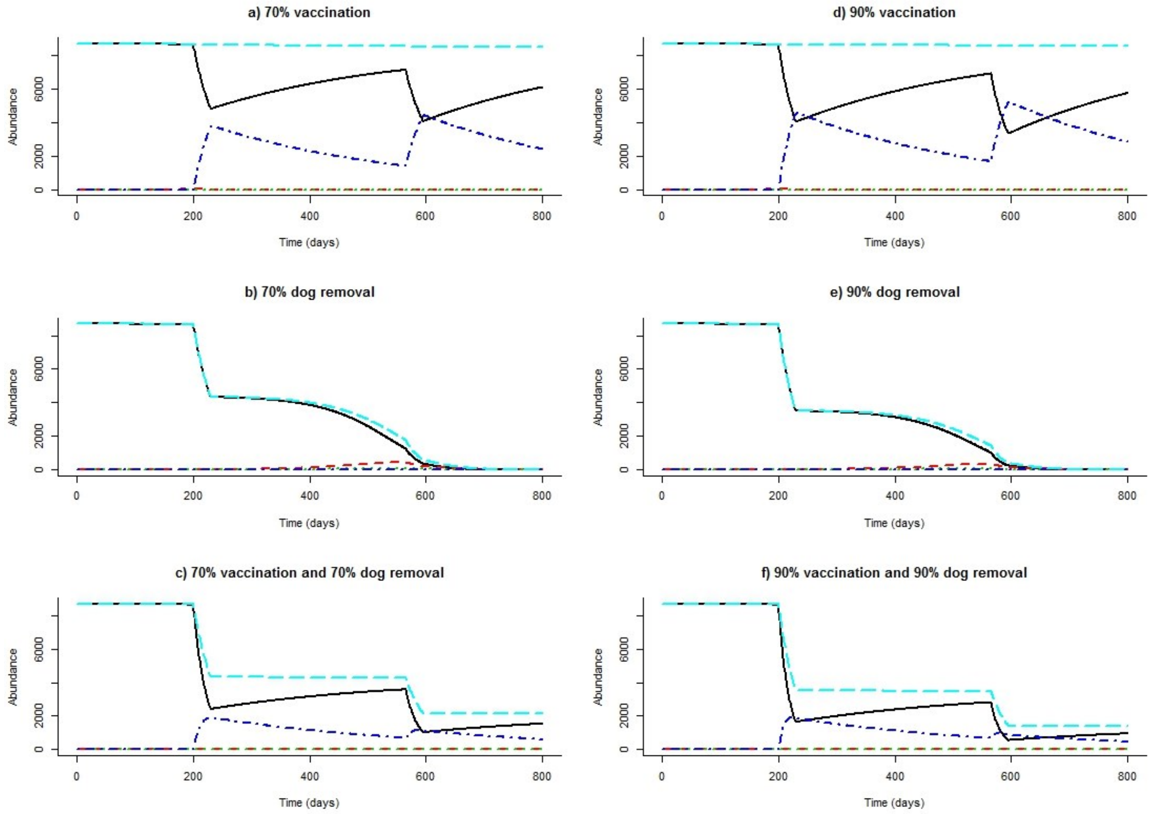


Figure 7-8 Example simulation runs for 0.7 (left column) and 0.9 (right column) of the wild dog population vaccinated (a), (d), removed (b) (e) and combined vaccinated and removed (c), (f), with a contact rate of 0.71 contacts per dog per day. Control strategy was implemented annually. Lines represent total population (light blue longdash), susceptible (black solid), removed (immune) (blue dotdash), exposed (red dashed) and infectious (green dotted) individuals. Time is in days.

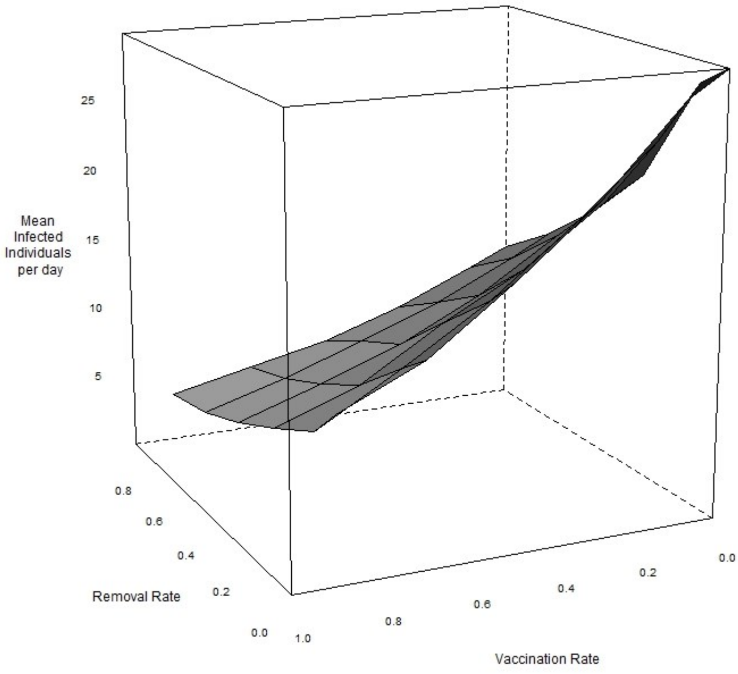


Figure 7-9 Response surface showing the interaction between vaccination and removal rates expressed as mean infected wild dog individuals per day, based on 1,000 simulation runs per control combination. Light to dark shading depicts fewer to greater numbers of infected individuals.

7.4.7 Discussion

All three dog populations identified and characterised here, expressed different responses to a rabies incursion despite being the same species. By developing simple state-transition models, we found that free-roaming domestic dogs residing in remote Indigenous communities were at highest risk of contracting and spreading rabies. For that group, the disease spread rapidly through the population, predominantly due to high contact rates. In reality, this occurs because of poor restraint of dogs, through a lack of fencing or tethering or both. This reflected scenarios seen in developing countries, where rabies remains a serious threat to human and animal lives (World Health Organisation 2005, Tenzin & Ward 2012). In contrast, it appears that in the wild dog population, rabies would likely remain at low levels for an extended period of time, limiting chances for localised detection and increasing rabies infection on a larger geographic scale. Due to relatively low contact rates, free-roaming domestic dogs in north-east NSW provided the lowest risk for rabies maintenance and spread in the dog populations assessed. Although free-roaming domestic dogs in peri-urban areas of north-east NSW may be exposed intermittently to infected wild dogs, the rate at which these interactions occur are not sufficient to create an epidemic in that dog group. Similar experiences have been observed in developed countries elsewhere, where rabies exposure from wildlife reservoirs and subsequent infection in domestic dogs is minimal (Rupprecht *et al.* 1995, Holmala & Kauhala 2006, Dyer *et al.* 2014).

To reduce the likelihood of an epidemic, response times to a rabies incursion must be rapid for some dog groups. This is particularly important for the free-roaming domestic dog population in remote northern Australia, where modelling illustrates a rabies epidemic is likely to occur within one month of an infected individual entering the community (Figure 7-3). High contact rates within this population (Sparkes *et al.* 2014b) mean that successful control of rabies would require extensive vaccination at the onset of a rabies incursion into the population, or at the very least, confinement of dogs to the home residence. In contrast, the time to vaccinate is not as critical for low contact rate populations (i.e. wild and free-roaming domestic dogs in north east NSW), with a longer lag phase observed prior to an epidemic and eventual population crash. However, due to the relatively long period between initial infection and an epidemic, rabies may go undetected in wild dogs for a long time.

On its own, the removal of dogs was not an effective rabies management strategy for any population modelled. Indeed, it increased the mean number of infected individuals when used in conjunction with low vaccination rates for the northern Australian free-roaming domestic dog population (Figure 7-5). Due to the cultural significance of dogs in Indigenous communities (Constable *et al.* 2010), forced removal of dogs from communities would also likely result in mistrust of authorities, encourage undesirable behaviours such as hiding dogs or moving them between communities, thereby potentially increasing the geographical spread of rabies in Australia: this behaviour has been observed in Indonesia (Bingham 2001, Windiyaningsih *et al.* 2004). Similar to rabies endemic regions in developing countries, high population turnover among free-roaming community dogs may limit the effectiveness of programs to vaccinate them (Hampson *et al.* 2009, Zhang *et al.* 2012, Conan *et al.* 2015). An increase in the number of annual rabies control programs and improved dog management that reduces annual birth rates and encourages confinement of pet dogs could help to ensure sufficient animals are vaccinated or removed from the susceptible state.

The control of rabies in wildlife populations is notoriously difficult (e.g. fox and raccoon rabies in the United States, Canada and Europe; Rupprecht *et al.* 1995, Smith 1996, Freuling *et al.* 2013). Our modelling suggests that a similar scenario would be expected in Australian wild dog populations. Although reducing the wild dog population through dog removal reduced the mean number of infectious individuals per day (Figure 7-7), it did not prevent a crash in the population at either the 70% or 90% removal rates (Figure 7-8), suggesting that removal alone would likely not be successful for rabies control in Australian wild dogs. Further, previous work in rabies endemic regions has found that culling was likely to disrupt dog social structures and increase contact rates between susceptible individuals, potentially increasing rate of spread (Aubert 1992, Rupprecht *et al.* 1995, Smith 1996, Morters *et al.* 2013).

Oral vaccination of wildlife has proven to be effective at controlling and even eliminating rabies in reservoir species such as the red fox and raccoons (*Procyon lotor*) in parts of Europe, Canada and America (Sterner *et al.* 2009, Müller *et al.* 2012, Freuling *et al.* 2013). If these findings for other reservoir species correlate with effective oral vaccination campaigns in dogs, our results suggest that a similar approach could be successful here. While 100% vaccination and removal rates are modelled here (Figure 7-9), campaigns would be unlikely to achieve 100% coverage within wild dog populations due to limited accessibility. However, current aerial wild dog control activities can effectively remove up to 90% of wild dog populations in some regions (Fleming & Ballard 2014). As such, if rabies were to enter Australia, target vaccination rates of up to 90% could be considered achievable.

To achieve high vaccination rates, an oral rabies vaccination program must also account for the removal of baits by non-target animals (Allen *et al.* 1989, Fleming 1996). Wildlife including foxes, feral pigs (*Sus scrofa*) and feral cats (*Felis catus*) are numerous throughout mainland Australia (West 2008) and will consume and cache baits, making them unavailable to dogs (Allen *et al.* 1989, Glen & Dickman 2003, Fleming & Ballard 2014). Bait delivery above the targeted vaccination rate may assist in maximising bait availability for wild dogs.

Despite the threat of a rabies incursion into Australia, only one parenteral rabies vaccine is approved for use in Australia, and is only approved to vaccinate animals for export (Animal Health Australia 2011). If the vaccine was to be used in the advent of a rabies incursion, it must firstly be approved for domestic use through the Australian Pesticides and Veterinary Medicines Authority (http://apvma.gov.au/node/6). Similarly, oral rabies vaccines would need to be approved for use in Australia, with the approval process potentially taking many months or years (1 to 18 months; http://apvma.gov.au/node/1088), depending on the type of registration required. Delaying control activities and increasing the time-to-control will likely result in an increase in the geographical spread of rabies, making the disease harder to eradicate, particularly from wild dog reservoirs. To this end, it is critical that research that facilitates rapid vaccine registration (e.g. identifying non-target effects, vaccine efficacy and appropriate delivery systems for Australian environments) be initiated to enable authorities immediate access to vaccines if (or when) rabies breaches Australian borders.

Traditionally, rabies models account for a single dog category when considering rabies spread in dog populations. Our research illustrates that each dog group is associated with differing rabies disease dynamics, so should be considered as independent groups or ‘species’ when modelling disease spread. These differences are based primarily on the dogs’ ability to roam and contact other susceptible individuals. Based on the risk of disease transfer, susceptibility and potential to implement control, Australian dog communities should be disaggregated and the AUSVETPLAN for the control of rabies in Australia (Animal Health Australia 2011) consequently revised and updated for improved rabies preparedness.

Like much previous work (e.g. Hampson *et al.* 2009, Carroll *et al.* 2010), the state-transition models used here assume homogenous mixing of individuals within the population. Dogs are highly social animals and their interactions are not random (Thomson 1992b; Sen Majumder *et al.* 2014, Sparkes *et al.* 2014b) and the complex sociality of dogs (Morters *et al.* 2013, Sparkes *et al.* In prep) likely explains the lack of empirical support for the implicit assumption that rabies transmission is a function of dog density (i.e. density-dependency) (Morters *et al.* 2013). Hence, alternative models that account for the different dog categories and heterogeneity in dog behaviours could strengthen predictive capabilities for rabies incursions and are recommended (e.g. Boehm *et al*. 2009, Cross *et al*. 2012, Reynolds *et al*. 2015).

Contact rates used within these models are based on best available data for Australian scenarios and include contacts where individuals are in close proximity; not just bite data. This could overestimate contacts within each population. However, not all individuals within a population can be monitored at once (e.g. due to logistic constraints), particularly the crepuscular and cryptic wild dogs. Indeed, many direct physical contacts would likely go undetected with the currently available observation technology, leading to an underestimation of contacts. Hence, we have used the best available information here. Once more research has been undertaken and estimates improved, these models could be updated to improve accuracy and predictive capabilities for a rabies incursion in Australia.

Although simple models have been used here to demonstrate differences amongst dog groups, it would be beneficial to develop improved stochastic models to further explore how rabies could spread in Australia, especially considering the complexities that exist within and between different dog communities. The interactive application of the stochastic, spatially explicit model of Dürr & Ward (2015) to the three groups of dog identified here also holds potential.

Future research should also focus on understanding inter- and intra-specific interactions of other susceptible species, including foxes, feral cats and native animals and their interactions with the disaggregated dog groups to improve our understanding of how they could contribute to the spread and maintenance of rabies in Australia.

Appendix 7-1: Model parameters. Parameter, description, value^ and source of parameters used in the rabies simulation models; stochastic values follow either a Uniform distribution (Unif(Min, Max)) or a beta-pert distribution (Pert(Min, Mode, Max)).

Parameter	Description	Value^	Source
Disease parameters			
ptrans	Probability of transmission	**0.45**	Hampson *et al*. 2009, Zhang *et al*. 2011
σ	1/Incubation period	**0.045**	
	Incubation period	22.3 days (20.0-25.0 at 95% CI)	Hampson *et al*. 2009
α	Disease death rate	**0.208**	1/Infectious period
	Infectious period	4.8 days (Range: 2.9-5.7 days)	Hampson *et al*. 2009, Zinsstag *et al*. 2009, Carroll *et al.* 2010
vacef	Vaccine efficiency	**0.89%**	Sage *et al*. 1993, Kennedy *et al*. 2007, Minke *et al*. 2009, Berndtsson *et al*. 2011
vacloss	Loss of immunity from vaccine (1/365 days)	**0.003**	Assumption; vaccine provides 1 year immunity

Scenario 1 – Free-roaming dogs residing within a remote Australian Indigenous Island community			
N$^{\#}$	Initial start population	**326 dogs**	Sparkes *et al*. 2014b
B	Natural birth rate	**0.002**	(Annual births/365/Initial start population)
	Annual births	237 pups	(Initial start population*% female and entire*Litters per entire female*Pups per litter)
	% female and entire	26.32%	J. Sparkes unpub. data, N = 95
	Litters per entire female	0.52 litters	Reece *et al*. 2008, Acosta-Jamett *et al*. 2010, Gsell *et al*. 2012
	Pups per litter	5.31 pups	Reece *et al*. 2008, Acosta-Jamett *et al*. 2010, Gsell *et al*. 2012, Morters *et al*. 2014
d	Natural death rate	**0.0019**	(Annual deaths/365/Initial start population)
	Annual deaths	230	(Initial start population*P of mortality for adults + Annual births*P of mortality for <1yr old)
	P of mortality for <1yr old	0.48	Reece *et al*. 2008, Morters *et al*. 2014
	P of mortality for adults	0.36	Reece *et al*. 2008, Morters *et al*. 2014
Contact	Contact rate per dog per day	**Unif(0, 23.8)**	Sparkes *et al*. 2014b
Scenario 2 – Wild dogs			
N$^{\#}$	Initial start population	**8701 dogs**	(Wild dog density*State Forest and National Park area)
	Wild dog density	0.31±0.53 dogs km^{-2}	McIlroy *et al*. 1986, Thomson 1992, Corbett 2001, Fleming *et al*. 2001, Sparkes, Ballard, Fleming *et al*. In press.
	NE-NSW State Forest and National Parks area	28,259km^{2}	National Park and State Forest area within 3 LLS boundaries: Hunter, North Coast and Northern Tablelands

B	Natural birth rate	**0.004**	(Annual births/365/Initial start population)
	Annual births	11,281 pups	(Initial start population*%female*prop females sexually mature*litters per female*pups per litter)
	% female	46%	J. Sparkes unpub. camera data, N = 44
	Proportion of females sexually mature (across all ages)	0.70	Jones and Stevens 1988
	Litters per female	0.79 litters	Thomson *et al*. 1992
	Pups per litter	5.1 pups	Thomson *et al*. 1992, Corbett 2001, Fleming *et al*. 2001
d	Natural death rate	**0.003**	(Annual deaths/365/Initial start population)
	Annual Deaths	11,038	(Initial start population* P of mortality for adults + Annual births*P of mortality for <1yr old)
	P of mortality for <1yr old	0.67±0.02	J. Sparkes unpub. camera data, N = 11, Corbett, 2001
	P of mortality for adults	0.40±0.34	J. Sparkes unpub. collar data, N = 11, McIlroy *et al.* 1986, Thomson *et al*. 1992
Contact	Contact rate	**Pert(0.07, 0.71, 1.99)**	(Contacts km^{-2}*Daily activity range)
	Contacts km^{-2}	0.2 ±0.2 Range: 0.02-0.56	Sparkes, Ballard, Fleming *et al*. In press.
	Daily activity range	3.56 ± 4.98km^2	Ballard, Sparkes, Meek *et al.* unpub. data, N = 4041 days, 23 dogs
Cull	Routine culling	**0.001 dogs day^{-1}**	Assumption

Scenario 3 – Free-roaming domestic dogs			
N$^\#$	Initial start population	**120,000 dogs**	(Prop dogs free-to-roam*NE-NSW domestic dog population)
	North-east NSW domestic dog population	0.46 million dogs	Office of Local Government 2015
	% domestic dogs free-to-roam	26%	Sparkes, Ballard, Fleming *et al.* In Prep.
B	Natural birth rate	**0.0005**	(Annual births/365/Initial start population)
	Annual births	19,809 pups	(Initial start population*Prop female and entire*Litters per entire female*Pups per litter)
	% female and entire	10.84%	Sparkes, Ballard, Fleming *et al*. In Prep.
	Litters per entire female	0.51 litters	Di Nardo *et al.* 2007
	Pups per litter	3 pups	Di Nardo *et al.* 2007
d	Natural death rate	**0.0004**	(Annual deaths/365/Initial start population)
	Annual deaths	19,531 dogs	(Initial start population*P of mortality for adults + Annual births*P of mortality for <1yr old)
	P of mortality for each age class	varied Range: 0.02-1	Di Nardo *et al*. 2007
	Mean age at death	11 years	Michell 1999
	% dogs in each age class	varied	Sparkes, Ballard, Fleming *et al.* In Prep.

Contact	Contact rate	**0.02**	(Contacts km^{-2}*Daily activity range)
	Contacts km^{-2}	0.016 ±0.025 Range: 0.003-0.075	Sparkes, Ballard, Fleming *et al*. In press.
	Daily activity range	0.26 ± 1.88km^{2}	Sparkes, Körtner, Ballard *et al.* unpub. data, N = 892 days, 21 dogs
Between-group transmission: Free-roaming domestic dogs and wild dogs, north-east NSW			
Contact		**0.00012 contacts/dog/day**	
	(Prop dogs free-to-roam*NE-NSW domestic dog population*(Attacks per year/Free-roaming dog population)+Non-violent dog contacts)		
	Non-violent contact	0.000115 contacts/dog/day~	Sparkes, Ballard, Fleming *et al*. In press.
	Attacks on domestic dogs	19.35 attacks yr^{-1}	Local Land Services domestic dog reported attacks, north-east NSW
	North-east NSW domestic dog population	0.46 million dogs	Office of Local Government 2015
	% domestic dogs free-to-roam	26%	Sparkes, Ballard, Fleming *et al*. In. Prep.

^ Bolded parameter values are presented as daily increments per dog

[#] For all scenarios, S = Initial start population – 1, E = 1, I = 0 and R = 0

Appendix 7-2: Global and local sensitivity analysis parameters, code and results for free-roaming domestic dogs residing within a remote Indigenous community (Tiwi Islands) and free-roaming domestic and wild dogs in north-east New South Wales

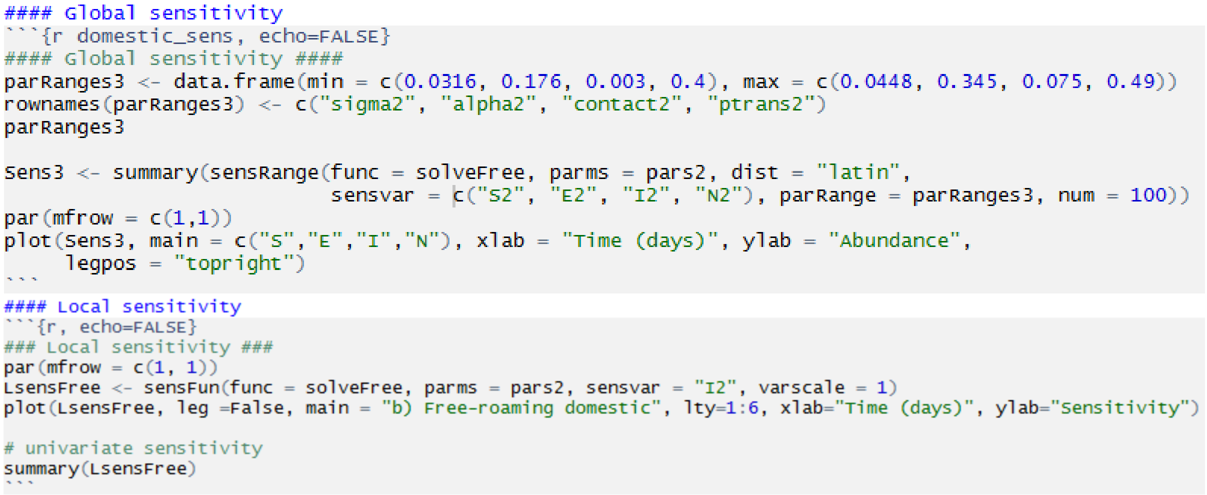
Minimum and maximum values for parameters used for the Global sensitivity analyses*

Parameter	Min	Max
Free-roaming domestic dogs, Tiwi Islands		
σ	0.0316	0.0448
α	0.1760	0.3450
Contact rate^	0.0010	24.0000
ptrans	0.4000	0.4900
Free-roaming domestic dogs, north-east New South Wales		
σ	0.0316	0.0448
α	0.1760	0.3450
Contact rate^	0.0030	0.0750
ptrans	0.4000	0.4900
Wild dogs, north-east New South Wales		
σ	0.0316	0.045
α	0.1760	0.345
Contact rate^	0.0700	1.990
ptrans	0.4000	0.490

* Values are based on ranges provided in Appendix 7-1

^ Due to contact rates overwhelming the Global Sensitivity analyses at these Min and Max values, the analyses were subsequently run with contacts = Min: 3.0, Max: 7.0

R code for Global and Local Sensitivity Analyses for one dog population, free-roaming domestic dogs, north-east New South Wales



~~~
#### Global sensitivity
```{r domestic_sens, echo=FALSE}
#### Global sensitivity ####
parRanges3 <- data.frame(min = c(0.0316, 0.176, 0.003, 0.4), max = c(0.0448, 0.345, 0.075, 0.49))
rownames(parRanges3) <- c("sigma2", "alpha2", "contact2", "ptrans2")
parRanges3

Sens3 <- summary(sensRange(func = solveFree, parms = pars2, dist = "latin",
                           sensvar = c("S2", "E2", "I2", "N2"), parRange = parRanges3, num = 100))
par(mfrow = c(1,1))
plot(Sens3, main = c("S","E","I","N"), xlab = "Time (days)", ylab = "Abundance",
     legpos = "topright")
~~~
Local sensitivity
```{r, echo=FALSE}
### Local sensitivity ###
par(mfrow = c(1, 1))
LsensFree <- sensFun(func = solveFree, parms = pars2, sensvar = "I2", varscale = 1)
plot(LsensFree, leg =False, main = "b) Free-roaming domestic", lty=1:6, xlab="Time (days)", ylab="Sensitivity")

# univariate sensitivity
summary(LsensFree)
```
```

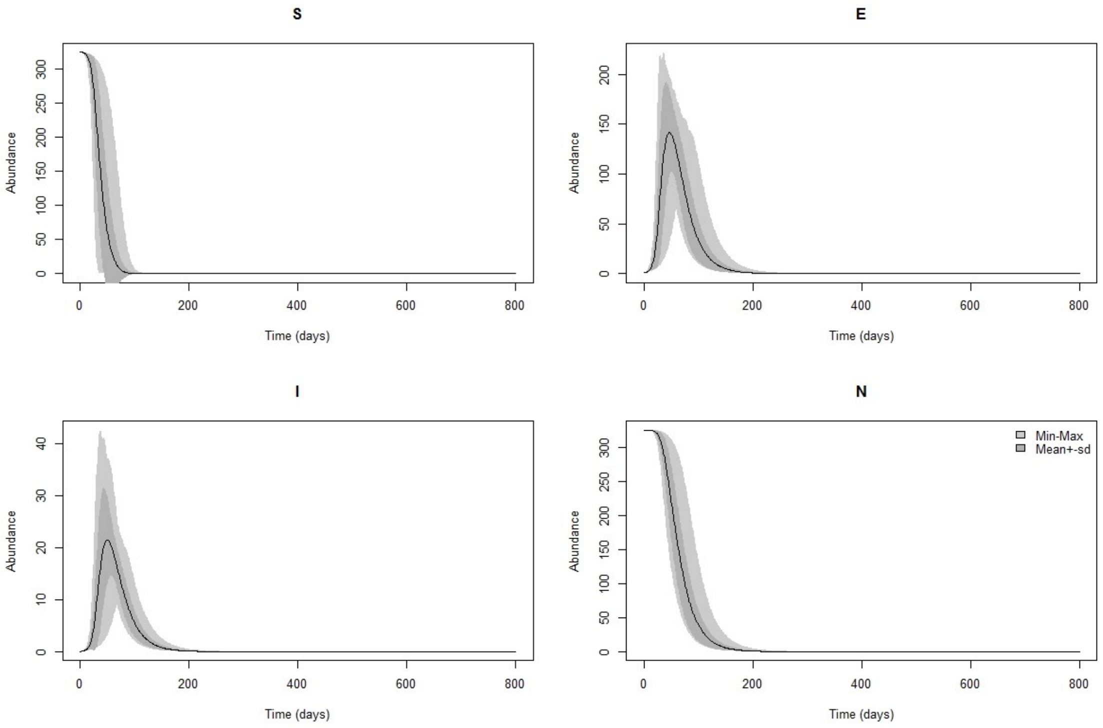


Figure A1: Global sensitivity analyses results for free-roaming domestic dogs within a remote indigenous community, northern Australia, for each state variable S, E, I and N
```

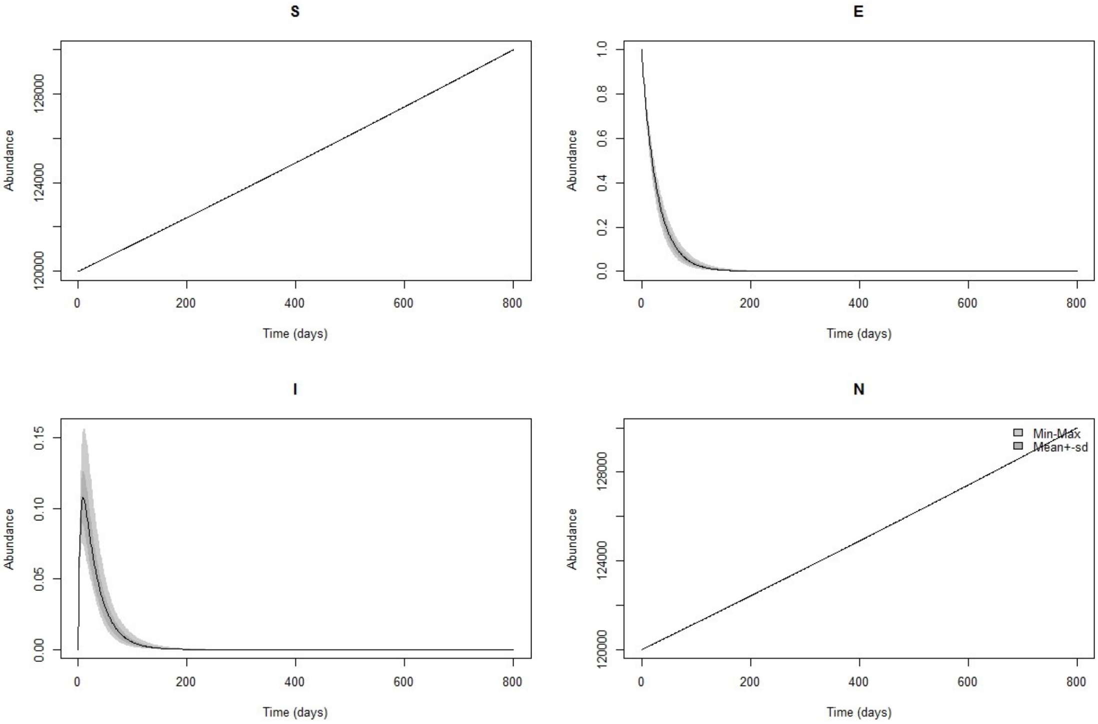


**Figure A2: Global sensitivity analyses results for free-roaming domestic dogs in peri-urban north-east New South Wales, Australia, for each state variable S, E, I and N**

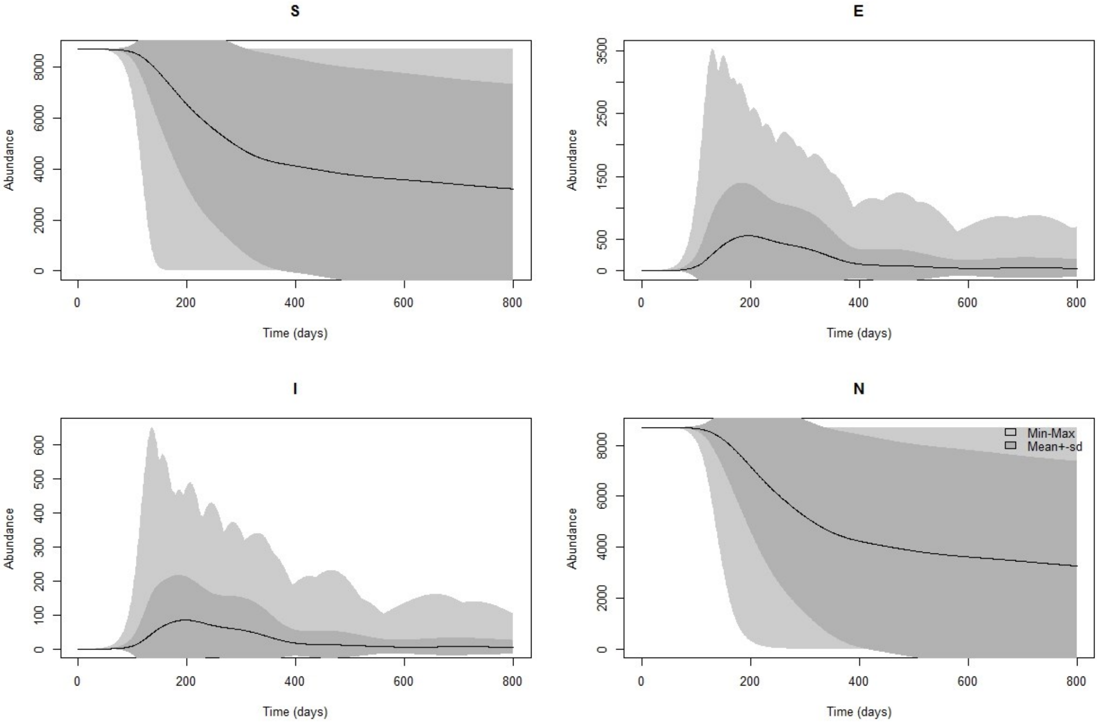
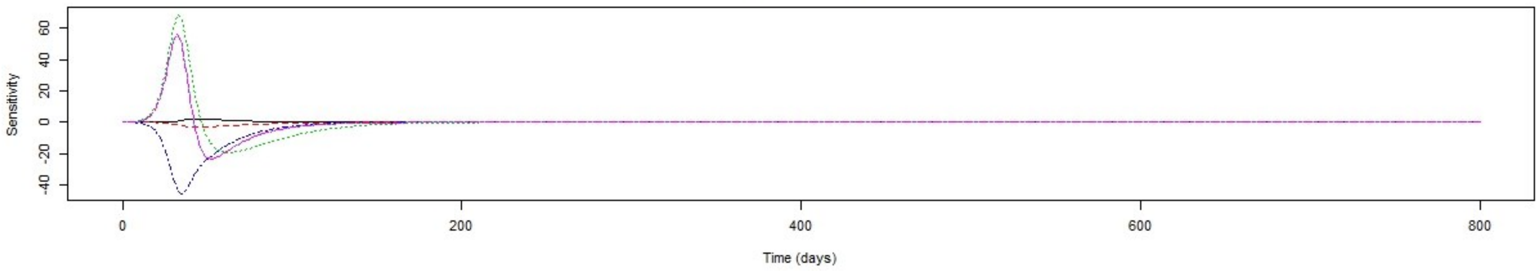
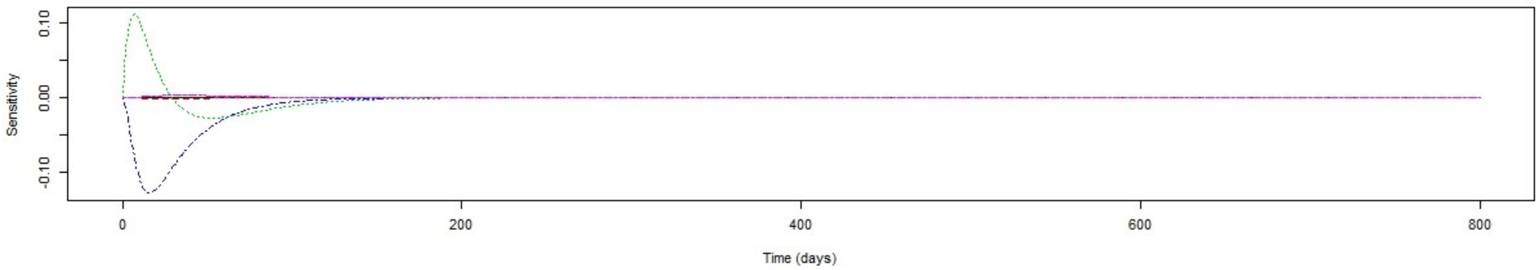


**Figure A3: Global sensitivity analyses results for wild dogs in peri-urban north-east New South Wales, Australia, for each state variable S, E, I and N**

a) Free-roaming domestic dogs, Tiwi Islands



b) Free-roaming domestic dogs, north-east NSW



c) Wild Dogs, north-east NSW

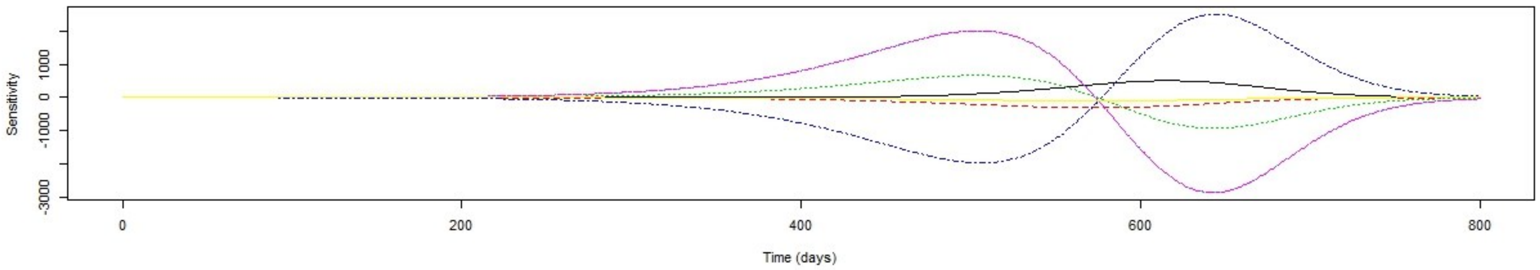


**Figure A4: Local sensitivity analyses for a) Free-roaming domestic dogs residing with a remote indigenous community, b) Free-roaming domestic dos in peri-urban north-east New South Wales and c) Wild dogs in peri-urban north-east New South Wales. Colours and line styles denote: Birth —; Death ---; σ ....; α ._._; contact – – –; ptrans - · - · -; cull —**

# Appendix 7-3: Ordinary differential equations for the simulation of control strategies for free-roaming domestic and wild dog populations

Prior to control:

Eq. S1 $\frac{dS}{dt} = (\mathrm{B} - \mathrm{d}) * \mathrm{S} - \beta * \frac{\mathrm{I}}{\mathrm{N}} * \mathrm{S} - \mathrm{cull} * \mathrm{S}$

Eq. S2 $\frac{dE}{dt} = \beta * \frac{\mathrm{I}}{\mathrm{N}} * \mathrm{S} - (\sigma + \mathrm{d}) * \mathrm{E} - \mathrm{cull} * \mathrm{E}$

Eq. S3 $\frac{dI}{dt} = \sigma * \mathrm{E} - (\alpha + \mathrm{d}) * \mathrm{I} - \mathrm{cull} * \mathrm{I}$

Eq. S4 $\frac{dR}{dt} = 0$

During control:

Eq. S5 $\frac{dS}{dt} = (\mathrm{B} - \mathrm{d}) * \mathrm{S} - \beta * \frac{\mathrm{I}}{\mathrm{N}} * \mathrm{S} - \mathrm{cull} * \mathrm{S} - (\mathrm{vac} * \mathrm{vacef}) * \mathrm{S} + \mathrm{vacloss} * \mathrm{R} - \mathrm{kill} * \mathrm{S}$

Eq. S6 $\frac{dE}{dt} = \beta * \frac{\mathrm{I}}{\mathrm{N}} * \mathrm{S} - (\sigma + \mathrm{d}) * \mathrm{E} - \mathrm{cull} * \mathrm{E} - (\mathrm{vac} * \mathrm{vacef}) * \mathrm{E} - \mathrm{kill} * \mathrm{E}$

Eq. S7 $\frac{dI}{dt} = \sigma * \mathrm{E} - (\alpha + \mathrm{d}) * \mathrm{I} - \mathrm{cull} * \mathrm{I} - \mathrm{kill} * \mathrm{I}$

Eq. S8 $\frac{dR}{dt} = (\mathrm{vac} * \mathrm{vacef}) * \mathrm{S} + (\mathrm{vac} * \mathrm{vacef}) * \mathrm{E} - (\mathrm{d} + \mathrm{vacloss} - \mathrm{B}) * \mathrm{R} - \mathrm{cull} * \mathrm{R} - \mathrm{kill} * \mathrm{R}$

Post control:

Eq. S9 $\frac{dS}{dt} = (\mathrm{B} - \mathrm{d}) * \mathrm{S} - \beta * \frac{\mathrm{I}}{\mathrm{N}} * \mathrm{S} - \mathrm{cull} * \mathrm{S} + \mathrm{vacloss} * \mathrm{R}$

Eq. S10 $\frac{dE}{dt} = \beta * \frac{\mathrm{I}}{\mathrm{N}} * \mathrm{S} - (\sigma + \mathrm{d}) * \mathrm{E} - \mathrm{cull} * \mathrm{E}$

Eq. S11 $\frac{dI}{dt} = \sigma * \mathrm{E} - (\alpha + \mathrm{d}) * \mathrm{I} - \mathrm{cull} * \mathrm{I}$

Eq. S12 $\frac{dR}{dt} = -(\mathrm{d} + \mathrm{vacloss} - \mathrm{B}) * \mathrm{R} - \mathrm{cull} * \mathrm{R}$

# STATEMENT OF ORIGINALITY

We, the PhD candidate and the candidate's Principal Supervisor, certify that the following text, figures and diagrams are the candidate's original work.

| Type of work | Page number/s |
|---|---|
| Journal article and all encompassing information | 196-225 |

Name of Candidate: Jessica Sparkes

Name/title of Principal Supervisor: Dr Wendy Brown

[redacted] 12 December 2015

Candidate Date

[redacted] 12 December 2015

Principal Supervisor Date

## STATEMENT OF AUTHORS' CONTRIBUTION

We, the PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

| | **Author's Name** | **% of contribution** |
|---|---|---|
| **Candidate** | Jessica Sparkes | Conception and design (70%)<br>Data collection (100%)<br>Analyses (80%)<br>Manuscript development (70%) |
| **Other Authors** | Steven McLeod | Analyses (20%)<br>Manuscript development (7%) |
| | Guy Ballard | Conception and design (15%)<br>Manuscript development (8%) |
| | Peter JS Fleming | Conception and design (15%)<br>Manuscript development (5%) |
| | Gerhard Körtner | Manuscript development (5%) |
| | Wendy Y Brown | Manuscript development (5%) |

Name of Candidate: Jessica Sparkes

Name/title of Principal Supervisor: Dr Wendy Brown

[redacted]

12 December 2015

Candidate

Date

[redacted]

12 December 2015

Principal Supervisor

Date

# 8 Conclusion

Despite the imminent risk of a canine rabies incursion from Indonesia, Australia is under-prepared for a rabies outbreak. Viewed in its current context, the rabies AUSVETPLAN, which was predominantly based around a fox rabies biotype entering Australia, is overly simplistic and outdated. Because our closest rabies-endemic country, Indonesia, harbours the canine rabies virus strain, I expect this biotype to be the most likely to infiltrate Australian borders, hence my thesis focused on the introduction and spread of canine rabies virus through the Australian dog population, rather than the fox rabies virus biotype. The application of the findings from this body of research could improve preparedness for a canine rabies outbreak in Australia, and has improved our knowledge on the ethology and population dynamics of several extant dog populations.

I used a range of methods including questionnaires, mark-recapture studies, camera traps and GPS telemetry to collect data on important parameters for rabies modelling in Australia. The dog populations I studied ranged from completely restrained domestic dogs, relying solely on humans for their resources, through to wild dogs (including dingoes), which did not rely on humans for food or shelter. These populations were located in identified high risk areas for a rabies incursion and subsequent spread; in northern and eastern Australia. Subsequently, I developed simple state-transition models to assess how each dog population responded to a theoretical rabies incursion.

Because Australia is currently free of terrestrial rabies, I had to make assumptions and draw on published literature from rabies-endemic countries, to estimate parameters for the transmission factors associated with the rabies virus. One assumption that cannot be overlooked is that rabid dogs behave similarly to healthy dogs. Because it is unethical to release rabies infected dogs, limited information exists on the movement behaviour of rabid individuals. However, Butler (1998) collared several free-roaming domestic dogs in Zimbabwe, South Africa which subsequently became rabid. He found that there were no significant differences in the movement behaviour of rabid dogs compared to other healthy collared individuals (Butler 1998). However, this information was based on intermittently collected radio telemetry data and reports from the dogs' owner and other community members. Regardless, this information is the best available and because we do not have rabies in Australia to quantify any potential alterations in behaviour in the Australian landscape, I have modelled rabies transmission based on this assumption.

Through the development and distribution of a questionnaire, I was firstly able to develop an understanding of dog ownership and dog demographics of residents in peri-urban north-east New South Wales (NSW). As a result of undertaking the survey, I found that restrained domestic dogs in north-east NSW are numerous, with an estimated 340,000 restrained dogs owned. These dogs have limited opportunity to interact with other dogs and wildlife, unless supervised by humans. Subsequently, this dog type was associated with a low risk of rabies maintenance and spread in Australia. Further, these dogs would likely be highly accessible for vaccination campaigns, decreasing risks associated with the transmission of rabies between dogs and humans.

Working dogs, including dogs used for hunting, are unlikely to contribute greatly to the maintenance of rabies, but they do have the potential to spread the disease over large distances through human mediated translocation events. Through devising and distributing a questionnaire targeted towards people that use dogs to hunt animals, I was able to gain greater insight into hunting dog use in eastern and northern Australia. Hunters reported that they travelled in excess of 500km to undertake hunting activities with their dogs. With 50% of hunters surveyed stating they encountered wild dogs when hunting, the risk of a hunting dog encountering a rabid wild dog would also likely be high. However, the movement behaviour and activity pattern of dogs while hunting is largely unknown and therefore, the true risk of rabies infection for this dog type is unclear. Further research to track hunting dog movements would provide greater insight into the risk that these dogs pose to rabies spread in Australia.

Despite limited knowledge on hunting-wild dog interactions, hunters that traverse long distances and hunt in remote regions of Australia, particularly northern Australia, may still prove a useful resource for identifying unusual behaviour in wild dogs, which may be associated with a rabies outbreak. To improve the chances of detecting rabies in wild dogs, education programs targeting hunters’ knowledge of exotic diseases, including rabies, should be developed, while encouraging people to report unusual activity to authorities. This action alone may help to reduce time to detection of rabies in the wild dog population, allowing response strategies to be implemented and the disease contained to a smaller area.

Because both surveys I undertook during my studies were anonymous, this precluded follow-up of non-respondents and could have created some bias in the results presented. However, because of the sensitive nature of the information I was attempting to collect, the best opportunity for obtaining truthful responses was to make the surveys anonymous. For example, due to the regulatory and emotional environment relating to dog ownership, respondents pets' ability to roam and/or use of dogs for hunting in general, it could be expected that responses received were from respondents that perceived they were more communally responsible and therefore 'doing the right thing'. If there was bias in my data, then my results would be negatively biased, which implies that the under-reporting of contentious issues, such as losing dogs, letting dogs roam, the occurrence of dog bites and the observed proportion of dogs that were not microchipped and registered, results in underestimates of reality. Hence, any use of these data for modelling purposes would likely be a conservative estimate of the true rate of these activities.

Free-roaming domestic dogs, where they are allowed to roam unsupervised outside of the owner's property, posed a greater challenge for characterising rabies spread in Australia. Rabies spread through free-roaming dogs in the remote Wurrumiyanga island community, northern Australia, would likely be rapid, predominantly due to high contact rates, high dog density and limited containment. However, I was only able to estimate contact rates of these dogs through the collection of GPS telemetry data, where I defined a contact as occurring when two or more collared dogs were less than 20m apart. This definition was based on GPS collar accuracy and would likely overestimate true interactions between these individual dogs. However, I was not able to collar all dogs within the community and the GPS units only logged the dogs' position every 15 minutes, which also limited opportunities to detect interactions. The limitations with the technology employed would likely result in an underestimation of interactions between individuals and hence, conservative parameter estimates.

It is also important to note that not all the interactions I recorded would result in the potential for rabies transmission between individual dogs. Rabies virus transmission requires contact with a mucous membrane of an infectious individual, and includes contact such as dog bites, sexual activity, consumption of infected tissue and licking of mucous membranes during social interactions. Although the collection of data on direct physical contacts and the recording of every dog bite would be ideal, current technologies preclude this. The methods I used to collect contact information are the best available at present. I used a threshold value of 20m based on realistic assumptions of the potential for interactions to occur and the accuracy of the technology I employed. Until technologies to record direct physical contact and bites are developed, the data I collected throughout my thesis provide the best possible estimate to base model predictions for rabies spread in Australia. In this context, it is important to compare my model predictions with those presented for rabies-endemic countries.

Similar to international experience, simulated dog removals to prevent rabies spread in the Wurrumiyanga island community, was counter-productive and would likely be met with resistance from community members. Vaccination rates in excess of 70% of the dog population would provide an effective barrier against rabies spread in this community, but would need to be implemented rapidly to ensure humans and dogs were protected. Unfortunately, because Australians are unfamiliar with rabies symptoms, initial detection could be delayed, allowing the rabies virus to spread throughout the community before the virus is detected in their dogs. Programs to educate community members on the symptoms of rabies need to be developed and implemented now, particularly in high risk areas of northern Australia. This will ensure time to detection and response times are minimised.

Because densities of free-roaming domestic dogs and associated interactions in north-east NSW were much lower than those observed for free-roaming domestic dogs on the Tiwi Islands, rabies persistence and spread through this dog population would likely be limited in NSW. However, these dogs would pose a significant threat to human health, because interactions with rabid animals may go undetected. An understanding of the frequency and duration of free-roaming dog activity is needed to determine the risk of contact with wild dogs and other free-roaming domestic dogs. The use of GPS telemetry and proximity loggers on free-roaming dogs will help to uncover roaming behaviour among this dog type and strengthen predictive capabilities of epidemiological models.

Due to high densities in areas of high risk for a rabies incursion, combined with limited human contact and relatively high contact rates, wild dogs are likely to pose the greatest threat for maintenance and spread of rabies in Australia. The state-transition models I developed highlighted that rabies would likely remain at low levels within the north-east NSW wild dog population for over a year prior to an epidemic becoming apparent. This was despite defining a contact as occurring when two or more individuals were less than

50m apart. However, likely counteracting the inflated definition of a contact was that I was only able to monitor a small area in front of each camera trap. Because of the crepuscular and shy nature of wild dogs, direct observations were impossible to make and those observations that could be made are usually exceptionally brief, particularly in the structurally diverse and often dense environments I was monitoring. In addition, human presence, when detected by wild dogs, alters their behaviour and contacts measured in such circumstances would be confounded by observer effects. Hence, camera traps were the most appropriate method available for remotely measuring rates of contact for wild and free-roaming domestic dogs within north-east NSW.

The long period of low infection rates for wild dogs could allow rabies to go undetected in the wild dog population for many months, allowing for greater spatial spread. Consequently, a control program would need to be implemented over a large area to ensure containment. This would greatly increase costs of control and may allow time for the disease to become endemic in the wild dog population, making eradication impossible. Definition of fine scale wild dog movements and quantification of their interactions through the use of GPS telemetry collars and proximity loggers is required to determine the scale at which control should be implemented and would complement data collected within this thesis.

Through recent advancements in DNA fingerprinting, it may also be possible to track gene flow between dogs and therefore identify relatedness between individuals to determine contact rates (i.e. through matings) and movements of individual animals (Corbett 2001, Jin & Wang 2005, Cullingham *et al*. 2008). This could prove an economically efficient and less labour-intensive method for understanding wild dog movements at a landscape scale compared with telemetry collars, as samples could be collected from the hundreds of dogs culled annually in control programs across Australia. A coordinated approach to collection, storage and analysis of samples would be required to ensure broad application, not only for its contribution to disease mitigation planning, but also for determining the scale at which current control programs should be implemented.

Unfortunately, no rabies vaccine is currently approved for domestic use in Australia. Research to progress the registration of parenteral and oral rabies vaccines, that can be used safely and are approved for use in Australia is urgently required. In particular, research into the effects of the rabies virus vaccine on non-target animals, including native wildlife is important. For example, spotted-tail quoll (*Dasyurus maculatus*), birds, possums and macropods have been documented to take poison baits targeted for the destruction of wild dogs and foxes in Australia (Fleming *et al*. 2000, Koertner 2007, Dundas *et al*. 2014). Similarly, wildlife could consume vaccine baits, which could negatively impact native populations if they react negatively to the vaccine, while also reducing the availability of the baits to dogs. Similarly, the role that other pest animals, including feral cats and foxes, might play in the spread and maintenance of sylvatic canine rabies in Australia should be assessed.

Because of differences in human-associated sociological values of dogs and the different roles they play in Australian society, and subsequent varied ethology and population characteristics identified within my thesis, a generic ‘one-dog-fits-all’ approach to a rabies incursion is unlikely to yield effective results. However, I was only able to collect information from four dog populations, including all four dog types I identified throughout my thesis. Because I identified contact behaviour differences between dog populations, more research is required to determine whether dogs of the same type, but residing in different regions and therefore, populations across Australia, behave similarly. Specifically, studies on wild and free-roaming domestic dogs and their interactions should be undertaken in regions where rabies is likely to have immediate and significant impacts, including in north Western Australia, the Gulf of Carpentaria and Far North Queensland. This will build on and strengthen parameter estimates described here. Because dogs are highly social animals, and their interactions are not random, models that use information provided here, but also take account of the heterogeneous nature of dogs, are also required.

In addition, a current skills database of personnel and equipment to draw upon in the advent of a rabies incursion should be constructed and remain relevant and accessible to authorities. Identifying personnel that are vaccinated against rabies, are experienced epidemiologists, ecologists, veterinarians and wild dog managers and trappers will help to reduce time to initial response. Development of a skills database will also aid in budgeting for a rabies incursion.

Despite the risk that rabies poses to wildlife, industry and people’s way of life, Australia is underprepared for terrestrial rabies. My research is a key first step in advancing rabies preparedness and if adopted, could help to improve Australia’s planned response to a likely incursion. Once more data becomes available, they should be integrated into epidemiological models to strengthen our predictive capabilities. To ensure the rabies AUSVETPLAN remains current, takes into account new research findings and reassesses the risk of rabies entering Australia, the plan should also be reviewed every few years. Further work, to improve reporting rates of dog bites and dog ownership, to enhance population estimates and extend our understanding of relevant dog behaviour, is also required to ensure Australia is adequately prepared for canine rabies.

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