SOCIAL AND SPATIAL ECOLOGY OF FREE-RANGING DOMESTIC DOGS

Submitted by

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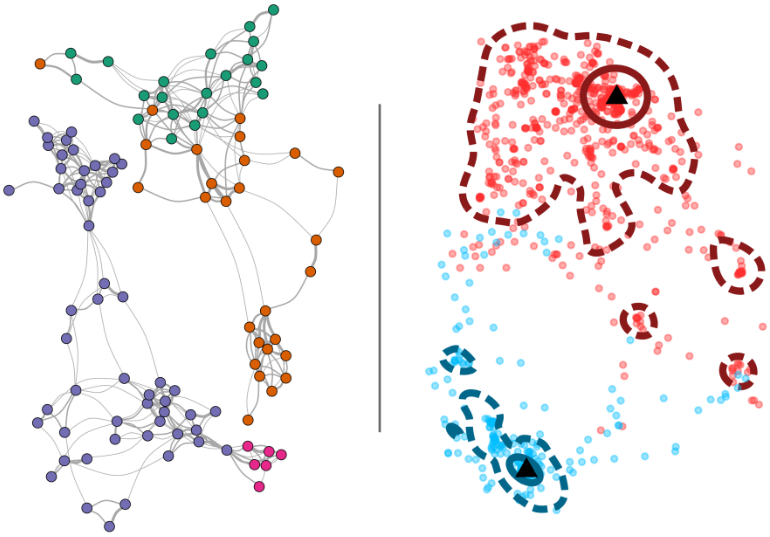

ABSTRACT

Controlling and preventing outbreaks of infectious diseases in human and non-human animals is a priority objective for public and animal health, and failure to do so can result in a significant loss of life and have adverse effects on the economy and on the conservation of biodiversity.

Free-ranging domestic dogs are reservoirs for several zoonotic diseases, and are currently the focus of two major public health programmes; the ‘Zero by 30’ strategic plan to eliminate dog-mediated rabies and the Guinea worm eradication programme. The management of these and other dog-mediated diseases would benefit from insights into the social and spatial ecology of free-ranging domestic dogs, and their relationships to the dynamics of disease transmission.

In this thesis, I explore spatial and temporal dynamics in the contact rates and space use of free-ranging domestic dogs in rural Chad; a region where the risks to humans of infection with rabies and Guinea worm are high.

I first describe static contact networks for free-ranging dogs, using novel proximity sensors, and then simulate the transmission of a communicable disease similar to rabies through the networks. My results show that there is considerable variation in the number and duration pf contacts between individuals, and that communities in the network were defined by household membership. Disease simulations showed that dogs with a higher ranked degree have a higher probability of starting an epidemic should they become infected, while those with a higher ranked eigenvector centrality tend to cause larger epidemics. Furthermore, in one settlement ranked eigenvector centrality was positively correlated with home range size. I demonstrate that dogs are not

equal in the epidemiological risks that they present and that there may be traits (e.g. drivers behind space use) that could identify individuals that present a higher risk.

I then explore dog space use using GPS loggers and continuous time movement models to calculate the dogs' home ranges and to investigate temporal patterns in their activity and space use. I find that dogs had larger ranges in the dry season, but that this was also when 70% of dogs can be more reliably found around their households. Owner activity explained some of the variation in dog space use, whereby dogs from households that went hunting had larger ranges in the dry season. These results demonstrate how dog spatial ecology can be used to inform disease management practices, such as vaccination campaigns, and highlight the potential to use targeted strategies at the household level.

Next, I use the detail of dyadic-level interactions to investigate the spatial-temporal variations in contact rates between dogs. I find that the probability that individuals were ever observed in contact and the hourly probability and duration of contacts should they have interacted, were all negatively correlated with the distance between the individual's households. Contact rates were higher around the household and village where they peaked between 5am-9am and again between 6pm-8pm. However, the duration of contacts were highest when they occurred outside the village. Evidence for the seasonal preferential mixing among the sexes was found, whereby male-male and male-female dyads had higher contact rates in the dry season.

Next, I quantify the exposure of free-ranging dogs to water sources in Chad; which are considered potential sources for Guinea worm infection. I use the

activity of dogs (based on GPS data) as a proxy for variation in exposure. I find that 85% of dogs had visited at least one water source, but that dogs with larger ranges had higher activity levels around water sources. In all field sites and seasons, no more than 4 water sources accounted for 95% of dog visits, and these were all <0.5 km from a household with tracked dogs. These results can be used to prioritise the chemical treatment of water sources that have the highest dog ‘traffic’.

Finally, I tie the results of this thesis together, and discuss the implications that they have for our understanding of the dynamics of disease transmission in free-ranging domestic dogs, and how this might be used to improve the management of dog-mediated diseases. I conclude that insights into the variations in dog ecology, particularly in their contact behaviour, can be useful in the management of dog-mediated diseases, and that relating contact behaviour to drivers of space use could inspire targeted strategies that are tailored to local socio-ecological contexts.

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Author’s declaration

Chapters 2, 3, 4, and 5 have been published or written for publication as co-authored academic papers. I developed the direction and research design for Chapters 2, 3, 4 and 5 in conjunction with Robbie McDonald. All authors contributed critically to the drafts and gave final approval for publication.

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Title images in this thesis are by Jared K. Wilson-Aggarwal.

CHAPTER 1:
GENERAL INTRODUCTION

1.1 EMERGING INFECTIOUS DISEASES

Diseases that are newly discovered, introduced or that re-emerge through a rapid increase in incidence, shift in their hosts or geographical range, are all classed as EIDs (Petersen et al. 2018). Historically, EIDs have caused substantial loss to human life, and examples include the Black Death pandemic (pneumonic plague; Kool & Weinstein, 2005), influenza pandemics (Potter, 2001) and the HIV/AIDs pandemic (Merson et al. 2008). Despite advances in the control, prevention and treatment of EIDs (Morens & Fauci, 2012), trends in the number and frequency of emergence and re-emergence events suggest they are on the rise (Jones et al. 2008).

The impact of EIDs can be far reaching and, beyond the obvious threat imposed to public health, they can have substantial 'knock on effects' for economics and conservation efforts. Economic impacts can include direct costs (e.g. costs of workforce and resources required for containment, prevention and recovery), losses to economic output (e.g. reduced productivity and trade) and the impact on future economic growth. The 2014 Ebola outbreak has been estimated to have had a global economic and social burden of US$53 billion (Huber et al. 2014), the 2003 SARS outbreak cost the global economy up to US$100 billion (Smith et al. 2006), while the annual global cost of Norovirus is estimated at US$64 billion (Bartsch et al. 2016). EIDs in livestock can also have significant impacts, and this is highlighted by the foot-and-mouth outbreak in 2001 that cost the economy £3.1 billion and involved the slaughter of over 4 million animals (Thompson et al. 2002). Furthermore, emergence events in wildlife have impacts on biodiversity, causing significant declines in wildlife populations, with some threatened with extinction (Smith et al. 2009). For example, outbreaks of trichomonosis has caused declines in some British bird populations (Robinson et al. 2010), haemorrhagic septicaemia has caused mass die offs in the critically endangered Saiga antelope (Kock et al. 2018), and the spread of chytridiomycosis has resulted in the decline and extinction of amphibian species across the globe (Olson et al. 2013).

Drivers of emergent infections are numerous and the majority stem from anthropogenic activity (Peterson et al. 2018). Human induced climate change is facilitating range shifts and expansions of disease vectors, such as mosquitoes, and causing the emergence of diseases in locations they have not been previously recorded (Tjaden et al. 2018). Furthermore, extreme weather events brought about by climate change are often followed by outbreaks of infectious diseases (McMichael, 2015). There are also more direct influences of human activity in causing emergence events, including the trade of wildlife (Karesh et al. 2005), habitat loss/alteration (Wilkinson et al. 2018), resource exploitation (Rohr et al. 2019) and the supplemental feeding of wildlife (Sorensen et al. 2014). It is clear that the drivers behind EID events are diverse however, a common theme is the increased exposure of humans and domestic animals to wildlife. This is emphasised further where the majority (60%) of past emergence events of diseases in humans have been shown to originate from non-human animals (Jones et al. 2008).

1.2 DOMESTICATION, DOGS AND DISEASE

The risk of EIDs at the human-wildlife interface is often amplified through the involvement of domestic animals (Cleaveland et al. 2001; Wolfe et al. 2007; Morand et al. 2012). Domestic animals, especially those that are free-ranging, can constitute a reservoir for disease (Han et al. 2016), and are capable of acting as ‘bridges’ for the transmission of zoonotic pathogens between both humans and wildlife (Caron et al. 2015). Examples of zoonotic emergent events that have involved domestic animals, include Guinea worm in domestic dogs (Hopkins et al. 2018) and Nipah virus in domestic pigs (Epstein et al. 2006). Moreover, the number of shared pathogens between humans and non-human animals appears to increase with the time since a species was domesticated (Morand et al. 2014).

Dogs *Canis familiaris* are among the earliest domesticated animals and, due to their close affiliation with humans, they are widespread with a global population of one billion (Gompper, 2014). Dogs share 47% of their known pathogens with wild mammals (Knobel et al. 2014) and 16% with humans (Morand et al. 2014). They exist on a continuum from companion animals that have restrained movements, to feral animals with loose connections to humans, and fully wild populations. However, due to their dependency on anthropogenic resources and their unrestrained movements, it is the free-ranging dog populations that have the greatest capacity to bridge the gap between humans and wildlife. Of concern to public health is the large number of zoonotic pathogens that dogs can transmit, including rabies, echinococcosis, Guinea worm and visceral Leishmaniasis. This threat extends to wildlife populations that can face the risk of extinction due to dog-mediated diseases (Doherty et al. 2017). An example of this is canine distemper, for which dogs are a reservoir, and which threatens populations of lions *Panthera leo* in Tanzania (Viana et al. 2015), Ethiopian wolves *Canis simensis* in Ethiopia (Gordon et al. 2015) and Giant pandas *Ailuropoda melanoleuca* in China (Yan et al. 2019).

Several zoonotic infections that dogs share with humans are considered neglected tropical diseases (Bodimeade et al. 2019), as they predominantly affect the poorest regions of the world, where resources for disease control are limited. Despite this, there are global efforts to try and control zoonotic diseases for which dogs are a reservoir. Most notable are (1) the ‘Zero by 30’ rabies campaign, which aims to eliminate dog-mediated rabies by 2030 (Jarvis, 2016), and (2) the Guinea worm eradication program, that hopes to globally eradicate the nematode parasite (Hopkins et al. 2018). These ambitious ventures highlight the challenges of managing multi-host pathogens and the need for a transdisciplinary approach.

1.3 DOG-MEDIATED RABIES

Rabies is a zoonotic disease in the *Lyssavirus* genus. It has a wide range of mammalian hosts and a near global distribution (Hayman et al. 2016). Infection typically occurs when the virus enters the body through a break in the skin, where it then migrates to the brain via the central nervous system and causes fatal encephalitis (Hemachudha et al. 2013). The virus has an incubation period of 1-2 months in humans, but this is highly variable and ranges from weeks to years. After the incubation period, the disease can manifest as either ‘furious’ rabies (symptoms include fluctuating consciousness, spasms and hydrophobia or aerophobia) or ‘paralytic’ rabies (symptoms include weakness and motor neuron disturbances). Although a vaccine has been developed, once symptoms begin, the disease becomes fatal.

In humans, around 99% of all cases are derived from rabid dog bites, and cases predominantly occur in Africa and Asia (WHO, 2018). Dog-mediated rabies is estimated to cause 59,000 human deaths every year and costs the global economy US$8.6 billion annually (Figure 1.1; Hampson et al. 2015). The risk of infection is generally associated with rural areas and the presence of free-ranging dog populations (WHO, 2018). Dogs are considered the main reservoir for rabies in humans (Lembo et al. 2008; Beyer et al. 2011), but the dog reservoir also threatens wildlife populations including the endangered Ethiopian wolf and African wild dog *Lycaon pictus* (Stuchin et al. 2018).

In the last century there have been significant advances in our knowledge on the epidemiology of rabies, and this has set us on a mission for zero human deaths from dog-mediated rabies by 2030 (Cleaveland & Hampson, 2017). It is widely accepted that this can be achieved through the mass vaccination of dogs alone (WHO, 2018). Due to the high turnover of dog populations, successful vaccination campaigns require an annual population coverage of 70% (Conan et al. 2015). While this is achievable, there are several barriers to elimination that include the distribution of resources, the need for socio-political motivation and the design of more sustainable and effective intervention strategies (Fahrion et al. 2017). A ‘One health’ approach has been advocated to help overcome the barriers to elimination and to reach the ‘Zero by 30’ goal (Cleaveland et al. 2014; Dürr et al. 2017). The ‘One Health’ approach recognises the interconnectedness of humans, animals and the environment, and advocates tackling public health issues through the collaboration between multiple sectors and the application of inter-disciplinary research (Degeling et al. 2015).

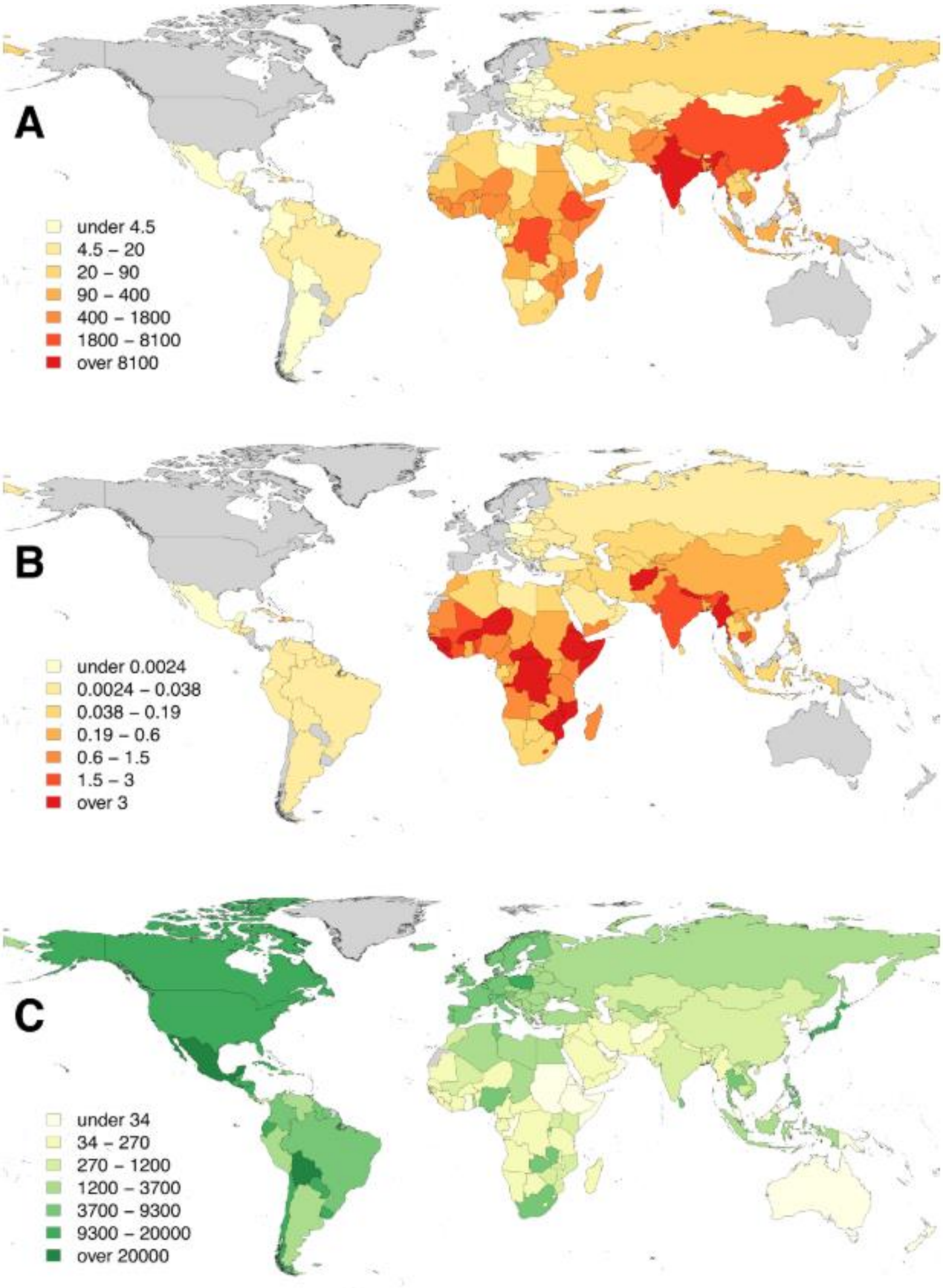

Figure 1.1. The distribution of the global burden of rabies: A) human rabies deaths, B) per capita death rates (per 100,000 persons), and C) expenditure on dog vaccination (per 100,000 persons). Countries shaded in grey are free from canine rabies. Reproduced from Hampson et al. (2015).

An ecological perspective is required to help eliminate dog-mediated rabies. Despite a century of research on the disease, there are still large knowledge gaps in our understanding of dog ecology, some of which are fundamental to transmission. For instance, little is known about the contact rates between dogs (Sparkes et al. 2015; Leung & Davies, 2017), and yet this is a crucial parameter in models that predict the spread of disease and that are used to determine optimal intervention strategies (Anderson & May, 1992; Barlow, 1996; Keeling & Eames, 2005). It has been increasingly acknowledged that dogs exist in various socio-cultural contexts, and that this requires locally adapted strategies to ensure access to 70% of the population (Taylor & Nel, 2015; Fahrion et al. 2017). Again, research on dog ecology and how it varies in these different cultural contexts could help design tailored strategies. Overall, a more rounded view of dog ecology could identify more optimised management practices, and this would alleviate issues of poorly distributed resources and could enhance the success rate of campaigns if access to individuals can be improved.

1.4 GUINEA WORM AND THE DOG RESERVOIR

Guinea worm disease is a debilitating infection of humans caused by the parasitic nematode *Dracunculus medinensis*. The transmission cycle of Guinea worm starts after a female worm emerges from its host and releases larvae into a water source, where an intermediate host (copepods) then ingest the larvae (Greenaway, 2004). The classic transmission pathway to humans is through the consumption of drinking water containing infected copepods (Figure 1.2). However, a novel pathway has recently been hypothesised, and transmission is now thought possible through the ingestion of tissue from a paratenic or transport host; such as fish or frogs that have themselves eaten an infected copepod (Eberhard et al. 2016; Cleveland et al. 2017). Once ingested, the copepods are killed by stomach acid that releases the worm larvae. Larvae then migrate out of the digestive tract and into the host’s connective tissues, where they mature and mate (Greenaway, 2004). Fertilized females continue to develop over the subsequent months, growing up to 1 m in length. After the 10-14 month incubation period, the female worm creates a painful blister on its host from which it emerges once contact with water is made.

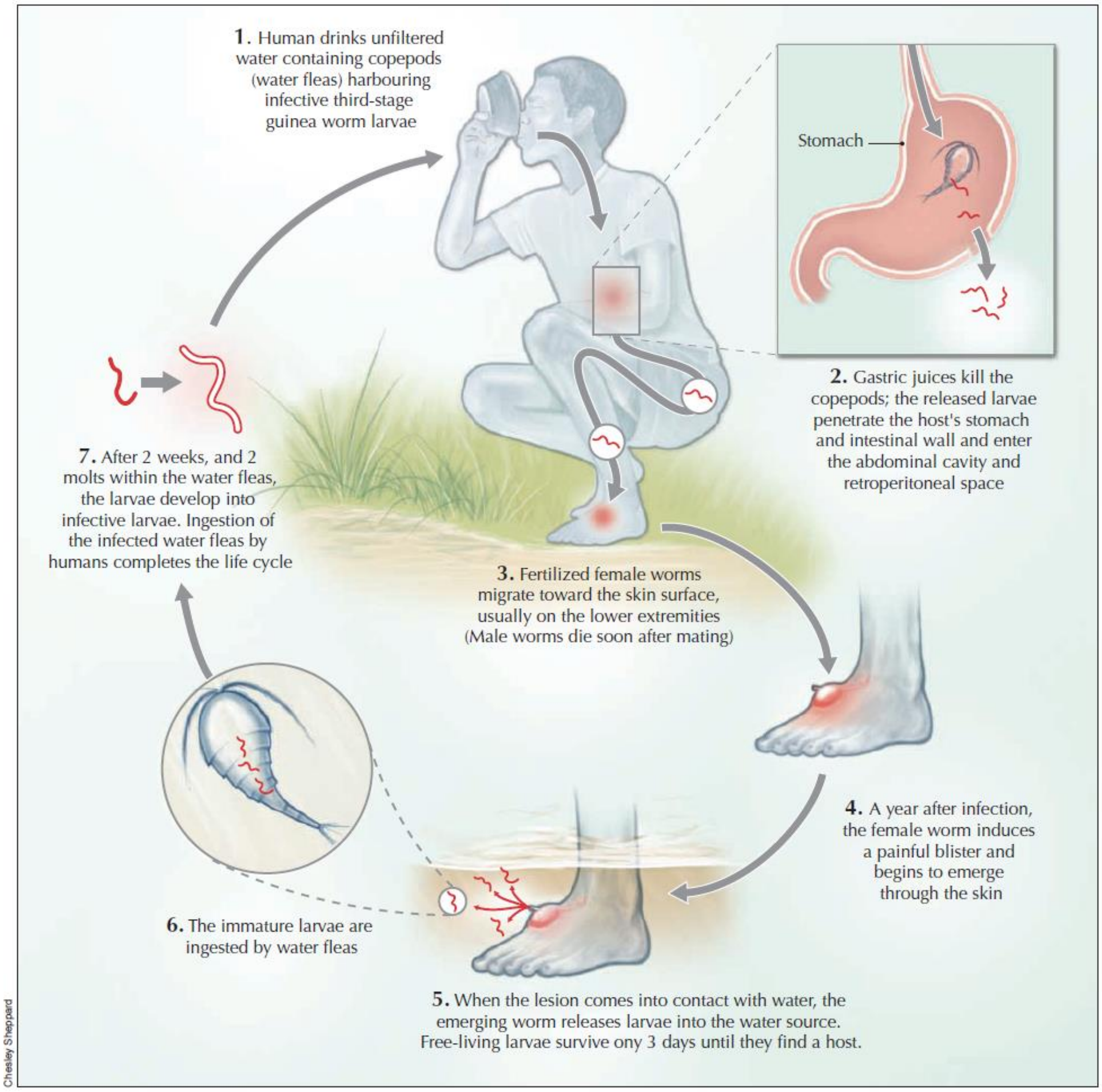

Figure 1.2. Life cycle of Guinea worm. Reproduced from Greenaway (2004).

Historically, Guinea worm disease has afflicted 3.5 million people per year across Asia and Africa (Watts, 1987), but global eradication efforts since the 1980s have reduced the number of human cases to only 28 in 2018 (CDC, 2019). Human cases have been reduced by applying a number of methods to break the cycle of transmission, including: the detection and isolation of cases, chemical treatment of water bodies to remove copepods and encouraging the filtration of drinking water (Biswas et al. 2013). While this has proved hugely successful, the final stage of the eradication programme faces major obstacles with insecurity in the remaining endemic areas and the recent detection of cases in non-human animals (Al-Awadi et al. 2014).

Of the few remaining endemic countries, infections in non-human animals have been detected in Chad, Ethiopia and Mali (Molyneux & Sankara, 2017). In 2018, infections were confirmed in 1069 domestic dogs, 32 domestic cats *Felis catus* and 1 olive baboon *Papio anubis* (CDC, 2019). Furthermore, recent evidence shows that emergent worms from human and non-human hosts are genetically indistinguishable (Thiele et al. 2018), suggesting that Guinea worm disease is a zoonotic infection. Therefore, even in the near-absence of human cases, non-human hosts could maintain Guinea worm in the environment, resulting in an ongoing low-level of infection in humans. The existence of a non-human reservoir could explain the situation in Chad, where no human cases were reported for 10 years, but in 2010 the disease re-emerged (Eberhard et al. 2014). Given their disproportionate representation in the number of non-human cases, domestic dogs are now recognised as a reservoir for the disease (Galán-Puchades, 2017). To achieve global eradication of Guinea worm, it is apparent that transmission must be interrupted in both human and non-human hosts.

While the transmission of Guinea worm to humans is fairly well understood, little is known about the epidemiology of the disease in any of its non-human hosts. It seems likely that the transmission pathways for non-human hosts are the same as for humans, but comparable control strategies are much harder to implement for free-ranging animals. Thus, to prioritise control efforts, a better insight into the ecology of non-human animal hosts, particularly dogs, in relation to Guinea worm infection is required (Molyneux & Sankara, 2017). Specifically, more information is needed on the relative exposure of dogs to sources of infection (e.g. activity around water sources associated with infection and amount of aquatic foods in the diet), and correlates between these metrics of exposure and infection are required to provide evidence based risk factors for dogs; see Appendix A for an investigation of this nature that was conducted in Ethiopia.

1.5 DISEASE ECOLOGY AND MANAGEMENT

A parameter fundamental to epidemiological theory is the contact rate between infected and susceptible individuals (May, 2006; Meyers, 2007). Historically, epidemiological models have made several assumptions about the relationship between contact rates and the transmission of disease, including that transmission is density dependent and populations mix both uniformly and at random (Begon et al. 2002). Density-dependent transmission suggests that infection rates, and therefore contact rates, increase with population density, and that a critical density threshold determines if an outbreak occurs (Anderson & May, 1997). In contrast, frequency-dependent transmission, which is often associated with heterogeneous mixing patterns, proposes that transmission rates are independent of population density and that epidemics are not determined by a density threshold (Begon et al. 2002). Another key concept in epidemiology is the basic reproductive number (R_0); the average number of secondary infections caused by a single infected host in a fully susceptible population (Anderson & May, 1992). Crucial in determining R_0, is the transmissibility of the pathogen, the infectious period and the contact patterns between the infected and susceptible (Meyers, 2007). If R_0 is less than or equal to one, the disease incidence declines, but if R_0 is more than one and each individual goes on to infect others, the infection has the potential to persist and spread in the population (Heffernan et al. 2005).

The distinction between density & frequency dependent transmission and homogenous & heterogeneous mixing is important, as these can determine the appropriateness of different management strategies. For instance, assumptions of density dependent transmission with random uniform mixing favours the culling or sterilisation of wildlife populations, with the aim of reducing the density of susceptible individuals to below the 'threshold' that disease epidemics will persist. However, in the last few decades evidence has emerged to show that heterogeneity in host contact behaviour is common place in social species (Stehlé et al. 2013; Rushmore et al. 2013; Hirsch et al. 2013; Hamede et al. 2009; Cross et al. 2013; Quevillon et al. 2015). Furthermore, observed contact heterogeneities among individuals have been shown to determine the dynamics of disease transmission (Craft et al. 2011; Drewe et al. 2010; MacIntosh et al 2012; Weber et al. 2013). This realisation has led to the integration of contact heterogeneities into agent-based disease models, which has allowed the consideration of novel management strategies such as targeted vaccination (Silk et al. 2019).

Another aspect of behaviour that is pertinent for disease transmission is an individual’s space use (Barlow, 1996). The movement of individuals in time and space can cause fluctuations in a population’s density and contact rates, which inevitably influences the patterns of transmission (Altizer et al. 2011). Examples include the peaks in disease incidence that are associated with the seasonal aggregations of some species (Hosseini et al. 2004; Reperant et al. 2010), the spatial constraints of disease by territoriality (Davies et al. 2015; Craft et al. 2011), and infections that are propagated by dispersal (Robertson et al. 2006; Nunn et al. 2008). The complex relationship between population density, contact rates and spatial movements can be challenging for disease control. This is highlighted in the transmission of bovine tuberculosis in the European badger *Meles meles*, where novel intervention strategies, such as ring vaccination (Smith et al. 2012), have been inspired by a complex system of demographic processes, density dependent dispersal and contact heterogeneities (McDonald et al. 2018).

In respect to dog ecology, there is mixed evidence for density and frequency dependent transmission processes for diseases such as rabies (Morters et al. 2013). Furthermore, as illustrated in the previous sections, it is apparent that little is known about the contact rates between dogs (Sparkes et al. 2015; Leung & Davies, 2017) or their spatial ecology. Although dogs are a domestic species they occupy a diverse array of socio-ecological contexts, each of which may elicit different social and spatial behaviours. Therefore, investigations into the individual level variations in contact rates and movements are required, with the aim of better informing our understanding of the transmission and control of dog-mediated diseases.

1.6 THESIS OUTLINE

The role of free-ranging dogs as a reservoir for diseases that can infect both humans and wildlife populations is now widely recognised. However, currently there are substantial knowledge gaps in our understanding of dog social and spatial ecology. In this thesis, I investigate the dynamics in the contact behaviour and spatial movements of free-ranging domestic dogs in rural Chad; where the risk of infection to humans for Guinea worm and rabies is high. I discuss how these new perspectives on dog ecology can help in the management of dog-mediated diseases.

Chapter 2 investigates the heterogeneity in contacts between free-ranging domestic dogs. I describe the contact network for dogs and use an agent-based disease model to highlight the implications of the observed network structure on epidemic outcomes for a disease comparable to rabies.

Chapter 3 provides a comprehensive analysis on the spatial movements of free-ranging dogs. I discuss how these movement patterns can be used to better inform disease management strategies, such as vaccination campaigns, that require access to a large proportion of the population.

Chapter 4 investigates the spatial-temporal dynamics of the contact behaviour between free-ranging dogs. I use a dyadic level analysis to describe the contact probabilities and contact durations between dogs in different seasons, at different times of day and in different locations.

Chapter 5 investigates the activity of free-ranging domestic dogs around water sources that are potential sources for Guinea worm infection. I discuss how these results can be used by the Guinea worm eradication program to prioritise resources used in the targeted treatment of water sources.

CHAPTER 2:

HIGH-RESOLUTION CONTACT NETWORKS OF FREE-RANGING DOMESTIC DOGS *CANIS FAMILIARIS* AND IMPLICATIONS FOR TRANSMISSION OF INFECTION

2.1 ABSTRACT

Contact patterns strongly influence the dynamics of disease transmission in both human and non-human animal populations. Domestic dogs *Canis familiaris* are a reservoir for several zoonotic infections, yet few studies have empirically determined contact patterns within dog populations. Using high-resolution proximity sensors, we characterised the contact networks of free-ranging domestic dogs from two settlements (n = 108 dogs, covering >80% of the population in each settlement) in rural Chad. We used these data to simulate the transmission of an infection comparable to rabies and investigated the effects of observed contact heterogeneities on epidemic outcomes. We found that dog contact networks displayed considerable heterogeneity, particularly in the duration of contacts and that the network had communities that were highly correlated with household membership. Simulations using observed contact networks had smaller epidemic sizes than those that assumed random mixing, demonstrating the unsuitability of homogenous mixing models in predicting epidemic outcomes. When contact heterogeneities were included in simulations, the network position of individuals initially infected had an important effect on epidemic outcomes. The risk of an epidemic occurring was best predicted by the initially infected individual's ranked degree, while epidemic size was best predicted by the individual's ranked eigenvector centrality. For dogs in one settlement, we found that ranked eigenvector centrality was correlated with range size. Our results demonstrate that observed heterogeneities in contacts are important for the prediction of epidemiological outcomes and that observable traits relating to an individual's network position hold potential for informing targeted disease management strategies.

2.2 INTRODUCTION

Heterogeneity in contact rates is influential in the epidemiology of both human and non-human animal diseases. In principle, variation in the contact rates among individuals affects their risk of acquiring and/or transmitting infections (May, 2006; Craft, 2015). Relationships between host social behaviour and the distribution of infections have been demonstrated in several wild animal host-pathogen systems, from tuberculosis in badgers *Meles meles* (Weber et al. 2013) and meerkats *Suricata suricatta* (Drewe, 2009) to nematodes in Japanese Macaques *Macaca fuscata* (MacIntosh et al. 2012). One driver of these relationships is the variation in contacts between individuals, which can influence the flow of infection through populations (Hamede et al. 2012; Reynolds et al. 2015). Therefore, in order to successfully manage some diseases, it is important to understand the dynamics of host contacts that facilitate the transmission of infection (Webster et al. 2016).

The number of infectious disease emergence events in humans has been increasing over time, and the majority of these are zoonotic in origin (Jones et al. 2008). This may, in part, be associated with the domestication of animals, as evidence suggests that the number of shared pathogens (between humans and non-human animals) increases with the time since a species was domesticated (Morand et al. 2014). This is because domestication increases the exposure of people and animals to a greater range of pathogens, and increases the risk of humans acquiring zoonotic infections (Karesh et al. 2012). If domestic animals are free-ranging, they are also more likely to interact with wild animals, further facilitating the transmission of disease between people and wildlife (Caron et al. 2015).

Dogs *Canis familiaris* are among the earliest domesticated animals and they share 16% of their known pathogens with humans (Morand et al. 2014) and 47% with wild mammals (Knobel et al. 2014). Amongst these pathogens is rabies, a viral zoonosis that poses a significant public health risk, responsible for approximately 59,000 human deaths annually (Hampson et al. 2015) and primarily transmitted to humans through the saliva of an infected dog when they are bitten (Warrell et al. 2004; Meslin & Warrell, 2013). Mathematical models can be applied to inform management efforts by predicting epidemics and, for rabies, these models are relatively well developed (Panjeti & Real, 2011). However, one of the challenges identified in controlling rabies is a lack of information on dog ecology (Fahrion et al. 2017) and variation in contact rates has been identified as being especially influential for epidemic outcomes in a number of modelling studies (Sparkes et al. 2016; Johnstone-Robertson et al. 2017). This is unsurprising given that dogs are social animals that exhibit pronounced between-individual variation in their behaviour (Bradshaw et al. 2009).

Collecting high resolution data on the contact rates between individuals is a major challenge, particularly for free-ranging animals. This lack of empirical data has meant that stochastic models have relied on assumptions that contact rates are density dependent or have included a frequency dependent function in the form of spatial and/or social scaling parameters to generate variation in the probability of contacts (Bradshaw et al. 2009; Beyer et al. 2011; Johnstone-Robertson et al. 2017). Although these assumptions are biologically sound, they fail to capture social phenomena that could influence disease transmission, such as assortative mixing (Newman, 2003) and clustering (Newman, 2009). Including observed contact data in stochastic models of communicable diseases could help better predict epidemics at a local scale and help identify novel management techniques (Newman et al, 2001).

To date, there has been only one study published that integrated observed contact rates of free-ranging dogs into a model for the transmission of rabies (Laager et al. 2018), in which the contact network of dogs was characterised over 3.5 days in an urban environment. They found that urban dogs formed communities that were defined by roads, which acted as a barrier to movement. When simulating outbreaks of rabies, the authors observed that major epidemics were avoided when 70% of the population were vaccinated and targeted management based on network measures increased the effectiveness of vaccination. However, it is unclear if this would also apply to rural dog populations, where the landscape and dog-human relationships are likely to be different to that in an urban environment (Gompper, 2014), where unowned dogs are rare, roads are few and where hunting, subsistence farming and fishing are more prevalent.

In this study, we used automated proximity loggers to generate high-resolution contact networks of free-ranging dogs in an area of rural sub-Saharan Africa, where dogs are susceptible to a number of zoonotic infections. We use these data to model the transmission of an infection that is epidemiologically similar to rabies. We test the effect of including observed heterogeneities in contacts between free-ranging dogs on predictions for epidemic size. Using a network model we simulate epidemics through random networks, the observed network characterised as binomial (present/absent) interactions and the observed network when weighted by the duration of interactions. The observed binomial network introduces non-random structures while maintaining uniformity and the observed weighted network adds non-random and non-uniform mixing. In addition, we investigate the effect of seeding different individuals with the infection. If contact heterogeneity influences epidemics it may be possible to predict epidemic outcomes using the network position and/or associated traits of the seeded individual.

2.3 METHODS

2.3.1 *Data collection*

Dogs were studied between June 24th and July 12th 2016 in two settlements, each comprising two neighbouring villages, located along the Chari River in the Guelendeng district of the Mayo-Kebbi East region of Chad. The settlement Kakale is located to the south-east of Guelendeng town and includes the villages Kakale-Mberi (10°53'0.79"N, 15°38'8.45"E) and Awine (10°48'6.34"N, 15°37'56.61"E). Kakale-Mberi is a linear settlement along a main (dirt) road that runs parallel to the Chari River. Awine is a dispersed settlement that is seasonally occupied by the people of Kakale-Mberi, who move there to cultivate crops. The settlement Magrao is comprised of the villages Magrao and Sawata (centred on 10°59'44.31"N, 15°29'29.27"E), located to the north of Guelendeng. Magrao is a dispersed village lying between the Chari River and the main road from Guelendeng to the capital, N'Djamena. Sawata is a smaller village that is surrounded by Magrao but is distinguished by different ethnicity and a higher prevalence of pastoralism.

All dogs had clear ownership and were associated with a specific household. They were all sexually intact. With the consent of owners, dogs were collared with standard nylon dog collars (Ancol Heritage). Puppies (less than 6 months of age) were not collared. Collars were fitted with two devices; (1) an i-GotU GT-600 GPS unit (Mobile Action Technology Inc., Taiwan) and (2) a wearable proximity sensor based on a design developed by OpenBeacon project (http://www.openbeacon.org/ and the SocioPatterns collaboration consortium (http://www.sociopatterns.org/. The GPS units were configured with a fix interval of 10 minutes and a sleep mode to extend battery life. The proximity sensors exchange one ultra-low power radio packet per second in a peer-to-peer fashion and, have been successfully deployed in several studies on humans (Stehle et al. 2013; Voirin et al. 2015). The exchange of radio-packets is used as a proxy for the spatial proximity of individuals wearing the sensors (Cattuto et al. 2010; Isella et al. 2011). Close proximity is measured by the attenuation, defined as the difference between the received and transmitted power. The attenuation threshold used in this deployment was selected to detect close-contact events (within 1-1.5 m), during which a communicable disease infection might be directly transmitted, either by airborne transmission or by direct physical contact. Additional data collected on the individual dogs included sex and body condition score (BCS; Laflamme, 1997). Due to low frequencies of some scores, we categorised them into poor (BCS ≤ 2) and moderate (BCS ≥ 3). Interviews using a standardised questionnaire were carried out at households to record the number of dogs owned and the dogs' ages, as recalled by the owner. A single observer estimated BCS and another conducted all household interviews. Dogs aged 12 months or less were classified as juveniles, dogs aged between 13 and 24 months were classed as sub adults and dogs older than 24 months were regarded as adults (Cafazzo et al. 2010). Since all households known to have dogs in the settlement were visited, the dog population size (excluding puppies) was calculated for each settlement by summing the reported number of owned dogs from each household.

2.3.2 *Data processing*

The proximity data were extracted from devices and cleaned by identifying corrupted sensors (where no data were available) or anomalous signals (such as continuous bursts of data). The GPS data were cleaned by removing erroneous fixes with speeds greater than 20 km/hr between locations. For both GPS and proximity data we discarded records collected on the first and last day of collar deployment in each village; providing time for the dogs to habituate to collars at the start and to account for the collection of the collars at the end of the field study.

Data analysis was conducted in R v3.3.3 (R Core Team, 2017) and Python v2.7. The R packages ‘sp’ v1.2-3 and ‘rgdal’ v1.2-5 were used to project the GPS data into the relevant coordinate reference system for Chad (EPSG:32634). The package ‘adehabitatHR’ v0.4.14 was used to calculate the dog’s total range (99% minimum convex polygons) and core range (60% kernel density estimate).

Networks were treated as undirected symmetric networks. Since dogs were not collared for the same number of days, the weights for the weighted networks were converted to the average number of seconds the dogs were in contact per day monitored. This was done by dividing the total duration in seconds over which a pair was in contact, by the shorter of the two periods in days for which the two dogs were collared. These weights were then $\log_{10}$ transformed. The global and local network metrics were calculated using the R package ‘igraph’ (Csardi & Nepusz, 2006). The network position of individuals was described using metrics most relevant to disease transmission (Silk et al. 2017a), including: degree (the number of unique connections of an individual), strength (the summed strength of all connections for an individual), betweenness (the number of shortest paths between other individuals upon which the focal individual lies), and eigenvector centrality (a measure of second order contacts whereby a higher score is assigned to individuals if they associate with highly connected individuals or many moderately connected individuals). To compute the probability density distribution of contact durations and the complementary cumulative distribution function (CCDF) of edge weights, we used the Python package 'Powerlaw' v1.4.1. Community membership describes individuals that are closely associated/clustered together and these groups were identified using the edge betweenness and Greedy algorithms in the Python package 'igraph' v0.7.1.

2.3.3 *Epidemic simulations*

The package 'Epimodel' v1.3.0 (Jenness et al. 2018) was used to build a Susceptible, Exposed, Infected and Removed (SEIR) network model of infection spread. Simulations were run on the observed binomial network, the observed weighted network and the null model (random networks). Random networks are traditionally used in network analysis to overcome the non-independence nature of contacts, and are typically constrained to biologically plausible scenarios. The null model for this study was that individuals mix randomly and so random networks were generated using the Erdős-Rényi model, conserving the observed number of nodes (individual dogs) and edges (connections). Every individual in the binomial and weighted networks was seeded with the infection and, for each seeded individual, 100 simulations of the model were run. For the null model, the same procedure was conducted, however, each simulation involved a different random network and all seeded individuals experienced the same set of 100 random networks. Simulations were run over 300 time steps (days). The network model assumed that (a) there was no recruitment or loss of individuals to the population (except the eventual removal of those infected), (b) the edges and weights of the network did not rewire over time or in response to infected or removed individuals and (c) individuals do not change their behaviour when infected.

For each simulation an initial seed (infectious individual) was selected at time step 1. At time steps 2-300, an edge list of infectious and susceptible individuals was made and transmission events were determined through a random binomial draw using the calculated per link transmission probability (β):

(1) $\beta = 1 - (1 - \lambda)^{\alpha}$

The probability of infection after being bitten (λ) was taken to be 0.49 (Hampson et al. 2009). To our knowledge, no data are available on the act rate (α; number of bites per partnership per day) of rabid dogs and it was therefore taken to be:

(2) $\alpha = \frac{\log(1-\beta)}{\log(1-\lambda)}$

Where β was calculated by assuming a constant value of the basic reproductive number (R_0) and by rearranging its definition in the heterogeneous mean-field approximation (Pastor-Satorras et al. 2015):

(3) $\beta = \frac{R_0 \, \mu \, \langle k \rangle}{\langle k^2 \rangle - \langle k \rangle}$

The mean degree ⟨k⟩ and mean square degree $\langle k^2 \rangle$ were extracted from the observed networks (see Table 2.1). The infectious period (μ) was randomly drawn from a gamma distribution (shape = 3.0; scale = 0.9; see Hampson et al. 2009 & Talbi et al. 2010). Simulations were run for a range of basic reproductive numbers found in the literature for rabies in dogs. The lower R_0 was set to 1.2, the mid value was 1.8 (Hampson et al. 2009) and the upper R_0 was 2.4 (Kurosawa et al. 2017). The transmission probability for different edge weights (β_{ij}) was calculated using equation 4:

(4) $\beta_{ij} = 1 - (1 - \lambda)^{\alpha_{ij}}$

(5) $\alpha_{ij} = \alpha \frac{w_{ij}}{1+w_{ij}} \times 2$

The weighted act rate (α_{ij}) was calculated through equation 5 which is modified from Reynolds et al. (2015). Here we assumed that α_{ij} was positively associated with the daily average of the total duration that individuals were in contact (w_{ij}), and in so doing, we applied a sigmoidal scaling function. This value was then multiplied by two to shift the mean of β_{ij} to β. The use of this scaling function is justified where biting is the main method of rabies transmission and only a short contact time is required. Once a transmission event occurred, a random draw from a gamma distribution was used to allocate an incubation period (shape = 1.1; scale = 20.1; see Hampson et al. 2009 & Talbi et al. 2010) and infectious period (see above for parameters). During the incubation period individuals were considered to be in the exposed category. Once the incubation period was over, the individual was classed as infected and could transmit the disease until such time as the assigned infectious period was over and the individual, along with its associated edges, was removed from the network. For this study, an epidemic was defined as disease transmission to at least one other individual.

2.3.4 *Statistical Analysis*

Differences in ranked network position (degree, strength, eigenvector centrality and betweenness) between nodal attributes (sex, age, BCS and home ranges) were identified by calculating t-statistics, using either t-tests or linear models. Observed statistics were compared to the distribution of test statistics from null models to identify if they were significantly different to those expected had individuals mixed randomly (Farine et al. 2015). Null models consisted of 10,000 random networks generated by randomly shuffling the node attributes while keeping the structure of the observed network the same. Homophily within the attributes age, sex and household was investigated by calculating the assortativity (r) coefficient using the ‘assortnet’ package in R. Again the observed coefficients were compared to the distribution of coefficients from null models. To see if community membership was determined by the dogs’ sex, age or household, we used the Normalized Mutual Information (NMI) score to scale the results between 0 (no mutual information) and 1 (perfect correlation). To investigate if there was a correlation between edge existence/weight and the distance between households, the ‘sna’ package v.2.4 in R was used to perform a quadratic assignment procedure (QAP) with 1000 permutations.

Generalised additive models (GAMs) were used to identify non-linear relationships between the averaged epidemic outcomes of simulations for seeded individuals and their ranked network position (degree, eigenvector centrality, and betweenness). Models were fit with family set to Gaussian and included a smoothing term (k = 3). Strength was not investigated in these models since no difference in epidemic size between weighted and binomial simulations was observed. Since measures of network position are often correlated, separate models were fitted for each measure of centrality and type of network. Akaike’s Information Criterion (AIC) and adjusted r^2 values were extracted and used to identify which centrality measure best explained epidemic outcomes.

2.4 RESULTS

2.4.1 *Network structure*

In Kakale, collars were successfully deployed for a mean of 8 days (range 2 – 9 days) on 48 dogs (86% of the population excluding puppies) from 28 different households (Figure 2.1). The distance between dog owning households ranged from 23 – 10,002 m. 8561 contact events were recorded between dogs in Kakale and the median contact duration was 20 seconds with a percentile (2.5 % - 97.5 %) range of 20 – 200 seconds. In Magrao, contact data were collected for a mean of 8 days (7 – 10 days) for 60 dogs (82% of the population) from 36 households. The distance between households ranged from 35 – 4758 m. 7361 contact events were recorded between dogs in Magrao and the median contact duration was 20 seconds, with a percentile range of 20 – 160 seconds.

The global structure of both networks revealed high levels of clustering and short average path lengths (Table 2.1). Furthermore, community analysis using the edge betweenness (EB) and Greedy (G) algorithms showed the dog populations in both settlements exhibited high modularity in the binomial network (Kakale: EB = 0.48, G = 0.51; Magrao: EB = 0.56, G = 0.57) and the weighted network (Kakale: EB = 0.57, G = 0.603; Magrao: EB = 0.60, G = 0.617). Magrao was the larger of the two networks and had a wider degree distribution ($k_{min} = 1$, $k_{max} = 17$) than that of Kakale ($k_{min} = 2$, $k_{max} = 14$). In both networks the degree distribution was homogenous (Kakale: coefficient of variation (CV) = 0.49, Magrao: CV = 0.48) while the distributions for the duration of contacts were highly heterogeneous (Kakale: CV = 1.88, Magrao: CV = 1.85), and the probability density distribution declined as contact durations increased (Figure 2.2).

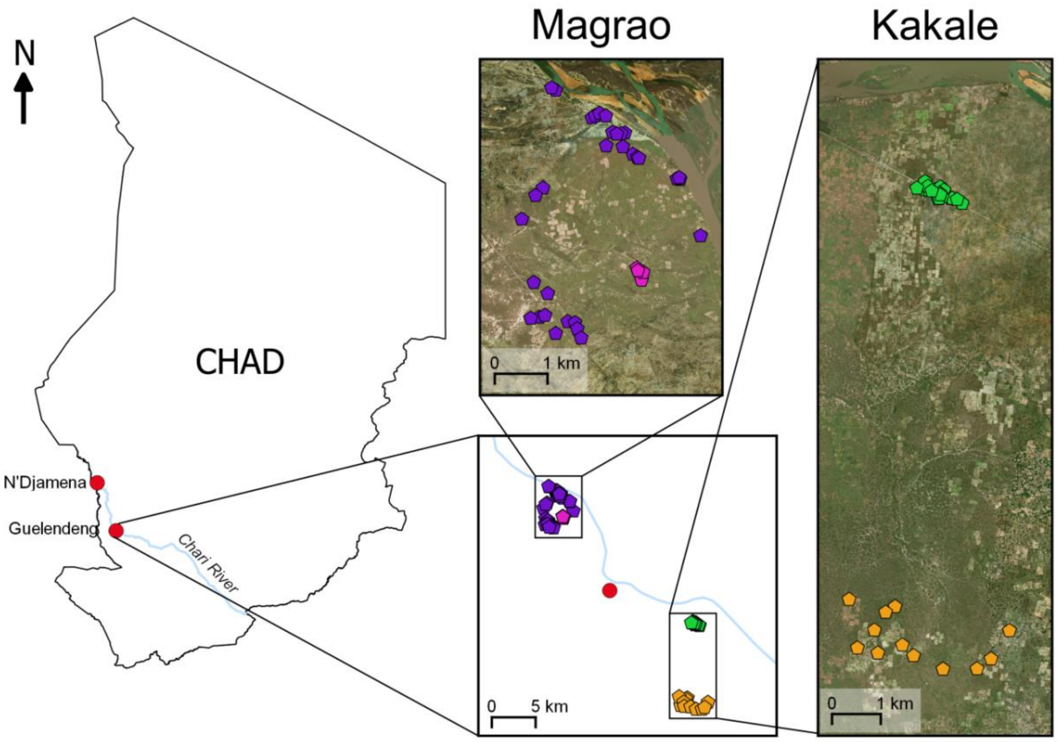

Figure 2.1. Locations of two settlements in rural chad at which contact patterns of free-ranging domestic dogs were quantified. Pentagons represent a household where at least one dog was collared. Villages include Magrao (purple), Sawata (pink), Kakale-Mberi (green) and Awine (orange). The satellite image was generated using the Esri world imagery basemap (sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community).

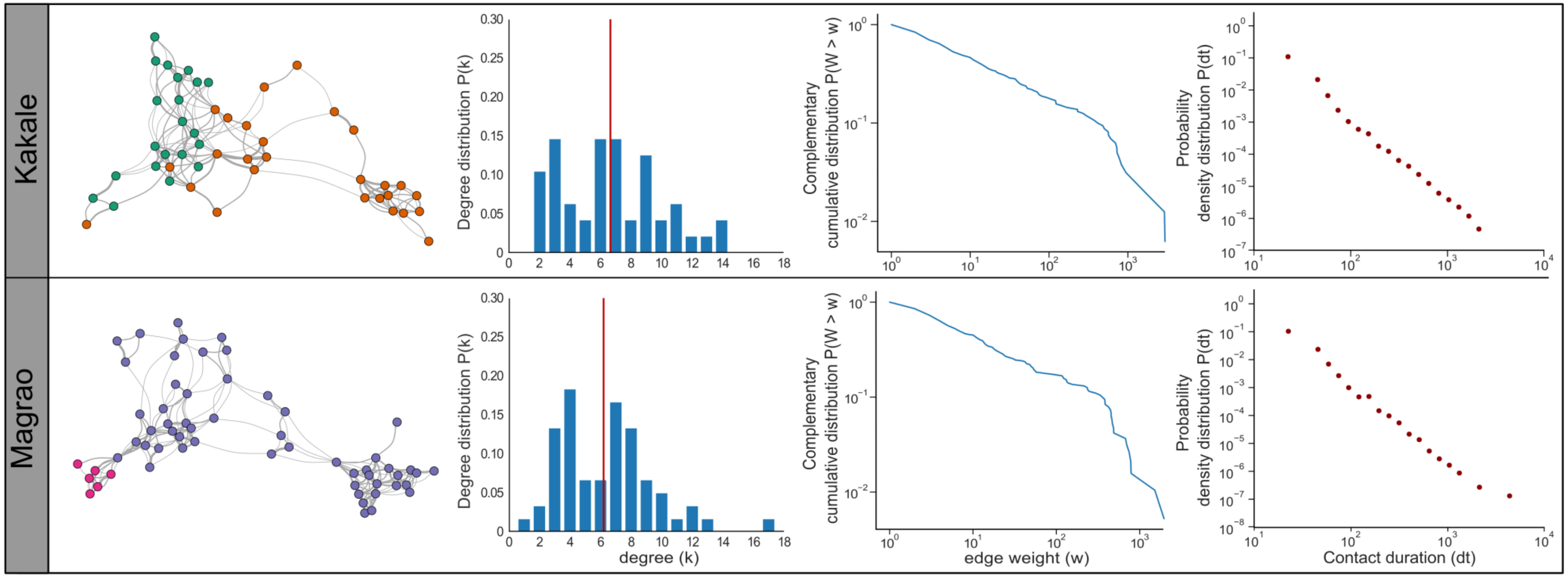

Figure 2.2: **The contact networks, degree distribution, edge weight distribution and probability density distribution of contacts between free-ranging dogs for two settlements in Chad.** In the networks, the circles represent individuals and the colours indicate the village that the dogs belong to: Kakale-Mberi in green, Awine in orange, Magrao in purple and Sawata in pink. The lines connecting individuals indicate that they have been in contact and the thickness of the lines are proportional to the logged daily average contact time between individuals. The red line of the degree distributions (probability that a randomly chosen node has degree ≥ k) indicates the mean degree (number of connections).

Table 2.1. Summary of individual attributes and the global and local network metrics for free-ranging dogs from two settlements, Kakale and Magrao, in rural Chad**.**

	Kakale	Magrao
Attributes		
Sex (male : female)	25 : 23	39 : 21
Age (adult : sub adult : juvenile)*	25 : 13 : 9	26 : 18 : 15
BCS (poor : moderate)**	24 : 24	15 : 40
Core range (km^2)***	2.28 ± 0.72	0.17 ± 0.05
Total range (km^2)***	20.77 ± 3.27	4.56 ± 0.66
Global network metrics		
Nodes	48	60
Edges	160	191
Edge Density	0.14	0.11
Diameter	7	8
Average path length	3.01	3.57
Clustering coefficient	0.51	0.50
Local network metrics		
Degree	6.7 ± 0.5	6.4 ± 0.4
Square degree	55.4 ± 7.2	49.9 ± 6.3
Strength	10.2 ± 0.7	9.1 ± 0.7
Eigenvector	0.32 ± 0.05	0.19 ± 0.03
Betweenness	47.1 ± 9.9	75.9 ± 16.8

The mean ± standard error is reported for spatial attributes and the local network metrics. Total range is the 99 % Minimum Convex Polygon and core range is the 60 % Kernel Density Estimate. Global network metrics include the number of nodes (individuals), number of edges (connections between individuals), diameter (longest path length), average path length and cluster coefficient (transitivity). Local network metrics include the degree (number of connections), square degree, strength (summed strength of connections), Eigenvector centrality (second order contacts) and betweenness (contribution to number of shortest paths).

*The age of one individual in both settlements was unknown. ** In Magrao, data for BCS was missing for 5 individuals. *** The spatial ranges of 9 individuals in Magrao and 3 individuals in Kakale were unknown.

2.4.2 *Individual attributes and network position*

Dogs in Magrao had substantially smaller ranges than dogs from Kakale, and the distribution of ranges was right skewed for both settlements (Appendix B Figure B1). Dogs in Kakale that had larger ranges had higher ranked eigenvector centralities and this was significantly different to null models (Table 2.2). Similarly, the home ranges of dogs in Kakale were positively correlated with their ranked degree, and this correlation was significantly greater than that of null models. In both networks, comparisons to null models revealed no significant association of any ranked network measures (degree, strength, eigenvector centrality or betweenness) with sex, age or body condition

.

Table 2.2. Relationships between the ranked network position of free-ranging domestic dogs from two rural settlements in Chad and their individual attributes.

	Ranked Degree		**Ranked Strength**		**Ranked Eigenvector Centrality**		**Ranked Betweenness**	
	t	p	t	p	t	p	t	p
				Male vs Female				
Kakale	-0.755	0.222	-0.237	0.404	-0.113	0.446	1.796	0.043
Magrao	1.735	0.045	1.530	0.069	1.060	0.147	-0.118	0.456
				Adult vs Juvenile				
Kakale	2.073	0.031	1.580	0.072	1.148	0.131	2.039	0.033
Magrao	0.754	0.233	-0.578	0.276	1.270	0.109	1.632	0.054
				Adult vs Sub Adult				
Kakale	0.501	0.306	1.258	0.106	0.048	0.484	0.012	0.488
Magrao	-0.905	0.490	-0.620	0.303	-0.013	0.494	1.002	0.161
				Sub Adult vs Juvenile				
Kakale	1.238	0.115	0.350	0.367	0.934	0.425	1.590	0.065
Magrao	0.480	0.237	0.905	0.452	1.363	0.124	0.456	0.316
				BCS (Moderate vs Poor)				
Kakale	1.266	0.103	1.570	0.057	0.061	0.472	0.041	0.481
Magrao	0.660	0.259	-0.205	0.414	1.921	0.033	0.760	0.224
				Core Range				
Kakale	3.603	**<0.001**	2.044	0.024	3.895	**<0.001**	-1.372	0.007
Magrao	0.822	0.217	0.232	0.420	0.508	0.317	1.897	0.029
				Total Range				
Kakale	2.936	**0.003**	1.708	0.048	3.915	**<0.001**	2.310	0.012
Magrao	1.035	0.164	0.116	0.459	0.703	0.243	2.403	0.008

Observed statistics for differences in ranked degree (number of connections), strength (summed strength of connections), Eigenvector centrality (second order contacts) and betweenness (contribution to number of shortest paths) are reported. Total ranges are based on 99 % Minimum Convex Polygons and core ranges are 60 % Kernel Density Estimates. P-values are for comparisons between the t-statistics of the observed and random graphs. P-values in bold are significant. The alpha level was corrected for multiple comparisons using the Bonferroni correction (α = 0.007).

All measures of community membership were strongly correlated with household membership in both the binomial networks (Kakale: NMI_{EB} = 0.622, NMI_G = 0.625; Magrao: NMI_{EB} = 0.739, NMI_G = 0.649) and weighted networks (Kakale: NMI_{EB} = 0.674, NMI_G = 0.70; Magrao: NMI_{EB} = 0.725, NMI_G = 0.713). Community membership had no significant relationship with either the dog's sex or age (Appendix B Table B1). When compared to null models, dogs in both settlements had a strong preference to associate with individuals from the same household and no assortative mixing patterns were found between dogs of a different/similar age or sex (Table 2.3). QAP tests found a significant negative correlation for the distance between households and the existence of an edge (Kakale: $r = -0.23$, $p < 0.001$; Magrao: $r = -0.4$, $p < 0.001$). A negative correlation was also found for the relationship between household distance and edge weight (Appendix B Figure B2. Kakale: $r = -0.22$, $p < 0.001$; Magrao: $r = -0.37$, $p < 0.001$).

Table 2.3. The binomial and weighted assortativity for the contact networks of free-ranging dogs from two settlements, Kakale and Magrao, in rural Chad.

Attribute	Settlement	Binomial		Weighted	
		r	p	r	p
Sex	*Kakale*	-0.051	0.381	-0.091	0.237
	Magrao	-0.075	0.206	-0.160	0.027
Age	*Kakale*	0.060	0.112	0.047	0.205
	Magrao	-0.015	0.405	-0.013	0.447
Household	*Kakale*	0.130	**< 0.001**	0.283	**< 0.001**
	Magrao	0.162	**< 0.001**	0.329	**< 0.001**

The assortativity between individuals of a similar sex, age and household in Kakale and Magrao. The r coefficient is for the observed network and the p-values are for the comparison between the observed coefficient and the distribution of those from null models. Significant p-values are in bold.

2.4.3 *Epidemic simulations*

For both settlements, larger R_0 values resulted in an increased risk of epidemics occurring and larger epidemic sizes (Figure 2.3, see Appendix B Figure B3 for the frequency distributions of secondary cases). In simulations when R_0 was 1.8 or 2.4, mean epidemic size was higher for random networks than that of simulations with observed contacts. Epidemic sizes for simulations using these random networks had a bimodal distribution, whereby epidemics either involved a large number of individuals or very few. In contrast, the distribution of epidemic sizes for observed networks had multiple peaks at intermediate sizes. The distributions of epidemic sizes differed for the two settlements, whereby Kakale had more intermediate peaks. Simulations with the lowest R_0 value (1.2) showed no discernible difference in mean epidemic sizes between the random and observed networks.

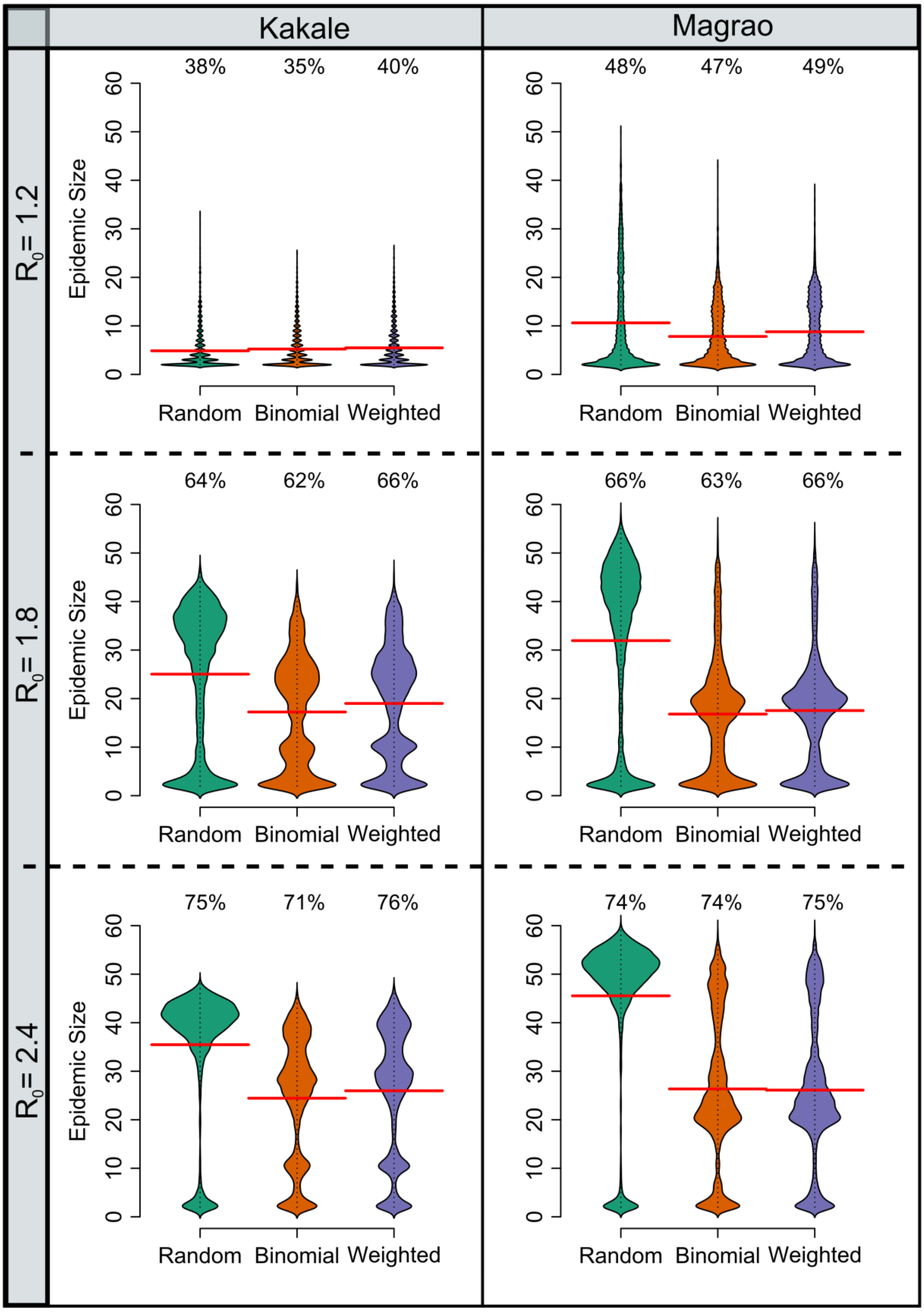

Figure 2.3. Simulated epidemic sizes of disease transmission through empirically determined contact networks for free-ranging dogs in two rural settlements in Chad. Bean plots show the distribution of epidemic sizes of simulations using the observed binomial and weighted networks and random networks: Kakale (n = 4800) and Magrao (n = 6000). All plots consider simulations where an epidemic occurred (the disease spread to at least one individual). The percentage of simulations that resulted in an epidemic is displayed above each bean plot. The horizontal red lines indicate mean epidemic size.

For the observed networks for both settlements, the seeded individual's ranked centrality measures (degree, eigenvector centrality and betweenness) were all positively correlated with the proportion of simulations that resulted in an epidemic (Appendix B Figure B4). The seeded individual's ranked degree was the best predictor for the proportion of simulations to result in an epidemic (Table 2.4), and at larger R_0 values the relationship between ranked degree and an epidemic outcome began to plateau for higher ranked individuals (Figure 2.4). As expected, the seeded individual's observed centrality measures did not correlate with the proportion of simulations to result in an epidemic in any of the random networks.

The seeded individual's ranked eigenvector centrality and ranked degree were positively correlated with the mean epidemic size in simulations on the binomial and weighted networks for both settlements (Appendix B Figure B5). Ranked eigenvector centrality was the best predictor of mean epidemic size (Table 2.4), and for simulations of Magrao at larger R_0 values, mean epidemic size plateaued for individuals with a higher ranked eigenvector centrality (Figure 2.4). The distributions of eigenvector centralities for dogs in each settlement (Appendix B Figure B6), were similar to the distribution of epidemic sizes in respective settlements. No correlation between the seeded individual's network position and mean epidemic size was found in any of the random networks.

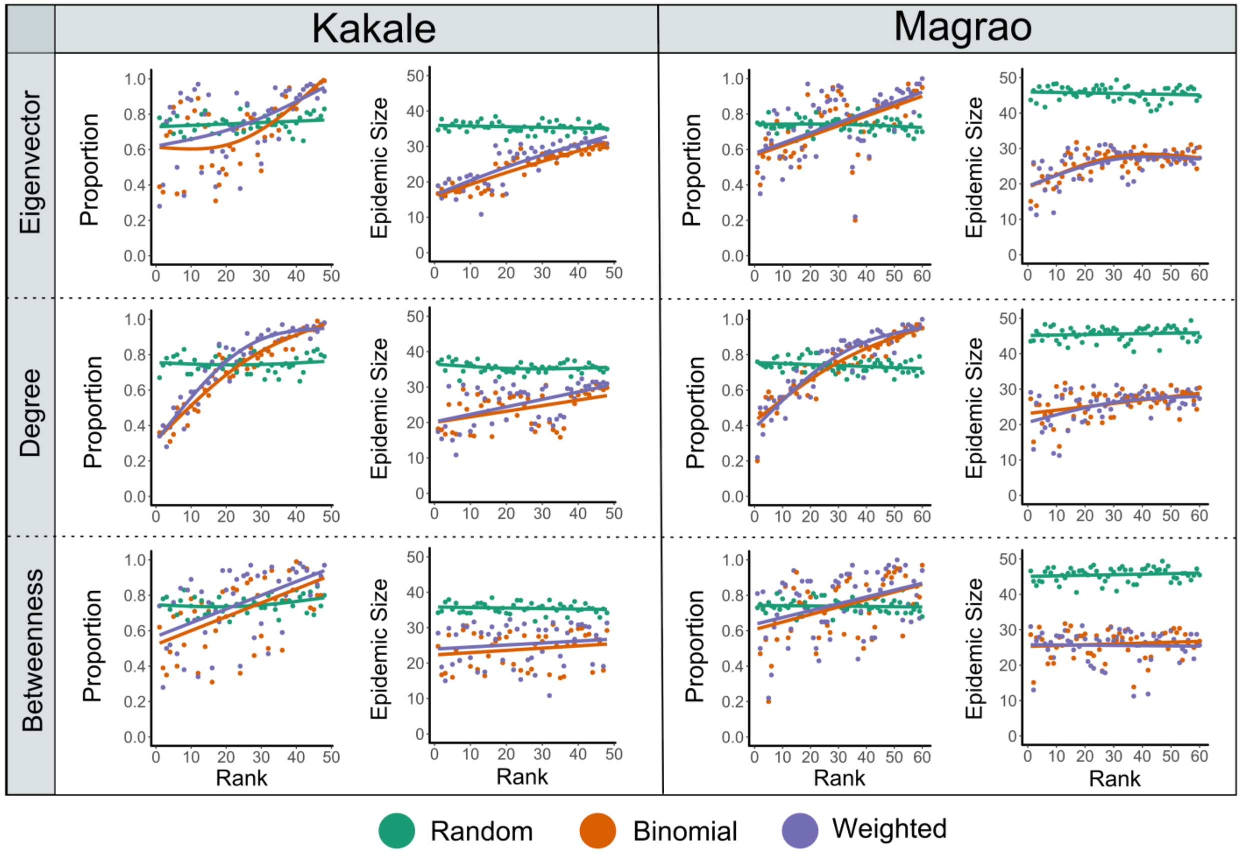

Figure 2.4. The relationship between epidemic outcomes simulated on contact networks of free-ranging dogs from two rural settlements in Chad and the seeded individual's ranked network position. Scatter plots for each settlement (Kakale and Magrao) show the seeded individual's ranked centrality measures (Eigenvector centrality (second order contacts), degree (total number of contacts) and betweenness (contribution to number of shortest paths)) plotted against the proportion of simulations that resulted in an epidemic (the disease was transmitted to at least one individual) and mean epidemic size. The mean epidemic sizes exclude simulations where the infection did not spread beyond the seeded individual. The data include the results for the random, binomial and weighted networks, and are for simulations when R_0 was set to 2.4. GAMs are fitted to the data to identify non-linear trends.

Table 2.4. Measures of model fit for the relationship between epidemic outcomes simulated on contact networks of free-ranging dogs and the seeded individual's network position. Networks were described in two settlements, Kakale and Magrao, in rural Chad.

	R_0	Network	Proportion of simulations that resulted in an epidemic						Mean epidemic size					
			Eigenvector centrality		Degree		Betweenness		Eigenvector centrality		Degree		Betweenness	
			r^2	AIC	r^2	AIC	r^2	AIC	r^2	AIC	r^2	AIC	r^2	AIC
Kakale	1.2	Random	0	-130	0.03	-131	0.07	-133	0.13	99	0.02	105	0	106
		Binomial	0.45	-72	**0.93**	**-169**	0.33	-64	**0.49**	**120**	0.18	144	0.04	151
		Weighted	0.32	-53	**0.86**	**-130**	0.42	-61	**0.56**	**132**	0.31	153	0.03	170
	1.8	Random	0	-166	0	-166	0	-166	0.01	206	0	207	0	207
		Binomial	0.36	-35	**0.92**	**-138**	0.36	-36	**0.68**	**234**	0.09	284	0	288
		Weighted	0.26	-31	**0.91**	**-132**	0.34	-37	**0.71**	**231**	0.24	277	0	291
	2.4	Random	0.03	-151	0	-149	0.09	-153	0.01	178	0.05	176	0	178
		Binomial	0.40	-40	**0.94**	**-148**	0.29	-32	**0.79**	**219**	0.18	285	0.01	294
		Weighted	0.24	-27	**0.91**	**-132**	0.28	-30	**0.69**	**253**	0.25	295	0	308
Magrao	1.2	Random	0	-197	0.06	-201	0	-197	0	233	0	232	0.15	223
		Binomial	0.33	-59	**0.87**	**-158**	0.14	-45	**0.73**	**188**	0.34	243	0	268
		Weighted	0.37	-58	**0.88**	**-159**	0.16	-40	**0.68**	**223**	0.36	264	0	292
	1.8	Random	0	-199	0	-199	0	-199	0	259	0.03	257	0	259
		Binomial	0.35	-53	**0.91**	**-173**	0.18	-39	**0.66**	**262**	0.30	304	0	325
		Weighted	0.29	-47	**0.85**	**-138**	0.10	-33	**0.54**	**292**	0.33	314	0	338
	2.4	Random	0.02	-222	0.05	-225	0	-221	0	255	0	255	0	255
		Binomial	0.34	-68	**0.87**	**-164**	0.19	-55	**0.49**	**299**	0.17	327	0	339
		Weighted	0.30	-53	**0.87**	**-151**	0.13	-40	**0.30**	**333**	0.24	338	0	355

The adjusted r^2 and AIC of fitted GAMs are reported for the seeded individuals centrality measures (Eigenvector centrality (second order contacts), degree (total number of connections) and betweenness (contribution to the number of shortest paths)). Results are reported for when R_0 was set to 1.2, 1.8 and 2.4, and for the random, binomial and weighted networks of both Kakale and Magrao. The best r^2 and AIC are highlighted in bold for each R_0 of the binomial and weighted networks.

2.5 DISCUSSION

We have gathered high-resolution data on the contacts among free-ranging domestic dogs living in two rural settlements in Chad, an area where rabies infection is endemic and regularly causes human fatalities. Using these data we have demonstrated the importance of including observed contact patterns when simulating the transmission of an infection comparable to rabies. We show that the observed contact rates between dogs are heterogeneous and that interactions were dominated by contacts that were short in duration and between dogs from the same household. In our model, for the transmission of infection, the inclusion of observed contact rates resulted in fewer epidemics occurring compared to when random mixing was assumed and, for all but the lowest R_0 values, epidemics were smaller in simulations using the observed networks. We also show that the seeded individual's first and second order contacts were strong indicators of epidemic outcomes, verifying that individuals differ in the risk they present for the transmission of infections. Furthermore, for dogs in one settlement, second order contacts were correlated with ranging behaviour, suggesting that observable traits exist which could inform targeted management strategies.

The transmission probabilities associated with the lowest R_0 value rarely resulted in an epidemic and, when one occurred, no more than a few individuals were infected. This meant that there was little difference in the overall mean epidemic size between simulations of random and observed networks. However, heterogeneity in contacts was still important in determining epidemic outcomes whereby the seeded individual's ranked degree was positively correlated with the proportion of simulations that resulted in an epidemic, and this was echoed in simulations with higher R_0 values. This finding demonstrates that, regardless of the transmission probability, dogs that are in contact with more individuals relative to the rest of the population are at higher risk of causing an epidemic should they become infected.

In simulations with all but the lowest R_0 value, the risk of a large epidemic was higher when infection started in dogs with a higher ranked eigenvector centrality, and this was further emphasised where the distribution of eigenvector centralities paralleled that of epidemic sizes for each settlement. The importance of an individual's eigenvector centrality in disease dynamics has also been shown in models for the transmission of *Mycobacterium bovis* in badgers (Silk et al. 2017b) and observed parasite infection in Japanese macaques (MacIntosh et al. 2012), where this measure was positively correlated with infection status. It appears that eigenvector centrality is a robust predictor of epidemic size and infection status because it describes how an individual is rooted into the network beyond their immediate connections.

We show that ranging behaviour was correlated with eigenvector centrality, but this was only true for dogs in Kakale. Both range sizes and eigenvector centralities were higher for dogs in Kakale than those in Magrao. This is likely due to anthropogenic variation in dog behaviour whereby some people in Kakale moved with their dogs between a permanent residence and a seasonally-occupied homestead, while people in Magrao tended to stay at one. The dogs that accompany their owners in travelling between permanent and seasonal homesteads will have larger ranges and this would influence the dog's network position by creating new contact opportunities. Nevertheless, the relationships between dog network position and epidemic outcomes were the same in both settlements. We also show that the distribution of dog owning households is important in determining contacts between dogs, with dogs more likely to have been in contact with and having stronger connections with dogs from closer households. However, it is important to note that this distance effect cannot fully explain the structure of the contact networks as many dogs from households in close proximity did not come into contact (Appendix B Figure B2). Although the dogs in this study were free-ranging, they were owned and anthropogenic influences on dog contact rates and ranging behaviour should not be overlooked, and understanding these would provide insight into disease management approaches.

For both settlements, there was no notable difference in epidemic size between simulations using the observed binomial and weighted networks. This result would suggest that including non-random mixing (whom individuals contact) in disease models is more important than including non-uniform mixing (contact duration/frequency). However, heterogeneities in edge weights are likely to be important and have been shown to further limit epidemic sizes when they are allowed to be dynamic in time (Ferreri et al. 2014). To further understand the effect of non-uniform mixing, future research should try to describe the temporal dynamics of free-ranging dog contacts over a timeframe relevant to the disease in question. Specifically, investigations should look for daily and seasonal differences in network structure and identify whether or not individuals occupy stable network positions.

The model of rabies transmission used in this study makes several assumptions that should be considered. First, individuals do not change their behaviour once infected. It is well known that rabies can manifest as either encephalitic (furious) or paralytic (dumb) and evidence suggests that, unless vaccinated, the furious form is more likely to develop in dogs (Tepsumethanon et al. 2016). However, it is not clear what determines the type of rabies an individual develops or if the different forms result in considerable deviations from the individuals' typical behaviour. Such deviations could result in changes to the contact network with either new connections being formed, the loss of connections or changes in the strength of connections. A second assumption is that when individuals were removed due to death, the network structure did not change. Removing these assumptions would require a rewiring of the network and this process should be biologically informed. Reynolds et al (2015) attempted to account for dumb and furious behaviours by assuming different frequencies of each and either changing the transmission probability (higher for furious and lower for dumb) or by altering the individual's contact behaviour (removing half their connections for dumb or doubling them for furious). They found that both methods produced similar results and the speed of transmission increased when there was a higher frequency of furious individuals and decreased with a higher frequency of dumb individuals. Although this effort to model behavioural change can be insightful, the methods of rewiring are not biologically informed and so should be interpreted carefully as they cover a limited number of possible scenarios in which the network could change. Solutions to such network dynamics are challenging as there is a lack of experimental data on the processes of network rewiring and, without this guidance, the number of potential modes of change is too computationally demanding to include in models. For diseases such as rabies it is unlikely that such data will ever exist given the ethical implications of such experimentation. However, understanding how a network rewires as individual states or community membership change could better allow network models to include such dynamics that are thought to be a major obstacle for controlling rabies (Hampson et al. 2009).

The inflation of predictions for epidemic size in models that do not account for observed contact heterogeneities are of particular concern when public health resources are limited (Rahmandad et al. 2008). This is the case for dog-mediated rabies in developing countries, where epidemics are preventable through vaccination but a major challenge is the high incidence of dog infections and human cases, combined with limited public health resources (Fahrion et al. 2017). Currently it is advised that successful vaccination campaigns require 70% coverage of the dog population (Coleman & Dye, 1996). However, through targeted management this might be reduced, helping alleviate costs. Further to work on urban dogs (Laager et al. 2018), our results show that even in a rural context, epidemic risk is not equal among individuals and suggest that, by identifying the network position of individuals and correlates thereof, targeted management could be feasible. We find evidence to suggest that the spatial ranging behaviour of dogs was associated with their network position, though anthropogenic influences clearly have a role in determining free-ranging dog movements and this deserves further investigation. Our research illustrates how a greater understanding of the social contact network of free-ranging dogs can help better inform the management of diseases such as dog-mediated rabies.

CHAPTER 3:

THE SPATIAL AND TEMPORAL DYNAMICS OF SPACE USE BY FREE-RANGING DOMESTIC DOGS IN RURAL AFRICA

3.1 ABSTRACT

Variation in the spatial ecology of animals can have a major effect on the transmission of infections and an improved understanding of host behaviours can inform control of zoonotic diseases. Little is known about the dynamics of space use by free-ranging domestic dogs *Canis familiaris,* which are globally widespread and act as a reservoir for several zoonotic diseases, including rabies. In this study we aimed to (1) characterise variation in dog space use, (2) determine the degree to which dog movements are predictable and (3) identify correlates of variation in patterns of movements. We deployed GPS loggers on dogs from six villages in rural Chad, and characterised the movements of 174 individuals in the dry season and 151 in the wet season. We found that seasonality was an important source of variation in space use, whereby home ranges were up to 38 times larger on average in the dry season than in the wet season. This seasonal variation was exaggerated by owner activities, with dogs in the dry season having ranges that were five times larger when they were from households that reported going hunting. 80% of dogs demonstrated daily patterns in their activity levels (speed), but just over half the dogs exhibited temporal patterns in their location (repeated space use). Furthermore, we show that in rural Chadian villages, the proportion of dogs found around their household where access for disease control interventions is easiest, is more reliably above 70% throughout the day in the dry season. These results highlight that, in rural Chad, disease interventions such as vaccination campaigns could access more dogs in the dry season, and the influence of human activity on dog movements presents opportunities for targeted interventions at the household level.

3.2 INTRODUCTION

Calls for a 'One Health' approach to tackle neglected tropical diseases (Cunningham et al. 2017) require that an ecological perspective is adopted to progress towards successful management of zoonoses. The spatial ecology of free-ranging animals is important for understanding disease transmission and dynamics (Altizer et al. 2011; Dougherty et al. 2018). The space use of individuals influences their contacts with others (Robert et al. 2012; Sanchez & Hudgens, 2015) and their exposure to environmental sources of infection (Padie et al. 2015; Tartu et al. 2018), both of which can determine the acquisition and onward transmission of infections (Boyer et al. 2010; Craft et al. 2011; Mysterud et al. 2016; McDonald et al. 2018). Knowing the spatial movements of free-ranging host populations can help forecast epidemics (Nobert et al. 2016; Tyne et al. 2017), while understanding predictors of space use can inspire novel or better-designed disease interventions. For example, knowledge of the seasonal dispersal behaviour of European foxes *Vulpes vulpes* was used to optimise the timing of vaccination campaigns against rabies in Europe (Vos, 2003; AHAW, 2015), understanding the migration patterns and habitat use of grey-headed flying-foxes *Pteropus poliocephalus* in Australia is helping to determine the management strategies for controlling the spread of Hendra virus (Plowright et al. 2017; Degeling et al. 2018), and in New Zealand, the spatial behaviour of brushtail possums *Trichosurus vulpecula,* has been integrated into models of surveillance, with the aim of determining if areas are free of bovine tuberculosis (Anderson et al. 2013; Livingstone et al. 2015). For the successful management of animal and zoonotic diseases involving free-ranging animal populations, the spatial ecology of individuals therefore needs to be considered when designing intervention strategies.

Free-ranging domestic dogs *Canis familiaris* are globally widespread and are frequently associated with public health concerns (Gompper, 2014). Dogs often constitute a reservoir for infections and facilitate the maintenance and transmission of zoonotic diseases such as rabies, echinococcosis, Guinea worm and visceral Leishmaniasis. Because the living conditions of domestic dogs are so variable, the management of dog-mediated diseases would benefit from an increased knowledge of the ecology of free-ranging individuals, so that intervention strategies might be tailored to local contexts (Slater, 2001; Fahrion et al. 2017; WHO, 2018). This is particularly true for dog-mediated rabies, where the majority of human cases occur in rural African and Asian communities, and the risk of human infection is increased with the presence of free-ranging dog populations (WHO, 2018). The ‘Zero by 30’ campaign aims to eliminate dog-mediated rabies by 2030 (Jarvis, 2016), and it is thought that this can be achieved through vaccination alone (Hampson et al. 2009), providing campaigns can achieve a 70% population coverage (WHO, 2018) Similarly, dogs have been implicated as reservoirs for Guinea worm, a zoonotic parasite which is close to being globally eradicated (Hopkins et al. 2018). However, access to the dog population is essential for surveillance and for control efforts such as the delivery of antihelminthics. With these examples in mind, it would be beneficial for intervention strategies to consider aspects of dog behaviour and ecology that determine the accessibility of individuals e.g. their home range and the probability of individuals being found around the household.

Studies on the spatial ecology of free-ranging dog are, perhaps surprisingly, somewhat rare and the majority of research has been motivated by the desire to control rabies. Among the most comprehensive studies on the movements of free-ranging dogs to date have been conducted in Northern Australia (Sparkes et al. 2016; Dürr et al. 2017; Hudson et al. 2017), a region that is presently free of canine rabies but where authorities are preparing for incursion of the infection from Indonesia. Dürr et al (2017) tracked 135 dogs over multiple seasons and found they had very small core and extended ranges, with a median of 0.35 ha (range: 0.17-2.33 ha) and 4.48 ha (range: 0.86-40.46 ha) respectively. Using the same study system, Hudson et al (2017) categorised dogs on the basis of their ranging behaviour, as either 'stay at home', 'roamers' or 'explorers', the former having extremely localised movements and the latter having relatively large ranges. Despite the use of different tracking procedures, observation periods and methods of home range estimation, similar range sizes have been reported in studies on the space use of dogs in Chile (Sepúlveda et al. 2015; Pérez et al. 2018), Kyrgyzstan (Van Kesteren et al. 2013), Mexico (Ruiz-Izaguirre et al. 2015) and India (Vanak & Gompper, 2010).

In terms of understanding variation in dog ranging behaviour, an interaction between the effects of sex and reproductive status on range size was found for dogs in Australia (Dürr et al. 2017), whereby neutered males had smaller ranges than intact males, but spayed females had larger ranges than intact females. In addition, seasonal variation in space use was identified, with individuals having larger ranges at the start of the rainy season, compared to at the end. Similarly, seasonality was important in determining the movements of domestic dogs in Ethiopia, where the mean home range was 30 ha in the wet season, compared to 590 ha in the dry season (Atickem et al. 2010). Dogs in Chile were shown to have larger ranges when they had higher body condition scores (Pérez et al. 2018), whereas in Kyrgyzstan variation in ranging behaviour remained largely unexplained by the traits of individuals investigated (Van Kesteren et al. 2013). Current evidence clearly indicates that the spatial movements of dogs vary in time and, the globally inconsistent predictors of space use imply that drivers behind this variation are not universal.

The spatial movements of individuals could determine their accessibility for disease interventions such as vaccination campaigns. If individuals can predictably be found at a particular location at a certain time, the number accessed might be increased through tailored field operations. Little is known about the variation in the periodicity of dog movements. Periodicity in location implies repeated visits to a particular place or places, and for free-ranging domestic dogs we would expect them to return repeatedly to their owner's household. Existing evidence suggests daily patterns are not geographically consistent, with one study in Kenya finding that dogs were most active and at greater distances from their household at 10am (Woodroffe & Donnelly, 2011), while a recent study in Australia found that dogs were furthest from their household at 6am and again at 6pm (Maher et al. 2019).In this study, we provide a comprehensive investigation into the dynamic spatial ecology of a large number of free-ranging domestic dogs from multiple rural villages in Chad. Using GPS loggers we characterise the variation in the dogs' ranging behaviour and investigated the predictability of their movements in time and space. Specifically, we quantify the dogs' home ranges, temporal patterns in their activity levels (speed), temporal patterns in repeated space use (location) and investigate times of the day when a high proportion of the population can be found around the household.

3.3 METHODS

3.3.1 *Field study timings and locations*

Fieldwork was conducted in rural Chad and dogs were collared in six villages (Figure 1) during the dry season (between 5th March and 17th May 2018) and again during the wet season (between 3rd August and 17th October 2018). Medegue (11°01'48.8"N 15°26'37.7"E) is a village in the district Guelendeng of the Mayo-Kebbi East region in the western central part of Chad. The remaining 5 villages are located in the district of Sarh in the Moyen-Chari region in the south of the country. Ngakedji (9°11'16.5"N 18°18'10.7"E), Kira (9°10'50.8"N 18°17'00.3"E) and Bembaya (9°11'33.6"N 18°17'42.3"E) are villages located approximately 10 km to the west of Sarh town. Approximately 40 km to the east of Sarh is the village Marabodokouya (9°19'42.3"N 18°43'20.0"E), (9°08'19.8"N 18°42'00.9"E) and ~20 km south of this settlement is the village Tarangara.

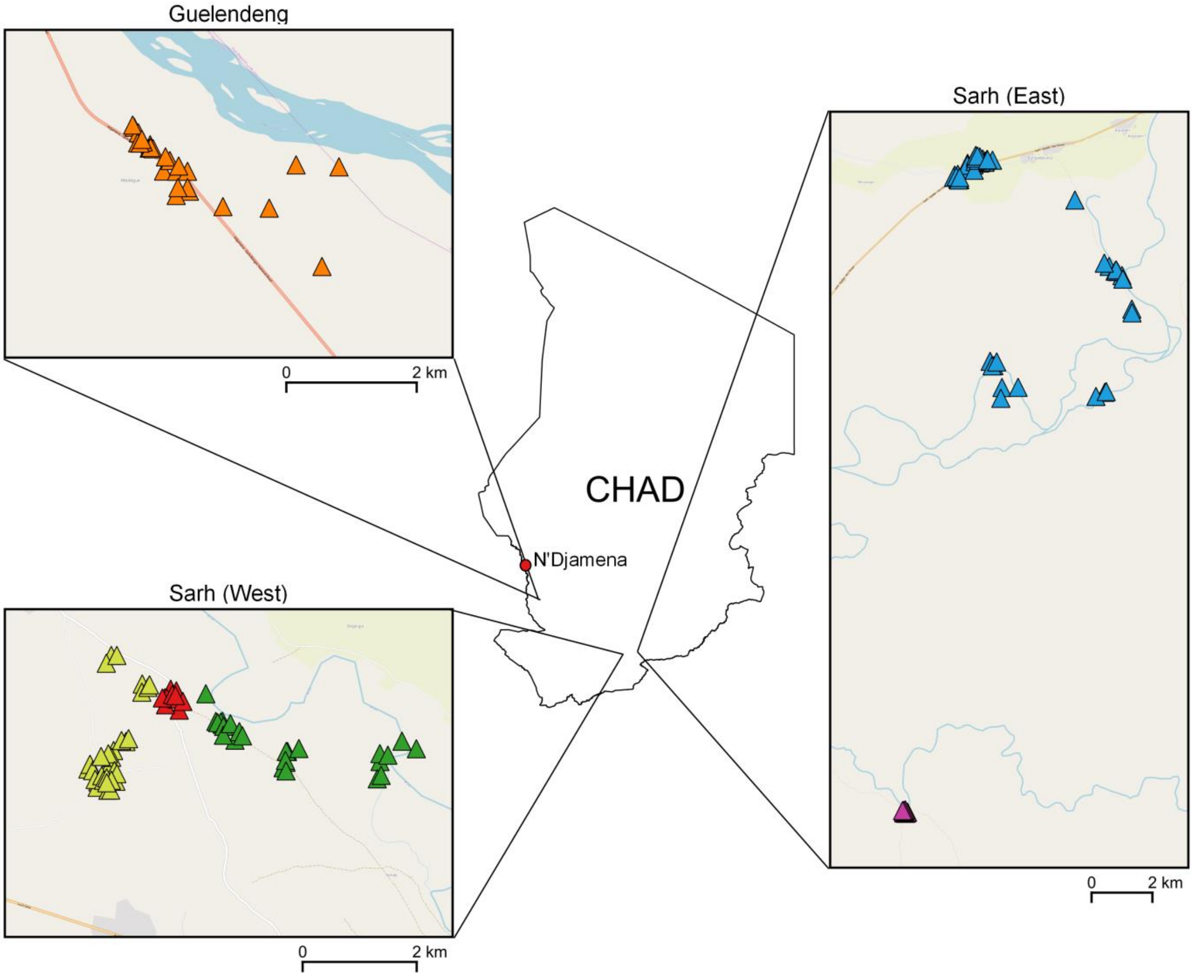

Figure 3.1. Locations of the districts and six villages in rural Chad and the human households in which at least one dog was collared. Triangles represent households from the different villages; Medegue (orange), Kira (yellow), Ngakedji (green), Bembaya (red), Marabodokouya (blue) and Tarangara (pink). Map data copyrighted OpenStreetMap contributors and available from https://www.openstreetmap.org.

3.3.2 *Data collection and processing*

After obtaining approval from the village chief, the field team conducted door-to-door visits to all households that owned dogs with the aim of collaring all the dogs in the village. The location of dog owning households was recorded using a handheld GPS and owners were asked whether or not they went hunting. The number of dogs reported to be owned in each household was summed to estimate the adult dog population for each village. For each dog, we recorded its sex and its body condition score (categorised into Poor: 1-2; Moderate: 3; Good: 4-5; Laflamme, 1997). With owner consent, dogs were collared with commercial dog collars (Ancol Heritage) that were fitted with an i-GotU GT-600 GPS logger (Mobile Action Technology Inc., Taiwan). The GPS unit was configured with a fix interval of 10 minutes. In each field season, an initial two week deployment was conducted immediately followed by a longer second deployment, where collars were fitted with a GT-600 unit modified with a larger battery.

After retrieving the collars and downloading data, the data were cleaned by removing locations taken up to 12 hours after the collar was deployed and 12 hours before collar recovery. Any likely erroneous GPS fixes with speeds greater than 20 km/hr between locations were removed. Data was discarded for times when dogs were known to have been tied up by their owners. GPS data were projected into the relevant coordinate reference system (EPSG: 32633) using the ‘sp’ and ‘rgdal’ packages (v1.3.1 & v1.4.4 respectively) in R (R Core Team, 2017).

3.3.3 *Home range analysis*

Continuous time movement models were used to estimate home ranges. Models were fitted and auto-correlated kernel density estimates (AKDE) calculated using the ‘ctmm’ package (v0.5.5), following the procedures set out by Calabrese et al (2016). Briefly, variograms were used to identify whether individuals were range-residents, and non-range-resident individuals were excluded from home range analysis. Movement models were then fitted to each individual’s spatial data separately, using maximum likelihood, followed by model selection based on the Akaike information criterion (AIC). The models considered included Ornstein-Uhlenbeck (OU) and Ornstein-Uhlenbeck with foraging (OUF). Once the best model was selected for each range-resident individual, the 95% AKDE ($AKDE_{95}$) and core AKDE ($AKDE_{core}$) were calculated. Core isopleths were determined through an individual-based approach, using an exponential regression to identify the ‘threshold’ isopleth (slope = 1) where the estimated home range area begins to increase more rapidly than the relative frequency of use (Vander Wal & Rodgers, 2012). The distributions for $AKDE_{core}$ and $AKDE_{95}$ were described using a gamma distribution fitted using maximum likelihood in the package ‘fitdistrplus’ (v1.0-14). Traditional home range analyses (minimum convex polygons, 50% and 95% kernel density estimates) were calculated using the package ‘adehabitatHR’ (v0.4.15).

The proportion of the dogs’ relocation points within a 50m radius of their household was used as a measure of how much time they spent around their household. The proportion of dogs that were around the household was calculated for each hour of each day that dogs were tracked. To estimate the amount of time dogs spent around the village, the proportion of relocation points within 100m of any household in the village that had dogs was calculated. Although crude, in the absence of known locations for all households in the village and considering the difficulties in defining boundaries of rural African villages, this method provides a conservative estimate of village area in the relevant terms of the spatial extent of dog-owning households. An alternative method would involve calculating a minimum convex polygon around the known household locations, but in situations where the households are widely dispersed, this method would over estimate space use in the village by including areas of unoccupied bush between households.

3.3.4 *Periodicity analysis*

To explore daily periodic patterns in space use (repeated visits to locations; latitude and longitude) and activity levels (peaks in speed) we followed the protocol set out by Péron et al (2016). Lomb-Scargle periodograms were used to identify the peak frequencies that most strongly contributed to variance in movement data. Due to the duration of the observation periods in this study, we focused on periodicities that were equal to or less than 24 hours.

Periodicity in activity levels was only investigated for individuals where an OUF model was selected for the home range analysis. This is because activity levels are characterised by speed, which can only be reliably estimated from models if the velocity autocorrelation is accounted for, as is the case with OUF models but not OU models. Instantaneous speed estimates were generated via the ‘ctmm’ package, using a function that simulates multiple realizations of the possible trajectory between observed locations and calculates a point estimate. To investigate patterns in the dog’s locations, periodic-mean models were fitted to the data and selected using AIC values. These models describe OU and OUF processes where the constant mean term is replaced with the movement process mean, modelled as a sum of sinusoids (Péron et al. 2017).

A null model approach was used to identify if the observed periodicity in location/speed was significant. The home range model for each dog was used as the null model and to simulate 150 datasets for predicted locations at the same sampling schedule as the observed data. For periodicity in activity levels, instantaneous speeds were calculated for each simulation. Periodograms were then computed for the simulated locations/speeds and a value for *P* was generated by calculating the proportion of simulated datasets that had larger values at the period of interest than that of the observed. Using data simulated from the periodic models, the time of the ‘peaks’ (maximum speeds or maximum distances from the household) and ‘valleys’ (minimum speeds or minimum distances from the household) in the periodicities were identified for each individual. To find the peaks and valleys in an individual location, general additive models (GAMs) were fitted to the estimates for the distance of relocation points to the household. To find the peaks and valleys for periodicities in speed, GAMs were fitted to the instantaneous speed estimates. The R package ‘MGCV’ (v1.8-24) was used to fit GAMs with family set to Gaussian and including a smoothing term (24 hr: k = 4; 12 hr: k = 6), and the package ‘quantmod’ (v0.4-15) was used to identify the peaks and valleys from the model estimates. Individuals with significant periodicities in location/speed were categorised into either 24 hr (one peak), 12 hr (two peaks), or <12 hr (more than 2 peaks) periodicity.

To determine the hourly variation in the proportion of tracked dogs that were around the household, for each hour of each day that dogs were tracked, the number of unique dogs with relocation points within 50 m of their household was summed and divided by the total number of dogs being tracked on that date at that time. This analysis considered all dogs regardless of if they had significant periodicity in their speed/location.

3.3.5 *Statistical analysis*

To investigate predictors of the dog's home range size, linear mixed-effect models with a Gaussian error structure were implemented using the package 'lme4' (v1.1-18.1; Bates et al. 2014). Model simplification was conducted using the package 'LMERConvenienceFunctions' (v2.1.0) through backward and forward fitting the fixed effects using AIC model comparison. To extract contrasts from models, the package 'emmeans' (v1.3.3) was used to estimate marginal means, estimates for contrasts, confidence intervals and p-values for pairwise comparisons using the Tukey method. Models were fitted with dog ID as a random variable and the response variable (either $AKDE_{95}$ or $AKDE_{core}$) was logged to meet assumptions of normality. Explanatory variables included sex, body condition score, village, whether the owner went hunting, the proportion of relocation points within 50 m of the household and the interactions between season and the aforementioned variables. In addition the number of days the dogs were monitored was included as a fixed effect. Preliminary analyses identified a strong positive relationship between the dogs logged $AKDE_{95}$ and logged $AKDE_{core}$ (Pearson's correlation: $r = 0.98$; $t_{323} = 100.56$; $p < 0.001$). We therefore present the results for the analysis of $AKDE_{95}$ in the main text, while results for $AKDE_{core}$ are provided in Appendix C.

General linear models were used to investigate whether or not the dogs exhibited predictable space use (the presence/absence of repeated visits to locations) or activity levels (presence/absence of periodicity in the dog's speed), as preliminary analysis showed that the variance for dog ID was zero when included as a random effect. A binomial error structure with a logit link function was used, and the explanatory variables and model simplification methods were the same as that used in previous models. For dogs that were found to have significant periodicity in their location/speed, similar models were fitted to identify correlates with the variation in the dog’s location/speed that was attributable to their periodicity in location/speed. These models used a Gaussian error structure and the response variable was either the dogs rotation deviance (η_p) or rotation speed (η_v), which correspond to the proportion of the variance in either the animal’s position or velocity that is caused by the periodicity in the mean, and are extracted from OU and OUF models respectively. Models for three individuals failed to converge when periodicity was included and were therefore excluded from the analyses.

3.4 RESULTS

3.4.1 *Home range*

In the dry season, 180 dogs were tracked successfully and of these, 174 dogs from 122 households were identified as range-resident (Table 3.1). Individuals were tracked for a mean of 37 days (range; 1-70 days). In the wet season, 159 dogs were tracked successfully and of these, 151 dogs from 107 households were identified as range-resident. Individuals were tracked for a mean of 35 days (range; 2-65 days). 77 individuals had data available in both the dry and the wet seasons. Reasons for dogs not having been collared or lacking spatial data in a field season included the dog being reported to have died (35 dogs) and inaccessibility due either to the dog's behaviour (10), the absence of the dog/owner when visiting a household (18) or inability to reach a household due to high waters (29). In addition, dogs were sometimes relocated, either by their owner moving to a different village (7) or to temporary housing nearer their crop fields in the wet season (11). For 37 dogs, no spatial data were available due to damaged GPS units or lost collars.

The $AKDE_{95}$ range of dogs differed between villages (Table 3.1), whereby dogs in Marabodokouya had ranges that were 2.7 (95% confidence limits; 1.2, 6.2) times larger than those of dogs from Kira ($z = 3.38$; $p = 0.010$) and 5.3 (1.7, 16.9) times larger than the ranges of dogs from Ngakedji ($z = 4.13$; $p = 0.001$). An interaction between season and village was found (Figure 3.2), with dogs from Bembaya having ranges that were 38.4 (12.2, 121.3) times larger in the dry season than in the wet season ($z = 6.22$; $p < 0.001$), and in Marabodokouya ranges were 6.7 times larger (3.4, 13.3) in the dry season ($z = 5.42$; $p < 0.001$). In the dry season dogs from hunting households had $AKDE_{95}$ ranges that were 4.5 (2.0, 9.9) times larger than the ranges of dogs from non-hunting households (z = 4.77; p < 0.001), but this was not the case in the wet season (z = 1.68; p = 0.333). The $AKDE_{95}$ ranges of dogs decreased by 3% (2%, 4%) for every 1% increase in the proportion of time they spent within 50 m of their household (t = -5.63; p < 0.001). Finally, for the 77 dogs that had data available in both seasons, there was a positive correlation between their $AKDE_{95}$ range in the dry season and wet season (r = 0.35; t_{75} = 3.18; p = 0.002). A summary of the home ranges estimated using the conventional KDE and MCP methods are presented in Appendix C (Table C1).

Table 3.1. Summary for the sample sizes of free-ranging domestic dogs from rural communities in Chad that were identified as range resident. For both the dry and the wet season, the number of dogs identified as range resident is reported for each village with the percentage of the adult population that the sample represents in brackets. The number of dogs of different sex and body condition are reported, as well as the number of dogs that belong to a hunting household.

Village	Season	n	Sex (female : male)	Body condition (poor : moderate : good)	Hunting household
Medegue	Dry	22 (73%)	11 :11	11 : 8 : 2*	1
	Wet	27 (71%)	13 : 14	5 : 16 : 2*	3
Kira	Dry	41 (91%)	22 : 19	7 : 17 : 16*	18
	Wet	36 (74%)	19 : 17	4 : 19 : 12*	15
Bembaya	Dry	12 (100%)	6 : 6	1 : 7 : 4	8
	Wet	18 (86%)	8 : 10	4 : 10 : 4	9
Ngakedji	Dry	19 (70%)	11 : 8	7 : 7 : 5	5
	Wet	13 (52%)	8 : 5	3 : 6 : 3*	4
Marabodokouya	Dry	64 (75%)	31 : 33	27 : 27 : 9*	44*
	Wet	57 (51%)	32 : 25	20 : 19 : 10*	40*
Tarangara	Dry	16 (76%)	12 : 4	3 : 10 : 3	12
	Wet	-	-	-	-
Overall	Dry	174 (79%)	93 : 81	56 : 76 : 39*	88*
	Wet	151 (65%)	80 : 71	36 : 70 : 31*	71*

* some individuals have missing information

Table 3.2. Parameters from movement models for the space use and periodicity of free-ranging domestic dogs in rural Chad. For each village and season the median and inter-quartile range for estimates are reported. Parameters include AKDE$_{95}$ and AKDE$_{core}$, as estimated from either Ornstein-Uhlenbeck (OU) or Ornstein-Uhlenbeck with Foraging (OUF) models. Speed estimates are derived from OUF models. Parameters from periodic models include the percentage of the dogs' variance in location that was explained by the periodicity in location (η_p; from both OU and OUF models), and the percentage of variance in the dogs' speed that is explained by their periodicity (η_v; from OUF models).

Home range models						Periodicity models		
Village	Season	n (OU:OUF)	AKDE$_{95}$ (km^2)	AKDE$_{core}$ (km^2)	Speed (km/hr)	n (OU:OUF)	η_p (%)	η_v (%)
Medegue	Dry	22 (9:13)	0.15 (0.07 - 0.39)	0.02 (0.01 - 0.04)	1.37 (0.91 – 1.76)	15 (6:9)	31 (19 - 44)	6 (4 - 9)
	Wet	27 (8:19)	0.57 (0.07 - 1.76)	0.08 (0.01 - 0.30)	1.49 (1.06 - 1.99)	15 (3:12)	36 (19 - 53)	7 (2 - 9)
Kira	Dry	41 (10:31)	0.26 (0.06 - 1.32)	0.04 (0.01 – 0.14)	1.07 (0.84 – 1.30)	26 (6:20)	23 (18 - 30)	4 (3 - 7)
	Wet	36 (13:23)	0.33 (0.14 - 0.70)	0.03 (0.02 - 0.07)	1.13 (0.99 – 1.53)	24 (4:20)	27 (21 - 31)	4 (5 - 16)
Bembaya	Dry	12 (1:11)	5.01 (0.36 - 17.82)	0.58 (0.04 - 2.08)	1.29 (1.16 - 1.36)	7 (1:6)	35 (33 - 36)	12 (4 - 16)
	Wet	18 (12:6)	0.05 (0.03 - 0.13)	0.01 (<0.01 - 0.02)	0.84 (0.75 – 0.93)	11 (8:3)	20 (13 - 28)	< 1 (< 1 - <1)
Ngakedji	Dry	19 (9:11)	0.11 (0.03 - 0.36)	0.01 (<0.01 - 0.05)	1.15 (0.90 - 1.65)	15 (6:9)	24 (13 - 29)	1 (1 - 2)
	Wet	13 (6:7)	0.12 (0.02 - 0.58)	0.02 (<0.01 - 0.10)	1.12 (0.71 - 1.42)	7 (2:5)	22 (16 - 30)	2 (1 - 3)
Mar	Dry	64 (5:59)	9.76 (0.57 – 19.81)	1.21 (0.12 - 2.59)	1.4 (1.06 – 1.64)	35 (1:34)	30 (16 - 44)	12 (5 - 17)
	Wet	57 (14:43)	0.65 (0.09 - 4.31)	0.08 (0.01 - 0.55)	1.09 (0.88 - 1.37)	27 (4:23)	29 (16 - 39)	4 (< 1 - 9)
Tarangara	Dry	16 (5:11)	0.36 (0.02 - 0.70)	0.07 (<0.01 – 0.17)	1.06 (0.73 - 1.36)	6 (3:3)	21 (17 - 24)	5 (3 - 5)
	Wet	-	-	-	-	-	-	-
Overall	Dry	174 (39:135)	0.54 (0.08 – 6.21)	0.08 (0.01 – 0.87)	1.26 (0.99 - 1.54)	104 (23:81)	27 (18 - 36)	6 (3 - 13)
	Wet	151 (53:98)	0.31 (0.07 - 1.06)	0.04 (0.01 - 0.13)	1.12 (0.93 - 1.42)	84 (21:63)	25 (16 - 36)	3 (1 - 6)

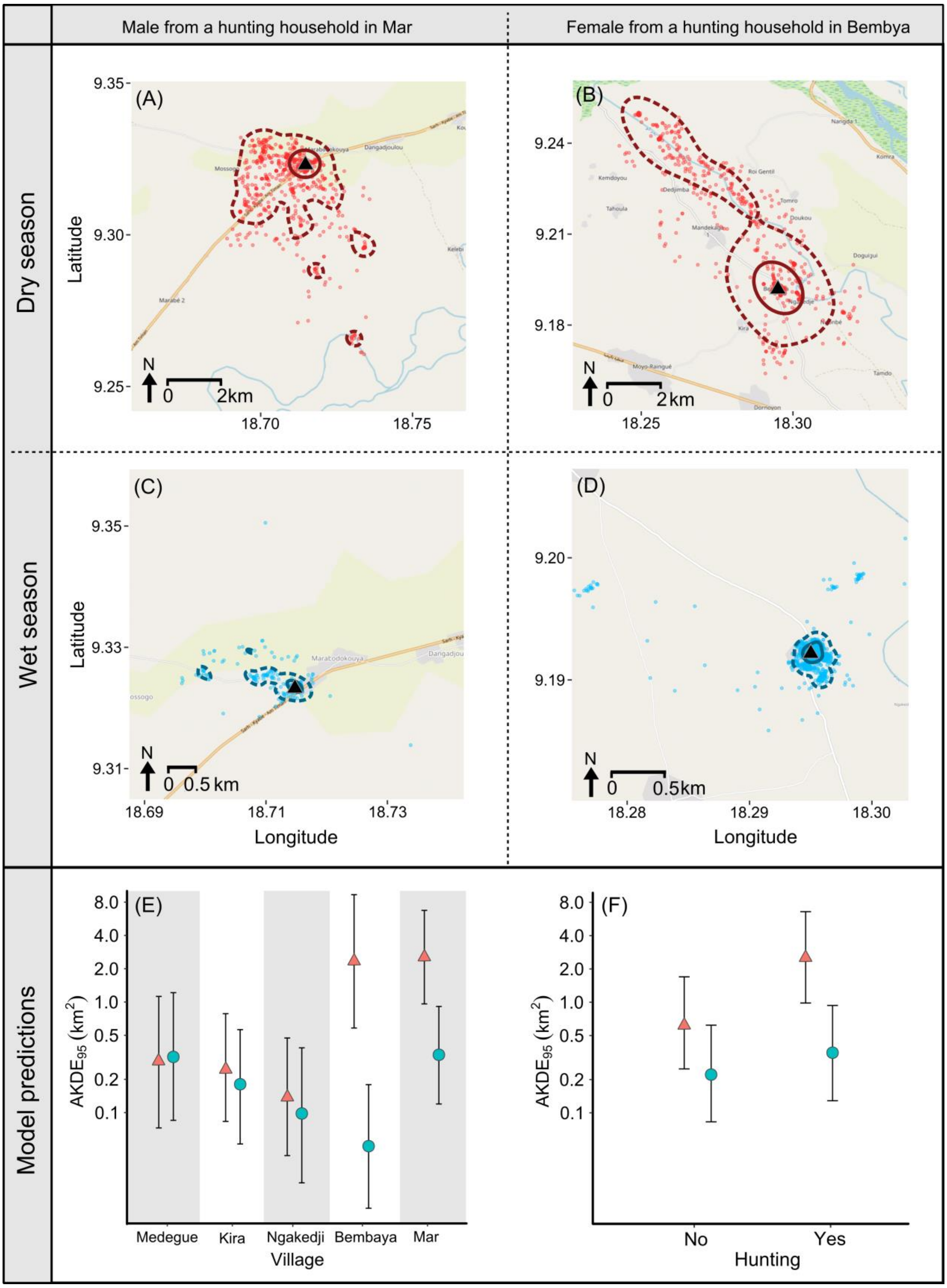

Figure 3.2. Variation in the home ranges of free-ranging domestic dogs in rural Chad. Maps A-D show the core (solid lines) and 95% (dashed lines) auto-correlated kernel density estimates (AKDE$_{core}$ and AKDE$_{95}$ respectively) for two exemplar dogs in the dry (red) and wet (blue) seasons, with a black tringle representing their household. Plot E shows the GLMM predictions of the AKDE$_{95}$ ranges for dogs from different villages in the dry season (red triangles) and wet season (blue circles). Plot F shows the model predictions of AKDE$_{95}$ ranges for dogs from hunting and non-hunting households in Marabodakouya (Mar) during the wet and dry seasons. Map data copyrighted OpenStreetMap contributors and available from https://www.openstreetmap.org.

3.4.2 *Periodicity in activity levels*

In the dry season, instantaneous speeds were estimated for 132 dogs, of which 54 (36%) exhibited a periodicity of 24 hours, 47 (41%) had a periodicity of 12 hours, 15 (11%) had a periodicity <12 hours, and 16 (12%) individuals had no periodicity. In the wet season, instantaneous speeds were estimated for 98 dogs, of which 64 (65%) individuals had a periodicity of 24 hours, 13 (13%) had a periodicity of 12 hours, 15 (15%) had a periodicity <12 hours and 6 (6%) had no periodicity. In both seasons, the activity of dogs exhibiting 24 hour periodicity peaked at 12 noon while those with a periodicity of 12 hours tended to show activity peaks around both 6am and 6pm (Figure 3.3).

The number of days that dogs were tracked was the only significant predictor for whether or not dogs had periodicity in their activity levels, whereby periodicity in speed estimates was more likely to have been identified in dogs that were tracked for longer ($z = 2.06$; $p = 0.040$). For dogs that did have periodicity in their activity levels, those from hunting households had 4% (2-6%) more of the variation in their speed explained by their periodicity in the dry season than in the wet season ($Z = 4.41$; $p < 0.001$). Furthermore, the periodicity of dogs from hunting households explained 3% (1-5%) more of the variance in their speed than that of dogs from non-hunting households in the dry season ($Z = 2.87$; $p = 0.004$). Finally, dogs in Marabodokouya had 3% (1-6%) more of the variation in their speed explained by their periodicity compared to dogs from Kira ($z = 3.72$; $p = 0.003$) and 5% (1-8%) more than dogs from Ngakedji ($z = 3.23$; $p = 0.020$).

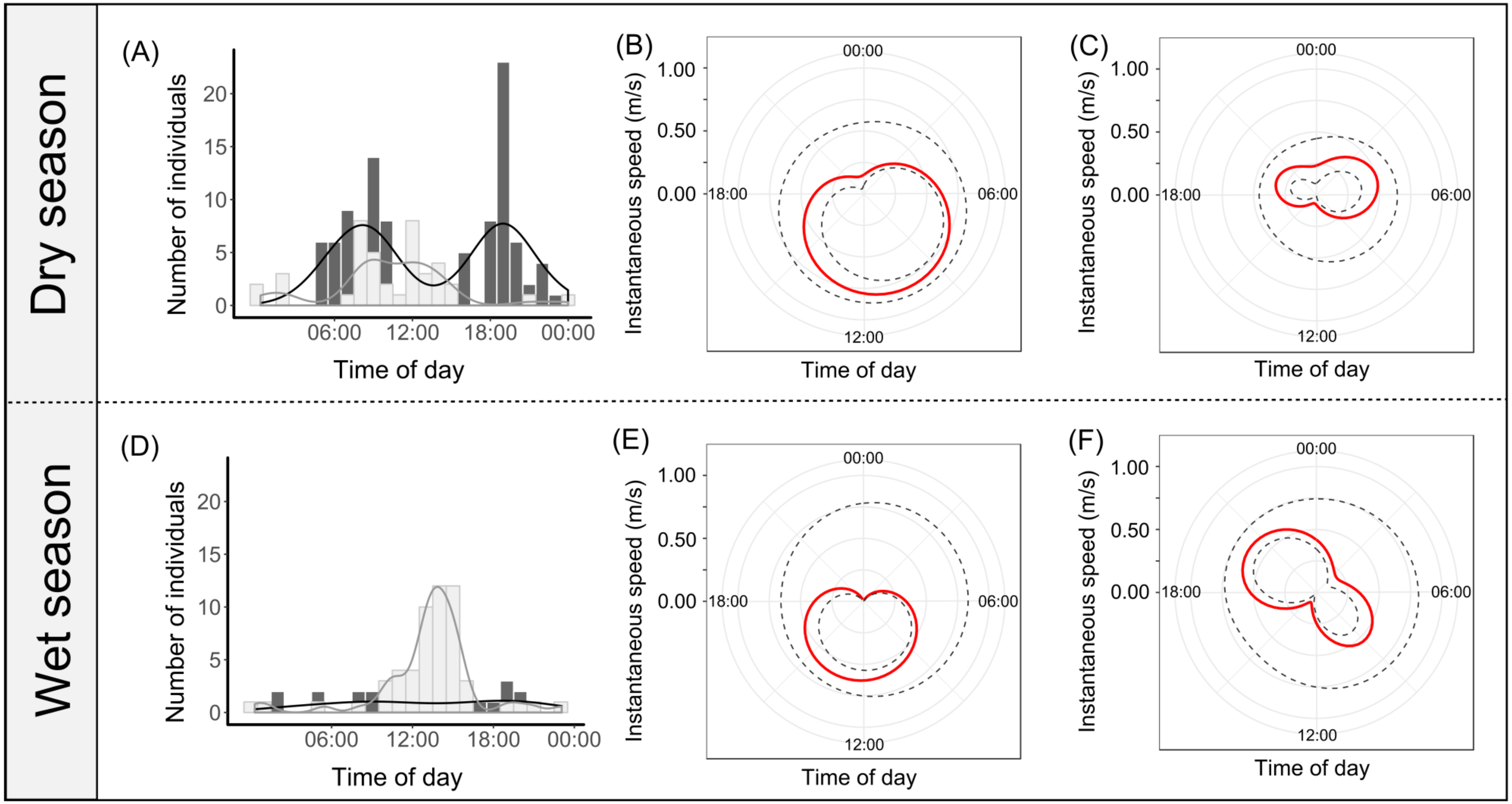

Figure 3.3. Periodicity in activity levels for free-ranging domestic dogs in rural Chad. Plots A and D show histograms and density curves for the time of peak activity for dogs with 12 hour (two peaks; dark grey) and 24 hour (single peak; light grey) periodicities. Radial plots show the speed estimates (in meters per second) from movement models for exemplar dogs at different times of the day. The red lines are fitted values from a GAM for the maximum likelihood estimates from movement models, and the grey dotted lines are fitted values for the upper and lower confidence intervals. Plots B and E are for two exemplar individuals showing 24 hour periodicity and plots C and F are for two individuals showing 12 hour periodicity.

3.4.3 *Periodicity in location*

Periodic patterns in location could be assessed in 171 dogs in the dry season, of which 81 (47%) individuals had a periodicity of 24 hours, 19 (11%) had a periodicity of 12 hours, 4 (2%) a periodicity < 12 hours, while 67 (39%) individuals exhibited no significant periodicity in their space use. Dogs with a 24-hour periodicity in their location were farthest from the household at ~12 noon (Figure 3.4), while dogs with 12-hour periodicity were at greater distances from their household between 6am and 12 noon and again between 6pm and 10pm. Periodic patterns in location could be assessed in 151 dogs during the wet season, of which 72 (48%) individuals had a periodicity of 24 hours, 6 (4%) had a periodicity of 12 hours, 3 (2%) had a periodicity < 12 hours, while 70 (46%) of individuals had no periodicity in their space use. The majority of dogs showing 24-hour periodicity were farthest from their household at ~12 noon (Figure 3.4).

Dogs with a good body condition were 4.3 (1.5, 12.0) times more likely to have periodicity in their location in the dry season than in the wet season. Periodicity in the dogs location was more likely to have been detected if they were tracked for longer ($t = 3.74$; $p < 0.001$). When dogs did have periodicity in their location, those that were tracked for longer had less of the variance in their location explained by their repeated movements ($t = -4.53$; $p < 0.001$). In addition, the proportion of explained variance in the dogs location decreased by 0.16% (0.07-0.27%) with every 1% increase in the proportion of time dogs spent around the household ($t = -3.19$; $p = 0.002$).

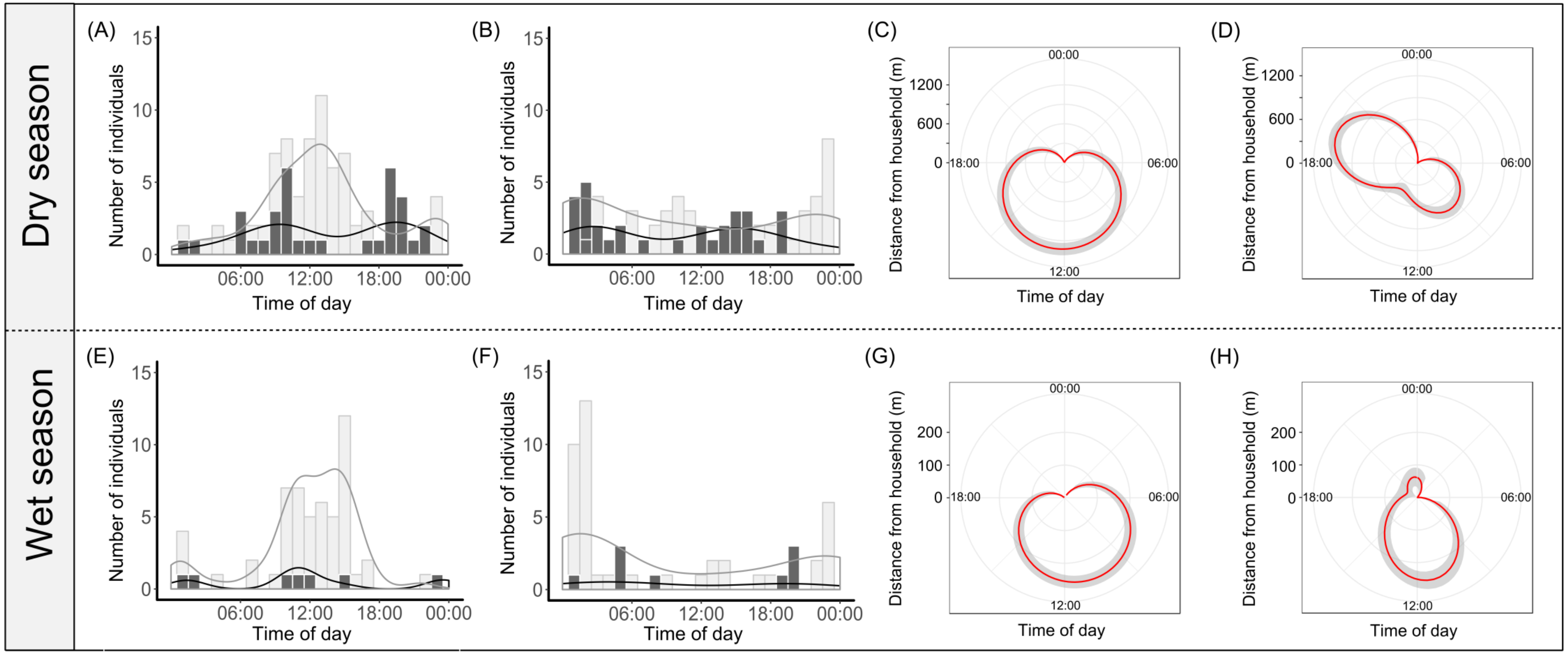

Figure 3.4. Periodicity in location for free-ranging domestic dogs in rural Chad. The histograms and density curves in plots A & E show the peak time of day at which dogs with 12 hour (two peaks; dark grey) and 24 hour (single peak; light grey) periodicity were farthest from their household. Plots B & F show the time of day that dogs were closest to their household. Radial plots show the periodicity in location for four individuals, where their distance from the household is plotted against time of day. The red lines are fitted values from a GAM and the grey shaded areas are the 95 % confidence intervals. Plots C and G are for two individuals with a 24 hour periodicity and plots D and H are for two individuals with a 12 hour periodicity.

3.4.4 *Proportion of time spent around the household*

In the dry season, a median of 72% (58 - 81%) of the dogs' relocation points were within 50 m of their respective households and 90% (79 – 95%) were around the village. In the wet season, 67% (52 – 78%) of the dogs' relocation points were around the household and 89% (82 – 96%) were around the village. In the wet season, the hourly pattern in the proportion of tracked dogs that were around their households was consistent between villages (Figure 3.5), and more than 70% of tracked dogs were around their households at ~6am and ~6pm, but this proportion dropped below 70% between 8am and 4pm. In the dry season, the hourly pattern was not consistent between villages; in three villages over 70% of dogs were around their household throughout the day, but in two villages the proportion dropped below 70% at ~7am and crossing above the threshold at ~12 noon.

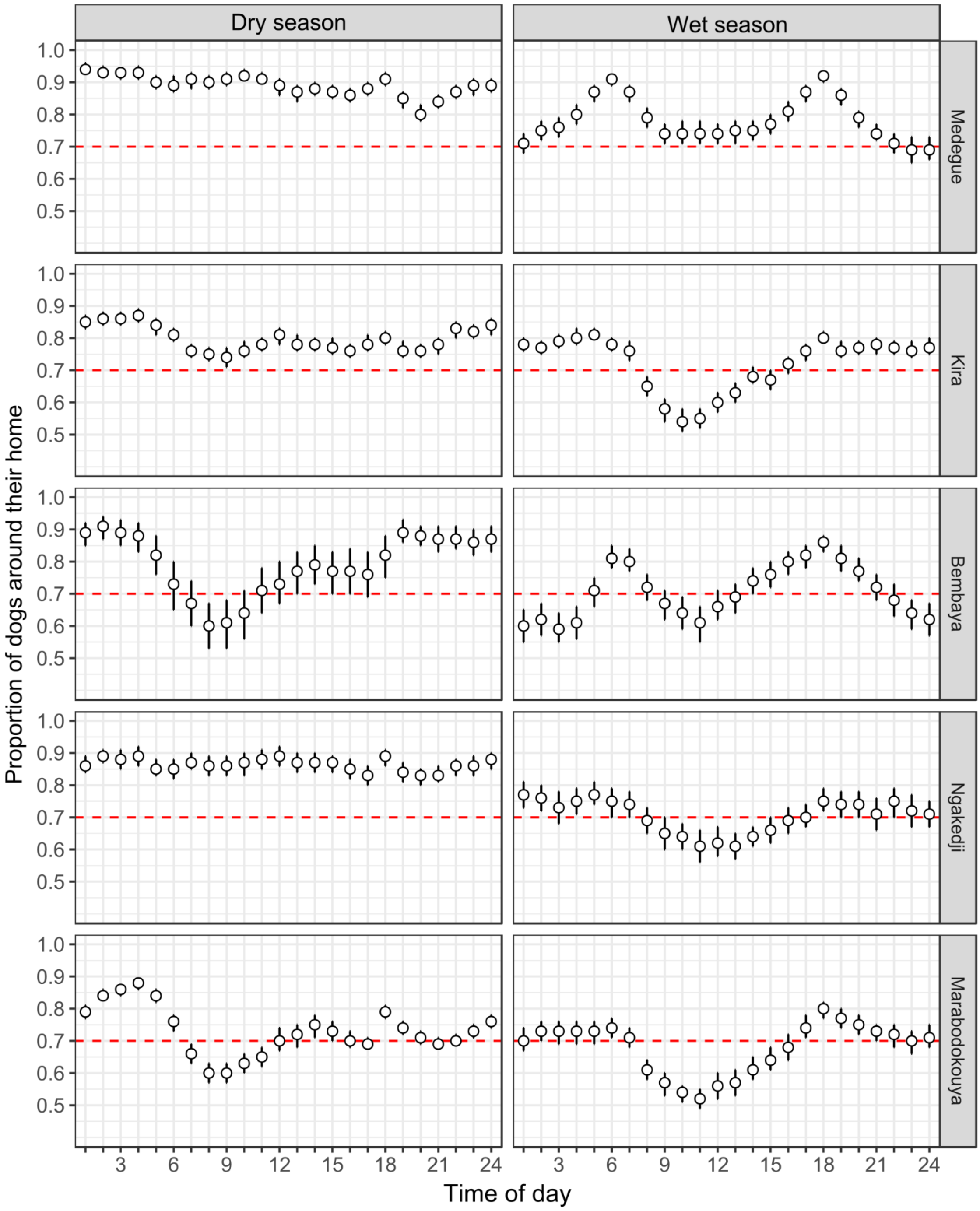

Figure 3.5. Temporal variations in the proportions of tracked dogs that can be found around their household at different times of the day. Dogs from 5 rural villages in Chad were tracked with GPS units in both the dry and wet seasons. Dogs were considered to be around the household if they had relocation points within 50m of their household. For each hour the mean and confidence intervals are plotted for the proportion of tracked dogs found around the household. The red dotted line represents the 70% threshold advised for vaccination campaigns.

3.5 DISCUSSION

This study quantifies the dynamics of space use for a large number of free-ranging domestic dogs in rural Chad, where dogs are implicated in the maintenance and transmission of numerous zoonotic infections, including rabies and Guinea worm disease, which are subject to control measures. In some villages, the dogs' home ranges varied seasonally and for some individuals these were up to 120 times larger in the dry season, compared to those in the wet season. Seasonal variation in ranges was increased by owner activity, whereby in the dry season, dogs from hunting households had home ranges that were five times larger on average than dogs from non-hunting households. While over 80% of dogs had predictable daily patterns in their activity levels (speed), and ~50% of individuals exhibited temporal patterns of repeated space use, there were clear seasonal differences in the periodicity of dog activity and location. In the wet season, the majority of dogs exhibited 24 hour cycles in their speed and location, while in the dry season two strategies were apparent, with dogs either having 24 hour or 12 hour cycles.

Our results suggest that, despite being unrestrained, the movements of dogs in rural Chad are governed to some extent by the routines of their owners. The owners' hunting activities in the dry season predicted their dogs ranging behaviours, but this was not the case in the wet season since, as reported by hunters, they tended to hunt less frequently in the wet season due to long grass making it harder to spot and capture game. The periodicity in the dogs' locations may also be human-mediated, given that dogs with larger ranges also had more of the variation in their location explained by their repeated space use. While patterns of repeated space use were detected in ~50% of individuals tracked, it is likely that these temporal patterns in location are more common than reported in this study, as the probability of detecting periodicity was positively correlated with the number of days that individuals were tracked. Nevertheless, the influence of owner activities on dog movements warrants further investigation to identify any nuanced effects of different occupational practices such as cattle herding, fishing and farming on dog movements.

From a global perspective, the home range estimates for dogs in this study were larger than that reported for other free-ranging domestic dog populations (Dürr et al. 2017; Hudson et al. 2017; Sepúlveda et al. 2015; Pérez et al. 2018; Van Kesteren et al. 2013; Ruiz-Izaguirre et al. 2015; Vanak & Gompper, 2010). Differences in the home range estimates for dogs across the globe may be a reflection of the various analytical methods used, with this study using continuous time movement models and previous studies using conventional home range methods (e.g. kernel density estimates, minimum convex polygons and Brownian movement models), which have been shown to underestimate home ranges (Noonan et al. 2019). However, when home ranges for dogs in this study were calculated using traditional methods, the range estimates were still larger than those reported in other studies (Appendix C Table C1). Similarly, while other studies have found evidence for 12 hour and 24 hour cycles in the dogs peak activity levels and location (Woodroffe et al. 2011; Maher et al. 2019), we find that the proportion of dogs exhibiting either of these strategies varies by season. When considered alongside previous research, our results highlight the variation in dog spatial movements and emphasise that predictors of dog space use are not globally consistent.

The variation in the spatial ecology of dogs described here has implications for disease transmission. An individual’s space use is often related to their contact rates (Robert et al. 2012; Vander Wal et al. 2014), which can determine the dynamics of disease outbreaks (Craft et al. 2011; McDonald et al. 2016). In a previous study on free-ranging dogs in rural Chad, individuals with larger ranges were found to have more second order contacts, and these individuals presented a greater risk of causing simulated disease epidemics should they become infected (Wilson-Aggarwal et al. 2019). Therefore, dogs from households whose owners participate in hunting may present a larger risk for disease transmission. Furthermore, as seen in simulated outbreaks of rabies in racoons *Procyon lotor* (Reynolds et al. 2015), the seasonality of dog movements described in this study could determine temporal variations in the risk of an epidemic occurring and the appropriateness of different disease management strategies. Therefore, models predicting the transmission of canine mediated diseases in rural Chad should consider both the seasonal and anthropogenic influences on dog movements.

The spatial dynamics of free-ranging dogs in this study can be used to design optimal field operations for controlling dog-mediated diseases. In the case of vaccination campaigns, possible strategies of accessing dogs include static point and door-to-door campaigns, which have been combined successfully in rural Tanzania (Kaare et al. 2009) and in Malawi (Gibson et al. 2016) to reach the advised 70% coverage. However, strategies involving house visits may be less effective if half the dogs are not predictably at their household. We show that, although dog ranges are smaller in the wet season, the proportion of dogs that are around their household drops below the advised 70% threshold during midday, and that this is consistent between villages. On the other hand, during the dry season, in three of the five villages more than 70% of the dogs could be found around the house at all hours of the day. The remaining two villages were those with dogs that generally had larger ranges, and here the proportion of dogs that could be found around the household dropped below the threshold at ~8am, and peaked above the threshold from 12 noon onwards. Therefore, it may be concluded that door-to-door campaigns in rural Chad are best conducted in the dry season since, in many of the villages reaching the advised 70% population coverage is more achievable. Furthermore, the relationship between owner activities and dog movements provides an opportunity for targeted interventions that are focused at the household level, i.e. households with owners that go hunting could be prioritised. This is supported by a study on urban free-ranging dogs in N'Djamena, which found that vaccination strategies targeting dogs based on their movement and contact behaviour could reduce the size of simulated epidemics of rabies (Laager et al. 2018). However, simulations of such intervention strategies would be required to identify if there was a benefit of targeted approaches in a rural context.

This study provides an insight into the variation of space use by free-ranging domestic dogs in rural Chad, and emphasises the importance of owner activities in understanding variation in their dogs' movements. In light of the 'Zero by 30' rabies campaign (WHO, 2018) and recommendations for locally adapted vaccination strategies to improve the access to individuals (Fahrion et al. 2017), our results highlight the potential for a 'One Health' approach that considers the spatial ecology of domestic dogs in the design and implementation of disease intervention strategies.

CHAPTER 4:

SPATIAL-TEMPORAL DYNAMICS OF CONTACT RATES AMONG FREE-RANGING DOMESTIC DOGS IN RURAL AFRICA

4.1 ABSTRACT

Forecasting and preventing epidemics can benefit from an understanding of the spatial-temporal dynamics of host contact rates, as these can determine variations in the risk of transmission. Free-ranging domestic dogs *Canis familiaris* have multiple shared pathogens with humans and wildlife, and managing canine-mediated infections is of interest to both public health and conservation concerns. We explored spatial-temporal variation in contacts among free-ranging dogs from six rural villages in Chad. We found that the distance between households was negatively correlated with the probability that individuals were ever observed in contact and negatively correlated with the hourly probability and duration of contacts should they have interacted. Interactions around the household and village peaked between 5am and 9am and again between 6pm and 8pm. The probability of contact events outside the village peaked between 5am and 8am. Contacts outside the village were of longer duration in the dry season than in the wet season and, in the dry season, contacts outside the village were longer than those within the village or household. We found evidence for seasonal differences in preferential mixing between the sexes. In the wet season, male-male contacts had a higher probability of occurring, and, if a pair had interacted, within-sex dyads had higher hourly probabilities of contact. In the dry season, if a pair had interacted, hourly contact probabilities were higher for male-male and male-female dyads. Although this study focused on within-village contacts, we observed rare between-village interactions; these were short in duration and mainly occurred around villages and during the dry season, when dogs ranged more widely. This study reveals clear spatial-temporal patterns in the contact behaviour of free-

ranging dogs, suggesting that contact rates have the potential to drive temporal variation in the incidence of canine-mediated diseases in rural areas.

4.2 INTRODUCTION

Interactions between individuals vary in time and space, and this can have implications for the transmission of infectious diseases (Silk et al. 2017a; Meyer & Held, 2017). Spatial-temporal patterns in contact rates between individuals can cause predictable increases in the incidence of infectious diseases in both humans and animals (Altizer et al. 2006). In humans, the increased contact between children during the school term has been shown to determine cyclic patterns for the incidence of measles (Bjornstad et al. 2002), chicken pox (Jackson et al. 2014) and influenza (Jackson et al. 2016). Examples in wildlife populations include the seasonal aggregation of birds during the onset of cold weather, that are synonymous with surges of conjunctivitis in house finches *Carpodacus mexicanus* (Hosseini et al. 2004) and avian influenza in water birds (Reperant et al. 2010). The observed association between the dynamics of contact rates and disease incidence occur because an individual’s contact behaviour can determine their susceptibility to infections (Drewe et al. 2011; Rimbach et al. 2015) and their propensity to transmit diseases (Lloyd-Smith et al. 2005; Lau et al. 2017). Therefore our capacity to forecast and control infectious diseases would benefit from knowledge of the temporal patterns of host contact behaviour.

Free-ranging dogs *Canis familiaris* share several pathogens with humans (Otranto et al. 2017) and with wildlife (Knobel et al. 2014), and managing dog-mediated diseases is often the focus of public health and conservation efforts. For domestic dogs in Africa, cyclic patterns have been observed in the incidence rates of rabies (Hampson et al. 2007) and canine distemper (Viana et al. 2015), but it is unknown as to what drives this periodicity. Such patterns of disease incidence could be explained by several interacting factors, including fluctuations in contact rates, climatic conditions and the renewal of susceptible individuals (Fisman et al. 2012). However, while the dynamics of dog populations are generally well studied (Morters et al. 2014; Conan et al. 2015), it is only in recent years that contact rates between free-ranging dogs have been successfully observed and quantified.

Few studies have provided a thorough account into the contact behaviour of free-ranging dogs, and those that have found significant between-individual variation in contact rates (Laager et al. 2018; Brookes et al. 2018; Wilson-Aggarwal et al. 2019). Dogs in northern Australia were shown to be highly connected with others in their village and, in general, the total time that each pair of dogs spent in association was 2-16 minutes a day (Brookes et al. 2018). A study of free-ranging dogs in rural Chad showed that individuals had heterogeneous contact rates, and that contacts were predominantly short in nature (Wilson-Aggarwal et al. 2019). Furthermore, contact rates were influenced by the distribution of dog owning households, with dogs more likely to interact and have longer interaction times when their houses were closer together. In one village, dogs that had larger ranges interacted with a greater number of individuals and had more second order contacts (Wilson-Aggarwal et al. 2019). In a study on urban free-ranging dogs in Chad, individuals were highly connected to others from nearby households, and the spatial structure of dog social communities were effectively characterised by elements of urban infrastructure e.g. main roads (Laager et al. 2018). Beyond the household, none of these studies identified preferential mixing patterns, however, a study on a managed population of dogs in north Australia, found reproductive status was important and a larger number of contacts were recorded for intact females and for neutered males (Sparkes et al 2014).

These studies have provided an aggregated 'snap-shot' account of the variation in the contact behaviour of free-ranging dogs, with observation periods of 3-10 days. However, it is not known if there are daily or seasonal variations in the occurrence of contact events or their durations, and yet these features can be important in determining disease epidemics (Volz & Meyers, 2009; Enright & Kao, 2018). For example, seasonal outbreaks of simulated rabies in racoons *Procyon lotor* are best explained by shifts in contact durations, rather than observed shifts in intersexual interactions or pulses in birth rates (Hirsch. et al. 2016). Moreover, evidence suggests that the temporal dynamics of contacts have larger influences on transmission dynamics when R_0 (average number of cases an individual will cause) is less than two (Chen et al. 2014), or when the disease shows low transmissibility and a long infectious period (Springer et al. 2017), as is the case with rabies (Hampson et al. 2009; Kurosawa et al. 2017).

In this study, we investigated spatial-temporal variations in the contact behaviour of a large number of free-ranging domestic dogs in rural Chad, where rabies remains endemic. We use proximity loggers to quantify the time, frequency and duration of close contacts that could facilitate the transmission of infections, and use GPS devices to identify the location of contact events. Specifically, we set out to identify if there is daily and seasonal variation in the tendency for individuals to contact each other, in their contact durations, and whether or not these temporal patterns vary by location.

4.3 METHODS

4.3.1 *Field study timings and locations*

Fieldwork was conducted in six rural villages in Chad (Figure 1) during the dry season (between 5th March and 17th May 2018) and again during the wet season (between 3rd August and 17th October 2018). The most northerly village, Medegue (11°01'48.8"N 15°26'37.7"E), is located on a main road in the Mayo-Kebbi east region in the western central part of Chad, and is approximately 15 km from the district town of Guelendeng. The remaining villages are all located in the district of Sarh in the Moyen-Chari region in the south of the country. These five villages can be split into two geographical sites, ‘Sarh east’ and ‘Sarh west’. Sarh west is approximately 10 km to the west of Sarh town and includes: Ngakedji (9°11'16.5"N 18°18'10.7"E), which stretches along the edge of a tributary from the Chari River; Kira (9°10'50.8"N 18°17'00.3"E) which is a large, nucleated village ~2 km from Ngakedji; and Bembaya (9°11'33.6"N 18°17'42.3"E) which is situated between the other two villages and is relatively small in size. Sarh east is approximately 40 km to the east of Sarh town and includes: Marabodokouya (9°19'42.3"N 18°43'20.0"E) which is a large village that is split into quartiers, where the principal quartier is located along the main road to Kyabé and several smaller quartiers are located along the river up to 10 km away from the road; and Tarako, which is a small, nucleated quartier of the village Tarangara (9°08'19.8"N 18°42'00.9"E), that is situated ~20 km south of Marabodokouya’s principal quartier and on a remote branch of the Chari.

With the consent of owners and the village chief, dogs were collared with standard nylon dog collars (Ancol Heritage). All collared dogs were sexually intact and had clear ownership and were closely affiliated with a specific human household. Puppies (less than six months of age) were not collared. We recorded the location of every dog-owning household visited using a handheld GPS. Since in each village all households known to have dogs were visited, the number of dogs owned by each household was recorded and summed to estimate the adult dog population. Additional data collected on the individual dogs included sex and age in months (as recalled by the owner).

Collars were fitted with two devices; (1) an i-GotU GT-600 GPS unit (Mobile Action Technology Inc., Taiwan) and (2) a wearable proximity sensor developed by the OpenBeacon project (http://www.openbeacon.org/) and the SocioPatterns collaboration consortium (http://www.sociopatterns.org/). The proximity sensors exchange one radio packet per second in a peer-to-peer fashion, and this exchange of radio-packets is used as a proxy for the spatial proximity of individuals wearing the sensors (Cattuto et al. 2010; Isella et al. 2011; Wilson-Aggarwal et al. 2019). Proximity is measured by the attenuation between devices, defined as the difference between the received and transmitted power. An attenuation threshold of -70 dbm was used in this study as it has been shown to detect close-contact events (within 1-1.5 m) in humans, during which a communicable disease might be directly transmitted, either by direct physical contact or by airborne transmission (Stehle et al. 2013; Voirin et al. 2015). In both field seasons, collars were deployed for an initial two weeks, and then replaced with collars containing a new proximity sensor and a new GPS logger modified with a higher capacity battery. The GPS units were all configured with a fix interval of 10 minutes.

Data processing

Processing of the proximity data was conducted in Python v2.7. After extraction from the logging devices, proximity data were cleaned by identifying corrupted sensors (where no data were available) and by removing data with anomalous signals (such as continuous bursts of data). To see if the contact events were recorded in an asymmetric way, inter-logger variability was assessed by comparing the number of packets emitted and received for all pairs of working sensors. The data from sensors were discarded if they showed deviations from the expected linear relationship between radio packets emitted and received. A contact event was defined by sensors exchanging radio packets for a minimum of 20 consecutive seconds. Contact events terminated if the sensors stopped exchanging radio packets in any of the subsequent 20 s breaks, meaning that the weights of interactions were characterised by multiples of 20 s.

Processing of the GPS data was conducted in R v3.3.3 (R Core Team, 2017) and the ‘sp’ v1.2-3 and ‘rgdal’ v1.2-5 packages were used to project all GPS data into the relevant coordinate reference system for Chad (EPSG:32634). The distance between the households for each observed pair of individuals (dyad) that could have come into contact was calculated. The GPS data for the dogs’ movements were cleaned by removing erroneous fixes with speeds greater than 20 km/hr between locations. To control for any effect of the researchers’ presence on the dogs’ behaviour and to give dogs time to adjust to the collars, we discarded both GPS and proximity records 12 hours after collar deployment and 12 hours before collar collection.

4.3.2 *Locating contacts*

To identify the locations where contact events were first initiated, continuous time movement models were fitted to the spatial data using the ‘ctmm’ package (v0.5.5). The models were used to simulate the possible location of individuals at times between the ‘known’ locations (recorded by GPS). For each individual, 30 realisations of their possible paths were simulated at an interval of one minute, excluding the period between the first collar being collected and the second collar being deployed. The time at which contact was first recorded by the proximity loggers was then used to extract the simulated locations of both individuals involved, or of just one individual if no spatial data were available for the other. The mean latitude and longitude of the simulated locations was taken to be the location of where the contact event was first initiated. This mean location was then categorised for each contact event as being either around the household (within 50 m of either of the individuals' households), around the village (within 100 m of any household that owned a tracked dog, excluding the individuals' households) or outside the village.

For each dyad, we recorded whether or not the individuals came into contact at any point during each season, how many contacts they had, the duration of each contact event, the daily probability of contacts (the total number of days a contact was observed divided by the number of days a contact could be observed), and the probability of contact during each hour of the day, in the household, village and outside the village (i.e. the number of hours that a contact occurred at time *i* and at location *j*, divided by the total number of hours that a contact could have been observed at time *i*).

4.3.3 *Statistical analysis*

General linear mixed-effect models (GLMMs) were used to investigate variation in the contact behaviour of dogs at the dyad level (rather than an individual level; Cross et al. 2012; Cross et al. 2013; Silk et al. 2017). Preliminary analysis suggested that contacts between individuals from different villages were exceptionally rare, and so statistical models were only run for data on contacts between individuals from the same village (within-village dyads).

To investigate predictors of whether or not a dyad ever came into contact during the observation period (0 for absence of a contact and 1 for the presence of contacts), a GLMM was fitted with a binomial error structure using the package ‘lme4’ (v1.1-18.1; Bates et al, 2015). Explanatory variables included dyad sex (categorised as male-male, male-female or female-female), age difference between individuals in months, the log (base 2) transformed distance between the individuals’ households (with 1 m added to all values), season, the interactions between the aforementioned variables and season, and finally region. The number of hours that both individuals in a dyad could have been observed in contact was included as a fixed effect to control for biases in observation times. Random effects consisted of the identity of each individual in a dyad (to control for individual variations in the tendency to have contact with others), the identity of the households to which each individual belonged (to control for household level variations in contact rates) and the village identity for both individuals (to control for village level variations in contact rates).

A GLMM was fitted with a binomial error structure to investigate spatial-temporal variations in the hourly probability of contacts. This model only used data for dyads that were observed to have been in contact. Because the response variable was a proportion, dyads that had less than 10 repeated observations for any hour were removed from the analysis, and the model was weighted by the total number of hours that each dyad could have been observed in contact at each hour of the day. Fixed effects were the same as in the previously-described model, with the exception of hours observed and with the addition of hour of day (as a categorical variable), location, and the interactions of these two variables with season. Random effects were the same as in the previous model, with the addition of dyad ID (to control for repeated observations).

To investigate spatial-temporal variations in the duration of contacts, a GLMM was fitted with a negative binomial error structure using the ‘glmmTMB’ (v0.2.3) package. Similar to the previous model, data for dyads that were not observed to have been in contact were excluded. Data on dyads from Tarako, Tarangara were also excluded as the missing data from the wet season caused errors when generating confidence intervals and predictions from the model. Fixed and random effects were the same as in the previously described model. For all models, the package ‘emmeans’ (v1.3.3) was used to estimate test statistics, *p*-values, odds ratios and confidence intervals for contrasts from the full model. The ‘DHARMa’ (v0.2.6) package was used to assess model residuals and goodness of fit.

4.4 RESULTS

Dogs were collared for a mean of 37 days (range; 1-70 days) in the dry season and 34 days (range; 2-65 days) in the wet season. Proximity data were successfully collected for 199 individuals in the dry season, and of these, 179 individuals had spatial data available. In the wet season 166 individuals had proximity data successfully collected, and 149 of these individuals also had spatial data available.

4.4.1 *Within-village contacts*

Of the 4254 potential within-village dyads in the dry season, 713 (17%) came into contact, and a total of 47,373 contact events were recorded (see Table 4.1 for a summary by village). Of the 3221 potential within-village dyads in the wet season, 533 (34%) came into contact, with a total of 33,259 contact events recorded. For dyads that were observed to have been in contact, the median daily probability of contact was 6% (inter-quartile range: 3–14%) in the dry season, and 10% (3–22%) in the wet season. In both seasons, the median duration of contact events was 20 s (20–40 s). In all villages, a higher proportion of contacts occurred within the village with a median of 44% (0–100%) of located contacts occurring within the village during the dry season and 75% (36–100%) in the wet season.

Table 4.1. Summary of the contacts between free-ranging domestic dogs from rural villages in Chad. For each village and season the adult dog population size is reported along with the number of individuals sampled, the number of potential within-village dyads that could have been observed in contact (due to overlapping deployments of proximity sensors), the number of observed within-village dyads that had recorded contact events, and the total number of observed contacts. The percentage reported for the number of dyads observed in contact, is calculated using the total number of observable within-village dyads, as opposed to the total number of dyadic pairs in the population. For dyads that were observed to have contacts, the median and inter-quartile range is reported for the duration of contacts (in seconds), the daily contact frequency (number of contacts divided by the total number of days monitored) and the proportion of GPS-located contacts that were around the household, within the village and outside of the village.

Village	Season	Pop.	Individuals sampled	No. of observable dyads	No. of dyads in contact	No. of contacts	Duration of contacts (s)	Daily frequency (%)	Prop. in the household (%)	Prop. within the village (%)	Prop. outside the village (%)
Medegue	Dry	30	26 (87%)	325 (75%)	62 (19%)	3814	20 (20 - 40)	6 (3 - 13)	0 (0 - 36)	51 (28 - 76)	11 (0 - 38)
	Wet	38	29 (76%)	355 (50%)	61 (17%)	4401	20 (20 - 40)	6 (3 - 17)	0 (0 - 12)	57 (48 - 100)	1 (0 - 47)
Kira	Dry	45	44 (98%)	942 (95%)	168 (18%)	15015	20 (20 - 40)	5 (2 - 14)	0 (0 - 32)	86 (41 - 100)	0 (0 - 6)
	Wet	49	36 (73%)	618 (53%)	210 (34%)	18529	20 (20 - 60)	8 (3 - 20)	0 (0 - 18)	93 (58 - 100)	0 (0 - 7)
Bembaya	Dry	12	12 (100%)	65 (98%)	46 (71%)	5586	20 (20 - 40)	12 (6 - 28)	20 (1 - 48)	55 (24 - 78)	0 (0 - 30)
	Wet	21	18 (86%)	151 (72%)	85 (56%)	4535	20 (20 - 40)	16 (5 - 30)	0 (0 - 25)	86 (49 - 100)	0 (0 - 4)
Ngakedji	Dry	27	27 (100%)	341 (97%)	47 (14%)	4499	20 (20 - 60)	9 (5 - 18)	6 (0 - 35)	65 (34 - 100)	0 (0 - 21)
	Wet	25	17 (68%)	136 (45%)	9 (7%)	649	20 (20 - 40)	9 (3 - 19)	50 (48 - 72)	29 (24 - 42)	0 (0 - 10)
Mar.	Dry	85	70 (82%)	2391 (67%)	347 (15%)	15693	20 (20 - 60)	6 (2 - 10)	0 (0 - 22)	14 (0 - 60)	60 (0 - 100)
	Wet	111	66 (59%)	1961 (32%)	167 (9%)	5145	20 (20 - 40)	11 (3 - 24)	0 (0 - 46)	50 (0 - 100)	0 (0 - 47)
Tarangara	Dry	21	20 (95%)	190 (90%)	43 (23%)	2766	20 (20 - 40)	5 (3 - 11)	48 (20 - 91)	48 (0 - 75)	0 (0 - 0)
	Wet	-	-	-	-	-	-	-	-	-	-
Overall	Dry	220	199 (91%)	4254 (76%)	713 (17%)	47373	20 (20 - 40)	6 (3 - 14)	0 (0 - 33)	44 (0 - 100)	4 (0 - 100)
	Wet	244	166 (68%)	3221 (38%)	533 (34%)	33259	20 (20 - 60)	10 (3 - 22)	0 (0 - 25)	75 (36 - 100)	0 (0 - 18)

4.4.2 *Probability of having had contact*

The marginal R^2 value (0.41) and conditional R^2 (0.69) suggests that both the fixed and random effects explain a substantial amount of the variation in the probability that a within-village dyad came into contact. The variance between individuals (τ00[ID1] = 1.01; Appendix D Table D1), households (τ00[Household ID2] = 0.63) and the villages (τ00[Village ID] = 0.13) suggests there was considerable variation between individuals in their tendency to have been in contact with others, but that there was little variation between villages.

For every doubling in the distance between the dyad individuals' households, the odds of them having had contact dropped by a factor of 0.49 (confidence intervals; 0.45-0.53; z = -18.25; p < 0.001; Figure 4.1). An interaction between season and sex was found, whereby the probability of a contact between males was 2.10 (1.23, 3.59) times more likely in the wet season than in the dry season (z = 2.712; p = 0.007). In the wet season, observed contacts between potential male-male dyads were 2.19 (1.07, 4.52) times more likely than female-female dyads (z = 2.55; p = 0.029). The odds of a contact having been observed between individuals increased by a factor of 2.56 (1.59, 4.13) for every 10-fold increase in the number of days observed (z =3.87; p < 0.001; Appendix D Figure D1).

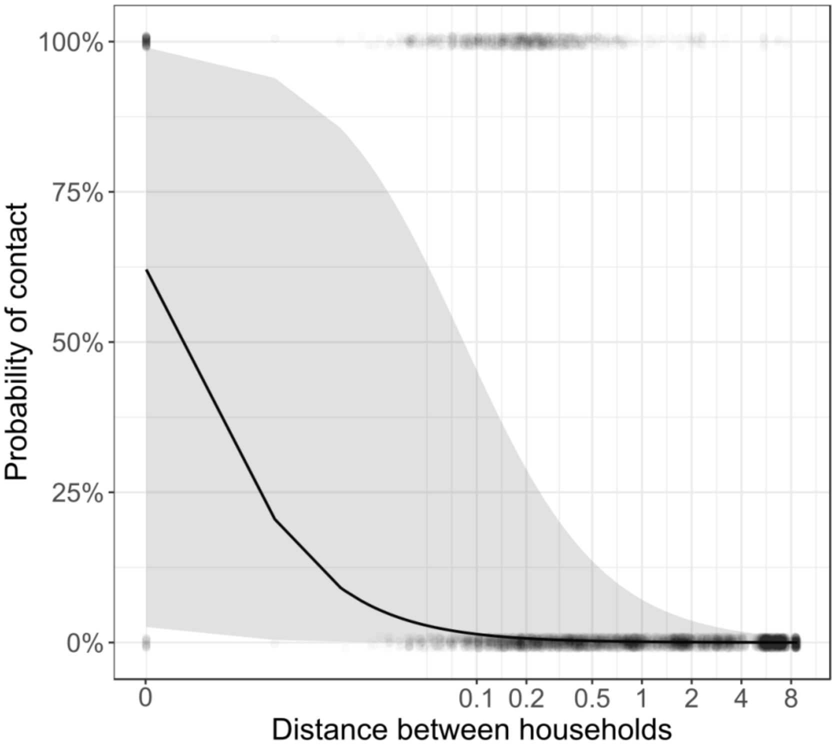

Figure 4.1. The probability of observing contact between potential dyads of free-ranging domestic dogs in rural Chad with increasing distance between the individuals' households.The predictions and confidence intervals are plotted from a general linear mixed model. The points are the raw data and have a jitter and alpha level applied. The x axis is on a logged scale.

4.4.3 *Hourly probability of contact*

The marginal R^2 (0.34) and conditional R^2 (0.56) suggest the fixed and random effects provided reasonable predictive power for the hourly probability of contact for dyads should the two individuals have been in contact. The between individual variance (τ00[ID1] = 0.22) and between household variance (τ00[Household ID1] = 0.29) in the hourly probability of contact was similar, while the between village variance was minimal (τ00[Village ID] < 0.01).

The hourly probability of contact reduced by a factor of 0.62 (0.60, 0.64) for every doubling in the distance between the individuals households ($z = -29.60$; $p < 0.001$). There was an interaction between sex and season, whereby the hourly probability of contact between female-female dyads was 1.64 (1.43, 1.87) times higher in the wet season than in the dry season ($z = 7.21$; $p < 0.001$), while the probability of male-male dyads was 1.26 (1.05, 1.52) times higher in the wet season ($z = 2.47$; $p = 0.013$). Furthermore, in the dry season, the hourly probability of male-male dyads was 1.57 (1.05, 2.36) times higher than female-female dyads ($z = 2.62$; $p = 0.024$), and male-female dyads were 1.45 (1.10, 1.90) times higher than that of female-female dyads ($z = 3.18$; $p = 0.004$).

The hourly probability of contact between dyads varied spatially, and was 1.56 (1.51, 1.62) times higher within the village than around the individual’s household ($z = 28.12$; $p < 0.001$), and 5.37 (5.05, 5.71) times higher within the village than outside of the village ($z = 63.56$; $p < 0.001$). Furthermore, the hourly probability of contact between individuals was 3.44 (3.23, 3.67) times higher around the household than outside the village ($z = 45.11$; $p < 0.001$). There was also an interaction between season and location, whereby the hourly probability of contact between dyads in the village was 2.13 (1.90, 2.38) times larger in the wet season than that in the village during the dry season ($z = 13.32$; $p < 0.001$; Figure 4.2).

Significant hourly variations were identified in the probability of contact for dyads (Figure 4.2; Table 4.2). The probability of contact peaked twice throughout the day, with one peak between 5 and 9am and a second peak between 6 and 8pm (Figure 4.2). While this pattern did not change between seasons, there was an interaction between season and time of day, and the probability of contact was noticeably higher in the wet season after 5pm (Table 4.2). There was also an interaction between time of day and location, where the probability of contact around the village and the individuals' households followed the aforementioned hourly pattern, but the probability of contact outside of the village had a smaller peak between 5 and 8am, after which it gradually declined throughout the day (Appendix D Table D2).

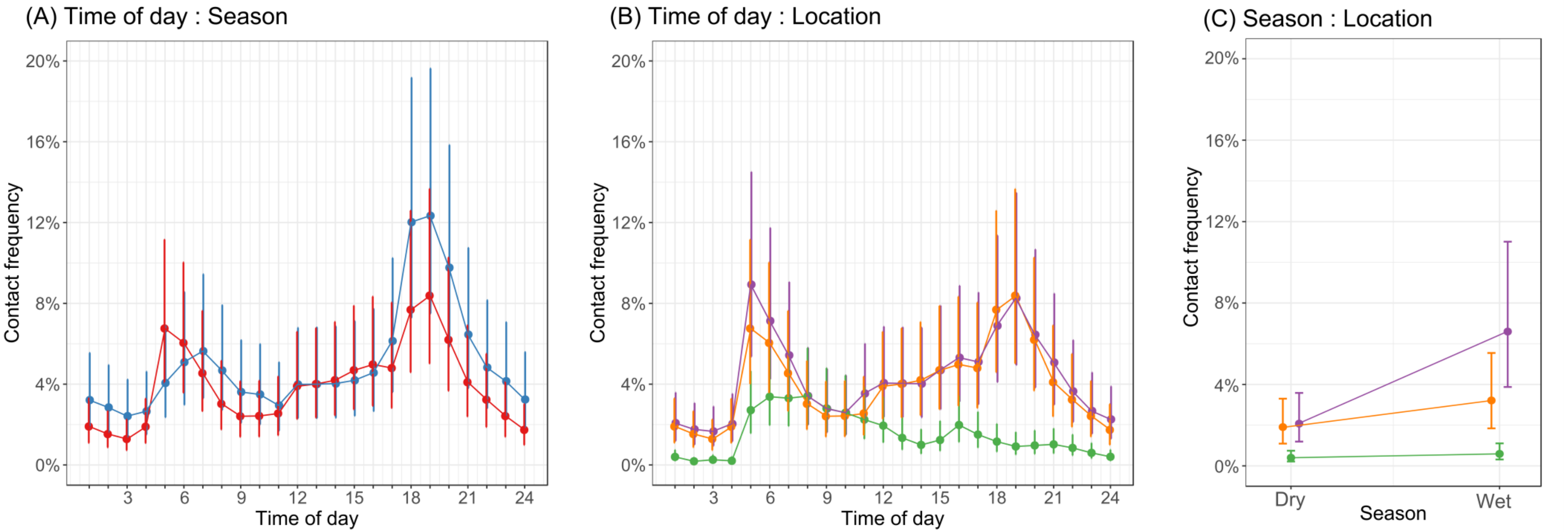

Figure 4.2. Temporal and spatial interactions affecting variation in the frequencies of contact among free-ranging domestic dogs in rural Chad. All predictions and confidence intervals are derived from general linear mixed models. Plot A shows the predicted frequencies of contacts between dogs at each hour of the day in the dry (red) and wet (blue) seasons. Plot B shows the predicted contact frequencies at each hour of the day in different locations; within 50 m of either of the dyadic individual's households (orange), within the village (purple) which is defined by a 100 m buffer around all households that own a dog while excluding the 50 m around either individual's household and outside of the village (green). Plot C depicts the models predictions for the frequencies of contacts between dogs at each of the different locations in the dry and wet season.

4.4.4 *Duration of contacts*

The marginal R^2 (0.70) and conditional R^2 (0.99) suggest that the model had strong predictive power, although the between-group variances was very low, suggesting that variation in contact durations was similar for different individuals (τ00[ID1] = 0.01), households (τ00[Household ID1] < 0.01) and villages (τ00[Village ID] < 0.01).

The duration of contacts for dyads reduced by a factor of 0.95 (0.95, 0.96) for every doubling in the distance between households ($z = -12.64$; $p < 0.001$). There was an interaction between the effects of the age difference between individuals and season ($z = -2.79$; $p = 0.005$), whereby in the wet season the duration of contact increased by 1.00 second (1.00, 1.01 seconds) for every month increase in the age difference between individuals, which was not the case in the dry season (Figure 4.3).

The interaction between the locations of contacts and season significantly affected contact durations; outside of the village contact durations were 1.35 (1.24, 1.48) times longer in the dry season compared to the wet season ($t = 6.62$; $p < 0.001$). Furthermore, in the dry season, contacts outside the village were 1.38 (1.29, 1.48) times longer than those within the village ($t = 10.73$; $p < 0.001$), and 1.40 (1.30, 1.51) times longer than those around the household (10.66; $p < 0.001$).

Seasonal variation in the duration of contacts at different hours of the day were identified (Figure 4.3). Contact durations in the wet season peaked twice, once between 5am-7am and again at 6pm. In the dry season, contact durations peaked three times, the first at 5am followed by a peak at 1pm and a third at 6pm. Spatial-temporal patterns were also detected, with longer contact durations outside of the village compared to those within the village or around the household, at almost all hours of the day.

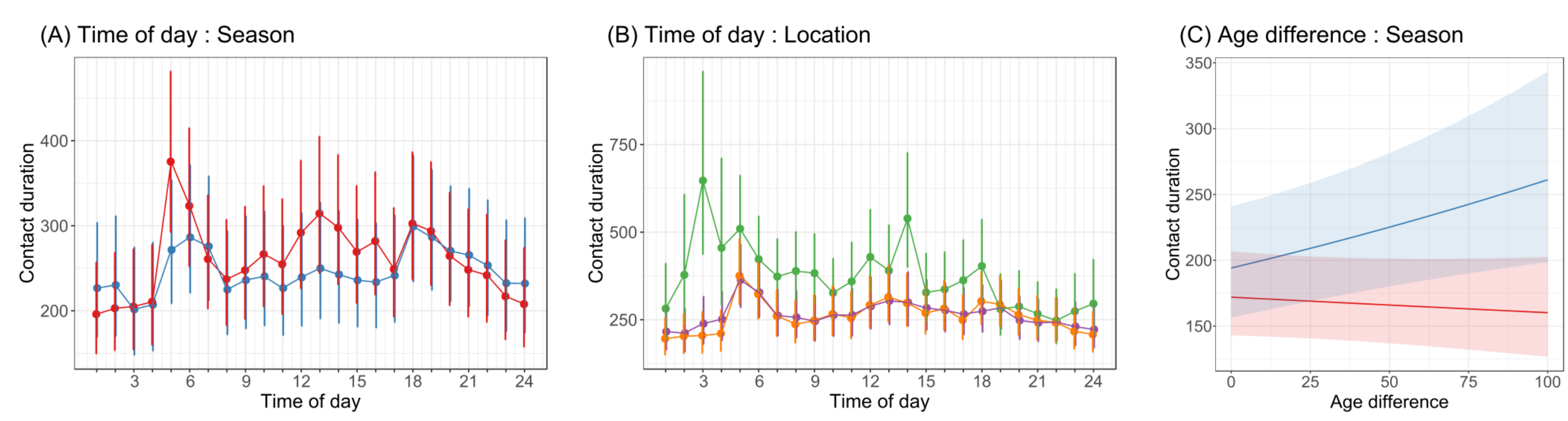

Figure 4.3. Spatial-temporal variation in the duration of contacts between free-ranging domestic dogs in rural Chad. All predictions and confidence intervals are derived from general linear mixed models and are presented in seconds. Plot A shows the predicted contact durations between dyads of dogs at each hour of the day in the dry (red) and wet (blue) seasons. Plot B shows the predicted contact durations at each hour of the day in different locations; within 50m of either of the individual's household (orange) and within the village (purple) which is defined by a 100 m buffer around all households that own a dog and excluding the 50m that defines either individual's household, and outside of the village (green). Plot C shows the predicted contact duration of contacts for dogs with different age differences in the wet (blue) and dry (red) seasons.

4.4.5 *Between-village contacts*

Between-village contacts were only observable in two of the field sites (in Sarh east during the dry season and in Sarh west during both the dry and wet seasons). During the dry season in Sarh east, none of the 5565 potential between-village dyads were found to have been in contact. In Sarh west, of the 3361 potential between-village dyads in the dry season, 25 (1%) came into contact, and 166 contact events were recorded with a median contact duration of 20 seconds (20 – 40 seconds; Table 4.2). Locations were estimated for 160 of the 166 contact events in the dry season, and of these 43 (27%) occurred within 50 m of one individual’s household, 101 (63%) occurred within the village, and 16 (10%) occurred outside of the village. In the wet season, only 3 (<1%) of the 1556 observed between-village dyads came into contact. A total of 5 contacts occurred, all of which were 20 seconds long and located within the village. These contacts involved two dogs from the same household in Kira that visited Bembaya on multiple days and came into contact with three dogs from different households.

Table 4.2. Summary of between-village contacts for free-ranging domestic dogs from rural villages in Chad. For each season and village in the field site ‘Sarh west’, the number of observable dyads is reported with the percentage of the total number of dyads for the population in brackets. The number of observed dyads that came into contact is reported along with the percentage that this represents from the total number of observed dyads in brackets. As well as the total number of contacts, the median and inter-quartile range for the duration of contacts is reported. A ratio of the locations of where contacts were located is reported for all located contacts.

illage	Season	No. of observable dyads	No. of dyads in contact	Total no. of contacts	Duration of contacts (s)	Location (household : within village : outside village)*
Kira	Dry	1699 (97%)	14 (1%)	54	20 (20 - 40)	1 : 48 : 3
	Wet	1250 (61%)	3 (<1%)	5	20 (20 - 20)	0 : 5 : 0
Bembaya	Dry	838 (97%)	21 (3%)	162	20 (20 - 40)	42 : 98 : 16
	Wet	944 (61%)	3 (<1%)	5	20 (20 - 20)	0 : 5 : 0
Ngakedji	Dry	1489 (97%)	15 (1%)	116	40 (20 - 40)	43 : 56 : 13
	Wet	918 (49%)	0 (0%)	0	-	-
Overall	Dry	2013 (97%)	25 (1%)	166	20 (20 - 40)	43 : 101 :16
	Wet	1556 (68%)	3 (<1%)	5	20 (20 - 20)	0 : 5 : 0

* Some contacts were not located

4.5 DISCUSSION

This study quantifies spatial-temporal variations in the within-village contact rates between free-ranging domestic dogs in rural Chad. The probability of the dogs in a dyad ever coming into contact, their hourly probability of contact should they have interacted, and the duration of their contacts were all negatively correlated with the distance between dog households. The hourly probability of interactions around the household and within the village peaked between 5am-9am and again at 6pm-8pm. While less common, the probability of contact events outside the village peaked between 5am-8am. Contacts outside the village were of longer duration in the dry season, when they were also longer than those within the village or household. Contact patterns for within- and between-sex dyads varied by season, whereby males were more likely to have been in contact in the wet season. When individuals had been in contact, contact probabilities throughout the day were higher for within-sex dyads in the wet season, and higher for male-male and male-female dyads in the dry season.

In two of the field sites studied (Sarh west and Sarh east) there was the opportunity to observe contacts between dogs living in different villages. Contact events were only recorded for between-village dyads in Sarh west, where the three villages under study were in close proximity (up to 2 km apart), relative to the distance between the two villages in Sarh east (~20 km apart). Given the negative relationship between the probability of contact for within-village dyads and the distance between the individuals' households, this absence of contacts between villages that are further apart is unsurprising. The contact events for between-village dyads in Sarh west were rare, accounting for less than 1% of all observed contacts. However, there was a clear seasonal difference in the occurrence of contacts for between-village dyads, with a greater number of dyads in contact and a greater number of contact events recorded in the dry season. Again, the spatial distribution of villages was important, as a greater number of the potential between-village dyads in Bembaya (which is situated between Kira and Ngakedji) were found to have had contact.

Peaks in the probability of contact around the household and within the village at ~6am and ~6pm, are in accordance with sunrise and sunset, the timings of which vary little throughout the year in Chad. Given the periodic patterns of repeated space use described for dogs in this study system (Chapter 2), the daily pattern of interaction is likely driven by dogs passing other dog owning households as they leave the village and again when they return to their household. The duration of contacts between dogs in this study were in line with that reported in previous studies (Brookes et al. 2018; Wilson-Aggarwal et al. 2019), with the majority consisting of brief interactions lasting 20-60 seconds. The longer duration of contacts outside of the village might suggest that these interactions are different to the type of contacts that occur around the village and household, and this may be of epidemiological importance if they involve more/less direct contact. Whether or not these patterns are driven by independent or owner-mediated movement is unclear. However, this distinction could be important for the management of diseases, since owner-mediated movements imply that there is an opportunity for dog owners to intervene and prevent contacts.

In contrast to previous studies (Laager et al. 2018; Brookes et al. 2018; Wilson-Aggarwal et al. 2019), we find evidence for the preferential mixing between sexes, and this varied by season with male-male dyads were more likely to have been in contact during the wet season. Whilst in this study we cannot determine the nature of contact events, aggressive interactions have been shown to be more common among male dogs (Pal, 2015), and this may increase the risk of disease transmission through behaviours such as biting. All dogs in this study were reproductively intact and the higher frequency of male-male and male-female interactions during the dry season may be indicative of a spike in mating behaviours. However, free-ranging dogs are generally thought of as non-seasonal breeders, and while there is a lack of research in this area, evidence for seasonal breeding has only been found for free-ranging dogs in India (Pal, 2011). A study in northern Australia provides further evidence for the effect of reproductive state on an individual's contact rates, where a higher number of contacts were recorded for intact females and neutered males in a managed population of free-ranging dogs (Sparkes et al. 2014). Given the current evidence, there is potential for the management of free-ranging dog populations to have unintended effects, whereby reducing the number of susceptible individuals through neutering campaigns could change transmission dynamics by altering the spatial-temporal patterns of dog contact behaviour.

Until recently, there has been a lack of empirical data on the contact rates of free-ranging dogs. This has meant that models for dog-mediated diseases have assumed that contact rates are density dependent, or have generated variation in the probability of contacts by applying frequency dependent functions in the form of spatial and/or social scaling parameters (Beyer et al. 2011; Johnstone-Robertson et al. 2017). Our results provide support for the use of a spatial scaling parameter in determining the contact rates between dogs from different households. This distance effect may also be relevant for contacts between dogs in different villages, but in rural Chad this might be complicated by seasonal differences in the dogs’ range sizes, that are larger in the dry season (Chapter 2) and may increase the probability of contact of individuals from different villages. By comparison, defining social scaling parameters requires more care, and for free-ranging dogs in rural Chad, the seasonal preferential mixing patterns between sexes should be included.

The contact patterns described for dogs here cannot on their own explain the 3-6 year cycles of canine distemper or rabies in free-ranging dog populations in Africa (Hampson et al. 2007; Viana et al. 2015). However, both contact frequency and duration can be important in determining whether an infection might be transmitted (Smieszek, 2009), and the importance of each depends on the infectiousness of the disease and its method of transmission (Cao et al. 2014; Toth et al. 2015). Furthermore, the seasonal variation in the contact behaviours of dogs reported here, could determine the size of outbreaks and the speed of transmission, depending on when and where the disease is first introduced. We might expect diseases with high transmissibility, such as canine distemper, to spread through a village faster in the wet season when contacts in the village are more frequent. Equally, we might expect larger outbreaks of diseases with both high and low transmissibility in the dry season, when contact durations are longer outside the village and interactions for between-village dyads are more probable.

In this study, we provide an in-depth account of the spatial-temporal patterns in the contact behaviour of free-ranging domestic dogs in rural Chad. While the spatial distribution of households and villages determined the contact rates and contact durations between individuals, we find evidence for preferential mixing among sexes and spatially explicit hourly patterns of interactions, both of which varied seasonally. These results have implications for the predictions of disease transmission in a domestic species that shares several pathogens with humans and wildlife.

CHAPTER 5:

EXPOSURE OF FREE-RANGING DOMESTIC DOGS *CANIS FAMILIARIS* TO POTENTIAL SOURCES OF INFECTION FOR GUINEA WORM *DRACUNCULUS MEDINENSIS*

5.1 ABSTRACT

The global campaign to eradicate Guinea worm disease, caused by the parasite *Dracunculus medinensis*, has been compromised by the emergence of infections in non-human hosts, particularly domestic dogs *Canis familiaris*. Dog infections have been found in several countries but are most abundant in Chad, where the distribution of infections follows the course of the Chari River. Infections in humans are acquired either via the classical pathway of drinking water contaminated with infected copepods, or through a possible novel route of consuming aquatic vertebrates that act as paratenic or transport hosts. Irrespective of the specific transmission pathway, water bodies along the Chari River are the sources of infection. In this study, we characterised the activity of dogs around natural water sources. GPS technology was used to track the movements of 298 free ranging domestic dogs across three climatic seasons, and in six rural villages in Chad where dog infections are frequently recorded. High-resolution satellite imagery was used to identify natural water sources. We found considerable temporal and spatial variation in the activity of dogs around water sources. Our results show that, in all seasons >85% of dogs had visited at least one natural water source. However, in any field site or season, no more than 4 water sources accounted for 95% of dog visits and these were all <0.5 km from a household with tracked dogs. Dogs from households that were closer to the Chari River and that had larger home ranges were consistently found to be more active around natural water sources. These results can be used to prioritise control efforts, such as the treatment of water sources with organophosphate temephos (Abate), whereby treatment of water sources close to villages that are subject to the greatest amounts of dog activity could be treated as a priority.

5.2 INTRODUCTION

Guinea worm disease, or dracunculiasis, is a profoundly debilitating disease that is caused by the parasitic nematode *Dracunculus medinensis*. The disease has historically infected humans throughout Africa and Asia, and it has been estimated that until recently the disease affected 3.5 million people living in 21 countries per year (Watts, 1986). Since the 1980s, a global campaign to eradicate Guinea worm disease has successfully reduced the number of human cases down to 28 in 2018 (CDC, 2019a), and the disease is now thought to be endemic in only 4 countries: Chad, Ethiopia, Mali and South Sudan (Hopkins et al. 2018), though Angola and Cameroon have recently experienced sporadic cases.

Despite the public health successes in reducing the incidence of human dracunculiasis, a large number of non-human animal infections have been detected in recent years, particularly in domestic dogs *Canis familiaris.* In 2018, infections were confirmed in 1069 domestic dogs, 32 domestic cats *Felis catus* and 1 olive baboon *Papio anubis* (CDC, 2019a). Furthermore, emergent worms from human and non-human hosts have been shown to be genetically indistinguishable (Thiele et al. 2018). The maintenance of the parasite in the environment by non-human reservoirs could, in addition to the challenges of surveillance, explain the apparent re-emergence of the disease in Chad after a 10 year hiatus of detected human cases (Eberhard et al. 2014). Even in the near-absence of human cases, Guinea worm evidently has the potential to persist in the environment as an ongoing source of infection for humans. Given the majority of detected non-human infections have been found in dogs, and 94% of dog infections in 2018 were found in rural Chad (CDC, 2019a), it appears plausible that dogs constitute a viable reservoir for infection. Since eradication of Guinea worm requires elimination in all hosts, these non-human infections now present a major obstacle for the final stages of the campaign.

The life cycle of Guinea worm starts when an adult female worm emerges from its host and releases larvae into a water source after a 10-14 month incubation period (Greenaway, 2014). Larvae are then ingested by an intermediate host (copepod crustaceans) where they develop into stage three larvae. The definitive host is then infected after ingesting the stage three larvae via either the classical or hypothesised novel transmission pathways. The classical transmission pathway is through drinking water containing the infected copepods. The novel pathway involves the ingestion of a paratenic or transport host, such as fish or frogs that have themselves eaten an infected copepod (Eberhard et al. 2016; Cleveland et al. 2017).

The reduction of human cases was achieved through methods of interrupting these cycles of transmission, and these included the chemical treatment of water sources with the organophosphate temephos (Abate) to reduce copepod populations, the provision of safe drinking water or filters to remove copepods from water, and, more recently, educating people on the importance of cooking fish before consumption (Eberhard et al. 2014). It is thought that similar methods can be used to reduce infections in dogs, and current control efforts include tethering suspect cases to prevent infected individuals contaminating water sources, and burying fish entrails to reduce the dogs' access to potentially contaminated food sources (Molyneux & Sankara, 2017). However, preventing dogs drinking from potentially contaminated water sources is clearly more difficult than in people, as dogs are free-ranging and only loosely controlled by their owners. For this reason, reducing copepod populations in water sources through chemical treatment with organophosphates remains one of the principal control strategies. Despite the continuation and intensification of these control efforts, dog infections continue to persist, and it is apparent that a better insight into the ecology of dogs in relation to Guinea worm infection is required to help inform appropriate control efforts.

The distribution of both human and dog infections in Chad follows the Chari River system, and the period for peak detection of new infections in dogs is between April and July (CDC, 2019b). Assuming incubation in the host of 10-14 months, the period of peak transmission is likely to coincide with the end of the dry season, when the river recedes to its lowest level and reveals ephemeral standing water sources. These ephemeral ponds are numerous, highly variable in size and are thought to be a source for Guinea worm infection (Eberhard et al. 2014), whether transmission is via classical or novel pathways. However, little is known about the interaction between dogs and water sources, which makes chemical control efforts harder, more labour intensive and more costly to implement. Furthermore, as seen from efforts to control vectors for malaria in sub-Saharan Africa, chemical treatment of water bodies can come with high operational costs (Derua et al. 2019). In Chad, such problems will be exacerbated by the dynamic hydrology of the Chari River. Thus, it is important to understand the activity of dogs around water bodies, so that resources and field operations can be prioritised or even targeted towards water sources that are disproportionately used by dogs.

This study explores the behaviour of free-ranging domestic dogs and their activity around water sources in rural Chad. We tracked the movements of dogs from six villages in which dog infections are frequently recorded, and have characterised the variation in dog activity around water bodies that are thought to be potential sources for Guinea worm infection. We aim to identify predictors for the dogs' activity around water bodies, which can then be used to inform control strategies, particularly in targeting and prioritising chemical treatment of copepod populations.

5.3 METHODS

5.3.1 *Field sites and timing of fieldwork*

Fieldwork was conducted in six villages in three areas of rural Chad (Figure 5.1). Medegue (11°01'48.8"N 15°26'37.7"E) is in Guelengdeng district of Mayo-Kebbi East region, in the western central part of Chad and is located ~15 km north from the town of Guelendeng on the main road along the Chari river. The other five villages were located in the district of Sarh of the Moyen-Chari region in the south of the country. Three villages lay close together, ~10 km to the west of the local capital town of Sarh (Sarh West area): Ngakedji (9°11'16.5"N 18°18'10.7"E) extends along the edge of a tributary from the Chari River, Kira(9°10'50.8"N 18°17'00.3"E) is a large, nucleated village ~2 km from Ngakedji, and Bembaya (9°11'33.6"N 18°17'42.3"E) is situated between the two. The other two villages were situated ~40 km to the east of Sarh (Sarh East area): Marabodokouya (9°19'42.3"N 18°43'20.0"E) is a large, dispersed settlement with its centre situated on the road to Kyabé, and multiple hamlets along the river bank, up to 10 km away from the main road, and Tarangara (9°08'19.8"N 18°42'00.9"E) is a small nucleated village ~13 km south of Marabodokouya, situated on a remote branch of the Chari that is cut off from the main river during the dry season forming a large pond.

Fieldwork was conducted in three field seasons; the dry season (between March and May 2018; 35°C mean daily maximum temperature, 10.3 mm mean total rainfall), the wet season (between August and September 2018; 27°C mean daily maximum temperature, 174.4 mm mean total rainfall) and the cool season (between January and March 2019; 28°C mean daily maximum temperature, 0 mm mean total rainfall). Temperature and rainfall information are reported for N’Djamena from the world meteorological organisation, (https://worldweather.wmo.int/en/home.html; accessed on 30/09/2019).

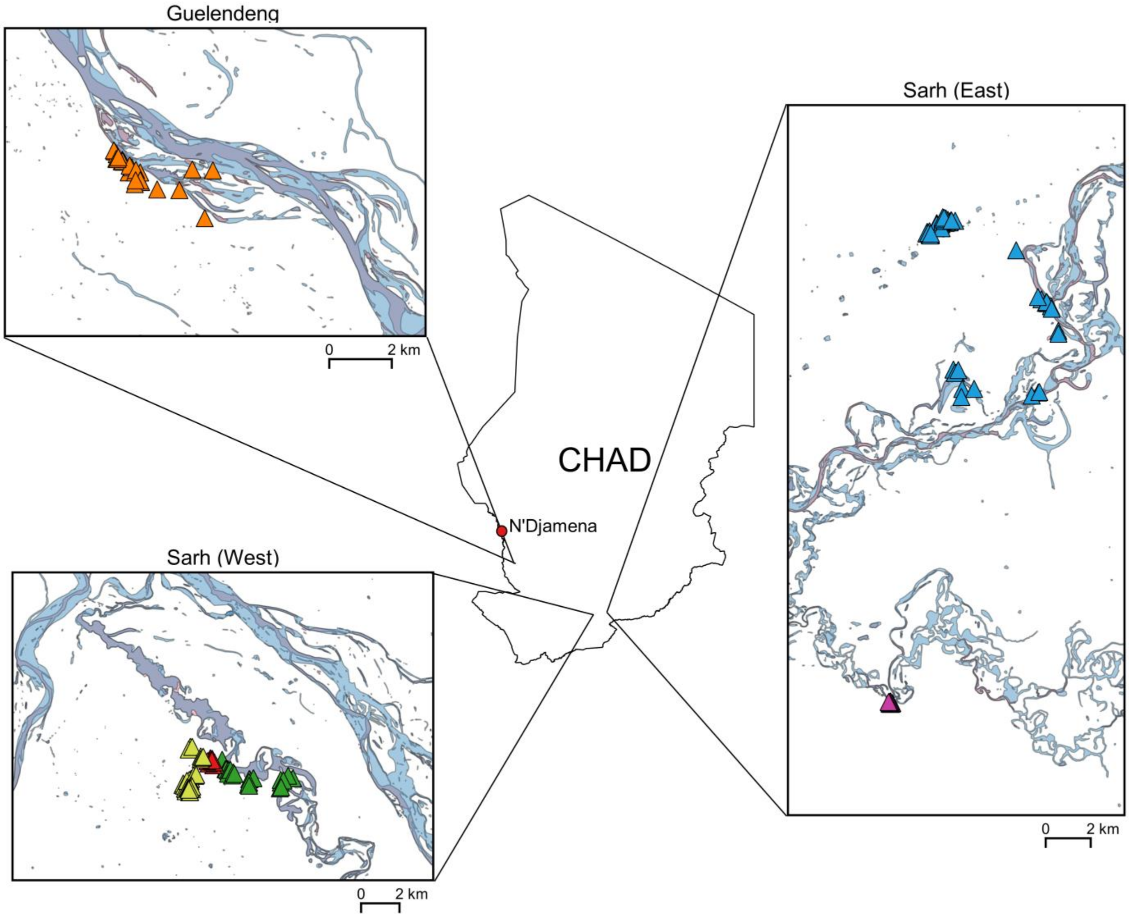

Figure 5.1. Field sites & natural water sources in rural Chad. Triangles represent a household where at least one dog was collared. Orange triangles represent households from the village Medegue in Guelendeng district. In the Sarh East area, blue triangles represent households in the village Marabodokouya and pink triangles are households from Tarangara. In the Sarh West area, yellow triangles represent the village Kira, green triangles the village Ngakedji and red triangles represent Bembaya. Vectorised water bodies from the satellite imagery are displayed for the wet season (blue) and dry/cool season (red).

5.3.2 *Dog space use*

After consent was provided by the village chief and dog owner, dogs were collared with retail dog collars (Ancol Heritage) fitted with a standard i-GotU GT-600 GPS unit (Mobile Action Technology Inc., Taiwan). After two weeks the collars were replaced with collars fitted with the same GT-600 GPS units, but which had been modified with a larger battery. The GPS units were configured with a fix interval of 10 minutes. GPS data were cleaned by removing locations taken up to 12 hours after the collar was deployed and 12 hours before collar recovery. Any likely erroneous GPS fixes with speeds greater than 20 km/hr between locations were removed. GPS data were projected into the relevant coordinate reference system for Chad (EPSG: 32633) using the 'sp' (v1.3.1) and 'rgdal' (v1.3.3) packages in R.

The dogs' home ranges were calculated using auto-correlated kernel density estimates (AKDE) from continuous time movement models. Models were fitted using the 'ctmm' package (v0.5.5) following procedures set out by Calabrese et al (2016). Variograms were used to check the autocorrelation structure of each individual's movement data. Individuals were excluded from home range analyses if there was no asymptote in the variogram, suggesting the individual was not monitored long enough or was exhibiting non-range resident behaviours, e.g. range expansion or dispersal. Movement models were fitted using maximum likelihood and model selection was determined by Akaike information criteria (AIC). Once models were selected, the 95% isopleth was extracted from models as an estimate for the dog's total range ($AKDE_{95}$).

5.3.3 *Water sources*

High resolution satellite imagery was obtained from DigitalGlobe for the three field sites. All satellite imagery was collected in either January or February 2018 and included red, green, blue and near infra-red bands from WorldView-2 & WorldView-3 satellites. Natural water sources were identified and vectorised using the Quantum Geographic Information System (v2.18.1) by visually searching the satellite imagery (a search area of 1463 km^2 for Sarh East, 486 km^2 for Sarh West and 147 km^2 for Guelendeng; Figure 1). Search areas for each field site were determined by creating a bounding box around all of the relocation points for dogs in the first field season. Water bodies were considered as present in the dry and cool season if water was visible in the satellite imagery. For identification of water bodies in the wet season, the boundaries of those identified for the cool and dry seasons were extended if visual evidence from the satellite imagery suggested they became larger (e.g. concentric rings caused by water evaporating in the surrounding soil). Similar evidence was also used to identify water sources that were present in the wet season but not in the dry or cool seasons, and to determine the likely boundaries of the river during the wet season. To ground-truth the location of vectorised water bodies, GPS locations of water sources around villages were taken in the field, and the proportion of these that were also identified in the satellite imagery was calculated.

5.3.4 *Activity around water sources*

To infer dog activity at water sources we used a similar approach to in a previous investigation conducted in Ethiopia (Appendix A), where for each dog we determined: the number of GPS location points within 100 m of a natural water source, the number of separate visits to water sources (defined by an interval of 30 minutes between GPS location points) and the number of unique water sources visited. The threshold distance of 100 m was chosen as preliminary analysis using the movement models showed that on average dogs moved 0.02 km/min (200 m per 10 minutes), meaning that if an individual had a GPS fix 100 m from a water source, they could reasonably have visited it and moved outside of the 100 m threshold within 10 minutes. For each water source, we measured: area, type (river or standing water), whether the water body was part of the river in the wet season, the distance to the nearest household with tracked dogs, whether it had been visited by a tracked dog during the monitoring period, the number of unique dogs that had visited, and the number of GPS location points within 100 m of the pond for all dogs.

5.3.5 *Statistical analysis*

Variation in whether or not dogs interacted with water bodies was analysed using a general linear mixed model (GLMM) with a binomial error structure. Explanatory variables included sex, logged (base 2) age, body condition, logged (base 10) $AKDE_{95}$ range, season, whether the dog was from a hunting household, whether the household provided water for their dogs, the logged (base 2) distance of the household from the river and the logged (base 10) number of days the dog was tracked. Region, village and household ID were included as nested random effects. Two further models were fitted with the same explanatory variables as the aforementioned model, but were used to investigate predictors for whether or not dogs interacted with (1) the river or (2) standing water bodies.

For dogs that had visited natural water sources, several GLMMs were fitted to investigate variations in the exposure of dogs to water sources. The first model investigated the number of unique natural water sources with which the dogs had visited, and used a Poisson error structure. A second model, fitted with a negative binomial error structure, investigated predictors for the activity of dogs around water sources, and used the number of GPS fixes that dogs had within

100 m of water bodies as a proxy for activity. The model for activity around water sources was re-run for activity just around rivers, and again for activity just around standing water bodies. Explanatory and random variables for all models were the same as in the aforementioned binomial models.

To investigate correlates with whether or not a water body was visited by a dog, a GLMM with a binomial error structure was built for each field season separately. Explanatory variables included the logged (base 10) area of the water source and the logged (base 2) distance of the water source from the nearest household with tracked dogs, while study site was included as a random variable. GLMMs with a negative binomial error structure and the aforementioned variables were used to investigate correlates with the number of unique dogs that visited each water source, and the number of trips by dogs to each water source. A generalised additive model (GAM) was used to relate the cumulative total of dog visits per water body to the logged (base 2) distance of the water body from a household with tracked dogs. The cumulative count of visits was made after ordering the water sources by the number of dog visits in descending order.

An information theoretic approach was used for the model selection of all GLMs and GLMMs, using ranked comparisons of corrected AIC (AICc) values. The top model set was selected using a difference in AIC (ΔAIC) of <2 from the top model, and model averaging was conducted over the top model set (Burnham and Anderson, 2002). Throughout the manuscript we report the more conservative full-averaged model results (as opposed to the conditional average results). Correlations between explanatory variables were investigated prior to analyses using Spearman’s rank correlation tests, and correlated variables were precluded from appearing in the same models. ‘lme4’ (v1.1-12) was used to conduct GLMMs, ‘MuMIn’ (v1.15.6) for model selection and ‘mgcv’ (v1.8.12) for GAMs.

5.4 RESULTS

Ranging data were collected for a total of 298 unique dogs. In each field season, dogs were tracked for a mean of 35 days, with a minimum observation period of 1 day and a maximum observation period of 70 days. 65 dogs had spatial data available in all three field seasons. Reasons for missing spatial data included loss or damage of collars and dogs dropping out of the study due to death, disappearance or relocation.

Of the dogs with spatial data available, those that were identified as range-resident and for which home ranges could be calculated, comprised 174 individuals in the dry season, 151 in the wet season and 190 in the cool season. The dogs' $AKDE_{95}$ ranges had a median of 0.54 km^2 (inter-quartile range: 0.08 – 6.21 km^2) in the dry season, 0.31 km^2 (0.07 – 1.06 km^2) in the wet season and 0.57 km^2 (0.09 – 3.39 km^2) in the cool season (see Table 5.1 for a summary be village). In all seasons, over 85% of tracked dogs interacted with a natural water source, but spent a median of ≤1% of their time around water sources. However, there were large variations in the activity of dogs around water sources, both between villages and seasons (Table 5.1).

In total, 1179 natural water sources were identified from satellite imagery for the dry/cool season, of which 842 of the standing water sources were part of the river system (Table 5.2). For the wet season 817 natural water sources were identified and, since the river was at maximum capacity, no standing water sources were part of the river system. Of the water sources with known GPS locations, 64 of 78 (82%) were detected in the satellite imagery.

Table 5.1. Summary for the activity of free-ranging domestic dogs around natural water sources in rural Chad. Reported for each field season and village is the number of individuals with spatial data, the number of individuals to have visited water sources (for standing water and the river in brackets), the AKDE$_{95}$ range of range resident individuals and the activity of dogs around water sources. Where relevant the median and inter-quartile range in brackets is provided. Data on individuals were excluded from metrics for the number of unique water sources visited and the activity around water sources if they were never recorded to visit the respective water source.

Village	Season	n	No. to visit a water body (standing : river)	AKDE$_{95}$ (km^2)	No. of unique water bodies visited	Activity around standing water (%)	Activity around the river (%)
Medegue	Dry	22	22 (22 : 14)	0.15 (0.07 - 0.39)	8 (5 - 10)	8 (2 - 63)	1 (<1 - 2)
	Wet	27	27 (22 : 27)	0.57 (0.07 - 1.76)	5 (3 - 9)	3 (<1 - 50)	12 (3 - 57)
	Cool	28	28 (28 : 19)	0.32 (0.08 – 1.29)	8 (4 - 12)	5 (2 - 39)	1 (<1 - 2)
Kira	Dry	41	31 (18 : 25)	0.26 (0.06 - 1.32)	1 (1 - 2)	<1 (<1 - <1)	2 (<1 - 4)
	Wet	38	32 (30 : 8)	0.33 (0.14 - 0.70)	2 (1 - 4)	<1 (<1 - 1)	<1 (<1 - 1)
	Cool	38	29 (19 : 25)	0.60 (0.05 – 2.61)	2 (1 - 2)	<1 (<1 - <1)	1 (<1 - 2)
Bembaya	Dry	12	12 (6 : 12)	5.01 (0.36 - 17.82)	2 (1 - 3)	1 (1 - 1)	8 (5 - 10)
	Wet	18	9 (0 : 9)	0.05 (0.03 - 0.13)	1 (1 - 1)	-	<1 (<1 - <1)
	Cool	14	13 (0 : 13)	0.41 (0.02 – 1.06)	1 (1 - 1)	-	3 (1 - 6)
Ngakedji	Dry	20	19 (1 : 19)	0.11 (0.03 - 0.36)	1 (1 - 1)	<1	17 (4 - 30)
	Wet	15	14 (2 : 14)	0.12 (0.02 - 0.58)	1 (1 - 1)	2	16 (4 - 43)
	Cool	19	19 (1 : 19)	0.13 (0.02 – 0.28)	1 (1 - 1)	<1	11 (4 - 47)
Mar.	Dry	68	60 (59 : 39)	9.76 (0.57 – 19.81)	6 (3 - 9)	2 (1 - 5)	<1 (<1 - 1)
	Wet	61	57 (46 : 19)	0.65 (0.09 - 4.31)	3 (1 - 5)	1 (<1 - 3)	12 (1 - 87)
	Cool	88	73 (71 : 31)	1.49 (0.16 – 5.61)	3 (2 - 7)	1 (1 - 5)	2 (<1 - 7)
Tarangara	Dry	17	17 (17 : 1)	0.36 (0.02 - 0.70)	4 (3 - 6)	38 (7 - 73)	<1
	Wet	-	-	-	-	-	-
	Cool	12	12 (12 : 1)	1.12 (0.16 – 2.87)	8 (3 - 10)	26 (7 - 55)	<1
Overall	Dry	180	161 (123 : 110)	0.54 (0.08 – 6.21)	3 (1 - 7)	1 (<1 – 5)	<1 (<1 - 5)
	Wet	159	139 (100 : 77)	0.31 (0.07 - 1.06)	2 (1 - 5)	<1 (<1 - 2)	<1 (<1 - 7)
	Cool	199	174 (131 : 108)	0.57 (0.09 – 3.39)	3 (1 - 7)	<1 (<1 - 5)	<1 (<1 - 3)

Table 5.2. Summary for natural water sources and the amount of dog activity they received. Where appropriate the median is reported with the inter-quartile range in brackets. Water bodies are considered part of the river system if the river flooded into them during the wet season. Summary metrics for the median number of unique dogs to visit each water body visited by dogs, and the median distance of water bodies visited by dogs from a household with tracked dogs.

Region	Season	No. of water sources	No. of water sources associated with the river system	No. visited by dogs	No. unique dogs	Distance from dog household (km)
Sarh East	Dry	623	445	110	2 (1 - 6)	1.43 (0.78 – 2.69)
	Wet	343	1	34	2 (1 - 7)	0.93 (0.33 – 1.55)
	Cool	-	-	119	3 (1- 6)	1.68 (0.93 – 4.51)
Sarh West	Dry	447	301	18	2 (2 - 4)	2.44 (1.41 – 2.68)
	Wet	279	1	21	4 (1 - 6)	1.19 (0.56 – 1.74)
	Cool	-	-	17	3 (2 – 4)	2.44 (1.38 – 2.61)
Guelendeng	Dry	109	96	39	3 (1 - 6)	0.35 (0.24 – 0.83)
	Wet	195	1	43	1 (1 - 4)	1.66 (0.24 – 2.35)
	Cool	-	-	32	6 (4 – 8)	0.32 (0.23 – 0.63)

5.4.1 *Probability of visiting water sources*

From the dog's perspective, the odds of individuals having been within 100 m of a natural water source, reduced by a factor of 0.34 (confidence limits: 0.23, 0.51) with each doubling in the distance between their household and the river ($z = 5.27$; $p < 0.001$; Figure 5.2). The odds of dogs having visited a water source increased by a factor of 7.27 (3.59, 14.73) with each 10-fold increase in their $AKDE_{95}$ range size ($z = 5.51$; $p < 0.001$; Figure 5.2). There was a marginal effect of sex, whereby the odds of females having visited a water source was 2.44 (1.03, 5.81) times that of males ($z = 2.02$; $p = 0.043$). In addition, the odds that dogs had visited a water source increased by a factor of 1.68 (1.04, 2.71) for every doubling in the days they were monitored ($z = 2.12$; $p = 0.034$).

The same predictors were found (with the exception of sex) when only considering whether or not dogs had visited standing water sources (distance from the river: 0.80 (0.66, 0.98); $z = 2.15$; $p = 0.031$; $AKDE_{95}$ range: 4.56 (2.77, 7.52) $z = 5.95$; $p < 0.001$); days monitored: 12.78 (3.69, 44.22); $z = 4.02$; $p < 0.001$). Again, when looking at whether or not dogs had visited the river, there was an effect of the household's distance from the river (0.33 (0.22, 0.49); $z = 5.46$; $p < 0.001$) and the dog's $AKDE_{95}$ range (7.17 (3.69, 13.91); $z = 5.82$; $p < 0.001$). However, there was also an effect of season whereby, compared to the dry season, dogs were less likely to have interacted with the river in the wet (0.23 (0.08, 0.63); $z = 2.85$; $p = 0.004$) and cool (0.44 (0.20, 0.97); $z = 2.03$; $p = 0.044$) seasons.

From the perspective of the water sources, in the dry season, the odds of a water source having been visited by a dog increased by a factor of 1.52 (1.11, 2.09) with every 10-fold increase in their size ($z = 2.60$; $p = 0.009$). In all seasons, the odds of a water source having been visited by a dog, decreased with every doubling in their distance from a household with tracked dogs (dry: 0.23 (0.18, 0.28); $z = -13.32$; $p < 0.001$; wet: 0.20 (0.14, 0.27); $z = 10.01$; $p < 0.001$; cool: 0.35 (0.30, 0.42); $z = 12.71$; $p < 0.001$).

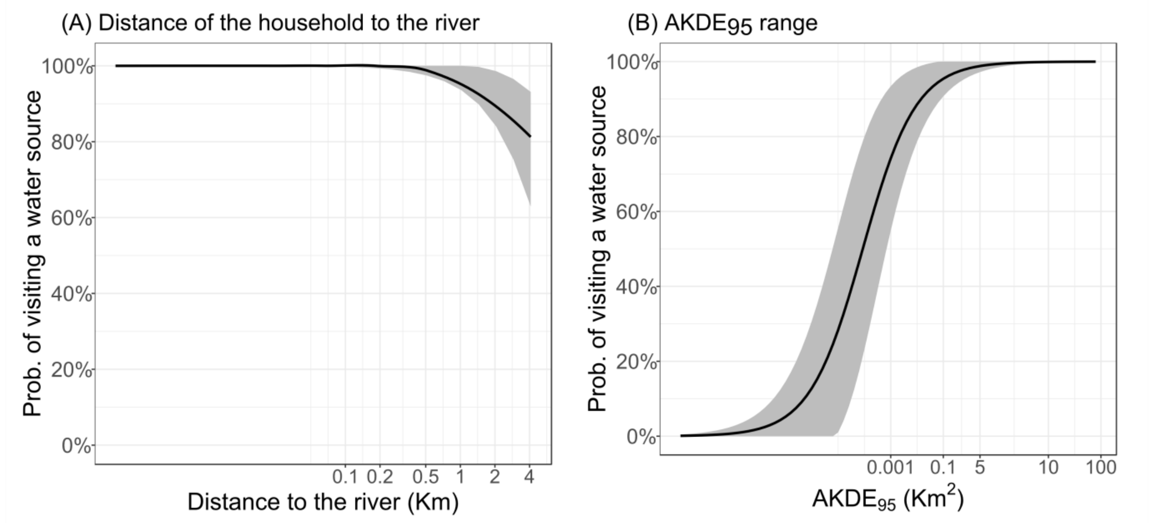

Figure 5.2. Predictors for whether or not free-ranging domestic dogs from rural villages in Chad had visited a natural water source. Predictions are from a general linear mixed model. Individuals were considered to have visited a water source if they had GPS fixes within 100 m of a water source. Plot A shows the predicted probability of individuals having visited a water source as the distance of their households from the Chari River increases. Plot B shows the predicted probability of having visited a water source at different $AKDE_{95}$ range sizes. In both plots the x-axis is on a log scale.

Unique water sources visited

From the dog's perspective, the number of unique natural water sources visited by dogs increased by a factor of 1.58 (1.45, 1.71) for each 10-fold increase in the dogs $AKDE_{95}$ range ($z = 11.05$; $p < 0.001$), and decreased by a factor of 0.92 (0.88, 0.95) for every doubling in the distance between their household and the river ($z = 4.84$; $p < 0.001$). The number of unique water sources visited increased by a factor of 2.04 (1.62, 2.58) for every 10-fold increase in the number of days the dogs were monitored.

From the perspective of the water sources, in all seasons, the number of unique dogs to have visited decreased with every doubling in their distance to a household with tracked dogs (dry: 0.74 (0.68, 0.81); $z = 6.93$; $p < 0.001$; wet: 0.71 (0.65, 0.76); $z = -9.14$; $p < 0.001$; cool: 0.71 (0.66, 0.77); $z = 8.50$; $p < 0.001$).

5.4.2 *Activity around water sources*

From the perspective of the dogs and for those that had visited a natural water source, the number of relocation points within 100 m of a water source reduced by a factor of 0.51 (0.47, 0.55) for every doubling in the distance between the dogs household from the river ($z = 16.67$; $p < 0.001$; Figure 5.3). The amount of time dogs spent around water sources increased by a factor of 1.63 (1.39, 1.92) with every 10-fold increase in their $AKDE_{95}$ range ($z = 6.00$; $p < 0.001$). There was also an effect of season (Figure 5.3), whereby in the cool season, the time that dogs spent around water sources decreased by a factor of 0.66 (0.48, 0.90) compared to that in the dry season ($z = 2.65$; $p = 0.008$), and by a factor of 0.74 (0.59, 0.93) compared to that in the wet season ($z = 2.59$; $p = 0.010$).

When only considering the activity of dogs around the river, the effect of the distance of the dog’s household to the river (0.54 (0.48, 0.60); $z = 10.43$; $p < 0.001$), the dog’s AKDE95 range (1.59 (1.34, 1.89); $z = 5.32$; $p < 0.001$) and number of days monitored (4.48 (3.19, 7.36); $z = 7.40$; $p < 0.001$) was unchanged. However, the effect of season showed that compared to the wet season, dog activity around the river decreased by a factor of 0.25 (0.16, 0.39) in the dry season ($z = 5.93$; $p < 0.001$) and by a factor of 0.16 (0.10, 0.24) in the cool season ($z = 8.48$; $p < 0.001$). Furthermore, the activity of dogs around the river was lower in the cool season than in the dry season, by a factor of 0.63 (0.44, 0.89; $z = 3.28$; $p = 0.001$). With the exception of season, the same effects were also found when only considering the activity of dogs around standing water (distance from the river: 0.73 (0.65, 0.81); $z = 5.81$; $p < 0.001$; $AKDE_{95}$

range: 1.38 (1.16, 1.65) z = 3.57; p < 0.001); days monitored: 3.75 (2.38, 5.90); z = 5.70; p < 0.001).

From the perspective of the water sources, when a water source was visited by dogs, the number of visits increased by a factor of 1.39 (1.19, 1.62) for every 10-fold increase in the water sources size in the dry season (z = 4.18; p < 0.001), and by a factor of 1.48 (1.21, 1.80) in the cool season (z = 4.18; p < 0.001). In all seasons, the number of dog visits received by a water source decreased with every doubling in their distance to a household with tracked dogs (dry: 0.45 (0.41, 0.50); z = -14.60; p < 0.001; wet: 0.42 (0.38, 0.47); z = 15.56; p < 0.001; cool: 0.44 (0.39, 0.50); z = -13.01; p < 0.001).

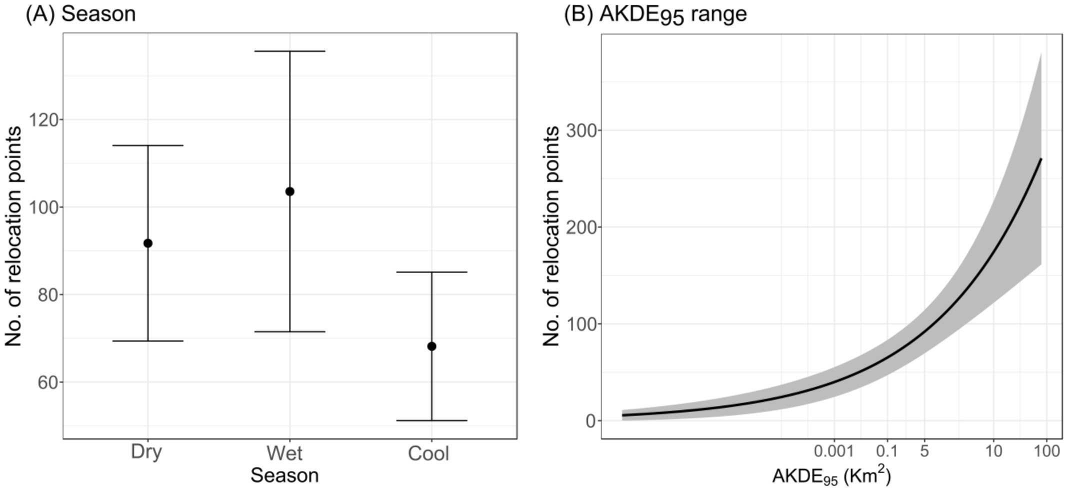

Figure 5.3. Sources of variation in the number of relocation points that free-ranging domestic dogs from rural villages in Chad had within 100 m of a water source. Predictions are from a general linear mixed model. Plot A shows the predicted number of relocation points that individuals would have around water sources in each season. Plot B shows the relationship between the dogs AKDE$_{95}$ range sizes and their predicted number of relocation points around water sources. In plot B the x-axis is on a log scale.

In all field seasons and at all field sites, only a few water sources accounted for 95% of dog visits, and these were all less than 0.5 km from a household with tracked dogs (Figure 5.4). In Sarh east, the river received the highest number of dog visits in all seasons, and in the dry season this was followed by standing water sources that originated from the river. During the wet season in Sarh east and all seasons in Sarh west, the river was the only water source to contribute towards 95% of the dog visits to water sources. In these instances, the shallow fitted lines for the relationship between the number of dog visits and the distance of water sources to the nearest household with tracked dogs, emphasises the small contribution that standing water sources had to the total count of dog visits. During all seasons in Guelendeng, the river was identified as one of the water sources contributing to 95% of dog visits to water sources, however, in the dry and cool seasons there were standing water sources originating from the river that received more visits than the river itself. During the wet season in Guelendeng, several standing water sources that were not associated with the river received a large number of dog visits, and this is in contrast to the other field sites, where such water sources never featured in those that contributed to 95% of dog visits. Finally, it is notable that the amount of dog activity at water sources in the southern field sites (Sarh west and east), is highest in the dry and cool seasons. In contrast, dog activity around water sources in the northern field site, Guelendeng, is highest in the wet season.

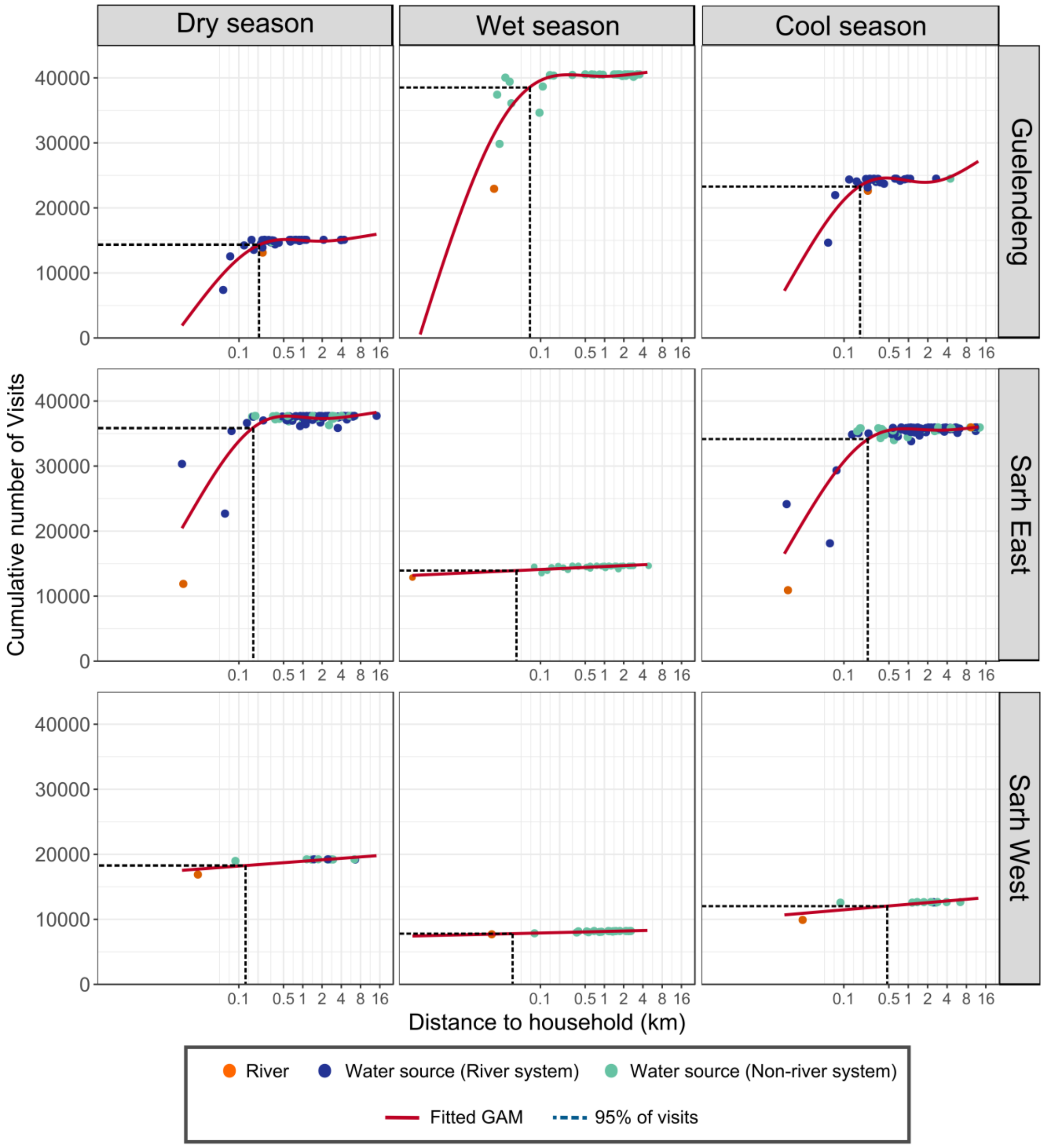

Figure 5.4. Relationships between the distance of water sources to households with tracked dogs and the number of visits from tracked dogs. The x axis is on a log scale.

5.5 DISCUSSION

The emergence of dog infections threatens the success of efforts to eradicate Guinea worm disease. We have characterised the activity of 298 free-ranging domestic dogs around water sources in rural Chad that may be potentially sources of worm infection. In so doing, we have shown that both dogs and water bodies are not equal in their exposure to potential sources of infection for Guinea worm. Across all three field sites and during each of three seasons, more than 85% of dogs had visited at least one natural water source. Dogs from households that were closer to the river and dogs with larger home ranges were consistently found to be more active around natural water sources. Furthermore, water bodies received more dog activity when they were larger and closer to a household with tracked dogs. It is striking, however, that in each season and field site, no more than four water sources accounted for 95% of dog visits, and these were all less than 0.5 km from a household with tracked dogs.

The temporal and spatial patterns of dog activity around water bodies in Chad, suggests there are seasonal and regional differences in the exposure of dogs to potential sources of Guinea worm infection. During the dry and cool seasons in the southern field sites, dog activity around water sources was higher than in the wet season and, in addition to the river, standing water bodies that were derived from the river received the majority of dog activity. This pattern of dog activity around water bodies follows that expected from what is known about the epidemiology of Guinea worm, with peak transmission in the dry season and water bodies associated with the river being the main sources of infection (Eberhard et al. 2014). In contrast, during the wet season in Guelendeng (the northern field site), the total activity of dogs around water sources was highest in the wet season. While in Guelendeng the river and a few of its associated water bodies received the majority of dog activity in the dry and cool seasons, the standing water bodies that appear in the wet season could provide an additional risk of infection if they are capable of acquiring and supporting copepod populations.

It is surprising that, regardless of the spatial or temporal context, the majority of dog activity around natural water sources was focused around no more than four water sources, and these were all less than 0.5 km from a household with tracked dogs. This finding makes the prospect of the targeted treatment of water bodies feasible. One strategy for the treatment of water sources might be to target or prioritise the water bodies receiving the highest dog activity during the time of peak transmission for Guinea worm, i.e. water bodies derived from the river and areas of the river that are within 0.5 km of a household with dogs, and during the dry season. In doing so, for the field sites studied here, only 28 (2%) of the identified standing water bodies would need treating. However, the river is clearly harder to treat due to its size and flow, which would quickly renew vector populations, and although chemical application is possible at known human entry points, those used by dogs may not be equally represented. While it is clear that some water sources should be prioritised for chemical treatment, it is currently not possible to detect the presence or prevalence of infected copepods in any water bodies. This means that, until a ‘pond-side’ test for the presence of Guinea worm in a water source is developed, a broader approach to targeting water sources is required, and targeting the treatment of water sources with the most dog activity would seem a reasonable means of prioritising use of resources.

While the predictors of dog activity at water bodies can be used as a measure of the dogs' exposure to potential sources of infection for Guinea worm, it is unclear if these predictors reflect the risk of infection. For instance, although larger water bodies received more dog activity in the dry season, it is not obvious how their size relates to their capacity to support copepod populations or the likelihood of them being infected with Guinea worm larvae. Similarly, it is not possible to determine if, or how often, dogs actually drank from the water bodies they are thought to have visited, or whether or not our measure of activity at water bodies is positively correlated with the probability of drinking from a water source. In addition, although 82% of water bodies with GPS coordinates were identified, the satellite imagery used to identify water bodies best reflected the cool season, and it is possible that the number of water bodies and their boundaries in the wet and dry season are not as accurately represented. However, this is not to say that there was a systematic bias in the detection of water sources, and so this is not expected to have a large impact on the results. The limitations in this study highlight the need for further investigation into the hydrology of the River Chari in relation to copepod ecology. Such studies would help to narrow down sites of potential infection and could be used to further inform targeted strategies for chemical treatment.

In the current absence of a test to diagnose the presence of infection in copepods in water bodies or in dogs, a basic understanding of the interaction between vectors and the worm's new, non-human animal hosts, is required to help guide the campaign to eradicate Guinea worm disease. This study has characterised one element of this system, and quantified variation in the exposure of dogs to natural water bodies in the worst affected areas of Chad.

This work highlights the potential for targeted control strategies to treat water bodies that receive a disproportionate amount of dog activity.

CHAPTER 6:
GENERAL DISCUSSION

6.1 BACKGROUND

Controlling and preventing epidemics of zoonotic diseases is of crucial importance for public health (Morens & Fauci, 2012). Free-ranging domestic dogs provide a reservoir for several pathogens that can infect humans (Bodimeade et al. 2019), and global efforts are being made to eliminate the risk that some dog-mediated diseases present to humans. These include the ‘Zero by 30’ rabies campaign (Jarvis, 2016) and the Guinea worm eradication project (Hopkins et al. 2018). However, there are some basic aspects of dog ecology that had not been well described, but which are fundamental to disease transmission and which could help design more informed disease management strategies. Specifically, the spatial-temporal heterogeneity in their contact rates was unknown and there was limited research on the dynamics of their spatial movements. In this thesis, I have provided a comprehensive account of spatial-temporal dynamics in both the contact rates and ranging behaviour of free-ranging domestic dogs in rural Chad; where dogs provide a reservoir for rabies and Guinea worm, and the risk of infection for both in humans is high. In this discussion, I will review the key findings of this thesis and, with particular reference to rabies and Guinea worm, I will discuss the implications that these findings have for the management of dog-mediated diseases.

6.2 KEY FINDINGS

Heterogeneity in the contact rates among individuals can strongly influence the dynamics of disease (May, 2006; Meyers 2007). In **Chapter 2,** I investigate this concept for free-ranging domestic dogs in two rural settlements in Chad. Despite it being evident that dogs are social animals (Bradshaw et al. 2009) and that contact rates are fundamental to disease transmission (May, 2006; Meyers, 2007), at the time of study there was no published literature describing a contact network for free-ranging dogs, and it is only recently that studies similar to the one presented here have emerged (Laager et al. 2018; Brookes et al. 2018). In describing the contact networks for dogs, I found that while there was variation in the contact rates of individuals, interactions were dominated by contacts of short duration, and that communities in the network were determined by household membership. I also found that, in one settlement, the individuals' second order contacts (eigenvector centrality) were positively correlated with their range size. Following this, I use agent-based models to simulate the transmission of a disease comparable in its characteristics to rabies through the observed contact network. I found that the position, within the contact network, of the individual first seeded with the disease, determined epidemic outcomes, whereby the risk of an epidemic occurring increased with the individual's ranked number of contacts (ranked degree), whereas the size of epidemics was positively related to the individual's ranked second order contacts. Through these results, I have highlighted that free-ranging domestic dogs have heterogeneous contact rates, and that individuals are not equal in their capacity to initiate disease epidemics or the size of epidemics they initiate. This led to my further investigation of the dynamics of contact rates, which I present in **Chapter 4**. The correlation between dog range size and the network position of individuals (relevant to disease transmission), suggested that targeted intervention strategies were feasible. However, a more in-depth understanding of the variation and drivers of space use is required, which I then addressed in **Chapter 3.**

The movement of individuals in time and space explicitly determines their interactions with others and their propensity to both transmit and acquire infections (Altizer et al. 2011; Dougherty et al. 2018). In **Chapter 3**, I explored temporal variation in the ranging behaviour of free-ranging dogs from six rural villages in Chad. Prior to this study, the temporal dynamics of dog ranging behaviour had only been extensively investigated in one population of community dogs in Northern Australia (Dürr et al. 2017; Maher et al. 2019). I used continuous time movement models to calculate home ranges and to describe the periodicity in the dogs' repeated space use and activity levels. I have shown that seasonality is an important source of variation in space use, with dogs having larger ranges in the dry season. Owner activity was also important, with dogs from hunting households having larger home ranges in the dry season than those from non-hunting households. These results demonstrate that there are considerable differences in the spatial movements of free-ranging dogs, and that, despite their free-ranging behaviours, some of this variation is mediated by the activities of their human owners. In **Chapter 2,** I showed that dogs with larger ranges have more second order contacts and a greater capacity to cause larger epidemics, should they become infected. My results in **Chapter 3,** suggest that targeted management strategies could be used at the household level to prioritise dogs with larger ranges (e.g. those from hunting households). Seasonal differences were found in the proportion of dogs that could be found around their household at different times of the day. In the dry season, over 70% of the population could be found around their household at all hours, except for dogs in two villages where less than 70% of individuals were around their household between 7am-11am. In the wet season, less than 70% of dogs were around their household between 8am-4pm, and this was consistent between villages. The ‘70% threshold’ is particularly relevant to dog vaccination campaigns against rabies, which require this level of population coverage to be successful (WHO, 2018), and my results highlight the variation in the access to dogs should interventions use a door-to-door strategy in rural Chad.

Dynamic patterns in the interactions between individuals can have implications for disease transmission and cause predictable pulses of disease incidence in time and space (Altizer et al. 2006; Silk et al. 2017; Meyer & Held, 2017). In **Chapter 4**, I conducted a thorough investigation into the spatial-temporal dynamics of contact rates between free-ranging dogs in six rural villages in Chad. Studies on where and when contacts occur between free-ranging domestic dogs are currently absent from the published literature, making this research a unique account of dog behaviour. I used high resolution proximity loggers to characterise the within-village contacts and a dyadic level analysis to describe the mixing patterns, probability of contact and the duration of contacts in time and space. I find that, similar to the results in **Chapter 2**, the probability of a contact occurring, the frequency of contact should two individuals have interacted, and the duration of contacts all decreased with increasing distance between the individuals’ households. Interactions around the household and village peaked between 5am-9am and again between 6pm-8pm, while contacts outside the village were not as common but peaked between 5am-8am. Contact durations followed a similar pattern, but a strong seasonal difference was found, whereby contacts outside the village were of longer duration in the dry season, and longer than both contacts in the village and household. I also found evidence for preferential mixing between the sexes that varied by season; male-male contacts had a higher probability of occurring in the wet season, and in the dry season, hourly contact probabilities were higher for male-male and male-female dyads, should they have interacted. While this study focused on contacts among dogs living in the same village (within-village contacts), between-village contacts were observed and found to be rare, but more common in the dry season where they tended to occur within the village. These results reveal clear temporal and spatial patterns in the contact behaviour of dogs that could have implications for the spread of disease.

Dogs have recently been identified as a significant reservoir for Guinea worm disease, and insight into their exposure to potential sources of infection is required to help inform the management practices of the global eradication campaign (Hopkins et al. 2018). In **Chapter 5**, I investigated the exposure of free-ranging domestic dogs in Chad to natural water sources; that are a potential source of Guinea worm infection. I found that, in all seasons, over 85% of dogs had visited at least one natural water source. Dogs spent less time around water sources in the cool season but, overall, dogs with larger ranges had higher activity levels around water sources. In addition, I showed that the majority of dog visits were to water sources that were within 0.5 km from a household with tracked dogs. My analysis provides an informed perspective on the variation in risk that different dogs and water sources have in facilitating the life cycle of Guinea worm. These results can be used to design control strategies with simple heuristics that enable prioritisation of dogs and water sources that present the greatest risk of transmitting/acquiring Guinea worm infection.

6.3 DOG ECOLOGY AND DOG-MEDIATED DISEASE TRANSMISSION

The contact rates and mixing patterns of individuals in a population are fundamental to our understanding of disease transmission and in informing our choice of control strategies (Anderson & May, 1992; Silk et al. 2019; McDonald et al. 2018). The explicit influence of an individual's spatial movements in determining their interactions with others makes the variation in individual space use another important consideration in disease ecology (Altizer et al. 2011). In this thesis, I have provided one of the first comprehensive descriptions of the dynamic social and spatial behaviour of free-ranging domestic dogs in rural Africa. I found that there were heterogeneities in several aspects of dog behaviour that are relevant for the dynamics of disease transmission.

6.3.1 *Contact heterogeneity*

In **Chapter 2**, I show that there is variation in the number of individuals that dogs interact with, and that substantial differences exist in the total duration of contacts that individuals had with others. These findings challenge models of dog-mediated diseases that have assumed homogenous mixing, and more broadly contribute to the growing literature that show social species do not mix randomly. The observed contact heterogeneities that I have presented here may, along with other processes such as high population turnover, help explain the failure of culling campaigns to reduce the incidence of disease in dogs (Windiyaningsih et al. 2004). The fact that some dogs interact with more individuals than others, suggests that there is the potential for 'super spreading events', where some individuals, 'super spreaders', contribute disproportionately to disease incidence and spread by causing unusually high numbers of new, secondary infections (Lloyd-Smith et al. 2005). Furthermore, variation in contact duration has particular importance for the transmission of communicable diseases that have low transmissibility, where individuals that have longer contact durations have an increased probability of transmitting a disease should they be infected (Smieszek, 2009).

In both **Chapter 2** and **Chapter 4**, the spatial distribution of the households with which dogs were affiliated determined interactions between individuals. This provides support for studies that, due to the absence of observed contact data, have used a spatial scaling parameter to determine contact rates when modelling disease in free-ranging domestic dog populations (Johnstone-Robertson et al. 2017). This spatial scaling of contacts seems appropriate at both the household and village level. However, my analysis in **Chapter 4** identified clear spatial-temporal patterns in the contact behaviour of dogs, and these patterns could result in seasonal variations in the duration and size of epidemics depending on when and where the disease is first introduced (Altizer et al. 2011; Reynolds et al. 2015). This may be further complicated by the evidence for preferential mixing between the sexes that varied seasonally (Nishiura et al. 2011). It would be beneficial for future studies to use simulations to determine which of these aspects of contact behaviour have the greatest impact on epidemic processes.

6.3.2 *Movement heterogeneity*

The spatial movements of individuals are inherently tied to the interactions they have with others (Altizer et al. 2011), and I demonstrate this in **Chapter 2**, whereby the ranges of dogs was positively associated with their second order contacts which was in turn related to their risk of causing larger simulated epidemics should they become infected. This inspired a more thorough investigation into the space use of dogs, and in **Chapter 3** I showed that dogs have larger ranges in the dry season, which may explain the findings in

Chapter 4 that indicate between-village contacts are more common in the dry season. The seasonal ranges of dogs clearly influence their interactions with others, and we might expect the incidence of communicable dog infections in rural Chad to peak in the dry season, when ranges are larger and contacts between villages are more likely. However, while periodic patterns of rabies and canine distemper have been described in dogs in Africa (Hampson et al. 2007; Viana et al. 2015), these are on the scale of 3-6 years, and a combination of factors may contribute to such patterns of disease incidence.

The spatial heterogeneity of dog space use described in this thesis helps illustrate the inherent link between an individual's movements and their interactions with others. Furthermore, these results suggest that identifying drivers in the variation of space use might help infer the epidemiological risks that different individuals present. This work also highlights that, despite being free-ranging, the owner's activity has a marked influence on dog movements and this should not be overlooked.

6.4 DOG ECOLOGY AND DOG-MEDIATED DISEASE MANAGEMENT

Several of the zoonotic diseases for which dogs provide a reservoir are classed as neglected tropical diseases and, as is the case for rabies and Guinea worm, these infections predominantly afflict people in regions that are resource limited (Bodimeade et al. 2019). Therefore, there is the need for control efforts to optimise operations to ensure that interventions successfully reduce disease incidence while also trying to alleviate the issue of limited resources. The results I report in this thesis can inform the management of dog-mediated diseases, and here I discuss how these findings might be applied to the efforts to control rabies and Guinea worm.

6.4.1 *Access to individuals*

Disease interventions often require access to individuals and, in the case of dog vaccination, a successful campaign requires 70% of the population to be accessed (WHO, 2018). It has been suggested that this can more reliably be achieved if campaigns are tailored to local contexts, and one consideration here is the local ecology of dogs (Fahrion et al. 2017). Furthermore, door-to-door methods are a reasonable strategy used in vaccination campaigns (Kaare et al. 2009; Gibson et al. 2016), but access to dogs requires them to be at their household. In **Chapter 3**, I found that, compared to in the wet season, 70% of dogs in rural Chadian villages were more likely to be around their households at all hours of the day in the dry season. These results suggest that there are seasonal and daily variations in the accessibility of free-ranging domestic dogs, and in Chad, door-to-door campaigns would be best conducted in the dry season. Furthermore, they give credence to the use of local dog ecology in tailoring interventions and optimising field operations. These temporal patterns of dog accessibility are unlikely to be the same for other free-ranging domestic dog populations around the world and in different contexts (e.g. urban populations). Therefore, field operations would benefit from studies into the temporal patterns of free-ranging domestic dog space use, as this knowledge provides the opportunities to improve the success of interventions that require direct access to individuals.

6.4.2 *Targeted control strategies*

Characterising the heterogeneities in the social and spatial behaviour of individuals can identify those that might present higher epidemiological risks should they become infected (Lloyd-Smith et al. 2005). The benefit of targeted strategies was recently demonstrated using simulated epidemics on a contact network for urban free-ranging domestic dogs in Chad (Laager et al. 2018). The findings of this study showed that targeting individuals based on their movement or position in the network substantially increased the impact of vaccination on epidemic outcomes. However, the feasibility of targeted management strategies requires that target individuals are readily identifiable through a common trait. In **Chapter 3**, I find that dogs from a hunting household have larger ranges in the dry season than dogs from non-hunting households. The positive relationship between range size and both contact behaviour (**Chapter 2 & Chapter 4**) and exposure to environmental sources of infection (**Chapter 5**), suggests hunting households may present an identifiable trait for which interventions might target or prioritise. However, for this to be realised several studies would be required to determine if dogs from hunting households actually present higher epidemiological risks (be it Guinea worm or rabies infection), and whether targeting control efforts in this context would improve the impact of vaccination campaigns. Furthermore, in rural Chad there are several other human related activities that could influence dog movements and which should be investigated e.g. cattle herding, fishing and farming small holdings. Nevertheless, these results highlight the potential for using local dog ecology to inform targeted disease management strategies.

The life cycle of Guinea worm (Greenaway, 2004) means that in rural Chad, the disease can be transmitted both from free-ranging domestic dogs to a water source and from a water source to dogs. However, one of the primary control measures is to chemically treat natural water sources that potentially harbour infected vectors (copepods). In **Chapter 5**, I described both the exposure of dogs in Chad to water sources and the exposure of water sources to dogs. I found that water sources that receive the highest exposure to dogs were all within 0.5 km of a household with tracked dogs. This provides an informed option for the targeted treatment of water sources and, for the eradication program, this could be particularly useful given that the treatment of water sources is resource intensive and the hydrological system in Chad is vast and complex, making it impractical to treat all water bodies. These results highlight how the ecology of dogs can be used to not only identify individuals that might disproportionately contribute to epidemics, but also identify environmental sources of infection that present greater epidemiological risks.

6.5 SOCIO-ECOLOGICAL CONTEXTS

Throughout this thesis I find evidence of anthropogenic influences on dog contact rates and movements, whether it be through the distribution of households or the activity of owners. Dogs exist in a wide range of socio-ecological contexts, from companion animals the movements of which are restrained, to feral animals with loose, if any, connections to humans, and fully wild populations. This thesis focuses on a specific area of this spectrum; free-ranging domestic dogs in a rural African context. It should be expected that this anthropogenic influence on dog ecology will show considerable global variation, and that this could also vary substantially on the local scale if there is high cultural diversity among humans. However, investigations into the anthropogenic influences on dog ecology could provide an insight into drivers of dog-mediated disease transmission and simple meausres that can optimise control efforts.

6.6 CONCLUSION

Preventing outbreaks of infectious disease is a key concern for public health, the health of livestock and that of wildlife. Domestic animals, particularly those that are free-ranging, provide a reservoir for zoonotic diseases. Free-ranging domestic dogs share several pathogens with humans and are currently the focus of two major public health programmes; the ‘Zero by 30’ strategic plan to eliminate dog-mediated rabies and the Guinea worm eradication programme. In this thesis, I provide a comprehensive investigation into the dynamics of the social and spatial behaviour of free-ranging domestic dogs in rural Chad. These insights have identified key seasonal and daily patterns in the contact behaviour and space use of individuals, shown that individuals are not equal in the risks they pose to disease transmission, related the influence of anthropogenic activity on space use, and highlighted the potential for targeted disease management strategies that are tailored to the local socio-ecological context. Overall, it is evident that studies of domestic dog ecology can contribute to a ‘One Health’ approach to tackling dog-mediated diseases.

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APPENDIX A

Ecology of domestic dogs *Canis familiaris* as a host for Guinea worm *Dracunculus medinensis* infection in Ethiopia

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Abstract

A programme for the global eradication of Guinea worm disease, caused by the parasitic nematode *Dracunculus medinensis*, has made substantial progress over the last three decades. However, the recent discovery of Guinea worm infections in populations of domestic dogs presents a major obstacle for the eradication programme. Dog infections have mainly been found in Chad, Mali and Ethiopia, where infections are apparently limited to parts of the Gambella region of western Ethiopia. Little is known about the epidemiology of the disease in non-human animals. While humans classically acquired Guinea worm infection by drinking water containing infected copepods, it has been hypothesised that dogs might additionally or alternatively acquire the infection via a novel pathway, such as the consumption of uncooked fish or frogs, as possible paratenic hosts, or which are functioning as transport hosts.

We characterised the ecology of free-ranging dog populations from three villages in Gog woreda, Gambella region, Ethiopia. We analysed their exposure to potential sources of Guinea worm infection, and investigated risk factors associated with the dogs' history of infection. The home ranges of 125 dogs and their activity around natural water sources were estimated using GPS tracking, and the diet of 119 dogs was described using stable isotope analysis. Owner questionnaires were carried out to describe dog husbandry and household characteristics, while the locations and features of natural water sources were determined through local knowledge and by searching high-resolution satellite imagery.

There were no clear correlates of past Guinea worm infection in dogs, other than that owners had apparently increased the frequency of the provision of clean water in response to previous infections and a marginal effect of increasing exposure risk with dog age. There was no effect of consumption of aquatic vertebrates (fish or frogs) on infection history and we found no evidence to support this hypothesised, novel transmission pathway. Variations in dog ranging behaviour, owner behaviour and the distribution and characteristics of natural water sources all influenced the exposure of dogs to potentially infectious water bodies. This initial study suggests that the classical transmission pathway should be the main focus of attention in future studies of Guinea worm infection in dogs in Ethiopia and in developing appropriate local control measures.

Introduction

Guinea worm disease is caused by the parasitic nematode *Dracunculus medinensis* and has historically infected humans across Asia and Africa [1]. Since the 1980s, global eradication efforts have reduced human cases from approximately 3.5 million per year to only 28 human cases in 2018 [2]. However, a significant number of infections in non-human animals have been detected in 3 of the 4 remaining endemic countries, with infections found in Chad, Ethiopia and Mali but none in South Sudan [3]. In 2018, infections were confirmed in 1069 domestic dogs *Canis familiaris*, 32 domestic cats *Felis catus* and 1 olive baboon *Papio anubis* [2]. These non-human infections, along with insecurity in the remaining endemic areas, present major obstacles for the eradication programme [4].

Recent evidence shows that emergent worms from human and non-human hosts are genetically indistinguishable [5]. Given the low numbers of human cases, this suggests that Guinea worm disease in humans is now effectively a zoonotic infection that is sustained by reservoir(s) in non-human animals. Therefore, even in the near-absence of human cases, non-human hosts are maintaining Guinea worm in the environment, resulting in an ongoing low-level of infection in humans. The existence of a non-human reservoir could, in addition to the challenges of surveillance, explain the apparent re-emergence of the disease in Chad, where no human cases were reported for 10 years prior to 2010 [6]. To prevent the re-emergence of Guinea worm after its elimination in humans and for eradication to be completed, transmission must be interrupted in non-human hosts. However, little is known about the epidemiology of Guinea worm in any of its non-human hosts.

The transmission cycle of Guinea worm starts after a 10-14 month incubation period when a female worm emerges from its host and releases larvae into a water body [7]. Here the larvae are ingested by intermediate hosts (copepods) where they develop into stage 3 larvae. Classically, transmission to humans is through the consumption of drinking water containing infected copepods [7]. It has recently been hypothesised that a novel pathway might also contribute to ongoing infections of humans and, to a greater extent, non-human animals. This hypothesised pathway requires the ingestion of tissue from a paratenic or transport host such as fish or frogs that have themselves eaten an infected copepod [8,9]. Human cases have been reduced by applying a number of methods, including: the detection and isolation of cases, chemical treatment of water bodies to remove copepods (using organophosphate temephos, Abate), encouraging the filtration of drinking water [10] and thoroughly cooking fish or discarding fish entrails [8]. These control strategies are much harder to implement for free-ranging animals and, although some of these measures are being applied to control dog infections, infections in dogs persist. Thus, to prioritise control efforts, a better insight into the ecology of non-human animal hosts, particularly dogs, in relation to Guinea worm infection is required.

Detected cases in dogs are found along major river systems in Chad and Mali, where they are spatially distributed in riverine and wetland habitats associated with the Chari [11] and Niger [12] rivers, respectively. In contrast, cases in Ethiopia are not concentrated along a major water source and are instead localised to a cluster of villages [13] in an area dominated by forest and smallholdings [14]. The different ecology of the affected area in Ethiopia compared to that in Chad and Mali has raised questions on the similarity of risk factors for transmission in non-human hosts [3]. This study aimed to outline the ecology of dogs in this part of Ethiopia and to identify potential risk factors associated with dog infections. Both the classical and novel transmission pathways for Guinea worm infection in humans are used to inform *a priori* hypotheses. Specifically, the study investigated dog husbandry, access to natural water sources and consumption of aquatic foods as potential correlates of previous worm infections.

Methods

Fieldwork was conducted in the Gog woreda of Gambella region in western Ethiopia, between 28th April and 15th May 2018. A total of 129 dogs, 98.5% of the resident adult population, were studied across three settlements; Ablen, Atheti and Wichini (centered on 7°37'19.7"N 34°23'25.9"E; Figure 1). For each household that owned dogs we recorded its location using a handheld GPS (Garmin Map 64S), and a questionnaire was used to gather information on whether the household members went hunting, the frequency of water provision for dogs (1-3 times a day and > 3 times a day), what they fed their dogs and the number of dogs in the household. For each dog we recorded its sex, age in months (as recalled by the owner), body condition score (BCS; score between 1 (emaciated) and 9 (obese)) [15] and whether the dog had ever had Guinea worm. BCS was binned into categories of poor (<= 2), moderate (3) and good (>= 4).

Dog space use

Dogs were collared for up to 14 days with off the shelf dog collars (Ancol Heritage), which were fitted with an i-GotU GT-600 GPS unit (Mobile Action Technology Inc., Taiwan). The GPS was configured with a fix interval of 10 minutes. GPS data was cleaned by removing locations taken 12 hours after collar deployment and 12 hours before collar recovery. Any likely erroneous GPS fixes with speeds greater than 20 km/hr between locations were removed. GPS data were projected into the relevant coordinate reference system for Ethiopia (EPSG: 32636) using the ‘sp’ and ‘rgdal’ packages (v1.3.1 & v1.3.3 respectively).

The dogs' home and core ranges were calculated using auto-correlated kernel density estimates (AKDE) from continuous time movement models. Models were fit using the 'ctmm' package (v0.5.5) following procedures set out by Calabrese et al (2016) [16]. Variograms were used to check the autocorrelation structure of each individual's movement data. Individuals were excluded from home range analyses if there was no asymptote in the variogram, suggesting the individual had not been monitored for long enough, or was exhibiting non-range resident behaviours, e.g. range expansion or dispersal. Movement models were fit using maximum likelihood and model selection was determined on the basis of Akaike information criteria (AIC). Once the models were selected, the 95% AKDE ($AKDE_{95}$) and core AKDE ($AKDE_{core}$) were calculated. To calculate the core range, for each individual an exponential regression was used to identify the isopleth where the estimated home range area begins to increase more rapidly than the relative frequency of use (slope = 1) [17]. To estimate the probability of finding each dog around their respective household, the number of relocation points within a 50 m radius of the household's location was divided by the total number of relocation points. In addition, the same was done for relocation points within 100 m of any household with tracked dogs, and this was used to estimate the probability of finding the dogs around the village.

DigitalGlobe satellite imagery of the field site was obtained for October 2018; red, green, blue and near infra-red bands from WorldView-3 & WorldView-2 satellites. Natural water sources were identified and vectorised using the QGIS platform by manually searching a 1365 km^2 area centred on the villages of interest. To ground truth the location of vectorised water bodies, GPS locations of water sources around villages were taken in the field. For each dog, we determined the number of relocation points within 100 m of a natural water source and water pumps, the number of separate visits to water sources (defined by an interval of 30 minutes between fixes) and the number of unique water sources visited. For each water source, we measured: area; distance to the nearest household with tracked dogs; whether it had been visited by a dog across the monitoring period; the number of unique dogs that had visited; the number of relocation points within 100 m of the water source for all dogs and for those dogs with a history of Guinea worm infection.

Variation in the size of the dogs' ranges was analysed using linear models (LMs). Only $AKDE_{95}$ was considered for analysis as it was highly correlated with $AKDE_{core}$ (rho = 0.99; $p < 0.01$). $AKDE_{95}$ was log-transformed to normalise its distribution and explanatory variables included village, sex, age, body condition, whether the dog was from a hunting household, frequency of water provision, number of days monitored and the distance of the nearest water pump and natural water source to the household.

Variation in the activity of dogs around natural water sources was analysed using general linear models (GLMs). The first model used a binomial error structure and considered whether or not dogs had visited a water source or not. Explanatory variables included village, sex, age, body condition, $AKDE_{95}$, whether the dog was from a hunting household, frequency of water provision, days monitored and the distance of the nearest natural water source and nearest pump to the household. Two additional models, with negative binomial error structures, were used to investigate activity around water for those individuals that visited water bodies. The response variables for these models were the number of relocation points around water bodies and the number of unique water bodies visited. Explanatory variables were the same as in the previous model, only the number of days for which a dog had been monitored was log-transformed and included as an offset.

To investigate predictors of whether or not a water source was visited by dogs, a binomial GLM was conducted. Explanatory variables included the logged$_{(\text{base }2)}$ area of the water source and the logged$_{(\text{base }2)}$ distance of the water source to the nearest known household with dogs. To identify predictors of the variation in dog activity around water sources for those visited by dogs, a negative binomial GLM was conducted. The number of relocation points around the water source was used as the response variable and the explanatory variables were the same as that in the previous model. A generalised additive model (GAM) was used to relate the cumulative total of dog visits per water source to the log-transformed distance of the water sources from a household with tracked dogs. The cumulative count of visits was made after ordering the water sources by number of visits in ascending order.

Dog diet

To identify principal food items, owners were asked (i) What they feed their dogs? (ii) What did they feed their dogs yesterday? and (iii) What they have seen other people’s dogs eating? Where possible samples of principal food items were sampled from the households and were otherwise sourced from the market in the nearby town of Pugnido (Gog) or opportunistically from local hunters and fishermen. On the day of collection, samples were dried and stored in ambient conditions. Items were sterilised in a sterlising oven for 6 hours at 140°C before, and in an autoclave, after importation. Prior to analysis, samples were freeze-dried and homogenised, and approximately 0.7 mg (± 0.1 mg) was weighed into a tin cup. For nitrogen depleted plant samples, 10 mg (± 0.1 mg) was weighed out and analysed in order to produce enough nitrogen for accurate isotopic characterisation.

For each dog, one whisker was plucked during collar collection. The whiskers were rinsed in distilled water, scraped to remove surface contaminants, sterilised and dried for 24 hours. They were then cut into 0.4 - 0.8 mg sections and sealed in a tin cup for analysis. To conduct stable isotope analyses of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), samples were analysed in a Sercon 2020 elemental analyser isotope ratio mass spectrometer. Stable isotope ratios are expressed as δ values in ‰, the ratio of heavy to light isotope relative to the isotopic ratios of an international standard for each element: the Vienna Pee Dee Belemnite (VPBD) for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$. Estimated mean precision between sample runs was ± 0.10‰ (± 0.01) for $\delta^{15}N$ and 0.08‰ (± 0.01) for $\delta^{13}C$, based on standards run within sample batches. A lipid-normalisation model was applied to $\delta^{13}C$ values of samples with a high lipid content [18, 19].

Relative contributions of food sources to dog diets was estimated using the ‘SIMMR’ package (v.0.3) [20] and isotope ratios were averaged across all whisker sections for each dog. This was done initially to estimate the diets of the whole dog population, and then to estimate the diets of individual dogs. Models were run for 1,000,000 iterations, with a burn-in of 50000 and thinning rate of 50. Gelman diagnostics were used to check model convergence. The ‘SIDER’ package v 1.0.0 [21] was used to generate trophic discrimination factors for dogs for $\delta^{15}N$ (3.68‰ SD 1·36) and $\delta^{13}C$ (2.82‰ SD 1·78), based on their diet type and phylogenetic position. Since dogs are omnivores, concentration dependence values (mean N/C) were added to the model [22].

Guinea worm infection

Field records of owner-reported Guinea worm histories were cross-checked with records of emergent adult worms from Ethiopian Dracunculiasis Eradication Program (EDEP). There was agreement in all but three records: Two owner-reported cases were not in the EDEP database, and for these the owner-reported records were used as they could represent undetected cases. The third discrepancy was a case recorded by the EDEP that was missing in the owner-reported records. To resolve this, we included the EDEP Guinea worm record as they are based on the collection of an emergent worm. Any EDEP records of emergent worms within 14 months post-fieldwork were also included, as transmission may have occurred at the time of the study.

A GLM with a binomial error structure was used to explore the correlates of individual level factors with the dogs' history of infection. Explanatory variables included sex, age, BCS, proportion of fish in the diet, $AKDE_{95}$, number of relocation points within 100 m of a water body, water provision, village and whether the dog was from a hunting household. A staged analysis was conducted in order to maximise sample size. The model was run first for all predictors (requiring the removal of data for individuals with missing data). All variables that appeared in at least 50% of top models for any of the three sets of Guinea worm infection records (EDEP, owner-reported, and finalised records) in this initial analysis, were then included in the final model. This ensures that any potentially important explanatory variables were retained for further analysis.

To identify traits of water sources that might be more likely to be visited by dogs with a history of Guinea worm infection, a binomial GLM was conducted.

Explanatory variables included the logged area of the water source and the logged distance of the water source to the nearest known household with dogs. A GLM with a Poisson distribution and offset for total number of visits was used to identify predictors for the variation in the activity of dogs with a history of Guinea worm around water sources. The number of relocation points within 100 m of the water source was used as the response variable and the explanatory variables were the same as in the previous model.

An information theoretic approach was used for model selection in all LMs and GLMs, using ranked comparison of corrected AIC (AICc) values. The top model set was selected using a difference in AIC (DAIC) of <2 from the top model, and model averaging was conducted over the top model set [23]. Results are expressed as full model-averaged coefficients for specific explanatory variables, often translated onto an interpretable scale, and 95% confidence intervals. For binomial epidemiological models, results are expressed as the odds of having had Guinea worm and as relative risks, with 95% confidence intervals from bootstrapping 10,000 times with replacement. Correlations between explanatory variables were investigated prior to analyses using Spearman's rank correlation tests, and correlated variables were precluded from appearing in the same models. In all models, village identity and distance from natural water sources were highly covariable and so were precluded from appearing together in models. Analyses were undertaken in R version 3.4.2 [24] and Quantum Geographic Information System (v2.18.1). 'lme4' (v1.1-12) was used to conduct GLMMs, 'MuMIn' (v1.15.6) for model selection and 'mgcv' (v1.8.12) for GAMs.

Results

Ranging behaviour

Collars were deployed on 131 dogs from 47 households (Table A1). Of these, 125 individuals were identified as range-resident. The mean number of days that dogs were tracked was 10 days, with a minimum observation period of 3 days and a maximum of 13 days. The median $AKDE_{95}$ for all dogs was 0.10 km^2 and 0.02 km^2 for the dogs $AKDE_{core}$ (Table A2). The median proportion of time that dogs spent around their household was 77 % (inter-quartile range: 61 – 89 %).

Range size was larger in older dogs (26.6% larger for every year older; 4.0 - 54.2 95% Confidence Intervals). Range sizes did not differ between villages. The sex, health, and whether the dog was from a hunting household or one that provided more water did not affect range size.

Activity around natural water sources

A total of 359 water bodies were identified. Of the water bodies with known GPS locations 60 of 99 (61%) were detected in the satellite imagery. Households with tracked dogs were a median of 406 m (312 – 513 m; Table A2) from the nearest natural water source. Of all the water bodies identified, 50 (14%) were visited by dogs during the study. The visited water bodies were a median of 742 m (43 – 230 m) from a household with tracked dogs and had a median area size of 225 m^2 (43 - 230 m^2). 27 water bodies accounted for 95% of all dog visits and these were all less than 1.5 km from a household with tracked dogs (Figure A2).

Natural water sources that were closer to a household were more likely to be visited by dogs than those at greater distances (Odds ratio of 0.20 (0.13, 0.32) as distance from a household doubles). Of the water bodies that were visited by dogs, those further from households experienced less dog activity (time spent by water bodies roughly halved (0.58 (0.39, 0.84)) each time distance from households doubles), while smaller water sources experienced more dog activity (0.73 (0.60, 0.91) of the activity time as size doubles).

Dogs in Atheti were more likely to have visited a natural water source than dogs in Ablen (Odds ratio of 13 (3.1, 55)). Dogs with larger ranges were more likely to have visited a water body (Odds ratio of 48 (6, 373); Figure A3), and dogs from a hunting household were less likely to have visited a water body (Odds ratio 0.13 (0.03, 0.62)).

Of those dogs that had visited a natural water source, dogs in poor health spent less time (proportionally 0.55 (0.38, 0.81) of GPS fixes) around water bodies than dogs in good health. Dogs in different villages spent different amounts of time near natural water sources. Those in settlements nearer natural water source systems spent more time near water bodies: dogs were predicted to have 7.6 (4.4, 13.2) and 2.8 (1.5, 5.2) times more fixes near water bodies in Atheti and Wichini respectively, compared to Ablen. All households reported providing water for dogs on at least a daily basis, but dogs from households that provided water more frequently (>4 times a day) spent less time near standing water (proportionally 0.65 (0.47, 0.90) of GPS fixes; Figure A3) than those dogs provided water 1-3 times a day.

There were only significant differences in the number of unique water bodies dogs had visited between different villages, with dogs in Atheti and Wichini visiting more water bodies than dogs in Ablen: 4.24 (2.70, 6.66) and 3.57 (2.24, 5.70) times the number of water bodies respectively.

Dog diet

Dog owners reported that they had either fed or had seen their dogs eat a range of items from maize, wild meat, livestock, vegetables and grain foods. Maize or a maize-based porridge were the most frequently reported items (47 out of 48 respondents), the next most commonly reported items were C3 plant foods (cabbage, beans, squash, rice and papaya; 17 respondents) and livestock meat (beef, goat and pork; 11 respondents). These were followed by wild meat (Olive baboon, wild bovid (antelope) species, rats, frogs, lion and unspecified; 8 respondents) and fish (4 respondents). Most people reported that they didn’t know what dogs from other households ate (27 respondents), or that they ate maize (13 respondents), with a range of other items which were only singly identified. Only 3 respondents reported that their own or others’ dogs ate faeces.

Owner reports of principal dietary items of dogs together with previous studies of dog diets in Chad [25] determined the initial collection of putative food sources. Once isotopically compared, these food items were formed into six groups: C3 plants, C4 plants, livestock, terrestrial wild food, aquatic wild food (comprising fish and frogs) and human faeces (Figure A4; Table A3).

Whiskers of 119 dogs were analysed, and their dietary composition estimated. Based on an estimate of dog whisker growth rate of 0.42 mm per day [25], these whiskers represented dog diets over a timespan of a little over 3 months (98 days; SD 21 days).

Isotopic analysis of dog whiskers and food sources correspond with owner-reported dog dietary composition; the majority of the diet of the dog population was composed of C4 plant sources (62%; 59 - 66 95% Credible Intervals). This was followed by faeces (17%; 11 - 22) and livestock meat (11%; 8 - 14) making up between 10-20% of the diet, then wild foods (aquatic: 2.6%; 1 - 4.3; terrestrial: 3.7%; 1.5 - 6.1) and C3 plants (4.2%; 1.1 - 8.3), each constituting <10% of the dogs' diets (Figure A4).

Correlates of Guinea worm infection

In initial models of the risk factors in predicting the history of Guinea worm infection, the age of a dog, its village, the frequency of water provision and the number of relocation points near water bodies, all appeared in at least 50% of one of the top model sets, and so were retained for further analysis. The proportion of aquatic food in the diet of dogs appeared in a proportion of 0.06, 0.17 and 0.24 of the respective top model sets for the three Guinea worm record datasets. Older dogs had higher chances of having had Guinea worm (Relative risk (RR) of 1.02 (0.99, 1.05) with each additional month of age), although this effect was marginal. Dogs which were reported to be provided water at least 4 times a day had a higher chance of having had Guinea worm than those provided with water, but less frequently (RR of 4.38 (1.6, 48.4); Figure A5).

Of the natural water sources which were visited by dogs over the course of the study, a water body was less likely to have been visited by a dog with a history of Guinea worm if it was further away from households (Odds ratio: 0.23 (0.08, 0.50) as distance doubles), and dogs with a history of Guinea worm spent more time around larger water bodies, compared to the general dog population (dogs with a Guinea worm history were located proportionally 1.22 (1.12, 1.33) more times around natural water sources as the area size doubled).

Discussion

We have provided a detailed account of the ranging behaviour and diets of free-ranging domestic dogs in rural Ethiopia, with the aim of understanding the potential pathways of Guinea worm infection in dogs, and therefore potential ways in which transmission might be interrupted. In this initial, short-term study in this disease system in Ethiopia, we found no evidence to support the hypothesised novel transmission pathway involving paratenic or transport hosts [8,9]; there was a general lack of dietary variation across the dog population and the contribution of aquatic foods (frogs and fish) to dog diets was small and uncorrelated with infection history. This is not to say that any putative novel transmission pathway, via paratenic or transport hosts, is not salient in this system, but suggests that either transmission via such hosts is not a major pathway, or that it is confined to very rare events and/or consumption of very low mass items that do not contribute significantly to dog diets. This is in contrast to Chad, where evidence suggests that dog infections are related to variations in the proportion of fish in their diet, over the range of about 10-20% [25].

We found that variations in dog body condition, dog husbandry and the range size of dogs were related to their exposure to potentially contaminated standing water bodies. These results identify factors affecting exposure to water sources and might be used to frame further investigations and measures in mitigation of potential risks of dogs in rural Ethiopia acquiring Guinea worm infection through the classical transmission pathway [7]. Management efforts in both Ethiopia and Chad, where studies of dog ecology in relation to Guinea worm infection have now been conducted, need to be tailored to the ecology of the affected areas and, in Ethiopia, there is more support for links between the classical transmission pathway and dog infections.

The positive effect of dog age on history of infection is a simple function of the duration of exposure. While this effect is intuitive, reflecting the fact that older dogs have had longer to acquire an infection, due to the relative infrequency of infection, this effect was marginal. It was also the case that older dogs had larger home ranges, which was associated with a greater probability of having visited a natural water body. Therefore, the increased ranges of older dogs could lead to increased exposure risk. Overall, dogs in these villages had small home ranges and the majority of their time was spent around the village. Although seasonal differences in ranging behaviour is expected [26], the ranges in this study are representative of dog movements at the start of the Guinea worm transmission season and when infection is thought most likely to occur [12].

Against a background of near universal provision of pumped groundwater to dogs, we identified an increase in the likelihood of a history of infection with respect to increasing frequency of water provision. This is counterintuitive, given that increased water provision might be expected to reduce the risk of infection, as dogs would be less reliant on potentially contaminated natural sources of water. The water provided to dogs comes from groundwater (aquifers) that cannot, at the time of collection, be contaminated with copepods or larvae. One possible explanation for the current result is that households reporting their current practice of providing water more frequently were doing so in response to owning a dog that had previously had an emergent worm. The Guinea worm eradication campaign has clearly had some success in educating rural communities in this region of Ethiopia on how to reduce risks of infection. Therefore, it is reasonable that the owners would respond to having had an infected dog by ensuring that clean water is readily available, thereby reducing the chance of reinfection. This response seems appropriate given that dogs provided with water more frequently were also found to spend less time around standing water bodies.

The distance of natural water sources from households was an important correlate of variation in the amount of dog activity they experienced, much of which is explained by the different locations of villages in relation to areas with the greatest concentration of water bodies. Water bodies closer to a household with dogs were both more likely to be visited by a dog, and a dog with a history of Guinea worm. Both the general dog population and infected dogs spent more time around natural water sources that were closer to households, however the wider dog population more frequently visited smaller water bodies, while dogs with Guinea worm spent proportionally more time around larger water bodies. This correlation with infection history could be due to the fact that larger water bodies will persist for longer during dry periods, and therefore have a greater potential to support copepod populations that could be infected with Guinea worm. From a management perspective, this knowledge of how dogs interact with water bodies can help tailor strategies for the control of copepod populations, initially targeting efforts towards systematic treatment of those with the most dog ‘traffic’. In this case, water sources within 1.5km of a household with dogs accounted for the overwhelming majority of interactions between dogs and natural water sources. In our use of satellite imagery to identify water sources, there was some difficulty in detecting small ephemeral water bodies which were identified in the GPS survey. While this may not substantially affect results, as it appears that larger water bodies are used most by dogs with a history of Guinea worm infection, improved detection rates might be achieved through the use of additional spectral bandwidths and/or machine learning techniques.

This study occurred during the onset of the rainy season in Gambella region [27], which corresponds to the beginning of the Guinea worm transmission season [12], thus the observed behaviour and diet of the dogs is reflective of the period in which infection likely occurs. However, if dog behaviour changes later in the season, different emphasis might be placed on alternative transmission pathways. It is also worth noting that, due to the current lack of a pre-patent diagnostic test, Guinea worm infections are only detected through the emergence of an adult worm, meaning individuals will be overlooked if they were exposed but did not successfully facilitate the completion of the parasite’s life cycle. In addition, the eradication program requires the containment of every case and, although necessary, this prevents the characterisation of dog behaviour during, or shortly after, worm emergence, which would explicitly identify the water bodies that are at greater risk of becoming sources of infection.

This study has identified correlates for the history of Guinea worm disease in free-ranging dogs in rural Ethiopia. It was found that dog owners may be responding to dog infections by taking positive measures to prevent further reinfection by providing clean drinking water for dogs. The provision of clean water, as well as improved body condition, in turn reduces the time dogs spend at natural water bodies. These findings suggest that there are multiple elements of owner behaviour, dog ranging behaviour and the characteristics of natural water sources which can influence potential exposure through the classical pathway of transmission (drinking contaminated water), and these can be targeted for more effective disease control.

Figures & tables

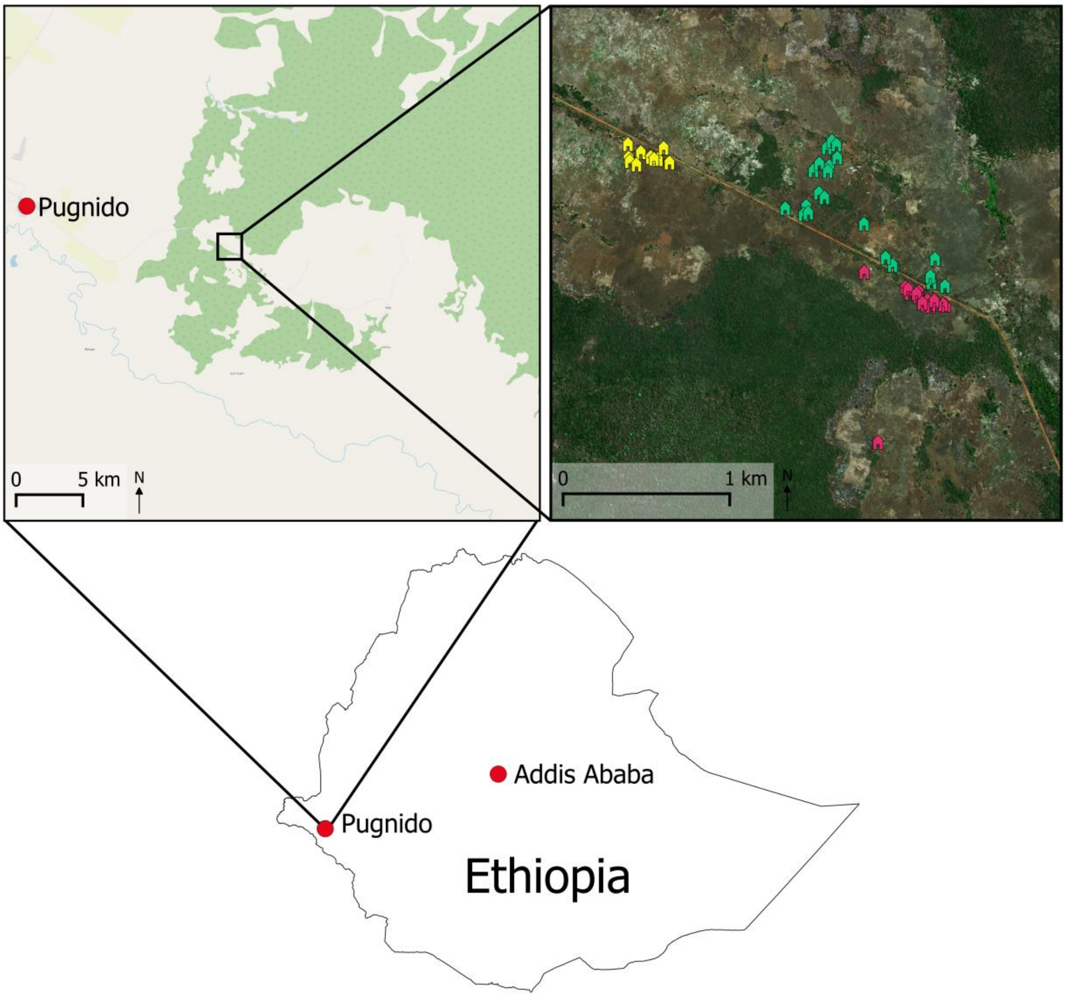

Figure A1: Locations of villages and households in which dogs were collared. The house symbols represent households from Ablen (yellow), Atheti (green) and Wichini (red) that dogs that were tracked. The maps include the base map from OpenStreetMap (https://www.openstreetmap.org) and the satellite image was generated using the ESRI world imagery basemap (sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community).

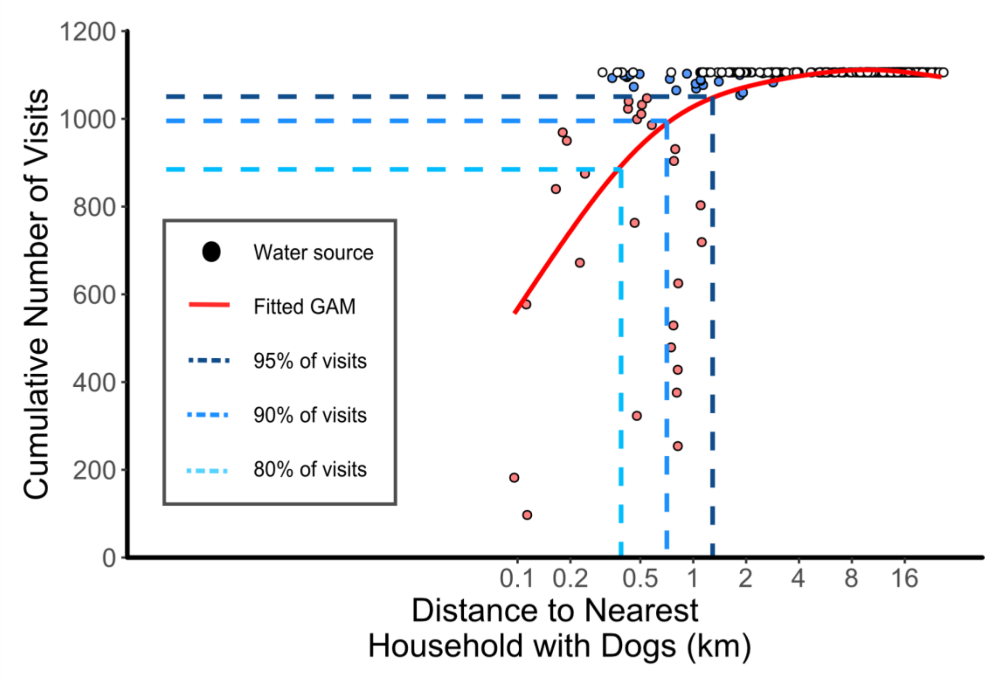

Figure A2: Dog activity around water sources in rural villages in Ethiopia. The graph to the left shows the cumulative total of all dog visits to water sources plotted against the distance of the water source to the nearest household with tracked dogs. The dashed lines indicate the distance from a household with dogs at which 80%, 90% and 95% of all dog visits are captured. Points represent water sources which account for 95% of visits (red), which have been visited but are not within the 95% threshold (blue) and those not visited by dogs (white). The red line represents the predictions from a GAM relating the cumulative number of dog visits to the distance of water sources from a household with a tracked dog.

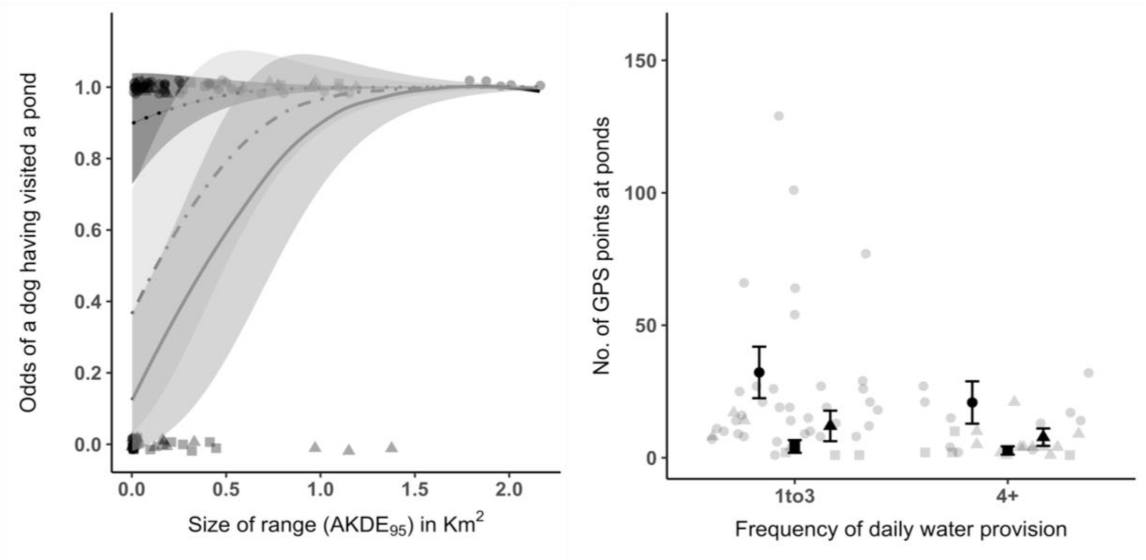

Figure A3: Dog ranging behaviour and exposure to potential sources for Guinea worm infection. A) The relationship between range size and the likelihood of a dog having visited a pond. Odds are predicted from the model of factors explaining whether a dog had visited a water body over the course of the study. B) The relationship between frequency of water provision and the amount of time spent near natural water sources (based on the number of relocation GPS fixes). Predictions are from the model of factors explaining the number of fixes within 100m of water body for those dogs which had visited a natural water source. The predictions are shown for dogs in the three villages: Atheti (dotted line; circles); Wichini (solid line; triangles) and Ablen (dashed line; squares). Other factors are held constant

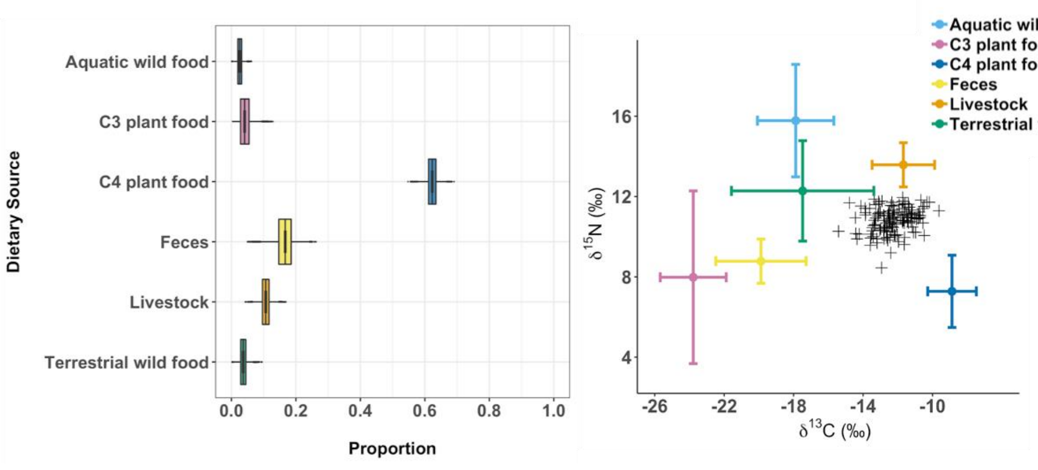

Figure A4: The dietary composition of dogs in three villages in Gog woreda, Ethiopia, as determined by stable isotope analysis of dog whiskers and putative foods. A) Estimates of the proportional contribution of each food group to the diet of the sampled dog population in as calculated by stable isotope mixing model analysis. B) The isospace of dogs and their dietary sources: the mean ± standard deviation error bars of the mean ± standard deviation error bars of $\delta^{15}N$ and $\delta^{13}C$ for the food groups; and the mean $\delta^{15}N$ and $\delta^{13}C$ values, averaged across all whisker sections for each individual dogs (black crosses). Trophic discrimination factors have been applied to adjust the relative position of sources upwards for both $\delta^{15}N$ and $\delta^{13}C$.

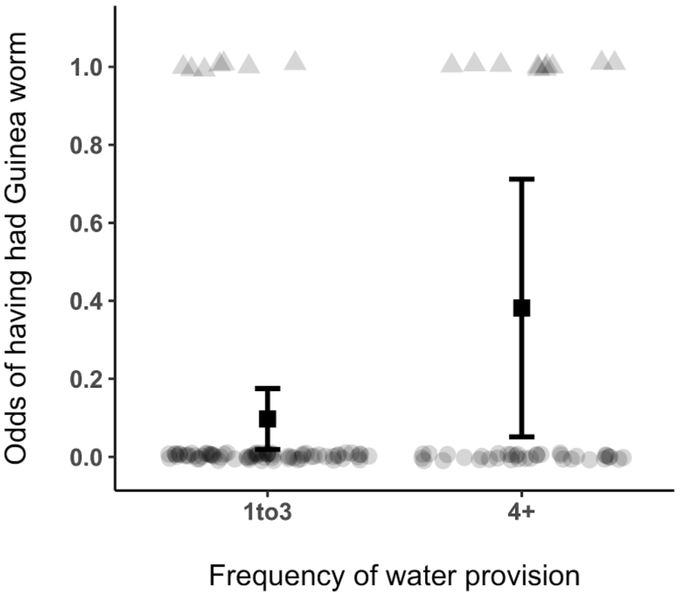

Figure A5: The relationship between the frequency of water provision and the Guinea worm infection histories of dogs in Chad. The odds, with 95% Confidence intervals, of having had Guinea worm are shown for dogs which are reported to be provided with water from 1 to 3 times a day, and at least 4 times a day. Odds are predicted from the model looking at the relationship between the history of Guinea worm infection, and with other predictive factors held constant. Results are presented for Atheti.

Table A1: Summary of all dogs studied in Gog, Ethiopia. Reported for each village is the number of dogs collared, their sex, age (mean ± standard error), body condition and the number of dogs with a history of Guinea worm (GW).

Village	No. dogs	Sex (F:M)	Age (months)	Body condition (Good: Moderate: Poor)	Dogs with GW history
Ablen	24	14 : 10	28 ± 4.7	9 : 6 : 8*	2 (8 %)
Atheti	68	37 : 31	34 ± 2.9*	19 : 30 : 16*	12 (16 %)
Wichini	39	19: 19*	29 ± 3.7*	8 : 26 : 3*	5 (14 %)
Overall	131	70 : 60*	32 ± 2.1*	36 : 62 : 27*	19 (15 %)

*some individuals had missing information

Table A2: Home range estimates and measures of the activity around natural water sources for free-ranging domestic dogs from rural villages in Ethiopia. A summary of the home range estimates for the 95% and core auto-correlated kernel density estimates ($AKDE_{95}$ and $AKDE_{core}$ respectively) are provided for each village. Summary statistics are also reported for the number of individuals with relocation points within 100 m of a water source, the number of unique water sources visited, proportion of time spent around water sources and the distance of households to the nearest water source. For the number of unique water sources visited and time at water sources, summary values exclude individuals that were not active around water sources. Where relevant, the median and inter-quartile ranges are provided for each parameter.

Village	n	$AKDE_{95}$ (km^2)	$AKDE_{core}$ (km^2)	No. of dogs to visit water sources	Unique water sources visited	Time at water sources (%)	Distance of household to nearest natural water source (km)
Ablen	22	0.14 (0.01 - 0.32)	0.03 (<0.01 - 0.07)	7	1 (1 - 2)	<1 (<1 - <1)	1.10 (1.06 - 1.13)
Atheti	65	0.08 (0.02 - 0.46)	0.01 (<0.01 - 0.08)	54	6 (4 - 8)	3 (1 - 6)	0.31 (0.23 - 0.36)
Wichini	38	0.12 (0.03 - 0.73)	0.02 (<0.01 - 0.17)	17	6 (4 - 7)	1 (<1 - 2)	0.46 (0.41 - 0.48)
Overall	125	0.10 (0.02 - 0.44)	0.02 (<0.01 - 0.07)	78	5 (4 - 8)	2 (1 - 5)	0.41 (0.31 - 0.51)

Table A3.The number of samples collected of each dietary group, and their constituent food items.

Dietary Group	**Food item**	**Sample count**	**Group total**
C3 plants	Pulses	11	52
	Grains	9	
	Vegetables	18	
	Fruit	14	
C4 plants	Maize	19	29
	Sorghum	5	
	‘Mash’	5	
Feces	(Human)	2	2
Fish	Lake fish	3	29
	River fish	7	
	Stream fish	19	
Frogs	(Assorted species)	10	10
Livestock	Chicken	5	12
	Beef	1	
	Goat	6	
Wild prey	Reptile	1	10
	Mammal	7	
	Bird	2	

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APPENDIX B

Methods

Duration of model runs

To ensure the presence of active exposed and/or infected individuals at the 300 day mark did not affect the final results or conclusions, we re-ran simulations for all networks of Magrao when R0 was set to 2.4. When allowed to run up to 730 days, the maximum epidemic duration was 454 days. We found that the distributions for epidemic size were unchanged, and the mean epidemic size did not change (mean epidemic size for: random = 46; binomial = 27; weighted = 26). Epidemics lasting longer than 300 days were either due to a few individuals that were assigned long incubation times or when an infection occurred towards the end of the 300 days. However, by 300 days the epidemics lasting more than 300 days had run their course and no new cases were produced after 300 days.

Table B1. Normalized Mutual Information (NMI) score for the relationship between the community membership of free-ranging dogs in two rural settlements in Chad and their attributes; sex, age and household membership.

Attribute	**Settlement**	**EB binomial**	**EB weighted**	**G binomial**	**G weighted**
Sex	*Kakale*	0.048	0.058	0.042	0.069
	Magrao	0.077	0.062	0.053	0.066
Age	*Kakale*	0.196	0.147	0.070	0.147
	Magrao	0.165	0.164	0.150	0.115
Household	*Kakale*	0.622	0.674	0.625	0.70
	Magrao	0.739	0.725	0.649	0.713

NMI scores closer to 1 imply a greater overlap between community membership and attributes. Community membership is calculated from observed binomial and weighted contact networks and calculated using both the edge betweenness (EB) and Greedy (G) algorithms.

Table B2: The duration of epidemics simulated on the contact networks of free-ranging dogs from two rural settlements in Chad.

Village	R0	Network	Duration (days)	Duration > 300 (%)
Kakale	1.2	Random	29 ± 1	0.01
		Binomial	28 ± 1	0.01
		Weighted	32 ± 1	0
	1.8	Random	102 ± 2	0.13
		Binomial	86 ± 1	0.05
		Weighted	95 ± 1	0.60
	2.4	Random	135 ± 2	0.09
		Binomial	112 ± 1	0.09
		Weighted	121 ± 1	0.08
Magrao	1.2	Random	51 ± 1	0.06
		Binomial	46 ± 1	0.02
		Weighted	52 ± 1	0.02
	1.8	Random	107 ± 2	0.20
		Binomial	84 ± 1	0.09
		Weighted	92 ± 1	0.07
	2.4	Random	139 ± 1	0.12
		Binomial	113 ± 1	0.16
		Weighted	117 ± 1	0.14

Results are reported for R_0 set to 1.2, 1.8 and 2.4, and for the random, binomial and weighted networks of the settlements Kakale and Magrao. Summary statistics are for simulations where at least one individual was infected by the seeded individual. The mean ± standard error are reported for the duration of epidemics that ended within the 300 days. The percentage of simulations that were longer than 300 days is also reported.

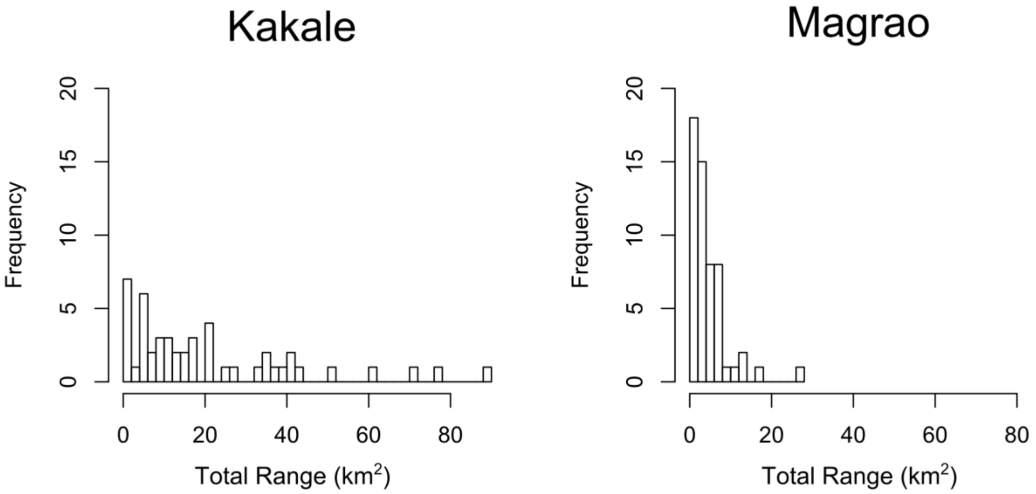

Figure B1. Frequency distribution of total ranges recorded for free-ranging dogs from two rural settlements in Chad**.** Total ranges are 99 % Minimum Convex Polygons.

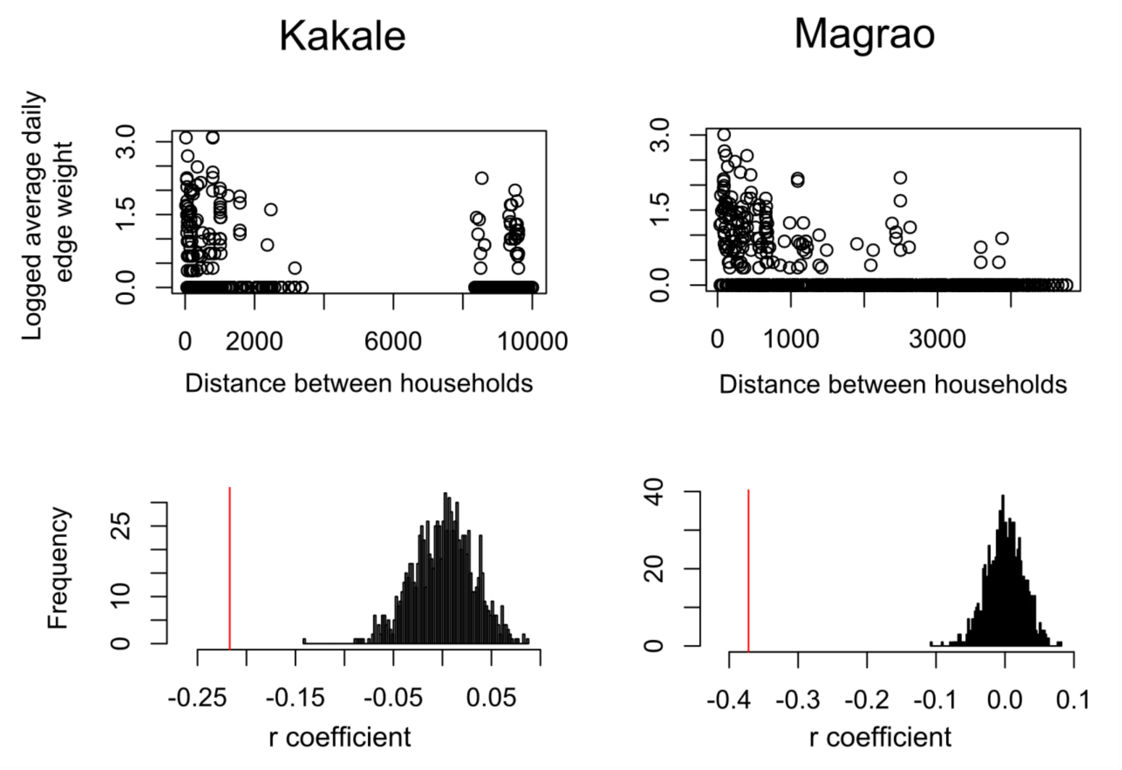

Figure B2. Relationships between the strength of contacts among free-ranging dogs in two rural settlements in Chad and the distance between their respective households. Scatter plots show the logged daily average edge weights between observed dyads in the settlements Kakale and Magrao against the distance (m) between their households. The histograms show the distribution of r coefficients calculated from permutations where edges were randomly shuffled. The red lines on the histograms indicate the observed r coefficient. For all plots, edges for individuals in the same household were excluded.

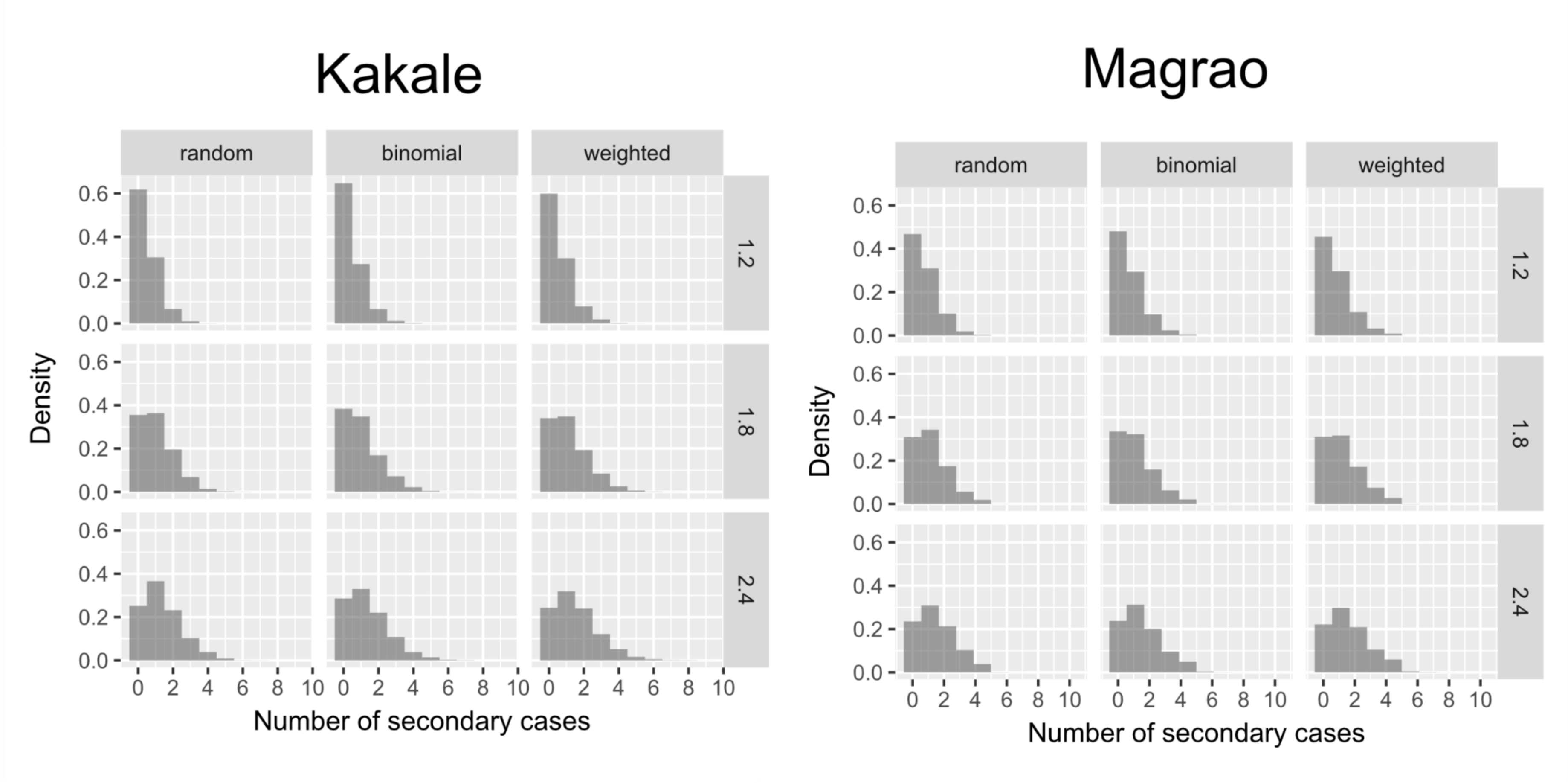

Figure B3. Number of secondary cases produced from epidemics simulated on the contact networks of free-ranging dogs from two rural settlements in Chad. Density plots for the number of secondary cases in simulations of the different networks (columns) of the settlements Kakale and Magrao and for the different R_0 values (rows).

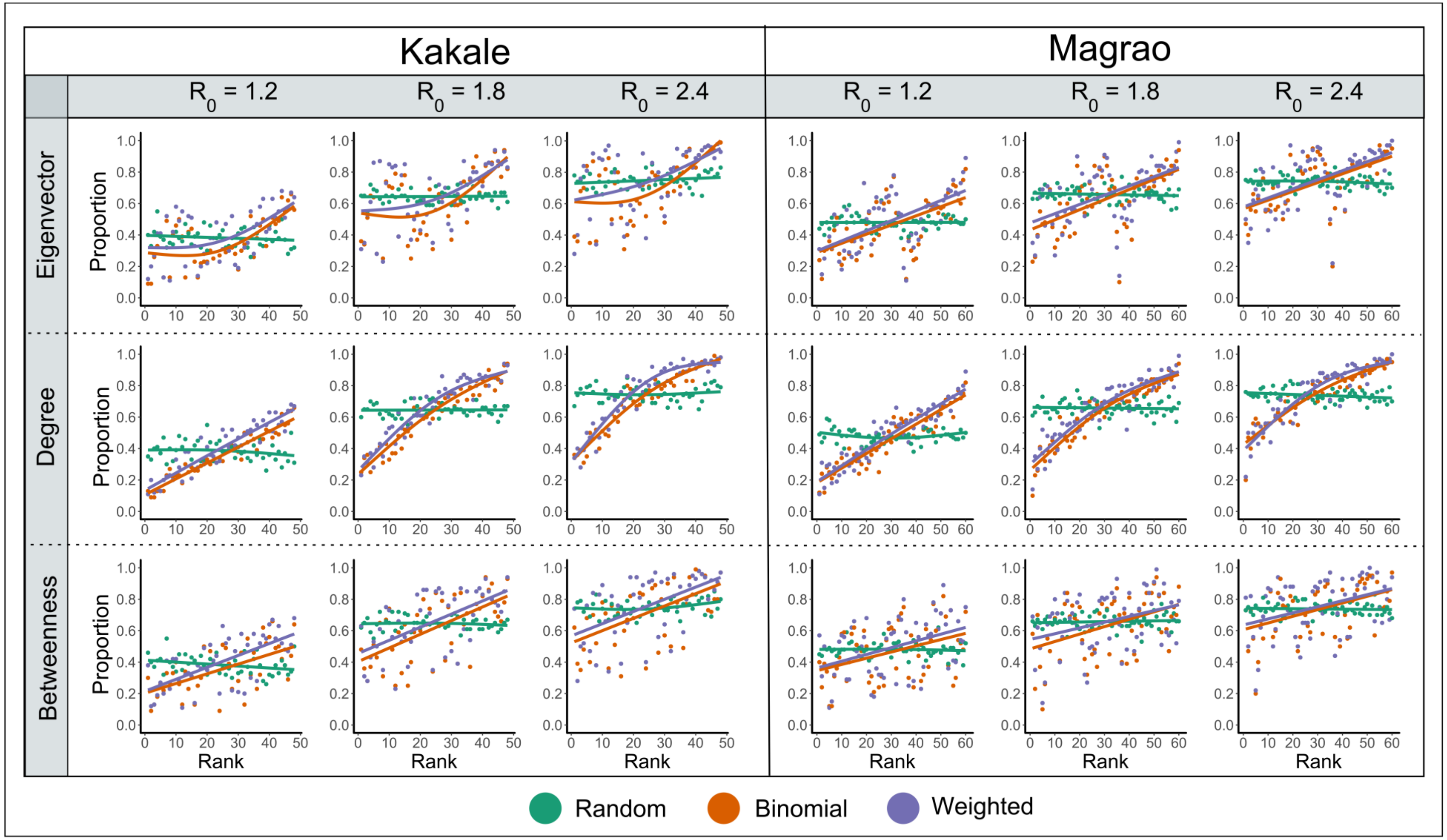

Figure B4. Relationship between the proportion of simulations to have an epidemic and the seeded individual's ranked centrality measures (eigenvector, degree and betweenness) when disease transmission is simulated through the contact networks of free-ranging dogs from two rural settlements in Chad. The scatter plots include the results for the random, binomial and weighted networks of each settlement (Kakale and Magrao), and are for each R_0 value modelled (1.2, 1.8 and 2.4). GAMs are fitted to the data to identify non-linear trends.

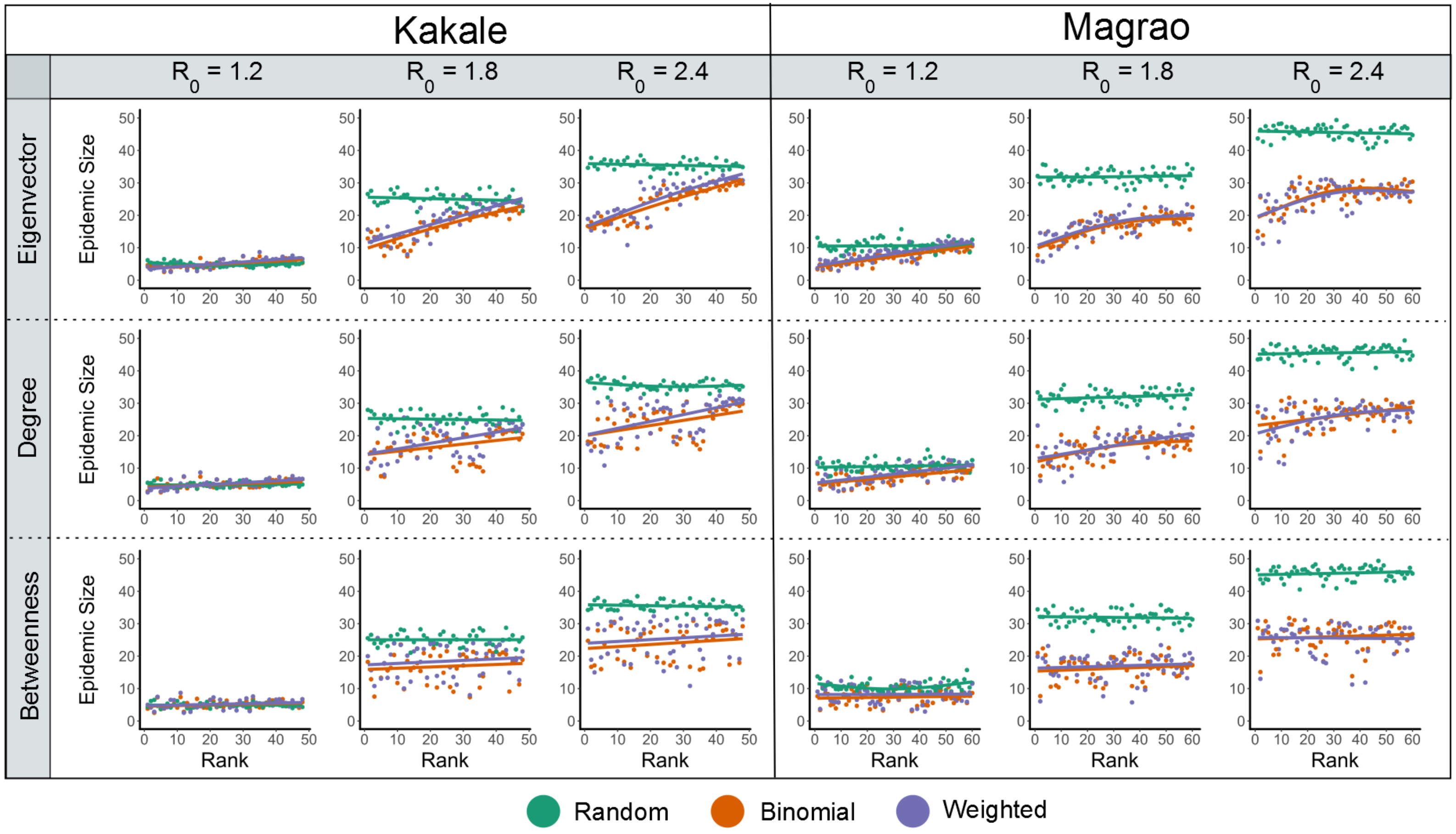

Figure B5. The relationship between the mean epidemic size of simulations and the seeded individuals ranked centrality measures (eigenvector, degree and betweenness) when disease transmission is simulated through the contact networks of free-ranging dogs from two rural settlements in Chad. The scatter plots include the results for the random, binomial and weighted networks of each settlement (Kakale and Magrao), and are for each R_0 value modelled (1.2, 1.8 and 2.4). The means exclude simulations where the infection did not spread beyond the seeded individual. GAMs are fitted to the data to identify non-linear trends.

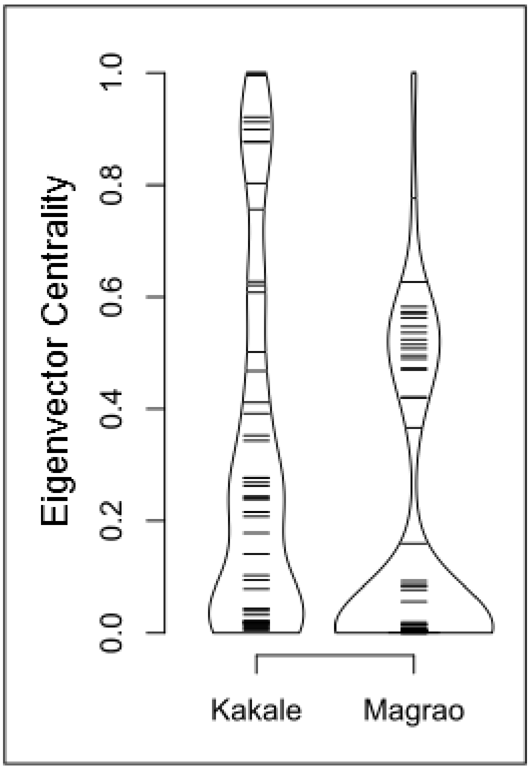

Figure B6. The distribution of eigenvector centrality scores for free-ranging dogs from two rural settlements in Chad. Bean plots are plotted for dogs from the settlements Kakale and Magrao.

Results

Variation in core range size

The $\mathrm{AKDE}_{\mathrm{core}}$ ranges of dogs differed significantly between villages, whereby the $\mathrm{AKDE}_{\mathrm{core}}$ of dogs in Marabodokouya were 3.5 (confidence intervals; 1.5, 8.0) times larger than those of dogs from Kira ($z = 4.24$; $p < 0.001$) and 5.6 (1.8, 17.7) times larger than the ranges of dogs from Ngakedji ($z = 4.26$; $p < 0.001$). Seasonal differences in the dogs $\mathrm{AKDE}_{\mathrm{core}}$ ranges were also found, but only for dogs from Bembaya which had ranges that were 29.2 (9.1, 93.4) times larger in the dry season than in the wet season ($z = 5.69$; $p < 0.001$) and dogs from Marabodokouya which had ranges that were 7.8 (2.6, 15.1) times larger in the dry season ($z = 6.17$; $p < 0.001$). The $\mathrm{AKDE}_{\mathrm{core}}$ of dogs from hunting households was 2.6 (1.6, 4.3) times larger than that of dogs from households that did not report going hunting ($z = 3.94$; $p = 0.001$). The $\mathrm{AKDE}_{\mathrm{core}}$ ranges of dogs decreased by 3% (2%, 4%) with every 1% increase in the proportion of time that they spent around the household ($t = -5.76$; $p < 0.001$).

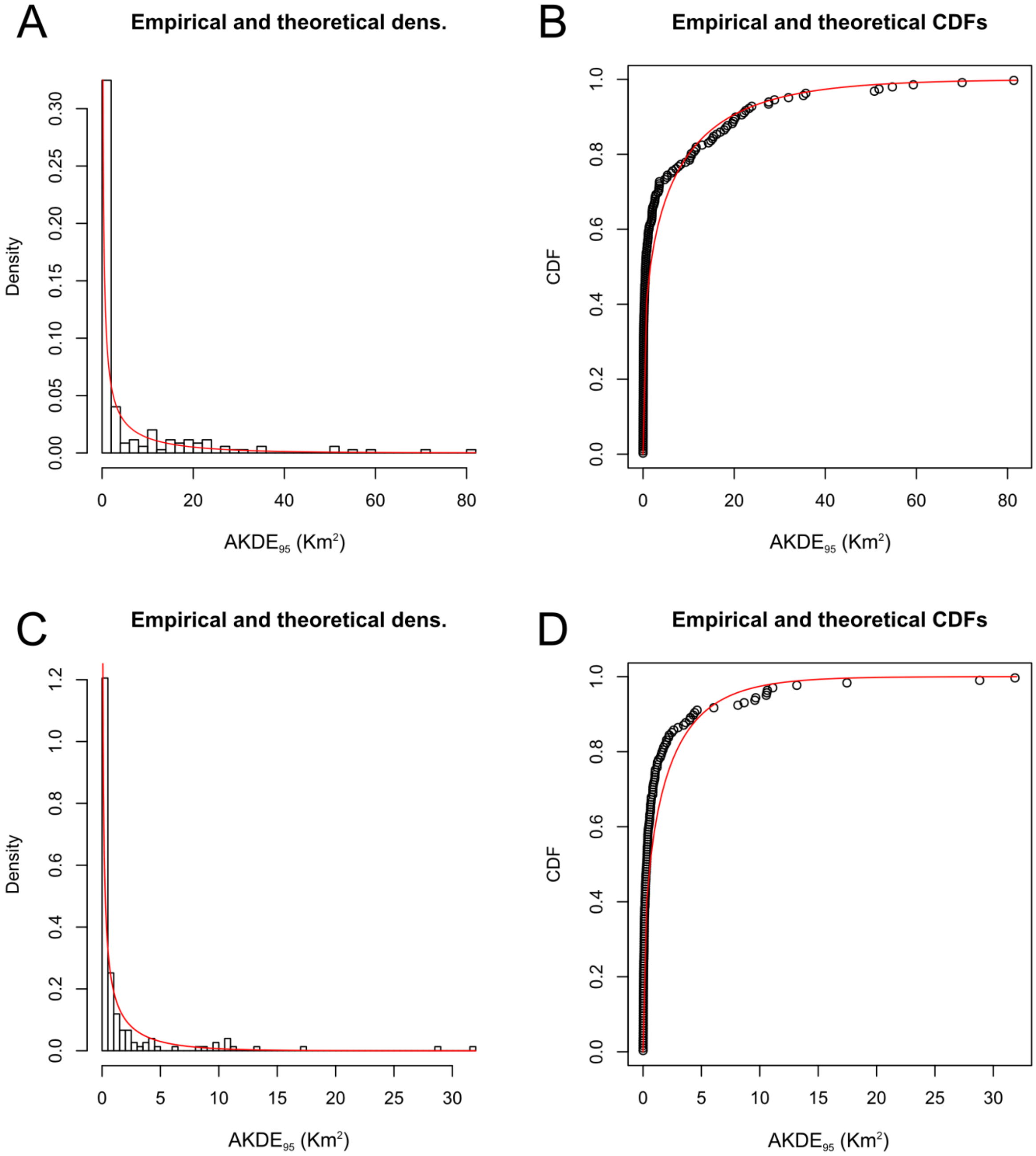

Figure C1. Fitted distributions for the 95% auto-correlated kernel density estimates ($AKDE_{95}$) of free-ranging domestic dogs from rural villages in Chad during the dry and wet seasons. Plots A & B are for the dry season and plots C & D are for the wet season. Plots A & C are histograms for the observed data with the fitted gamma distributions (red line; A: shape = 0.30; rate = 0.05; C: shape = 0.38; rate = 0.21). Plots B & D show the empirical cumulative distribution against the fitted gamma distributions (red line).

Conventional home range estimation methods

Table C1: Home range estimates using conventional methods for free-ranging domestic dogs in rural Chadian communities during the wet and dry seasons. The home ranges of dogs identified as being range resident were estimated using Kernel density estimates at the 95% isopleth (KDE_{95}) and 50% isopleth (KDE_{50}), and using minimum convex polygons (MCP). Range sizes are reported in km^2. The median is reported along with the interquartile range in brackets.

Village	Season	MCP	KDE_{95}	KDE_{50}
Medegue	Dry	4.12 (1.68 – 6.28)	0.19 (0.08 - 0.40)	0.01 (<0.01 – 0.04)
	Wet	7.26 (2.67 – 10.09)	0.68 (0.09 – 1.72)	0.06 (0.01 – 0.16)
Kira	Dry	8.46 (2.91 – 14.69)	0.29 (0.06 – 1.20)	0.03 (0.01 – 0.07)
	Wet	4.30 (2.82 – 7.05)	0.35 (0.19 – 0.91)	0.02 (0.01 – 0.05)
Bembaya	Dry	29.27 (6.08 – 44.01)	4.21 (0.74 – 14.20)	0.18 (0.05 – 0.61)
	Wet	0.68 (0.61 – 1.90)	0.06 (0.03 – 0.14)	0.01 (<0.01 - 0.02)
Ngakedji	Dry	1.57 (0.88 – 4.98)	0.12 (0.04 – 0.28)	0.01 (<0.01 – 0.03)
	Wet	1.08 (0.23 – 3.97)	0.19 (0.02 – 0.44)	0.02 (<0.01 – 0.06)
Marabodokouya	Dry	32.25 (12.10 – 58.28)	6.71 (0.52 – 16.99)	0.44 (0.05 – 0.92)
	Wet	5.40 (1.89 – 13.56)	0.72 (0.11 – 3.62)	0.05 (0.01 – 0.30)
Tarangara	Dry	8.67 (0.28 – 25.45)	0.36 (0.05 – 0.62)	0.04 (<0.01 – 0.11)
	Wet	-	-	-
Overall	Dry	9.50 (2.94 – 31.65)	0.56 (0.09 – 3.84)	0.05 (0.01 – 0.31)
	Wet	3.97 (1.35 – 8.21)	0.35 (0.06 – 1.12)	0.03 (0.01 – 0.09)

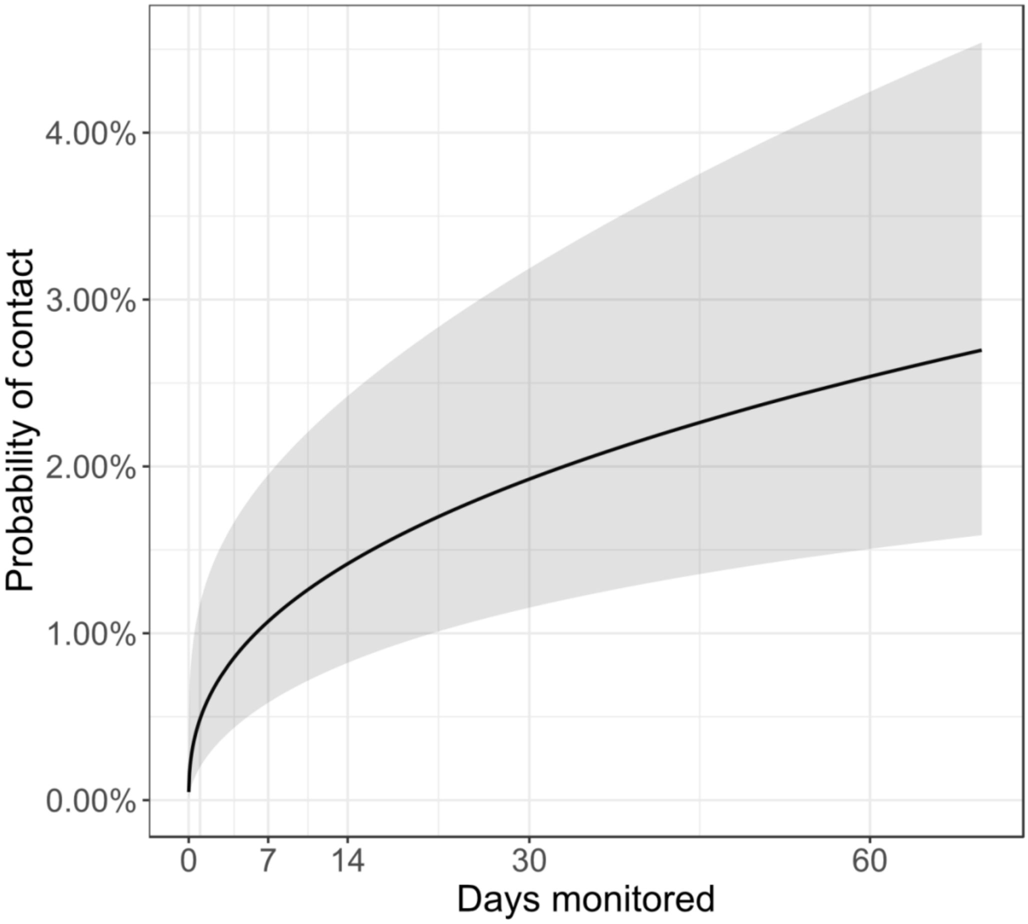

Figure D1: The probability of contact between free-ranging domestic dogs in rural Chad with an increasing number of days over which a potential dyad was observed. The predictions and confidence intervals are plotted from a general linear mixed model. The x axis is on a logged scale.

Table D1: Summary of mixed effect models for the probability of free-ranging domestic dogs in rural Chad ever having had contact, their hourly contact probability should they have been in contact and the duration of their contacts. For each model either the odds ratio or incidence rate ratio and confidence intervals (CI) are reported. For the random effects of each model the variance (σ^2), between-group variance (τ00), group size (Nτ00) and intra-class correlation (ICC) are reported.

Predictors	**Contact probability**		**Hourly contact probability**		**Contact Duration**	
	Odds Ratios	*CI*	*Odds Ratios*	*CI*	*Incidence Rate Ratios*	*CI*
(Intercept)	0.86	0.06 – 12.08	0.02 ***	0.01 – 0.03	182.93 ***	152.04 – 220.11
$\log_{10}$(hours monitored)	2.56 ***	1.59 – 4.13	-	-	-	-
$\log_2$(Household Distance)	0.49 ***	0.45 – 0.53	0.62 ***	0.60 – 0.64	0.95 ***	0.95 – 0.96
Sex [female-female]	*Reference*		*Reference*		*Reference*	
Sex [male-female]	1.48 *	1.03 – 2.13	1.45 **	1.15 – 1.82	1.01	0.94 – 1.08
Sex [male-male]	1.16	0.66 – 2.05	1.57 **	1.12 – 2.21	1.03	0.94 – 1.13
Age difference	1	0.99 – 1.01	1.01	1.00 – 1.01	1	1.00 – 1.00
region [Guelendeng]	*Reference*		*Reference*		*Reference*	
region [Sarh East]	0.35	0.10 – 1.20	0.71	0.42 – 1.21	1	0.89 – 1.12
region [Sarh West]	1.17	0.35 – 3.87	1.05	0.62 – 1.78	1.09	0.98 – 1.21
season [dry]	*Reference*		*Reference*		*Reference*	
season [wet]	0.83	0.33 – 2.12	1.73 ***	1.41 – 2.13	1.12	0.92 – 1.35
location [Household]	-	-	*Reference*		*Reference*	
location [Out.Village]	-	-	0.21 ***	0.15 – 0.29	1.41 *	1.02 – 1.95
location [Village]	-	-	1.09	0.91 – 1.31	1.09	0.91 – 1.32
hour [01]	-	-	*Reference*		*Reference*	
hour [02]	-	-	0.8	0.63 – 1.01	1.01	0.81 – 1.26
hour [03]	-	-	0.67 **	0.53 – 0.85	1.07	0.85 – 1.33
hour [04]	-	-	0.99	0.80 – 1.24	1.05	0.84 – 1.30
hour [05]	-	-	3.73 ***	3.11 – 4.47	1.91 ***	1.60 – 2.27

hour [06]	-	-	3.31 ***	2.76 – 3.97	1.64 ***	1.38 – 1.96
hour [07]	-	-	2.45 ***	2.03 – 2.95	1.32 **	1.10 – 1.59
hour [08]	-	-	1.61 ***	1.32 – 1.96	1.22 *	1.01 – 1.48
hour [09]	-	-	1.27 *	1.03 – 1.57	1.25 *	1.02 – 1.52
hour [10]	-	-	1.28 *	1.04 – 1.58	1.37 **	1.13 – 1.66
hour [11]	-	-	1.35 **	1.09 – 1.66	1.31 **	1.08 – 1.59
hour [12]	-	-	2.09 ***	1.72 – 2.53	1.49 ***	1.24 – 1.79
hour [13]	-	-	2.15 ***	1.77 – 2.61	1.60 ***	1.34 – 1.92
hour [14]	-	-	2.26 ***	1.86 – 2.74	1.53 ***	1.28 – 1.84
hour [15]	-	-	2.53 ***	2.09 – 3.06	1.36 ***	1.14 – 1.64
hour [16]	-	-	2.69 ***	2.23 – 3.25	1.43 ***	1.19 – 1.71
hour [17]	-	-	2.59 ***	2.15 – 3.13	1.25 *	1.04 – 1.50
hour [18]	-	-	4.28 ***	3.59 – 5.11	1.51 ***	1.28 – 1.79
hour [19]	-	-	4.71 ***	3.95 – 5.61	1.49 ***	1.26 – 1.77
hour [20]	-	-	3.40 ***	2.84 – 4.07	1.31 **	1.10 – 1.56
hour [21]	-	-	2.20 ***	1.82 – 2.66	1.26 *	1.05 – 1.51
hour [22]	-	-	1.72 ***	1.41 – 2.10	1.27 *	1.05 – 1.53
hour [23]	-	-	1.28 *	1.04 – 1.57	1.06	0.87 – 1.30
hour [24]	-	-	0.91	0.73 – 1.14	1.04	0.83 – 1.29
season [wet] * log2(Household Distance)	1.04	0.94 – 1.15	1.01	0.99 – 1.02	1.01	1.00 – 1.02
season [wet] * Sex [male-female]	0.92	0.59 – 1.44	0.64 ***	0.58 – 0.72	1	0.92 – 1.09
season [wet] * Sex [male-male]	1.89 *	1.05 – 3.41	0.77 *	0.63 – 0.94	0.95	0.84 – 1.08
season [wet] * Age difference	0.99	0.98 – 1.01	1	1.00 – 1.00	1.00 **	1.00 – 1.01
location [Out.Village] * season [wet]	-	-	0.87 **	0.79 – 0.95	0.71 ***	0.65 – 0.78

location [Village] * season [wet]	-	-	1.95 ***	1.84 – 2.07	0.97	0.92 – 1.03
hour [02] * season [wet]	-	-	1.11	0.86 – 1.43	1.01	0.78 – 1.30
hour [03] * season [wet]	-	-	1.11	0.86 – 1.44	0.87	0.68 – 1.12
hour [04] * season [wet]	-	-	0.83	0.64 – 1.06	0.86	0.68 – 1.11
hour [05] * season [wet]	-	-	0.34 ***	0.28 – 0.42	0.63 ***	0.52 – 0.78
hour [06] * season [wet]	-	-	0.49 ***	0.40 – 0.60	0.76 **	0.62 – 0.93
hour [07] * season [wet]	-	-	0.73 **	0.60 – 0.90	0.92	0.75 – 1.13
hour [08] * season [wet]	-	-	0.92	0.74 – 1.14	0.83	0.67 – 1.02
hour [09] * season [wet]	-	-	0.89	0.71 – 1.11	0.86	0.69 – 1.06
hour [10] * season [wet]	-	-	0.85	0.68 – 1.06	0.79 *	0.63 – 0.98
hour [11] * season [wet]	-	-	0.68 ***	0.54 – 0.85	0.75 **	0.61 – 0.93
hour [12] * season [wet]	-	-	0.60 ***	0.48 – 0.75	0.71 **	0.58 – 0.88
hour [13] * season [wet]	-	-	0.58 ***	0.47 – 0.73	0.71 **	0.57 – 0.88
hour [14] * season [wet]	-	-	0.56 ***	0.45 – 0.70	0.70 **	0.57 – 0.87
hour [15] * season [wet]	-	-	0.52 ***	0.42 – 0.65	0.78 *	0.63 – 0.96
hour [16] * season [wet]	-	-	0.53 ***	0.43 – 0.66	0.71 **	0.58 – 0.87
hour [17] * season [wet]	-	-	0.76 *	0.62 – 0.94	0.86	0.70 – 1.06
hour [18] * season [wet]	-	-	0.96	0.79 – 1.17	0.86	0.71 – 1.05
hour [19] * season [wet]	-	-	0.9	0.74 – 1.10	0.85	0.70 – 1.02
hour [20] * season [wet]	-	-	0.96	0.78 – 1.17	0.9	0.74 – 1.10
hour [21] * season [wet]	-	-	0.95	0.77 – 1.17	0.94	0.76 – 1.15
hour [22] * season [wet]	-	-	0.89	0.71 – 1.11	0.88	0.71 – 1.09
hour [23] * season [wet]	-	-	1.02	0.81 – 1.29	0.96	0.76 – 1.20
hour [24] * season [wet]	-	-	1.11	0.87 – 1.41	0.99	0.78 – 1.25
hour [02] * location [Out.Village]	-	-	0.57	0.32 – 1.00	1.3	0.76 – 2.23
hour[02] * location [Village]	-	-	1.06	0.81 – 1.39	0.95	0.73 – 1.25
hour[03] * location [Out.Village]	-	-	0.96	0.57 – 1.61	2.17 ***	1.37 – 3.45

hour[03] * location [Village]	-	-	1.19	0.90 – 1.57	1.02	0.78 – 1.35
hour[4] * location [Out.Village]	-	-	0.52 *	0.29 – 0.91	1.52	0.91 – 2.54
hour[4] * location [Village]	-	-	0.99	0.76 – 1.28	1.11	0.85 – 1.45
hour[5] * location [Out.Village]	-	-	1.86 **	1.28 – 2.70	0.95	0.66 – 1.35
hour[5] * location [Village]	-	-	1.24	1.00 – 1.54	0.87	0.70 – 1.08
hour[6] * location [Out.Village]	-	-	2.63 ***	1.83 – 3.79	0.92	0.65 – 1.30
lhour[6] * ocation [Village]	-	-	1.1	0.88 – 1.36	0.92	0.74 – 1.15
hour[7] * location [Out.Village]	-	-	3.48 ***	2.41 – 5.00	1.01	0.71 – 1.43
hour[7] * location [Village]	-	-	1.11	0.89 – 1.38	0.9	0.72 – 1.13
hour[8] * location [Out.Village]	-	-	5.47 ***	3.79 – 7.90	1.14	0.81 – 1.62
hour[8] * location [Village]	-	-	1.04	0.82 – 1.32	0.97	0.77 – 1.22
hour[9] * location [Out.Village]	-	-	5.64 ***	3.88 – 8.21	1.07	0.75 – 1.53
hour[9] * location [Village]	-	-	1.06	0.83 – 1.36	0.9	0.70 – 1.15
hour[10] * location [Out.Village]	-	-	5.15 ***	3.53 – 7.52	0.86	0.60 – 1.23
hour[10] * location [Village]	-	-	0.98	0.76 – 1.26	0.89	0.70 – 1.13
hour[11] * location [Out.Village]	-	-	4.24 ***	2.89 – 6.22	0.97	0.67 – 1.40
hour[11] * location [Village]	-	-	1.29 *	1.01 – 1.64	0.97	0.76 – 1.23
hour[12] * location [Out.Village]	-	-	2.37 ***	1.62 – 3.46	1.02	0.71 – 1.47
hour[12] * location [Village]	-	-	0.96	0.76 – 1.21	0.91	0.72 – 1.14
hour[13] * location [Out.Village]	-	-	1.57 *	1.06 – 2.33	0.85	0.59 – 1.24
hour[13] * location [Village]	-	-	0.92	0.73 – 1.17	0.86	0.68 – 1.08
hour[14] * location [Out.Village]	-	-	1.11	0.74 – 1.66	1.26	0.86 – 1.84
hour[14] * location [Village]	-	-	0.88	0.69 – 1.11	0.9	0.71 – 1.13
hour[15] * location [Out.Village]	-	-	1.23	0.83 – 1.83	0.89	0.61 – 1.29
hour[15] * location [Village]	-	-	0.92	0.73 – 1.15	0.93	0.74 – 1.16
hour[16] * location [Out.Village]	-	-	1.86 **	1.28 – 2.72	0.83	0.57 – 1.19
hour[16] * location [Village]	-	-	0.98	0.78 – 1.23	0.91	0.73 – 1.13

hour[17] * location [Out.Village]	-	-	1.47 *	1.00 – 2.15	1.07	0.75 – 1.55
hour[17] * location [Village]	-	-	0.98	0.78 – 1.22	0.98	0.79 – 1.22
hour[18] * location [Out.Village]	-	-	0.68 *	0.46 – 1.00	0.92	0.64 – 1.33
hour[18] * location [Village]	-	-	0.82	0.66 – 1.01	0.83	0.67 – 1.02
hour[19] * location [Out.Village]	-	-	0.49 ***	0.33 – 0.73	0.67 *	0.46 – 0.99
hour[19] * location [Village]	-	-	0.9	0.73 – 1.11	0.88	0.72 – 1.08
hour[20] * location [Out.Village]	-	-	0.71	0.48 – 1.06	0.77	0.53 – 1.13
hour[20] * location [Village]	-	-	0.96	0.77 – 1.18	0.87	0.71 – 1.07
hour[21] * location [Out.Village]	-	-	1.17	0.79 – 1.73	0.75	0.51 – 1.09
hour[21] * location [Village]	-	-	1.15	0.92 – 1.43	0.87	0.70 – 1.08
hour[22] * location [Out.Village]	-	-	1.23	0.82 – 1.86	0.73	0.49 – 1.08
hour[22] * location [Village]	-	-	1.04	0.82 – 1.31	0.89	0.71 – 1.12
hour[23] * location [Out.Village]	-	-	1.18	0.76 – 1.81	0.9	0.59 – 1.36
hour[23] * location [Village]	-	-	1.02	0.80 – 1.30	0.98	0.77 – 1.25
hour[24] * location [Out.Village]	-	-	1.12	0.70 – 1.78	1.02	0.66 – 1.58
hour[24] * location [Village]	-	-	1.2	0.93 – 1.55	0.99	0.76 – 1.27
Random Effects						
σ2	3.29		3.29		1.06	
τ00 [ID1]	1.01		0.22		0.01	
τ00 [ID2]	0.77		0.18		0.01	
τ00 [Household ID1]	0.43		0.29		< 0.01	
τ00 [Household ID2]	0.63		0.08		< 0.01	
τ00 [Village ID]	0.13		< 0.01		< 0.01	
τ00 [Dyad ID]	-		0.9		< 0.01	
ICC	0.47		0.34		0.02	
Nτ00 [ID1]	255		194		198	
Nτ00 [ID2]	160		203		197	
Nτ00 [Household ID1]	258		129		131	

Nτ00 [Household ID2]	161	134	129
Nτ00 [Village ID]	6	6	5
Nτ00 [Dyad ID]	-	1058	1060
Observations	7190	94656	20594
Marginal R^2 / Conditional R^2	0.407 / 0.688	0.338 / 0.561	0.70 / 0.99

* $p<0.05$ ** $p<0.01$ *** $p<0.001$

Table D2: Contrasts for model predictions of the hourly probability that free-ranging domestic dogs in rural Chad were in contact. For each hour of the day the odds ratio and confidence intervals are provided for the contrast between the probability of contact at the focal hour and to that three hours ahead, between the focal hour in the wet and dry season, and between contacts at the focal hour within the village.

Hour	**Hour hour[i] - hour[i+3]**		**Hour*season: hour[Dry] - hour[Wet]**		**Hour*location: hour[within village] - hour [outside village]**	
	Odds Ratios	*CI*	*Odds Ratios*	*CI*	*Odds Ratios*	*CI*
hour [01]	1.38	0.96 - 1.99	0.59 ***	0.48 - 0.73	7.91 ***	5.37 - 11.67
hour [02]	0.25 ***	0.18 - 0.34	0.54 ***	0.43 - 0.67	14.75 ***	8.59 - 25.31
hour [03]	0.25 ***	0.17 - 0.3	0.53 ***	0.43 - 0.67	9.85 ***	6.18 - 15.71
hour [04]	0.22 ***	0.16 - 0.3	0.72 **	0.58 - 0.89	15.08 ***	8.81 - 25.8
hour [05]	1.05	0.88 - 1.24	1.74 ***	1.48 - 2.04	5.28 ***	4.37 - 6.38
hour [06]	1.51 ***	1.28 - 1.79	1.22 *	1.04 - 1.42	3.3 ***	2.77 - 3.92
hour [07]	1.62 ***	1.37 - 1.92	0.81 **	0.69 - 0.94	2.52 ***	2.13 - 2.99
hour [08]	1.41 ***	1.18 - 1.68	0.64 ***	0.55 - 0.76	1.51 ***	1.26 - 1.79
hour [09]	1.03	0.85 - 1.23	0.67 ***	0.56 - 0.79	1.49 ***	1.23 - 1.81
hour [10]	1.09	0.89 - 1.33	0.7 ***	0.59 - 0.83	1.5 ***	1.23 - 1.84
hour [11]	1.17	0.95 - 1.45	0.87	0.73 - 1.04	2.4 ***	1.95 - 2.95
hour [12]	1.12	0.91 - 1.37	0.99	0.84 - 1.18	3.2 ***	2.58 - 3.97
hour [13]	0.77 ***	0.63 - 0.94	1.02	0.85 - 1.21	4.65 ***	3.62 - 5.96
hour [14]	0.66 ***	0.53 - 0.81	1.06	0.89 - 1.27	6.27 ***	4.74 - 8.3
hour [15]	0.55 ***	0.45 - 0.67	1.14	0.96 - 1.36	5.91 ***	4.58 - 7.64
hour [16]	0.71 ***	0.59 - 0.86	1.11	0.94 - 1.31	4.17 ***	3.38 - 5.15
hour [17]	0.87	0.72 - 1.05	0.78 **	0.67 - 0.92	5.28 ***	4.23 - 6.59
hour [18]	1.46 ***	1.21 - 1.77	0.62 ***	0.53 - 0.71	9.49 ***	7.54 - 11.94
hour [19]	1.93 ***	1.56 - 2.39	0.66 ***	0.57 - 0.76	14.61 ***	11.32 - 18.85
hour [20]	2.14 ***	1.7 - 2.7	0.62 ***	0.53 - 0.72	10.6 ***	8.26 - 13.6
hour [21]	2.23 ***	1.73 - 2.88	0.63 ***	0.54 - 0.74	7.78 ***	6.06 - 9.98
hour [22]	1.76 ***	1.34 - 2.31	0.67 ***	0.56 - 0.8	6.67 ***	5.05 - 8.83
hour [23]	1.93 ***	1.36 - 2.72	0.58 ***	0.48 - 0.7	6.84 ***	4.96 - 9.43
hour [24]	1.43 ***	1.02 - 2	0.54 ***	0.44 - 0.65	8.51 ***	5.85 - 12.39

* p<0.05 ** p<0.01 *** p<0.001