Integrating individual behaviour into simulations of disease management in Ethiopian wolves.



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A thesis submitted for the degree of

Doctor of Philosophy

Michaelmas 2019

For those that pursue a better world in a dark time.

Acknowledgements

I would like to thank my supervisors Claudio Sillero-Zubiri and Jorgelina Marino for their help and guidance throughout the whole process. WildCRU for providing me with a home over these years. The Ethiopian Wildlife Conservation Authority and Bale Mountains National Park for kindly letting me conduct research within Ethiopia. Eric Bedin, Muktar Abute and all the field staff at EWCP who helped me. The zoology department at Oxford University for the opportunity to study there. EWCP, WCN, Bornfree, Idea Wild, SoS and the EU commission for their help in funding the work. Tim Coulson and Angela Maclean for their support and criticisms. My parents for supporting me emotionally, financially and grammatically but failing to ward me off of science hard enough throughout my life. Fly and Qara for their assistance in prototyping GPS collars. And Leanne Massie for her continued support in the face of my constant complaining.

Abstract

Domestic animals are one of the primary global sources of disease due to their position at the interface between humans and wild environments. Wildlife that lives on this interface is extremely vulnerable to infectious disease. Disease has been a particularly prominent threat to wild carnivores that are already threatened through habitat loss or poaching. Outbreaks of disease have caused population declines in lions (*Panthera leo*), African wild dogs (*Lycaon pictus*), and Ethiopian wolves (*Canis simensis*). A specialised social canid, the Ethiopian wolf is restricted to the Afroalpine ecosystem of Ethiopia with no more than 500 individuals surviving; the species is ultimately threatened by a shrinking range, but the most immediate threats are rabies and canine distemper virus (CDV) transmitted by sympatric free-ranging domestic dogs (*C. familiaris*). A series of sequential and even concurrent outbreaks of these pathogens have led to severe declines in the largest population in the Bale Mountains; and an isolated small population to near extinction. The impact of disease on the last remaining Ethiopian wolf populations is currently mitigated by dog vaccination campaigns and reactive vaccination of the wolves. Successful and ongoing oral vaccination trials aim to use preventive wolf vaccinations to reduce the frequency and impact of outbreaks, but a better understanding is required of how to best apply different vaccination regimes (both of dogs and wolves) and dog management or exclusion strategies, proposed as part of an integrated approach in the National Action Plan for the conservation of the species. With this purpose in mind, custom-built monitoring devices were constructed to study the movement and behaviour of domestic dogs in sympatry with wolves using high resolution GPS and accelerometer data. These devices were deployed on 26 domestic

dogs in the Web Valley, Bale Mountains National Park, over multiple weeks in two seasons in 2018. Data (during day time and from when dogs left the village area) were analysed to determine dogs' extent of movement based on inter-point distances, their habitat preferences from Z tests of proportions of available to used habitat, and home ranges using 90% autocorrelated kernel density estimate. Dogs ranged out of villages to a mean distance of 727m (SD ±79.4m) away from their respective village within a home range of 3.0km^2 (SD ±0.63km^2) and showed a preference for grassland ($z = 192.35$, $df = 1$, $p = < 0.00001$), and drainage lines ($z = 54.396$, $df = 1$, $p = < 0.00001$). Deep learning was used on the accelerometer data to determine patterns in time allocation of activities throughout the day. Dogs exhibited two activity peaks: 07:00h to 10:00h and 14:00h to 18:00h, when they spent the majority of their time foraging or travelling. From long-term observations of wolf packs (focal pack observations and individual behavioural follows) equivalent home ranges were calculated as 10km^2 (SD ± 0.975km^2, $n = 253$, between 2007 and 2018) as well as movement and behavioural budget breakdown. A measure of overlap between the two species was developed to understand when and where the probability of disease transmission might be highest, calculating as overlap of function graphical area using integration. Dogs and wolves overlapped by 75% in active behaviours across the day and on average 48% of a dog's home range overlapped with wolf range. An epidemiological Agent-Based model including the two species, rabies and CDV, was parameterised with data on their movement, behaviour and demography, and published data on the dynamics of the diseases. When validated using historical disease outbreak data from the Bale Mountains population, the model produced a low root mean squared error of 3.74 for predicted population size and had a low linear sensitivity (less than 0.1) to input parameters. The validated model was used to simulate a variety of disease and management scenarios in the Bale wolf population. Under current disease management interventions (domestic dog vaccinations and reactive wolf vaccination in response to outbreaks) the population extinction

risk was predicted to be 17% (in 30 years), compared to 58% without management while the number of epizootics doubled without management. The model was run without reactive wolf vaccination which increased extinction risk by 10% with no effect on the number of epizootics compared to current management. Restricting dog movement to close to villages, or fewer dogs going into wolf habitat, removed extinction risk to 0% and reduced the incidence of epizootics by 50% in models. A parameter sweep of combinations of levels of vaccination coverage predicted that preventive wolf vaccination will be more effective and cost-effective at reducing epizootics in the wolves than dog vaccination at all levels of coverage. This is because the large number and turnover of dogs reduce effectiveness of dog vaccination in preventing outbreaks in the wolves. The most cost-effective strategy predicted was 70% of vaccination of the wolves with 0% dog vaccination. Until CDV vaccination is trialled and approved for wolves, it is better to retain high levels of dog vaccination to protect wolves from CDV, while using oral rabies vaccination in wolves to provide higher levels of rabies protection. This thesis showcases how custom-built monitoring devices, tailored to individual projects, have the potential to open up a wealth of new data sources and to improve the quantification of overlap between hosts for the modelling of transmission dynamics. The agent-based modelling framework developed could be expanded to numerous systems, particularly ones where domestic dogs are the primary host of disease. The model outputs provide guidelines for the implementation of preventive vaccination in wolves based both in its effectiveness as well as the long-term costs. The model also supports behavioural changes on the part of dog owners living next to the wolves as an effective measure that would require cooperation from all stake-holders. The model framework could be used globally to understand the impacts of behaviour on disease transmission and demonstrate the benefits of wildlife vaccination for species threatened by disease.

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Chapter 1

Introduction

Diseases of people and animals are a major burden on life and economies in the world (World Health Organisation 2013; Bloom et al. 2012; Hampson et al. 2015). Much of human history and scientific advances have been aimed at the prevention or curing of disease. Diseases have a range of different causes, from pathogens to our own genes. While we have developed medicines like antibiotics that have revolutionised the treatment of certain bacterial infections, we are still locked in an arms race with various viruses (Hoffmann, Schneider, and Rice 2015). Due to their incredibly rapid adaptability, viral diseases have proven to be some of the hardest to understand and control. Viral pathogens affecting people and other animals commonly have their origins in or depend upon animal hosts, either domestic or wild, which adds another layer of difficulty to their management (Canfield 1981).

Viruses typically have adverse effects upon their hosts; for instance they may lead to reduced growth, slow reproduction or loss of livestock species, posing a heavy economic burden for their owners (The World Bank 2012). Wildlife species that

live in human modified environments in sympatry with domestic animals, are at particular risk from disease (Gortazar et al. 2015). Some viruses represent a serious challenge to threatened species (Laurenson et al. 1998a) such as mountain gorillas threatened by Ebola (Walsh et al. 2007) or California condors impacted by West Nile virus (Chang et al. 2007). Scientists are only now beginning to take a more holistic view at the entire ecological system surrounding wildlife viral disease, including the pathogens, their vectors and the environment they exist in.

Despite our better understanding of virus-host transmission and spread, we still struggle to comprehend disease systems that have numerous interactions and variability, from the individual behaviours of infected individuals, such as travel rates and social activities, to the effect that subtle environmental differences, such as those in temperature or humidity (Eisenberg et al. 2007). For threatened species, where management of disease is a priority, this complexity can make it difficult to control diseases, and the management interventions put in place may be ineffective or have unintended consequences (Chauvenet et al. 2011). Better management must be built upon data, particularly data on the underlying behaviour of the species that are involved in disease transmission. These data then feed models of behaviour and management that can be used for prediction or analysis, expanding knowledge of a disease system. However, studying the behaviour of animals is no simple task, requiring intensive monitoring of individuals and posing different challenges depending on the species.

Techniques for the indirect, 24-hour monitoring of animal behaviour have advanced significantly in the last few years. From the humble origins of radio telemetry,

various wildlife tracking solutions have sprung up (Cochran and Brander 1969), becoming more advanced, easily available and cheaper over time. It is now be possible to design custom purpose GPS devices for research projects to gather exactly the information sought using a methodology that is tailored for the project (see below). In addition, there has been a large increase in the use of accelerometers to collect data on the behaviour of animals. Accelerometers provide far more comprehensive information than that from GPS-only collars and are capable of recording data at a far more intensive and prolonged rate than direct behavioural observations by an observer (Ravi et al. 2005). Accelerometers record movements via acceleration in m/s2 in up to three spatial axes. By observing an individual behaviour and validating recorded patterns of acceleration, it is possible to then derive whenever this behaviour occurs at a distinct period of the accelerometer data. The combination of GPS and accelerometers allows researchers to understand in far more detail how an animal moves around and uses its landscape (Brown et al. 2012). Movements present opportunities for inter or intraspecific interactions, which are the primary source of disease transmission events (Arthur et al. 2017). Despite the obvious importance of movements, in the past it has been difficult to both study and include these movements in models. On top of understanding the hosts or vectors, the dynamics and effects of the viruses themselves are still poorly understood. Understanding where outbreaks originate allows for better pre-emptive actions, stopping outbreaks before they begin. The generation of large quantities of these novel data however, necessitates the development and use of new computational techniques.

Accelerometer data in particular is generated at rates of many times per sec-

ond; this means that recording over a long period can quickly generate millions of data points. To manually classify all the patterns of behaviour across millions of data points would not feasible. When dealing with such big datasets, current methodologies are machine learning-based. Machine learning algorithms "learn" underlying patterns in the data to make predictions, using error to adjust a mathematical prediction formula (Bishop and Nasrabadi 2007). These require a training dataset of labelled data from which it can learn the patterns. The cutting-edge of machine learning algorithms is deep learning: using large amount of training data in methodologies that generally try to replicate how the brain learns. Accelerometer data are time-series data, and the current cutting-edge approach for time-series data is recurrent neural networks, a form of deep learning algorithm (Saleh, Hossny, and Nahavandi 2018). A recurrent neural network has an inbuilt state memory that is capable of taking the classification of the previous data point and using it to help make the next classification. This is commonly being used in behavioural classifications from accelerometer data, particularly from integrated exercise/sport-tracking devices such as smart watches and smart phones (Mannini and Sabatini 2010; Hirano and Maekawa 2013). Recurrent neural networks can classify the behaviour of individuals at a highly detailed level and give a summary of an individual's behaviour throughout the day. Once an individual's active behaviour is known, the way that it spatially moves is the next critical component to understand the whole picture.

Spatial analyses have become a mainstay of ecology (Fortin, Dale, and Ver Hoef 2016). The increase in the usage of GPS devices and satellite imagery means that finer scale understanding of the spatial behaviour of species is becoming possible.

Geographic information systems (GIS) have become a common tool for studying locations, as the costs of GPS have decreased and the accuracy of analysis has increased. Home range estimation from GPS collar data has advanced from minimum convex polygons, to kernel density estimates and now with further understanding of how one fix is not independent of the previous fix with the use of Autocorrelated Kernel Density Estimate (Fleming et al. 2015). This accounts for the fact that if an individual is in one location at one time, then the probability of being in any other location is dependent on the time and distance, so that no two GPS fixes in a time series are truly independent. This method leads to more robust estimation of an animal's home range. Habitat preference is also a common GIS analysis performed on GPS collar data. By linking individual locations to a habitat type, and knowing the available habitat breakdown, one can determine whether individuals have a preference for particular habitat types (Aarts et al. 2008). By understanding all these behaviours in vector species we can begin to understand how they can effect disease dynamics.

The traditional approach to understanding disease dynamics has been through the use of epidemiological modelling (Garner and Hamilton 2011). Models allows for the prediction or estimation of disease parameters such as the scale of epidemics or transmission. These use a standard framework of susceptible-infected-resistant (SIR),sometimes also including removed individuals (SIRR), where each individual is one of these four states and can transition between them as an infection spreads (Schneckenreither et al. 2008). Populations as a whole are then modelled in a series of matrix equations or differential equations with numbers of individuals in each state and transmission parameters describing the rate of change between

them. From such matrix models, one can predict the spread of a disease with a starting population size on the basis of the reproduction number of the disease. There are two types of reproduction number, the basic reproduction number or R_0, of an infection is the average number of secondary infections each case will cause while the effective reproduction number, or R_e, is the actual number of secondary infections depending on the current dynamics of the disease (Dietz 1993; Wilson 1996). Some SIRR models can be used to calculate R_0 when detailed outbreak data exist to back-cast the number of infected that occurred. These traditional models are used to trial disease management interventions (eg vaccination campaigns) by manipulating the number of susceptible or resistant individuals as a proxy for vaccination. This approach can miss many of the fine details, such as individual behaviours, which could be crucial to disease control (Bansal, Grenfell, and Meyers 2007). However, including these details can greatly increase the complexity of the model leading to less computational efficiency and longer run times, again requiring more computer power. Fortunately computers are advancing rapidly and models that would have once taken years to run before can now be done in days (Railsback et al. 2017).

With increases in computer power and availability of high-performance computer clusters, Agent Based Modelling (ABM, also referred to as individual based modelling) is increasingly used (Amouroux, Desvaux, and Drogoul 2008). ABM is a form of computational modelling for the simulation of individual agents and their interactions to see effects on the system as a whole (Coates and Schmid 1998). They are widely used for the modelling of infectious diseases (Pais et al. 2017). These have demonstrated that individual behaviours can have significant roles in

the spread of diseases, such as awareness of the infected status of other individuals, and enhanced transmission due to spatial use of resources in hotspots (Bonnell et al. 2010).

Nowadays we have the tools to not just unravel deeper mysteries of the disease system, but to predict computationally in far more detail than previously the impacts of disease management interventions. An ideal system to do this in is the Ethiopian wolf (*Canis simensis*) in the Bale Mountains of south-eastern Ethiopia, where viral diseases impact both people, their domestic animals and an endangered wild carnivore (Marino et al. 2013). With the availability of detailed historical behavioural and demographic data and fresh data on the movements of disease vectors, the Ethiopian wolf – domestic dog system is ideally suited for an ABM. By allowing individuals within the population to have varying demographic, behavioural or disease parameters, and to interact with other individuals within the system, ABMs provides a far more powerful or realistic representation of the system, giving insights into previously unknown properties and allowing far more detailed modelling, thus increasing predictive power.

The Ethiopian wolf (Figure 1.1) is endemic to the Afroalpine ecosystem of Ethiopia. It is the world's rarest member of the Canidae (family of wolves, dogs and foxes) and Africa's most endangered carnivore (Sillero-Zubiri, Hoffmann, and Macdonald 2004). There are fewer than 500 individuals left and none in captivity, surviving only in a few isolated Afroalpine enclaves above 3,000m asl (Marino 2003; Marino and Sillero-Zubiri 2011)(Figure 1.2a). The wolves are threatened by canine-borne diseases and loss of habitat due to the spread of subsistence agriculture and live-

stock grazing in Afroalpine ranges (Sillero-Zubiri, King, and Macdonald 1996; Laurenson et al. 1998a; Marino 2003; Johnson et al. 2010). Pastoralists are moving further up into the Afroalpine due to the pressures of an increasing demand on arable land and grazing pasture in the surrounding fertile highlands (Asresie 2015). The local Oromo population are primarily pastoralists, relying on meadows and moorlands for the grazing of livestock; indeed Ethiopia has one of the highest proportion of its population still reliant on grazing animals (Leta and Mesele 2014; Asresie 2015). Villages within the Afroalpine area are generally small hamlets, a collection of 2-20 households each typically belonging to a family, often with close family members occupying adjacent households. Most houses have a livestock paddock to contain the livestock overnight. Most of these villages are located on the edges of fertile valleys where the livestock then move to graze.



Figure 1.1: An Ethiopian wolf in the Bale Mountains National Park. Photo J. Foley

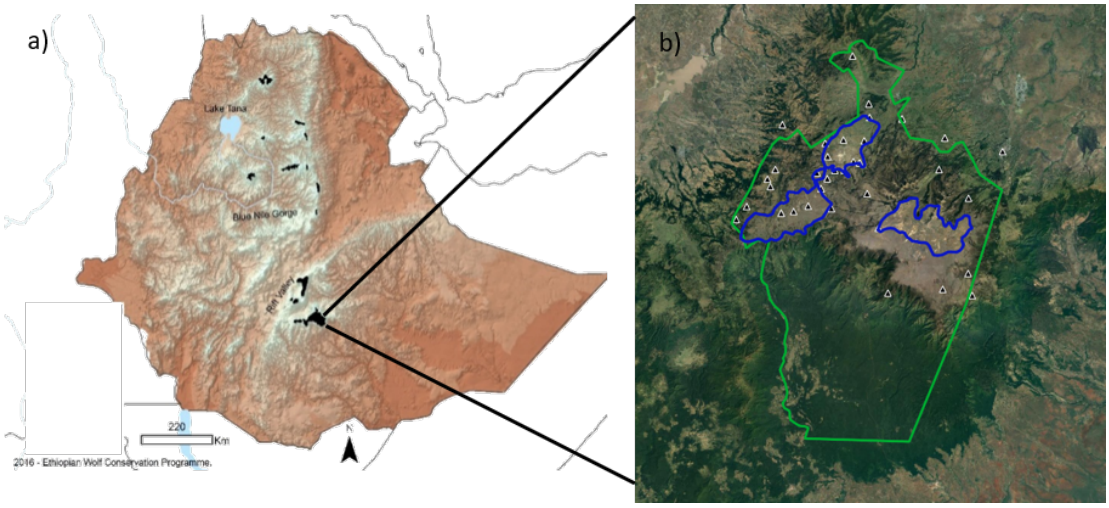

Figure 1.2: a) Ethiopia, with the Afroalpine ecosystem shown in black. b) Bale Mountains National Park indicated in green with village locations as triangles; optimal wolf habitat marked in blue.

Ethiopia's Afroalpine ranges are sometimes referred to as the "roof of Africa" (Kingdon 1990) rising in places to heights well above 4,000m (Figure 1.3). This height makes it much colder and wetter than much of the surrounding areas in Africa. This highlands are considered as a "Water Tower" for the whole of the eastern Africa region, providing water to much of Ethiopia and surrounding countries such as Somalia and Kenya (Viviroli and Weingartner 2008). Afroalpine areas in Ethiopia are biodiversity hotspots (Gehrke and Linder 2014), with higher number of endemic species than nearly any other area of equivalent size in the world, featuring an unparalleled variety of endemic bird species (Clouet, Barrau, and Goar 2000), a host of rodent species (Sillero-Zubiri and Gottelli 1995), iconic herbivores (e.g. mountain nyala, *Tragelaphus buxtoni*) (Evangelista, Norman, and Swartzinki 2012), an endemic primate (the gelada baboon, *Theropithecus gelada*) (Dunbar 1980) and the flagship of the Afroalpine ecosystem, the Ethiopian wolf (Marino 2003). The wolves are the primary predator of the abundant rodent populations,

particularly giant mole rats (*Tachyoryctes macrocephalus*) in the Bale Mountains, which are themselves ecosystem architects of the area, meaning that the wolves play a critical role in maintaining this delicate yet vital habitat (Sillero-Zubiri, Tattersall, and Macdonald 1995; Skilba et al. 2017). The abundant water and remote open land are what draws in pastoralists looking for fresh pastures to graze their livestock on. The world's largest population of Ethiopian wolves, ranging between 150-300 adults is found in the Bale Mountains National Park, with highest densities found in the Web Valley (Figure 1.2b). Up to 87% of the Afroalpine ranges where the wolves are found have been designated as protected areas (Ethiopian Wildlife Conservation Authority. 2017) but despite this designation, there is still large scale encroachment due to ineffective enforcement. Encroachment by pastoralists and their herds brings the wolves into contact with domestic dogs. (*Canis familiaris*).

The dogs living in Afaoalpine areas are owned by individual households, and although they are free-ranging they are not considered to be feral; however they often do not receive enough food at home and need to hunt or scavenge to supplement their diet (Atickem et al. 2010). In doing so village dogs perform a hygienic role around households eating garbage and human excrement (Atickem, Bekele, and Williams 2009). The dogs are free to roam out of the village and some are frequently sent out with the livestock into wolf habitat. This presents a valuable foraging opportunity but also allows for competitive interactions (Atickem, Bekele, and Williams 2009) with, and disease transmission to, the wolves and other wild carnivores. Dogs, and in some cases livestock (Jibat, Mourits, and Hogeveen 2016), are a reservoir of diseases that can spread to the wolves, particularly rabies and ca-



Figure 1.3: Afroalpine habitats taken in Webb Valley of Bale Mountains National Park. Photo J. Foley

nine distemper virus (CDV) (Sillero-Zubiri 1996; Laurenson et al. 1998b; Randall et al. 2004; Johnson et al. 2010; Gordon 2013)(. These diseases are lethal to both dogs and wolves, while rabies is also a significant threat to humans and livestock. When outbreaks occur among Ethiopian wolves, they can wipe out significant parts of the population and, in the smaller populations, lead to local extinctions (Haydon, Laurenson, and Sillero-Zubiri 2002; Johnson et al. 2010; Marino et al. 2017). This risk is compounded when outbreaks of both diseases occur concurrently or sequentially (Gordon et al. 2015; Marino et al. 2017). The wolves are social and live in close-knit social groups at high density (Marino et al. 2012), which means that diseases can spread at a rapid rate once an individual is infected (Haydon, Laurenson, and Sillero-Zubiri 2002).

Social behaviours create prime opportunities for the transmission of disease as they require direct contact between individuals; this has been shown to be particularly true with rabies in canids (Sterner and Smith 2006). The Ethiopian wolf is a pack living cooperative breeder. They live in close packs of between 2 and 18 individuals, depending on resource availability and territory size (Sillero-Zubiri and Gottelli 1995; Marino, Sillero-Zubiri, and Macdonald 2006; Marino et al. 2013). Unusually among social canids, Ethiopian wolves forage individually yet they engage in complex group greetings, allo-grooming, tandem mark patrols, and generally sleep in small groups (Sillero-Zubiri and Macdonald 2004). Each morning the pack wolves will greet each other, play and then patrol their territory border, scent-marking with urine and faeces, signalling their presence to other wolves (Sillero-Zubiri, Johnson, and Macdonald 1998; Van Kesteren et al. 2012). During the day, while foraging, they will often be in close proximity to each other in small parties of 2-3. A dominant pair breeds each year, producing between 1 and 7 pups, while most members of the pack assist with the raising of the offspring. During the breeding season, social proximity is even higher; often pregnant females solicit food off other pack individuals and the den site becomes a social hub, where individuals meet at the end of the day and socialise (Sillero-Zubiri and Macdonald 2004; Ashenafi et al. 2005), a potential hotspot of infection. The wolves maintain close proximity to each other, frequently contacting each other during interactions such as greetings and play, presenting numerous opportunities for transfer of rabies and CDV, along with intestinal parasites (Van Kesteren et al. 2015) and other diseases such as mange or canine parvovirus (Laurenson et al. 1998a).

Rabies is a highly lethal zoonotic infection, and a major threat to the health of people and animals globally (Hampson et al. 2015). Rabies and other closely related viruses are RNA viruses in the Lyssavirus genus, part of the Rhabdoviridae family. Extant rabies viruses are fairly recent in origin with estimations of their origins being within the last 1500 years (Nadin-Davis and Real 2011). It is particularly prevalent in Africa and Asia (Knobel et al. 2005) where the management programmes that have been used in developed countries are not employed (Scientific Panel on Animal Health and Welfare 2016; Ma et al. 2018). The virus infects the nervous system of mammalian species and in nearly all species the immune system is completely unable to fight off the infection. It is generally spread from one individual to another by bite as the virus replicates in the salivary glands as well as the nervous system, and then enters the body when a bite occurs (Jackson 2002). Rabies has variable incubation times depending on the host species and even within species; in dogs it is generally 2-8 weeks. This variability is due to how long it takes for the virus to begin initial reproduction, spread to, and fully infect the nervous system and brain (Jackson 2002). The virus causes many symptoms in the infected individual, including photophobia, hydrophobia, excess salivation, while the lethality comes from extremely high fever that damages the brain (Jackson 2002). Infected individuals can experience extreme behavioural changes, termed as furious rabies, with approximately 80% of infected dogs being furious while the remaining 20% experience "dumb" rabies that inhibits the nervous system leading to partial paralysis (Shuangshoti et al. 2016). If furious, an animal will become highly aggressive and attempt to bite any other animals that they come across. Sometimes this aggression is so extreme that individuals will engage in a "rabid run" where they travel large distances to attack and infect

any animals they can find until they finally succumb to the disease (Hueffer et al. 2017). Despite there being a proven and widely available vaccine (first developed in 1885), and not being a highly infectious disease, with a global reproduction number (R_0, the number of secondary infections from each case) of <2 (Dietz 1993; Kaare et al. 2009), rabies has proven to be difficult to eliminate possibly due to the many host species, including nearly all warm-blooded mammals (Knobel et al. 2005). Within Ethiopia rabies has a higher incidence than in most African countries (Aga, Hurisa, and Urga 2016), most likely due to the high prevalence of domestic animals and livestock as a source of zoonosis, with some possible external sources such as bats or wild carnivores. In Ethiopia rabies is responsible for the deaths of approximately 2,600 people each year, a rate far higher than that observed elsewhere (Jemberu et al. 2013). On top of lives lost, rabies in Ethiopia has an economic cost on the people, with an incidence rate in cattle of between 11% and 21% and can cost herders up to USD $1,000 in a year per household, representing a significant amount of lost income (Jibat, Mourits, and Hogeveen 2016).

Canine distemper virus is a single strand RNA virus of the Paramyxoviridae family along with similar diseases such as measles and mumps. These viruses are extremely widespread and found in numerous animal host species and some are capable of becoming zoonosis and infecting humans (Thibault et al. 2017). In recent years there has been a rise in the number of cases of CDV spilling over from domestic dogs and cats to wildlife all over the world (Nagao et al. 2012; Sakai et al. 2013; Feng et al. 2016). This is most likely due to the increase in the number of domestic dogs, and stray dogs as well as the interconnectedness of populations thanks to human movements. CDV, despite its name, can cross species

and even genera boundaries easily, and it has been found to infect a wide range of species, some highly endangered, all over the world, including the Iberian lynx (*Lynx pardinus*) (Millán et al. 2009), rhesus macaque (*Macaca mulatta*) (Sakai et al. 2013), and Caspian seal (*Pusa caspica*) (Kuiken et al. 2006). CDV has been particularly damaging to threatened canid species such as the island fox (*Urocyon littoralis*)(Timm et al. 2009) and African wild dog (*Lycaon pictus*)(Prager et al. 2012). Unlike rabies, CDV poses a different threat in that it does not require direct contact to be spread between individuals. CDV is spread through bodily fluids, generally mucus, and can survive outside the body in fluids left behind (generally urine or faeces) or even the soil for quite some time, particularly in cold environments (Appel and Gillespie 1972). If the virus is then inhaled by an animal that investigates these fluids, or accidentally ingests them, then the virus will infect that individual (Beineke et al. 2009). While CDV itself does not directly result in death in many species, it weakens the immune system leading to fatal secondary infections with pulmonary infections as the most common (Appel and Summers 1999). In general CDV is not as lethal as rabies but due to its method of transfer, and the ability to persist in the environment it is more infectious. Long-term monitoring data of Ethiopian wolves in the Bale Mountains has shown recurrent CDV outbreaks, indicating that the wolves are highly susceptible to CDV and experiencing high lethality when infected (Gordon et al. 2015).

There have been several major catastrophic disease outbreaks recorded in the Bale Mountains over the last three decades (Figure 1.4). The first in 1991 led to the deaths of 41 out of 53 known individuals and demonstrated the threat that rabies can pose to the species (Sillero-Zubiri, King, and Macdonald 1996). During the

next main rabies outbreak reported, in 2003, the first vaccination intervention was trialled, with the capture and vaccination of at-risk wolves (Randall et al. 2006). There were other rabies outbreaks in 2006, 2008, and 2014 with local declines of between 50-75%, followed by a more or less rapid recovery (Johnson et al. 2010; Marino et al. 2013). Reactive interventions to create a cordon sanitaire of vaccinated wolves were also implemented in 2008-2009 and 2014-2015 (Ethiopian Wolf Conservation Programme 2019). For the first time in 2008 the origins of the virus could be determined through sequencing techniques (Marston et al. 2015). Two major outbreaks of CDV in 2011 and 2015 showed that this pathogen can also cause high mortality among Ethiopian wolves, for which a vaccine is currently undergoing trials (Ethiopian Wolf Conservation Programme 2019). The threat to the continued existence of the wolves and the need for study and monitoring lead to the establishment of the Ethiopian Wolf Conservation Programme (EWCP) in 1995 which has been working to protect the wolves from these diseases using a variety of management strategies (**marino2011**; Ethiopian Wildlife Conservation Authority. 2017). There has been considerable work toward the development of an integrated disease management plan that uses multiple management techniques with a focus on vaccination ((Randall et al. 2006; Ethiopian Wolf Conservation Programme 2019), and an integral part of the National Action Plan for the conservation of the Ethiopian wolf (Ethiopian Wildlife Conservation Authority. 2017). The work developed in this thesis offers a contribution to these management aims.

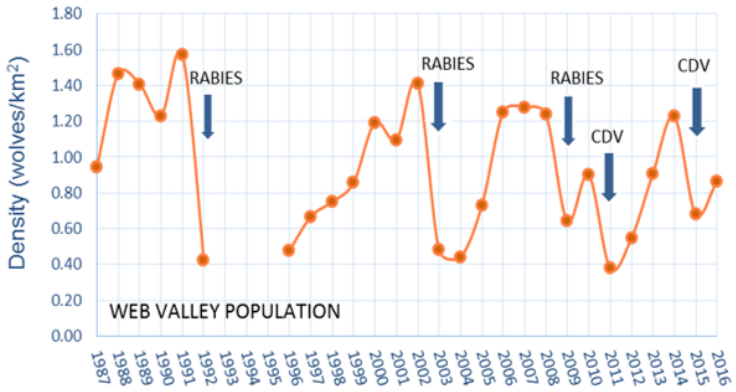

Figure 1.4: Ethiopian wolf population density over the last 30 years with known outbreaks marked when they occur. Credit Ethiopian Wolf Conservation Programme (2016)

As the most common source of rabies and CDV in Ethiopian wolves, EWCP periodically vaccinates domestic dogs against rabies, in and around wolf habitats, and against CDV in key areas of Bale Mountains National Park. While domestic dogs being the primary source of disease to the wolves is an assumption it is backed up by genetic evidence and the dynamics of the system. The system itself has a very low density of other carnivore species that could be a reservoir of the diseases, while the density of domestic dogs is extremely high with them being one of if not the most abundant carnivore in the area meaning that they are the most likely source by sheer numbers. This is contrasted to other ecosystems where dogs are not the most common carnivore and there are large populations of other carnivores which can be a reservoir of the diseases. While there are bats in the area they are unlikely to be the source of rabies as phylogenetic work on the rabies virus in the Ethiopian wolf found it belongs to Africa-1a lineage of rabies viruses most commonly from domestic dogs (Marston et al. 2015). Phylogenetic work on CDV showed that samples from a previous outbreak clustered closer to viral sequences

from CDV in China than even from neighbouring Tanzania (Marston et al. 2017) which suggests that the outbreak did not come from a local source, such as one of the other carnivores, while domestic dogs often travel around Ethiopia.

To prevent outbreaks of rabies, WHO recommends a vaccination threshold of 70% (World Health Organisation 2013), which is customarily achieved by EWCP vaccination campaigns around the wolf habitat in Bale (Ethiopian Wolf Conservation Programme 2019). However, with the high turnover of dogs observed in the Bale Mountains, maintaining this threshold does not last, and periodic outbreaks still occur. Other methods of disease control have been suggested such as restricting the number of dogs in wolf habitat (Ethiopian Wildlife Conservation Authority. 2017) or reducing human encroachment (Nelson 2011), but it has proved difficult to actually implement any of these suggestions. Any form of human behavioural change is difficult to achieve due to perceptions of livestock predation and the perceived impact change will have on livelihood (St. John, Edwards-Jones and Jones, 2010). The situation in Bale, and the concerted efforts by EWCP and others to combat viral disease there, offers a good example of a "One Health" approach, where veterinary medicine, human medicine, and wildlife research can all be accomplished in a single project (American Veterinary Medical Association 2008). Prevention of disease in domestic animals and wildlife can help to protect people from disease and prevent the loss of livelihoods that goes with it. One Health initiatives are increasingly adopted by governments and private agencies with the goal of uniting human and veterinary medicine. One Health has been gaining increasing traction worldwide as a method of approaching health, from the view of the system as a whole rather than focusing on individual species and the dis-

eases occurring within them, with particular emphasis on antibiotic resistance and zoonotic diseases (Robinson et al. 2016). This approach has many benefits over traditional human or veterinary medicine, using a far more realistic viewpoint by considering the myriad of interactions that exist in a system. So far, few systems have tested whether this is a successful approach to disease management including Ebola in the Democratic Republic of Congo and Rift valley fever in Tanzania (Coker et al. 2011). While the Ethiopian wolf presents an ideal system to test this paradigm, designing strategies that utilise One Health principles, however, require a deeper understanding of the system and a novel approach to management.

Currently, vaccination of Ethiopian wolves only occurs reactively when there is an outbreak of disease in an area, but a proactive approach may well prevent outbreaks before they spread (Haydon et al. 2006). An oral vaccine for rabies was successfully trialled in the wolves (Sillero-Zubiri et al. 2016) and trials of a parenteral CDV vaccine are ongoing; these could be used in a preventive manner, before outbreaks occur. With this proactive approach as part of a possible solution to disease mortality, it is now a priority to understand how we can best apply all these tools in developing successful disease management strategies and inform policy. This first requires a greater understanding of the dynamics of disease vectors in the system, particularly how dogs and wolves move through the landscape and interact. Vector behaviour and movements are the principal components of disease transfer and require intensive data collection to understand them fully. The first step in studying animal behaviour is being able to find and track individuals.

An ABM of wolves and dogs has applications beyond just understanding disease

dynamics in these species. Management strategies such as vaccination thresholds or limits to dog coexistence with the wolves can be explicitly simulated. This can be done much faster and cheaper than experimentally trialling management strategies and then scaling them up. As with any model, this is not the real world at work but a representation of the system, based upon assumptions and hypotheses, but these simulations and recommendations can be useful to guide trials or possible intervention strategies. This technique has applicability in a range of systems beyond the Ethiopian wolf and this work serve as a proof of principle for a methodology which could speed up the implementation of wildlife disease management worldwide. ABMs have been criticised for their large data requirements and for using uninformed guesses to match reality when these data are not available (Beikirch et al. 2018). Fortunately, with three decades of data to draw upon, the Ethiopian wolf system is ideal for accurate parameterisation. There have also been criticisms on the use of ABM for causal inference (Grüne-Yanoff 2009), but this has been widely refuted by the modelling community (Niazi, Hussain, and Kolberg 2017) through the simulation of counter-factual scenarios (El-Sayed et al. 2012). What is needed for Ethiopian wolves is the simulation of management not an understanding of causation and an ABM is has the capability to provide informed results.

Outputs from previous modelling by Haydon et al. (2006), suggested that low coverage vaccination strategies of the wolves would be effective in reducing or preventing rabies outbreaks. An ABM of Ethiopian wolves can go beyond to investigate this threshold of vaccination and numerous others, with more accurate representations of the wolf and dog behaviours. The effectiveness that past and

current management has had on population persistence can be directly modelled to evaluate success. The relative effectiveness of dog vaccination and preventative wolf vaccination can be compared. The cost of management interventions can be directly incorporated into the model so the cost-effectiveness of dog or wolf vaccination can be assessed to not just see which is more effective but where money should be directed to. How robust these predicted management strategies would be to variability in parameters, such as population dynamics, can also help to inform future management. Below I outline the process by which I went about collecting the necessary data, constructing a model, delivering model outcomes, and discussing their application.

Thesis Outline

Chapter 2: Open source, low cost modular GPS collars for the monitoring and tracking of wildlife.

The process by which custom GPS collars can be built using the open source Arduino microelectronics platform. These can be customised to collect specific data as required and the housing can be 3D printed to best fit the components or the species it is being placed on.

Chapter 3: Who let the dogs out? Habitat use and behaviour of domestic dogs, a primary source of disease in Ethiopian wolves.

Using the custom-built GPS collars to collect behavioural data on domestic dogs in the Bale Mountains. GPS analysis and deep-learning on the accelerometer data were used to determine home ranges, habitat preference, movement speeds and

hourly time allocation of specific behaviours.

Chapter 4: Spatial and temporal overlap of Ethiopian wolves and domestic dogs: implications for disease transmission and management.

Using data from long-term monitoring of Ethiopian wolves in Bale Mountains to quantify home ranges, habitat preference, movement speed and hourly breakdown of behaviours. This was then used with the dog data from Chapter 3 to quantify the overlap between the two species, both the spatial use and the temporal behavioural breakdown.

Chapter 5: A scalable agent-based model of viral diseases in Ethiopian wolves and the primary host, domestic dogs.

Construction of an ABM of Ethiopian wolves, domestic dogs and diseases in the system. The model was parameterised using the data from Chapters 3 and 4 and available epidemiological data on the diseases. It was then validated against previous outbreak and demographic data collected on the wolves.

Chapter 6: Recommendations from in-silico trials for integrated disease management for Ethiopian wolf protection.

Using the model from Chapter 5 to simulate null, current and possible management scenarios. Simulations included restricting dogs' movement to certain distances from their household and a large parameter sweep to find the optimal vaccination strategy, not just for effectiveness of controlling disease but also cost-effectiveness.

Chapter 7: Discussion

Synopsis of the results and discussions on the broader applicability of the key results on the wider fields of behavioural ecology, conservation and epidemiology.

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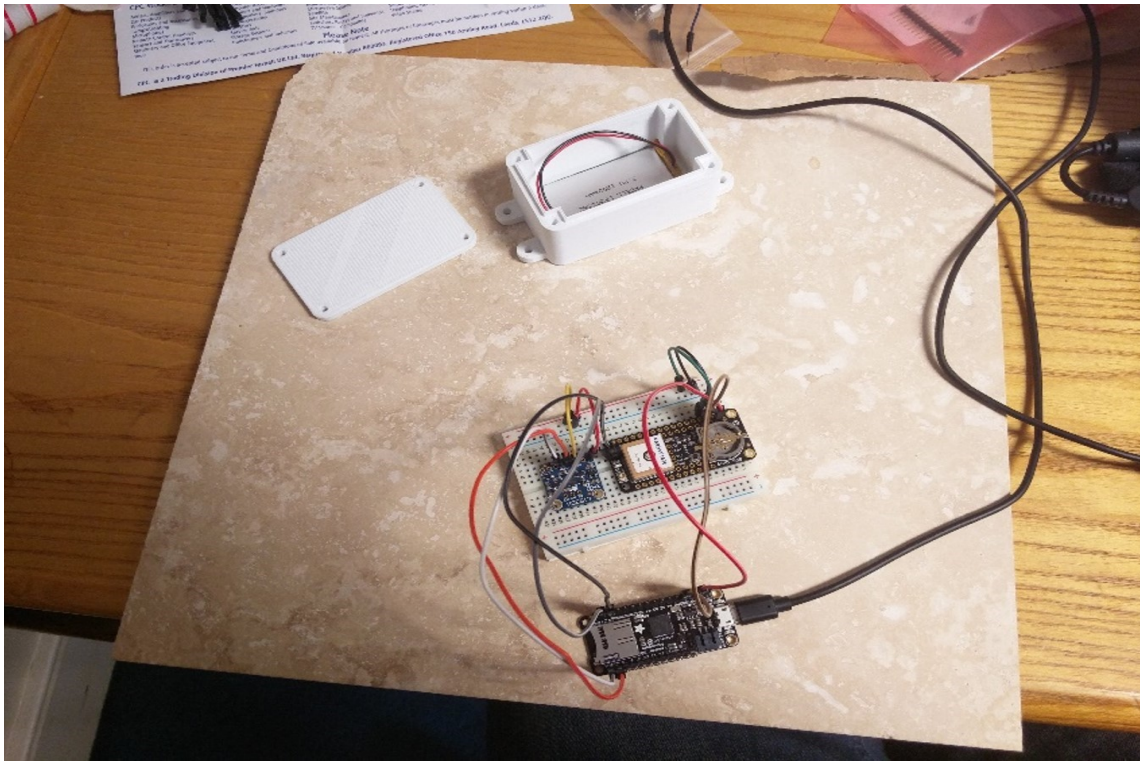
Chapter 2

Open source, low cost modular GPS collars for the monitoring and tracking of wildlife.

This chapter is currently in press in *Methods in Ecology and Evolution* as Foley & Sillero-Zubiri (2019).



2.1 Abstract

Monitoring the movements and behaviour of wildlife using radio telemetry or GPS devices has been critical to the fields of ecology and conservation over several decades. For many field projects however, commercially available devices can be expensive and may not always be ideally suited for collecting desired data. I present a low-cost solution of customisable tracking devices based on the open source Arduino system. These devices can be custom designed for specific studies and easily programmed to collect desired data. Custom-built collars with GPS and accelerometer units were trialled on 30 free-ranging domestic dogs in rural Ethiopia. These collars collected high-resolution data at a frequency of 10 fixes per hour and accelerometer data at 10hz over a 10 day period, at a cost of approximately £100 ($130 USD) per collar. These devices can be placed on any species that can handle a weight of 15.4g plus battery and housing. The current configuration weighs approximately 240g which would be suitable for any animal above 8kg living in terrestrial environments.

2.2 Introduction

GPS technology, pioneered in the 1990s (Wingenroth 1993; Rempel, Rodgers, and Abraham 1995), was transformative for wildlife telemetry. These devices give highly accurate location data through triangulation by satellites, without need to track the individuals on the ground or from the air. Data collected from GPS collars is increasingly becoming a powerful tool for the research and monitoring of animals. GPS data can be used to determine animals' home ranges, daily activity patterns, habitat utilisation and has applications in planning for the management of species (Morris 2003). With the rise of big data and machine learning (Goldberg and Holland 1988; John Walker 2014), our ability to analyse increasingly large or complex data, obtained during GPS collar studies of wildlife, has dramatically increased.

Modern GPS collar technology can now capture information from wildlife that was not previously accessible or utilised in scientific research such as audio signals, accelerometer data or video which allow classification of behaviours and interactions that were not possible with earlier GPS collars (Moreau et al. 2009). Accelerometers measure the force of acceleration in three axes which occur when the sensor is moved. By correlating to individual behaviours, patterns of acceleration can be validated and extrapolated across the full data. From this, behavioural patterns can be recognised (Ravi et al. 2005) and daily activity patterns and other metrics of collared individuals broken down, in far more detail than previously possible. Accelerometers record data up to hundreds of times per second and constantly throughout the day, which is impossible with direct behavioural observations; al-

lowing an understanding in far more detail of how an animal moves and uses its landscape (Brown et al. 2012)

Significant recent advances in wildlife telemetry have made GPS collars readily available and less expensive due to reduction in prices in the components, mass production and increased competition from newer companies (Hebblewhite and Haydon 2010; Thomas, Holland, and Minot 2011; Jung et al. 2018). GPS tracking devices are becoming the standard in wildlife research and monitoring work. However, commercial wildlife devices can still cost thousands of dollars each depending on the study species and required features, due to the need for custom-built species-specific devices; companies need to recoup costs for research and development, and typically lack a market to scale up production. This represents a high cost for any field study and can prove to be even more difficult for wildlife projects where GPS collars are a prerequisite and funding is limited and highly competitive. Globally there is an increasing need for wildlife monitoring and lower cost devices provide an opportunity to alleviate some of the financial burden that comes with the requirement to purchase GPS collars. This has implications for any projects working with wildlife, allowing larger projects to monitor many more individuals, or institutions in developing countries and NGOs with limited funding to begin their own monitoring projects.

Until recently, the only options for wildlife telemetry were generally the high cost commercial solutions that often included sensors recording unnecessary data or were missing sensors for recording the specific data a project relies on, requiring further modification. Customisation of commercial devices to allow for collection

of specific data types, such as raw formats, or at desired frequency to meet the requirements of a specific study or species is possible with direct consultation with the manufacturers. However, this customisation generally comes at an increased expense while lower cost commercial devices come at the price of heavily reduced features (Jung et al. 2018). To avoid expense or to gain features there has been a rise in recent years of researchers building their own devices (Clark et al. 2006; Fischer et al. 2018). This has generally come with the caveat that researchers have worked with engineers or computer scientists to develop devices that are highly specific and difficult to replicate (Wijers et al. 2018).

Thanks to the development of open source microelectronics platforms such as Arduino, Raspberry pi and Micropython it is now possible to build these devices with little previous knowledge or experience of electronics. Being open source, there are numerous manufacturers competing to produce the chips, driving costs down, and a wealth of examples and guides with which to programme devices. These platforms are designed to be modular and have chipsets for almost any purpose. Modular GPS collars based on these can be designed from inception to contain components that collect specialised data, which allows for optimisation of programming and structural design. This provides a low-cost means to develop custom devices for a research project without expert domain knowledge and could help improve and expand wildlife telemetry globally. The objectives of this chapter are to describe the construction, testing and usage of one such device based on one of these platforms that is capable of being easily replicated and modified by almost any user.

2.3 Methods

I constructed custom-built GPS collars with accelerometers using the open source electronics and programming platform, Arduino (Fisher and Gould 2012). The primary component of the device was a MicroController board with an onboard micro SD card storage. There are varieties of such Ardunio boards that are compatible with the devices, depending on the storage, power, shape, species weight or size requirements of the project. The MicroController used in this trial was an Adafruit Feather m0, weighing 5.3g and measuring 47mm x 28mm. Soldered onto the board was a separate GPS board (an Adafruit Feather GPS Breakout) with a GPS chip with 66-band antenna and a backup 3V 250mAh button cell battery, weighing 8.8g and measuring 47mm x 28mm. Wired onto the processor board was an Adafruit LIS3DH 3-axis accelerometer, weighing 1.3g and measuring 25mm x 25mm. The test units were powered by a 4400mAh rechargeable Lithium ion battery pack (weight 98g). It should be noted that any size battery with a JST connector or a micro USB can be used depending on the power or weight requirements of the study or species that the device will be deployed on. The battery will often be the bulkiest and heaviest component of the device. Each component draws a specified power during usage, the lowest being the accelerometer which draws 2mAh during usage, the GPS board had the highest power usage at 20 mAh while active, the microprocessor draws 11mAh while writing to the SD card.

To protect the components from damage I designed a custom plastic housing, 3D printed with a Makerbot Replicator 2 printer (build volume of 28.5 x 15.3 x 15.5 cm, https://www.makerbot.com/)(Figure 2.1). The 3D printed housing was then

coated in a clear polyester resin that helped increase the weather resistance of the housing and provided added durability; the housing was sealed with a lid around which a rubber seal was glued to ensure water could not get in. The housing for the test units was attached to a conventional durable leather dog collar fastened with a metal buckle. The housing of these devices was specifically designed for use on free-ranging domestic dogs which were highly aggressive to conspecifics wearing collars requiring protection from bites. Depending on the species or environmental requirements, different housing solutions could be applied, and 3D printing allows complete customisation.

I programmed the devices using the Arduino repositories based on the C++ language (Stroustrup 2000). The programming allows for the frequency of data collection to be easily changed by altering parameters in the setup code for both GPS and accelerometer individually. If desired, devices can be programmed to sleep if there was no movement detected in the accelerometers over a user defined time period to improve battery life.

The completed test collars were extremely lightweight (240g), with nearly all the weight associated with the strap and battery (Table 2.1); there is further potential to reduce weight by using different components, smaller batteries, housing or straps. The total weight of these collars was similar to commercially available products for the same species size that vary between 200-300g. Figure 2.2 provides full step-by-step instructions for construction of the electronics. Code, specifications and construction instructions are available in the supplementary material or online.

Table 2.1: Cost and weight specifications of each component in the trialled devices.

Part	Cost (£)(USD)	Mass (g)	% Of Total Mass
MicroController board	22.50 ($29.25)	5.3	2.2
GPS board	40.00 ($52.00)	8.8	3.6
Accelerometer	9.40 ($12.22)	1.3	0.5
Battery	4.00 ($5.20)	95	39.5
Micro SD	3.00 ($3.90)	0.5	0.2
Collar	13.75 ($17.88)	118	49.1
Plastic Housing	4.00 ($5.20)	11	4.5
Total	96.65 ($125.65)	240	100

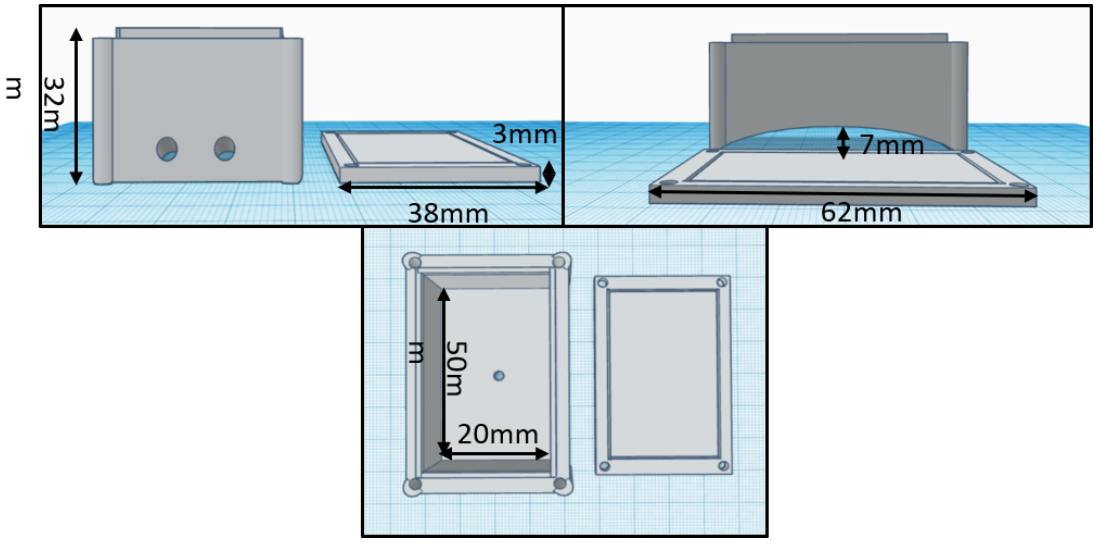


Figure 2.1: 3D model used for the 3D printed housing. A rounded bottom was used to better fit the housing with the curve of the neck. Four 3mm screws connected the lid to the body of the housing. Two larger 4mm screws on each side went through the leather collar to attach the housing.

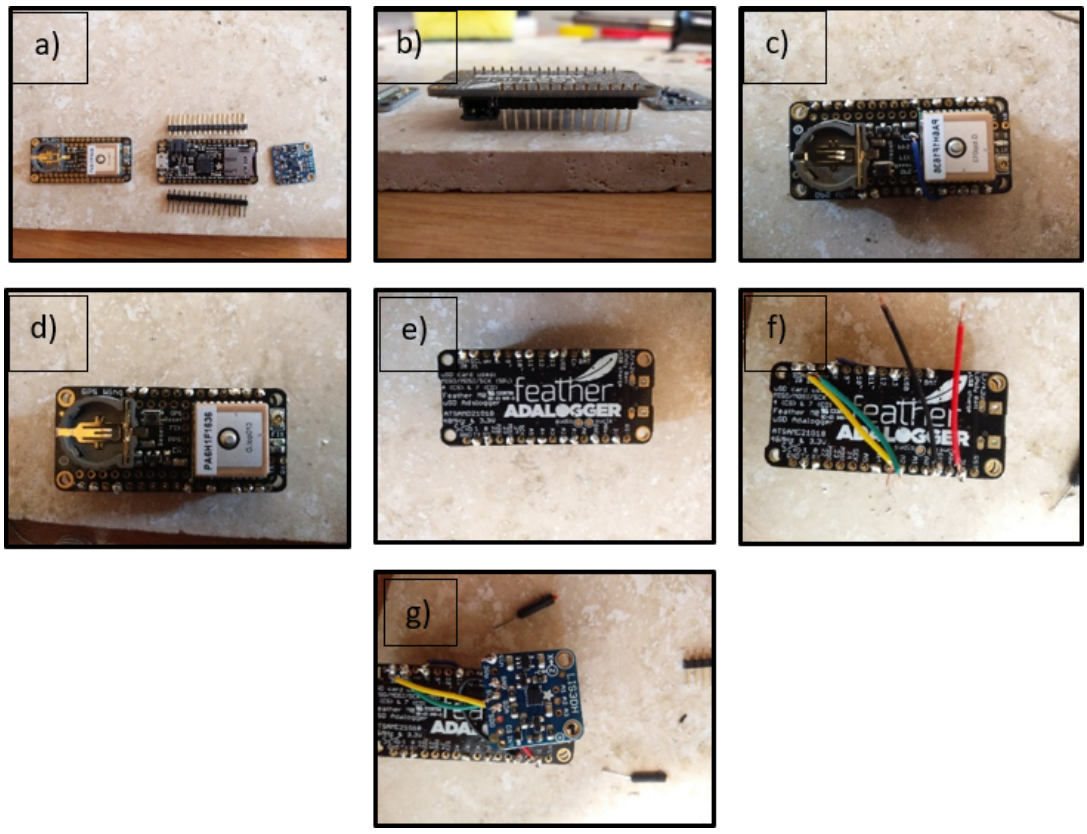


Figure 2.2: a) Starting components from left: GPS board, MicroController board with header pins, accelerometer. b) First step was to place the header with the smaller pins through the controller board. c) Solder the pins into the board making sure that at least the gnd, 3V TX and RX were securely connected. d) Solder the GPS board onto the longer pins above the controller board. e) Solder a wire that connects a data pin in the controller board to the enable pin in the GPS board. f) Solder wires onto the 3V (red) gnd (black), SCA (green) and SDA (yellow). g) Solder the wires into their corresponding pin on the accelerometer.

2.3.1 Performance Evaluation

The performance of the devices was evaluated using similar measures to Jung et al. (2018). Overall performance was taken from deployment success rate, measuring

how many devices were working on deployment, and the early failure rate, measuring how many of the devices stopped collecting data earlier than expected. The GPS was evaluated using the fix success rate, determined by the proportion of failed fixes out of the total number of scheduled fixes for each device. A fix was determined to have failed to be acquired if after three minutes the device was not providing a latitude and longitude and this was recorded in the data as "No Fix". The accuracy of fixes of the device, being the error of each fix measured in meters was calculated using the horizontal dilution of precision (Langley 1999) (HDOP), a measure of the impact of satellite position on accuracy, as 2 X mean HDOP X device accuracy. HDOP measurements are provided by the chips inbuilt software using the transmitted location, angle and number of satellites. The quality of accelerometer data was examined using a K statistic cut off method based on distance between points and mean amplitude, clustering the differences together to see if there are clusters of data which are extremely different from the mean (Slaven et al. 2006). Accelerometer drift was tested by looking for consistent shifts of measured acceleration over a long recording period.

2.3.2 Performance of Free Ranging Dogs

Twenty-five of these devices were constructed and deployed on 30 domestic dogs in two separate deployments; 12 in the wet season (March to October) and 18 in the dry season (November to February) in the Bale Mountains National Park of southern Ethiopia. Here dogs are owned, but are free to move in and out of their villages, and thus considered free-roaming, where they act as a vector of disease for the Ethiopian wolf (Canis simensis)(Laurenson et al. 1998). At 240g, collars did

not exceed 3% of the animal's weight, which is a recommended threshold (Wilson 1996; Sikes 2016). In this trial anaesthesia was not required for collaring, the help of the dog owners was recruited to handle them. The collars were programmed to collect high-resolution data, with GPS fixes on a 6-minute interval and accelerometer at 10 Hz over a 10-day period with the devices not programmed with a sleep function. These devices were programmed to collect data over a short period, as the high intensity data was a feature of this study. However, these devices can also be used over longer time periods and collect data at different rates depending on the requirements of the project. The devices themselves are capable at recording data in the GPS at up to 10Hz and 5kHz in the accelerometer and should be adjusted as per the needs of a study.

Across all the deployments only one device did not record data and was deemed to be a failed deployment, a further 6 devices during deployments failed early, providing a total deployment success rate of 77.6% (23/30). This was comparable to many commercial devices (Habib et al. 2014). A comparison of commercially available collars deployed on Australian mammals by Matthews et al. (2013), found that 48.6% of collars deployed failed early, with 30% of collars having intermittent failures during deployment. However, Jung et al. (2018) had an 89% overall deployment success rate on over 100 collars of a single brand and type deployed. Collins et al. (2014) compared custom devices to commercial devices where their custom devices had a high failure rate (7/8) which suggests that the devices trialled here may be more reliable than other custom devices but does highlight the risk that could occur with custom devices. During deployment there was a mean fix success rate of 99.57% $\pm$ 0.15% with a range of 98.4% - 100%, however the study

area was in an open high altitude area and acquisition rates may be lower in dense canopy forests (Vance et al. 2017). The devices are capable of a 1.8m accuracy of fix however, with a mean HDOP error of 4.9 ± 4.2 the mean fix accuracy was 14.76m, this HDOP error is slightly higher than the mean of many commercial collars at 3.0 (Matthews et al. 2013). Some 98% of data were clustered together in a K score of < 10 indicating a large proportion of high-quality data. There was no evidence of drift in accelerometer data at the programmed frequency of collection however, any drift that might be occurring would have been removed during analysis as it passed through a high pass filter prior to analysis (Takeda et al. 2014). The frequency of data collection chosen in this study, at 10Hz, is lower than many other accelerometer devices however, with the advent of more advanced machine learning methods this is becoming more than sufficient for behavioural classification, with classification now being possible with as low as 1Hz (Studd et al. 2019).

The 3D printed housing was resilient enough to take impact from the dogs including biting by con-specifics, movement through rough terrain and mud, and exposure to varied environmental conditions including high and low temperatures (-8°C to +28°C) and heavy rain. All housing survived the deployment without being pierced or breached by water. Despite the lack of apparent damage to the housing it is possible some of the failures were caused by impact from con-specifics as noted for other species (Jung and Kuba 2015), but this could not be explicitly tested for. The housing can be used in harsh conditions and could be deployed in a variety of other environments, including both hot and cold areas. However, the device would most likely need to be adjusted if used in aquatic environments or if there is a high

likelihood of prolonged submersion. 3D printing allows the user to customise the size, shape and attachments of the housing to be varied, based on what is needed and is a key tool in the modularity of the devices.

2.4 Discussion

Under the data collection parameters the collars were drawing a total of approximately 7.77 mA, which would allow for a maximum battery life of 23.6 days at this sampling rate. The GPS is the largest power draw accounting for 6.66 mA or 85% of the power draw. If the GPS sampling rate was reduced to 1 fix per hour there is a hypothetical battery life of 103 days under a 1.77 mA draw. There is a possibility that battery life was hampered by the large temperature oscillations in the Ethiopian highlands (varying between -8°C to +2°C over 24 hrs), the batteries performed below estimates made from usage in a stable environment in the United Kingdom however this was not tested. While the estimated battery life is lower than many commercial GPS collars, which often state multi-year battery lives, further improvements and efficiency changes in the programming may bring this up to competitive levels. Magnetometers have become commonly used in conjunction with accelerometers as they can assist with calibration and provide a wealth of added features for behavioural classification; they were not trialled in this device for space, weight and power reasons but would make an excellent complement to other such devices.

The devices trialled had no satellite or radio reporting components, meaning they were required to be collected from the collared animals and data downloaded from

the onboard SD card; however, these could be added by attaching further components such as a radio transmitter depending on size limitations. GPS reporting would require a satellite network subscription. An easy addition of a GSM board would be capable of sending the data in a text allows the devices to not require collection or satellite subscription at a low cost if this is required and relevant GSM networks are available. It should be noted that accelerometer data rapidly becomes very large due to the high frequency of data collection and will likely be too large to send via GSM. It may be better to send GPS location data via GSM and then supplement it with the accelerometer data once the device can be recovered. There are also post-processing algorithms that can be part of the device programming which can extract summary statistics or, using pre-calibrated classifiers, even behavioural classifications which can then be sent over GSM instead of the raw data. It is important to note that these algorithms require both memory and processor capacity within the device so must be lightweight and will come with an increase in power draw.

2.4.1 Conclusions

The custom-built devices reported here are a simple proof-of-concept of a modular device that can be customised and built from the ground up to fulfil the exact needs of a given study. With the use of 3D printing, customised housing can be as light or resilient as required and be shaped ideally for the species that it is being deployed on. The components used in these devices are relatively inexpensive and readily available from numerous retailers. Little background knowledge is needed to construct and programme a working device and a large deal of support

is available online including guides, tutorials and help forums. There is still much scope to improve upon the basic devices presented here and the device concept represents a platform that could be widely used across numerous research areas. The inexpensiveness and high usability of the devices mean that there is an opportunity for a far greater level of wildlife monitoring in many systems without incurring a large cost.

2.4.2 Ethics Approval

All work in this paper was performed under full ethical approval after review from Oxford University and an approved permit from the Ethiopian Wildlife Conservation Authority. Permission to collar the free roaming dogs was granted by the owners of the dogs after conversations with them about the aims of the study. These conversations represent informed consent on the part of the dog owners, who all reside within Bale Mountains National Park and have experience with the research aims of the larger project through the dog vaccination campaigns. Only owners who gave consent had their dogs collared and collaring was performed during handling that was for routine vaccination. Many owners were able to place the collars on their own dogs.

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Chapter 3

Who let the dogs out? Habitat use and behaviour of domestic dogs, a primary vector of disease in Ethiopian wolves.



3.1 Abstract

Domestic dogs are increasingly recognised as a threat to many threatened species. In particular, they are key hosts of rabies and canine distemper virus (CDV) that have been shown to infect wildlife species globally. Ethiopian wolves face a clear and present risk from domestic dogs, as they suffer from periodic outbreaks of both diseases. Using custom built GPS data loggers, I collected data on the movements and behaviour of 26 free roaming domestic dogs that travel and forage daily within wolf habitat in the Bale Mountains National Park, South-eastern Ethiopia. These data were analysed for home ranges, habitat preference, and movement speeds, using deep learning analysis to classify behaviours and understand high risk areas and times of the day for disease transmission to the wolves. Domestic dogs spent the majority of their time in their villages or within 1.2km of their village; fixes outside of the villages were on average 727m (SD = ±79.36m) away during the dry season and 538m (SD = ±94.82m) in the wet season. Individual home range sizes averaged ∼3km2 (SD = ±626m2). They displayed clear habitat usage patterns, favouring grassland and drainage lines. Most of their time was spent resting (52%, range 35% - 70%), with two peaks of activity in mid-morning and mid-afternoon. The area within a 1.2km radius from villages would have the highest risk for disease transfer as well as the habitat preferred by dogs, particularly if wolves show similar preferences, because of higher probability of contact with wolves. Opportunities for disease transmission will also be high during dog Peak active hours, either through increasing contact whilst travelling or leaving infectious residue in foraging hotspots.

3.2 Introduction

Diseases are often transmitted between wildlife, domestic animals and humans at the interface where they overlap (Lloyd-Smith et al. 2009). While much of the focus of study is into zoonotic diseases where wildlife or domestic animals can transmit diseases to humans (Greger 2007; Graham et al. 2008) in many situations domestic animals are acting as a disease source to endangered species (Alexander and Appel 1994; Michel 2002). Understanding the behaviour of the domestic animal sources is a critical step in understanding the transmission of diseases into endangered species. Diseases can have multiple different hosts, each with their own distinctive pattern of behaviour and movements across a landscape (Ostfeld, Keesing, and Eviner 2008). Thus, infection rates among species would differ and without understanding these patterns, predictions or control measures could be dramatically inaccurate and ineffective.

An individual's behaviour over the course of the day and in different locations can prove important in terms of disease transmission (Bansal, Grenfell, and Meyers 2007). The movement of an infected host will determine the spatial overlap while time allocated to different behaviours will determine the temporal overlap. While foraging, an infected host can leave disease traces across a landscape in the form of infected saliva, faeces or urine; reproductive activities such giving birth can also leave infectious residue (Wambua et al. 2016). Resources that are consumed by multiple individuals, such as water sources or carcasses, could be a potential source of infection due to transfer of fluids (Bonnell et al. 2010), and this is especially the case for canids and felids, who are particularly driven by olfaction, and

always alert for cues in urine which can contain pathogens. Activities that require close proximity to others pose higher risks, such as social intraspecific interactions (Walsh et al. 2007; Hamede et al. 2009). The spatial world that a disease host inhabits also plays a critical role. For example, geographic boundaries such as rivers or cliffs present potential boundaries to infection as well (Wheeler and Waller 2008). Areas that are more heavily used by hosts and susceptibles are more likely to have transmission events. Knowing the time spent in different behaviours, where the behaviour occurs, and the associated transmission risks, will allow a more accurate estimation of the transmission potential of a host. One particularly prolific host for numerous diseases is the domestic dog (*Canis familiaris*).

Domestic dogs are recognised as a primary source of disease in many terrestrial systems (Hughes and Macdonald 2013). Numerous helminth parasites can be transferred between domestic dogs and humans (Otranto et al. 2013), and other organisms carried by dogs such as fleas, ticks or mites also transmit diseases to humans (Ogden et al. 2000; Bitam et al. 2010). Domestic dogs are the most common source of transmission of rabies to humans as well as to the charismatic carnivores that are often the target of conservation efforts (Macdonald 1993). Domestic dogs also carry and transmit canine distemper virus (CDV), a disease increasingly threatening wild carnivore populations (Kuiken et al. 2006; Millán et al. 2009; Feng et al. 2016). Transmission of rabies requires direct contact, including puncture of the skin (Hampson et al. 2010) while CDV can be transmitted not just through direct contact but also through infected excretions left in the environment (Appel and Gillespie 1972). Humans have introduced domestic dogs in many landscapes and as their numbers increase, they are becoming the most abundant carnivore

and potential reservoir populations of disease. Domestic dogs used for livestock guarding in Serengeti have been implicated as the primary host leading to multiple outbreaks of CDV and rabies in lions (Cleaveland et al. 2000). To counter disease outbreaks, domestic dog populations are vaccinated in many parts of the world (Kaare et al. 2009; Franka et al. 2013). With better understanding of hosts' behaviours, targeted vaccination could effectively compliment wide scale campaigns, reducing the required coverage or cost. One threatened species for which domestic dogs are the primary source of disease is the Ethiopian wolf (*Canis simensis*).

Ethiopian wolves are endemic to the Afroalpine ecosystem of Ethiopia and found only in a handful of montane enclaves above 3,000m, where they live in packs of between three and thirteen with a mean of $\sim$ six and low quality areas living mostly as pairs (Sillero-Zubiri and Gottelli 1995b; Marino et al. 2012; Marino et al. 2013). With fewer than 500 surviving, and none in captivity, Ethiopian wolves are listed as Endangered by the IUCN (Marino and Sillero-Zubiri 2011). The wolves are highly social, defending a communal territory averaging approximately 10km^2 (Sillero-Zubiri and Gottelli 1995b) and, unlike most other wolf species, are solitary hunters of diurnal small mammals (Sillero-Zubiri and Gottelli 1995a; Sillero-Zubiri and Macdonald 2004). The wolves are primarily threatened by habitat loss due to range restriction however, the most immediate threat to these wolves is from diseases transmitted by domestic dogs (Laurenson et al. 1998; Marino et al. 2013) brought into wolf habitat by pastoralists or free-roaming out of villages. These dogs serve a traditional role of livestock protection from predators and keeping villages clean by consuming waste (Atickem et al. 2010; Eshete et al. 2018; Eshete, Marino, and Sillero-Zubiri 2018). Households in Afroalpine areas rely on

small-scale agriculture for subsistence owning a small herd of goats, sheep and/or cattle. Most households own one or multiple dogs who are allowed to move in and out of the homestead and village; some follow their owners when they take out their livestock and at times venture away from them, roaming freely in wolf habitat (Atickem, Bekele, and Williams 2009; Perry, Marino, and Sillero Zubiri 2018). They generally subsist on a meagre diet of whey, cereal husks and left overs, as well as scraps and human faeces. When out in wolf habitat they have been observed to hunt rodents, potentially competing with wild carnivores, and previous studies have shown that they scavenge off carcasses, they also pick up unknown small scraps from the ground making foraging trips in wolf habitat a significant food source (Atickem, Bekele, and Williams 2009; Atickem et al. 2010; Perry, Marino, and Sillero Zubiri 2018).

The wolves in the Bale Mountains, where the largest population of wolves resides, experience periodic outbreaks of rabies (Sillero-Zubiri, Gottelli, and Macdonald 1996; Randall et al. 2004; Johnson et al. 2010) and CDV, which spread rapidly within a pack and result in high wolf mortality (Gordon et al. 2015; Marino et al. 2017). Long-term management of these diseases in the Bale Mountains landscape includes domestic dog vaccination campaigns, targeting villages within and surrounding wolf range, coupled with reactive vaccination of wolves against rabies during outbreaks (Randall et al. 2006). Oral rabies vaccination has been tested (Sillero-Zubiri et al. 2016) and approved to now be deployed while a test of a CDV vaccine in wolves is ongoing (Ethiopian Wolf Conservation Programme 2016). In depth knowledge of the mechanism of diseases transmission can improve the design and implementation of these interventions. Previous studies of free roaming dogs

in Bale looked into their diet and behaviour (Atickem, Bekele, and Williams 2009; Perry, Marino, and Sillero Zubiri 2018) from direct observations and follows of dogs in wolf habitat. To improve our knowledge of free roaming dogs' behaviour in depth monitoring of multiple individuals at a time is required. Hotspots for disease transmission can then be derived from dog behaviours and time budgets that will increase interspecific interactions and/or put wolves at higher risk of contact with CDV viruses in the environment. Dog behaviour will also inform management options that revolve around manipulations of dog behaviour or demographics through changes in the owners' husbandry practice.

This study aims to use high frequency GPS locations and accelerometer data to increase understanding of dogs' movements and behaviour both within wolf habitat the Bale Mountains, and inside neighbouring villages across the dry and wet season. GPS locations will be analysed to determine how much time domestic dogs spend in wolf habitat, to what extent they roam out of the village and how active they are, to derive high risk areas for disease transmission. Individual home ranges will be calculated to provide insights into habitat preferences and potential overlap between wolves and dogs. The accelerometer data will be used to construct a detailed twenty-four-hour time budget of dog behaviours, to identify active periods and possible temporal transmission hotspots.

3.3 Methods

3.3.1 Study area

This study was conducted in the Bale Mountains National Park (BMNP) in the Web Valley. BMNP is in south-eastern Ethiopia and has a total area of 2400 km^2, ranging from 1500m to over 4000m above sea level. The Web Valley is approximately 70km^2 of optimal wolf habitat (Gottelli and Sillero-Zubiri 1992). The landscape comprises multiple habitat types previously incorporated into a detailed vegetation map of the Bale Mountains (Tallents and Macdonald 2011). The map was derived from a Landsat image with a 30m x 30m pixel size, each classified into one of seven habitat types: *Erica* moorlands, wetlands, lava flows, *Hellichrisyum*, shrubland, *Alchemilla* grass, bare soil and herbs and drainage lines.

3.3.2 Data collection protocol

GPS collars constructed under a protocol described in by Foley & Sillero-Zubiri (2019) (Chapter 2) were placed on 26 domestic dogs in the BMNP, split across two deployments: one in the wet (April – October) and one in the dry (November – March) season (Table 3.1). Dogs of one year of age or older were chosen opportunistically to target individuals that regularly went out into wolf range, as these were the individuals of greater interest in the context of disease transmission to the wolves. As local people prefer males dogs, our sample was equally biased. The collars recorded location data at a rate of 6 minutes between fixes and accelerometer data at 10hz. During the collar period collared dogs were followed and recorded in videos performing behaviours that can later be classified to accelerometer data.

Table 3.1: The breakdown of data collected during GPS collar deployments.

Season	No. Collared Dogs	No. Villages	No. GPS Fixes	No. records Accelerometer
Dry	15	4	23,828	22,633,200
Wet	11	3	14,717	14,005,400

3.3.3 Movement patterns in respect to village

Using the data in Table 3.1, patterns of dog behaviour in areas overlapping d with wolf habitat were derived. Using the known village of origin for the dog as reference, the distance from that village to all GPS points of an individual was also calculated, using inter-locus distance calculations in QGIS (QGIS Development Team 2019), to provide the extent to which the dogs travelled outside their village. Further analyses were performed in R (R Development Core Team 2011).From the time stamp and the distance from the village of each point it was deducted when dogs were in and out of their village. The distance and time between each fix were used to calculate movement speed between the fixes; all movement speeds were then combined into a distribution of movement speeds for all dogs. When there was no movement between fixes these were classified as periods of rest, and movement was classified as activity, to get a simple measure of active time across all fixes per dog.

3.3.4 Home range analyses

Home ranges were calculated using 90% autocorrelated kernel density estimates (AKDE) (Fleming et al. 2015) excluding fixes within 100m to village, to better understand habitat utilisation outside the village using the ctmm package (Fleming

et al. 2020). These kernels represent the extent of movement as well as the rate of usage within that extent. AKDEs also take into account the nature of GPS fixes as time series data. Autocorrelation means that if an individual is in a location at one time, the chances of it being in a drastically different location at the next time is fairly low, causing the data to be skewed by each prior fix. AKDEs apply a correction statistic to each location's probability function based on the time between the previous location. This methodology is a standard part of continuous time movement modelling.

3.3.5 Habitat preference analyses

Using the vegetation map each GPS location was classified based on its habitat type. Potential errors due to GPS accuracy (mean error 14m, compared to the 30m map pixel size) were considered unlikely to have serious implications. A series of random points, the same number as the total of fixes from each dog, were generated within each animal's home range to represent availability of each habitat type; these random locations were then classified using the habitat map. Comparing the proportion of each habitat in the random points to the fixes that are recorded within each habitat for each dog across the entire collared period can show if dogs were preferentially selecting, avoiding, or indifferent to certain habitat types as a function of their availability (Aarts et al. 2008). To get an overall habitat preference for dogs a series of random points were generated in the total extent of dog movements and the proportion of these were compared to the fix locations of all dogs. These were statistically confirmed using z tests of proportions (Lawley 1938). by performing a z test on the proportion of fixes that

are of that habitat out of all fixes to the proportion that habitat makes up out of all available habitat. Again, fixes within 100m from villages were excluded. Due to the nature of the data, it was not possible disentangle whether habitat usage and preference was affected by the presence of humans or livestock.

3.3.6 Dog activity analyses

Analyses of accelerometer data provided a breakdown of daily activity patterns for the domestic dogs. Identifying accelerometer patterns over given time periods extracted from direct observation in videos allowed for the recognition of specific activities, which were then extrapolated across all accelerometer data to classify the entire dataset (Ravi et al. 2005). All accelerometer data was initially run through an unsupervised k-means machine learning algorithm built in python (Van Rossum and Drake 2003) which found the most common patterns and matches data to a cluster (Petitjean et al. 2014). Sequences of 100 datapoints corresponding to 10 seconds worth of data were used for clustering and further analysis. The clusters were then validated by comparison with data classified to specific behaviours from simultaneous videos taken of collared dogs (n = 47 videos of n = 12 different dogs). The validated behaviours were termed lying down, sitting, foraging, eating and travelling:

"Lying down": no acceleration being measured in the x or y axes and only gravity being recorded.

"Sitting": same as lying down but a shift of some negative acceleration in the Y axis from the heads angle being different and being impacted by gravity.

"Foraging": From the videos and behavioural observations (Perry, Marino, and

Sillero Zubiri 2018) any time dogs walk they appeared to be actively foraging, looking around with heads close to the ground, and "foraging walk" is a dominant behaviour in free-roaming dogs in Bale, as well as in wolves (Sillero-Zubiri and Macdonald 2004). Low level acceleration on the X axis was then classified as foraging as it is a slow walk.
"Eat": when the dog's head was directly dipped down to investigate or eat something and could be detected by shifts in acceleration in the Y and Z axes.
"Travelling": high level of acceleration in the X axis and represented higher intensity travel behaviours.

Using the data from the videos and hand selected high quality data from the matching cluster allowed the construction of a training dataset of classified data of 2,455 series each of 100 data points for a total of 245,500 data points in 409 minibatches. This training dataset was then used to train a long-short term memory recurrent neural network through bootstrapping and iterative training built in the Julia programming language (Bezanson et al. 2017). A long-short term memory recurrent neural network is a form of deep learning algorithm that classifies a series of data points as a batch while able to take into account all the surrounding data points (Saleh, Hossny, and Nahavandi 2018). The training dataset was randomly divided into 90% training and 10% testing at each training iteration. Data was fed into the neural network in 10 second windows in a minibatch of 1 minute of data. Each 10 second window was then classified into a behaviour as a batch; backward propagation, based on error between the predicted behaviour and the true value, trained the neural network to improve prediction accuracy. This hybrid learning approach is becoming a standard method for dealing with big data (Hirano and

Maekawa 2013). After training for 3,000 iterations the LSTM RNN had an overall testing accuracy of 97%, with a true positive rate of 92% and a false positive rate of 1.8% and a training accuracy of 98% with a true positive rate of % and a false positive rate of 0.4%. Due to the similarity between training and testing accuracy the model was deemed to not be overfitting. Overfitting is defined as where the model is learning the training data itself, not the underlying patterns that are important leading to a high accuracy during training with a significantly lower accuracy for testing. The method was 4.5 times more accurate on true positives compared to a random chance allocation (20%) and was on par with other accelerometer classification algorithms that use higher resolution and accessory data (Wijers et al. 2018), this can be considered a highly accurate model (Table 2).

Table 3.2: Confusion matrix of the LSTM RNN, classifying domestic dog behaviour from accelerometer patterns with accuracy for each classification and false positive rate.

	Forage	Eat	Travel	Sit	Lie Down
Forage	94.2%	1.3%	0%	0%	3%
Eat	2.8%	93.4%	0%	0%	2%
Travel	0%	0%	100%	0%	0%
Sit	0%	3.9%	0%	94.4%	11%
Lie Down	5.2%	2.6%	0%	5.6%	84%

Once the neural network was trained all collar data was run through it to classify the data into each behaviour over each 10 second period. Each collar was classified individually as a complete time series and then each hour extracted and combined with the same hour across all dogs to create an average dog detailed time allocation of the proportion of each behaviour in any given hour by an average dog across the day.

3.4 Results

3.4.1 Movement patterns in respect to village

The dogs were usually out of their village between 09:00h and 15:00h; only sporadically dogs left the village during the night (Figure 3.1), these were rare occurrences with less than 6% of the data being outside the village between 19:00h and 07:00h. Dog stayed within 100m of their household 72% (range = 54% - 85%) of the time during the dry season and 64% (range = 42% - 81%) in the wet season. When outside of the village, 90% of fixes fell within 1.2km of their village, regardless of season (Figure 3.2). In the dry season the mean distance away from village of origin was 727m (SD = ±79.36m) with a maximum extent of up to 4.5km in the dry season. In the wet season dogs stayed closer to the village with a mean of 538m (SD = ±94.82m) (Figure 3.3) and a maximum extent of 4.5km. Dogs travelled slowly; 90% of speed estimations from distances between each 6 minute fix fell into less than 3km/h, with a mean of 1.2km/h (Figure 3.4). No distance was travelled at all between 70% of all pairs of fixes in the dry season and 62% of all fixes in the wet season.

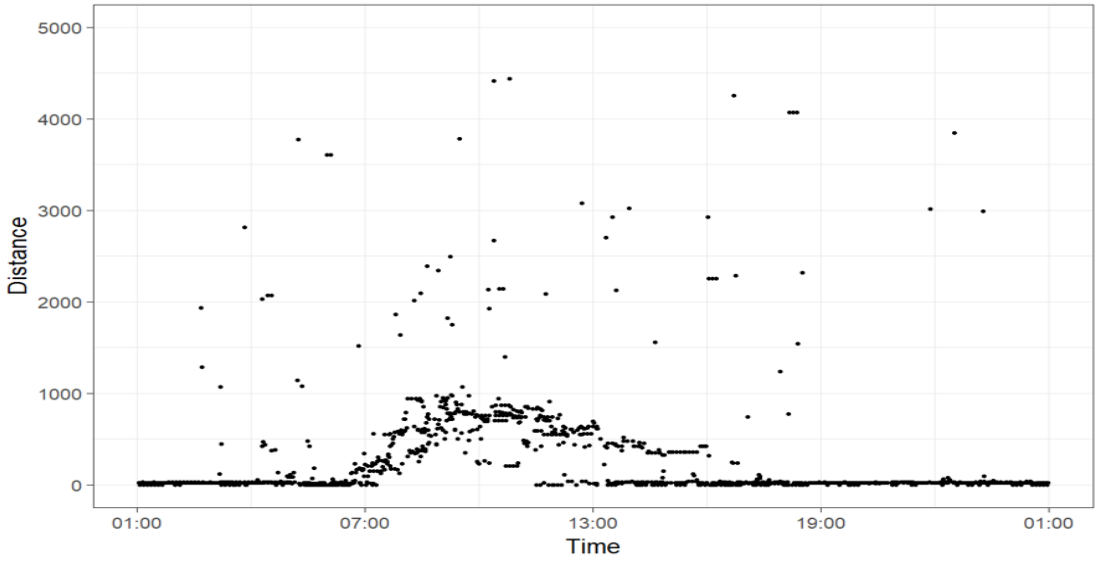

Figure 3.1: Distance travelled from the village in meters against the time in the day for a sample dog over the entire collared period in the dry season (approximately 10 days).

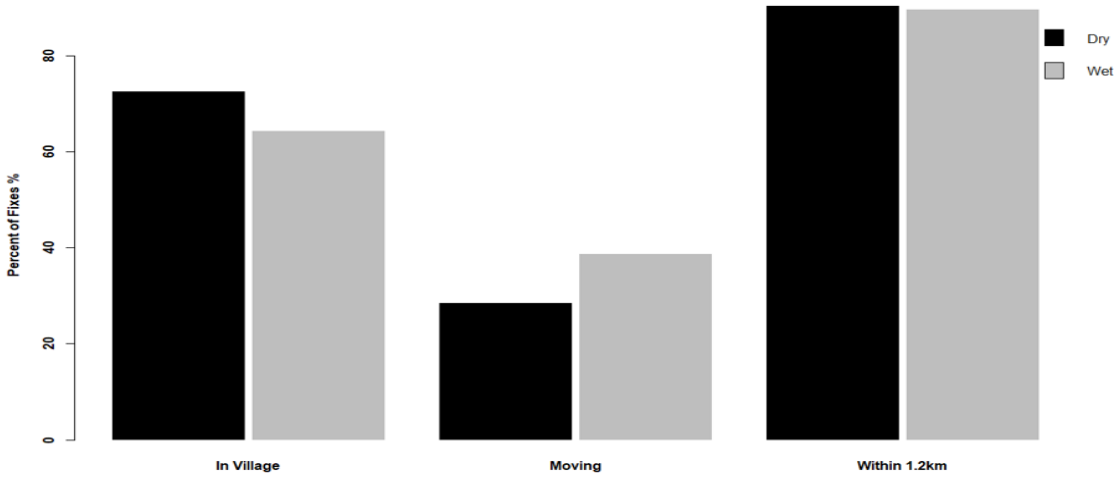

Figure 3.2: Percentage of dog GPS fixes that were in the village, moving (with distance travelled between the previous fix), or within a 1.2km radius of the village across all dogs per season (where 90% of all data fell) n = 26 dogs over two approximately 10 day collaring periods.

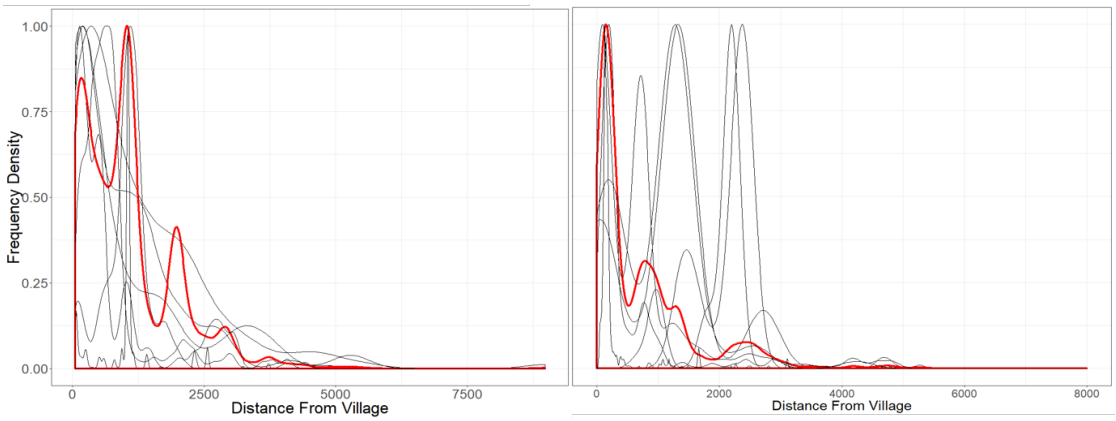

Figure 3.3: Density plot of fixes at various distances from the village for each dog as black lines, with average values represented in red in the dry season (left) and wet season (right) n = 26 dogs over two approximately 10 day collaring periods.

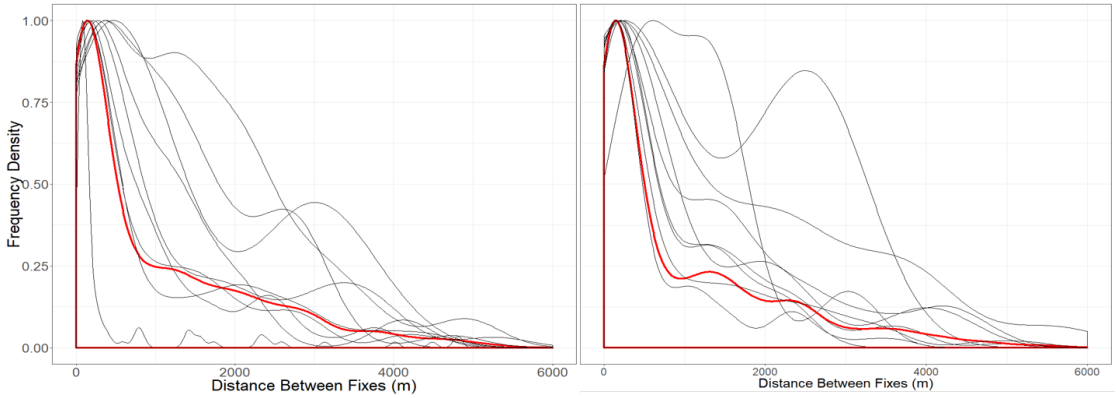

Figure 3.4: Speed of movement, represented as distances between each pair of successive fixes of each dog in black, with averages in red in the dry season (left) and wet season (right) n = 26 dogs over two approximately 10 day collaring periods.

3.4.2 Home range

Excluding fixes within 100m from village of origin, the mean home range area of the samples dogs during the dry season was 3km^2 (SD = $\pm$0.626km^2)(90% kernel, figure 3.5). The shape of the area was highly variable, depending on the individual and the surrounding terrain (figure 3.6). In the wet season, the home range size was 2.9km^2 (SD = $\pm$584m^2) and the shape was again highly variable.

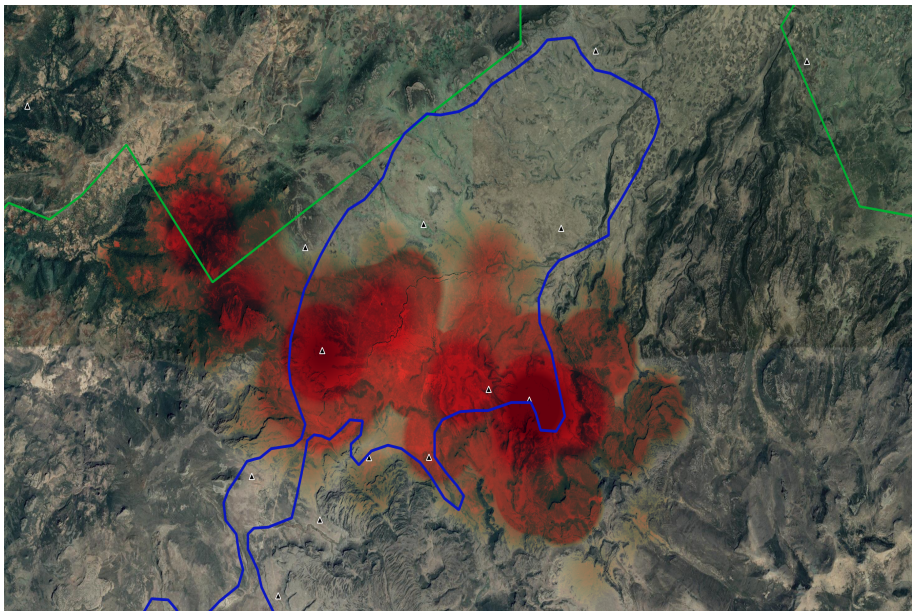

Figure 3.5: Autocorrelated kernel density estimate home ranges of domestic dog collars in the dry season presented as heatmaps, darker shades mean higher occupancy. Triangles are villages. Blue outline delimits the boundary of optimal wolf habitat. Green outline is the boundary of the Bale mountains national park.

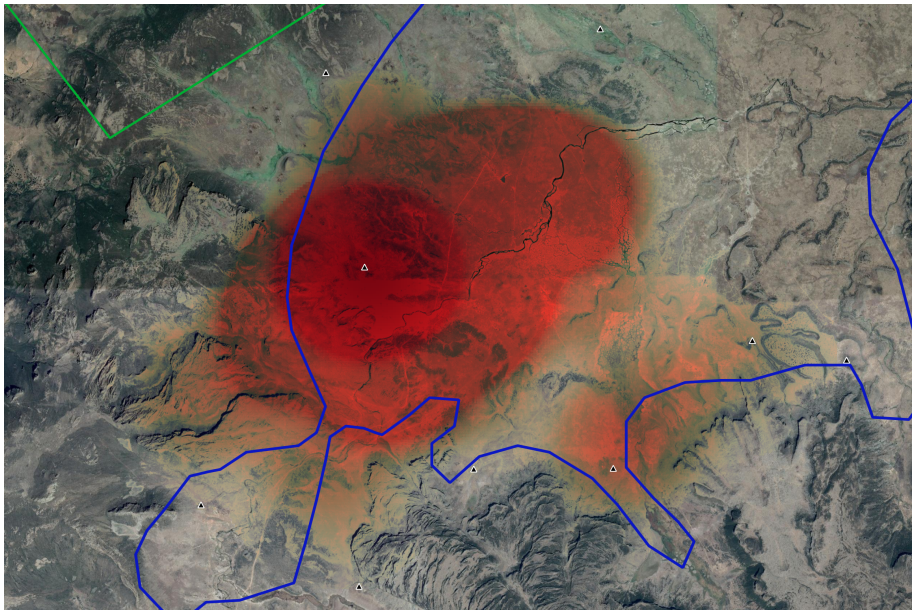

Figure 3.6: Autocorrelated kernel density estimate home ranges of a single domestic dog from GPS fixes in the dry season presented as heatmaps, darker shades mean higher occupancy. Triangles are villages. Blue outline delimits the boundary of optimal wolf habitat. Green outline is the boundary of the Bale mountains national park.

3.4.3 Habitat use by dogs

In the dry season, across all dogs, they largely preferred drainage lines ($z = 192.35$, $df = 1$, $p = < 0.00001$), wetlands ($z = 131.05$, $df = 1$, $p = < 0.00001$), *Alchemilla* grassland ($z = 6.75$, $df = 1$, $p = 0.0009$), and *Erica* heathland ($z = 131.05$, $df = 1$, $p = < 0.00001$) above the random availability of these habitats. Dogs showed an aversion to lava flows ($z = 150.16$, $df = 1$, $p = < 0.00001$) and shrubland ($z = 157.65$, $df = 1$, $p = < 0.00001$) compared to availability of each habitat type (Figure 3.7). In the wet season there was a shift in preference, so that the only habitats above random were *Alchemilla* grassland ($z = 54.396$, $df = 1$, $p = <$

0.00001) and drainage lines (z = 428.42, df = 1, p = < 0.00001). Wetlands (z = 29.23, df = 1, p = < 0.00001) and *Erica* heathland (z = 101.27, df = 1, p = < 0.00001) were now avoided (Figure 3.5).

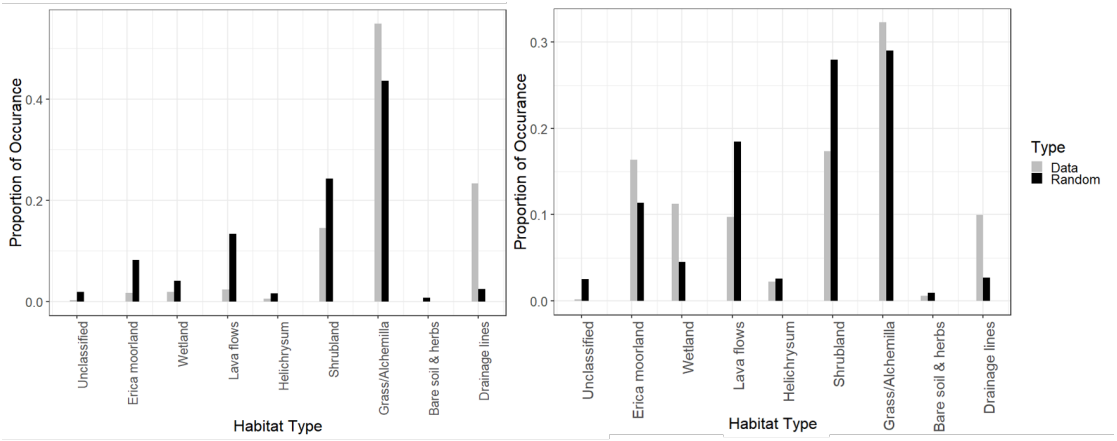

Figure 3.7: Dog habitat preferences by season, comparing the proportion of fixes in each habitat type out of all fixes against the proportion of that habitat within total dog range. Dry season on left and wet season on right n = 26 dogs over two approximately 10 day collaring periods.

3.4.4 Dog activity

Once this trained algorithm was run using all the available accelerometer data, an hourly breakdown of behaviour could be deduced (Figure 3.6). In general, there were two peaks of dog activity during the day. During the hot dry season, the first peak of activity began at 07:00h and extended until 10:00h, followed by a second smaller peak beginning at 14:00h and ending at 18:00h. In the cold wet season this pattern reversed with the larger peak at 14:00h and a smaller peak beginning at 07:00h. The dogs spent a large amount of their time resting, with as much as 75% time lying down during the night; even during activity peaks, 30% of time

was spent resting. The most common active behaviour was foraging.



Figure 3.8: Proportion of time (for each hour) in the day spent performing each behaviour from the LSTM machine learning model, with dry season on the left and wet season on the right, pooling data from all 26 dogs over the two approximately 10 day collaring periods.

3.5 Discussion

Dogs spent the majority of their time in their villages (¿65%), including typically throughout the night. They were out of their villages for periods of eight hours between morning and early afternoon. This pattern meant that there is only a risk of direct contact with the wolves for a small part of any 24hr period. As any foray outside the village could leave potentially infectious exudate, the potential for CDV disease transmission was still high in those areas used by dogs even when opportunities for direct dog-wild contact were limited in duration. With dogs concentrated in villages, most disease transmission events between dogs will occur within villages. These infected individuals then pose a risk to the wolves, when

some travel out into wolf range, either with livestock, other dogs or on their own. Perry, Marino, and Sillero Zubiri (2018)showed dogs spent 40% of their time with livestock or people while out in wolf range. Most dogs within villages do not roam out into wolf habitat and even some dogs that do roam do not leave the village every day.

The core usage areas, within 1.2km from villages, is where disease transmission events between dogs and wolves will most likely occur. These core areas are where livestock were most commonly found, and with them the accompanying dogs. Forays beyond the core array were probably brief foraging trips, or trips searching for socialising or mating opportunities with dogs from other villages. Opportunities to minimise transmission risk exist if dogs were restricted to a smaller area around the village. Indeed, the official park policy is to restrict dog movement to within 100m from their homes to reduce the risk area (Nelson 2011). Even a reduction of a few hundred meters distance out of the village can reduce the total risk area by a huge amount. Enforcement of this policy has however yet to be truly enforced by management authorities and pastoralists still desire to keep dogs with livestock for protection, so this option would require active participation from all stakeholders.

The distance travelled between most 6 minute fixes was fairly short, with a mean of 122m. Dogs did not move far from their villages, but they were active when away from them. Particularly in the morning, dogs moved with the livestock (Perry, Marino, and Sillero Zubiri 2018) which in general progress slowly while grazing. When travelling small distances with livestock, dogs were also foraging regularly over a small area. There were also large movements at the end of the

day, when dogs return to the village from further away, other larger movements may have been exploratory forays to search for new foraging spots. During periods of longer movements dogs would be more likely to transmit diseases. As CDV can be left in the environment, covering a larger distance creates a larger area were animals can become infected. Larger distances covered also increase the likelihood of encountering or interacting with another individual, thus increasing the risk of disease transmission from that dog (McCallum, Barlow, and Hone 2001). During the wet season there was a higher proportion of fixes with distance travelled between them, perhaps due to seasonal variation and changes in habitat availability they must travel more to reach livestock grazing spots or foraging locations. This may be due to habitats becoming waterlogged thus more difficult to travel to or no longer being optimal foraging areas. There was an increase in the proportion of the foraging behaviour in the wet season, possibly due to the lower availability of quality foraging habitats, which could account for the difference in proportion of inter-fix movement between seasons. When in the village, dogs were mostly foraging most likely for any available scraps. The seasonal difference that dogs were more active in the villages and over night during the wet season may be down to social changes between seasons or availability of food within the village.

Dog home ranges were extremely variable between individuals. The average dog home range was $3km^2$ however, the shape of the range differed between dogs. The shapes reflected mainly regularly used routes of travel and preferred grazing areas, as the dogs' movements were partially dependent on those of livestock and humans. Still, dogs, as well as livestock, encounter wolves during the day (Atickem, Bekele, and Williams 2009; Perry, Marino, and Sillero Zubiri 2018). As dogs do

not often venture too far away from their village, dogs from the same village will have a large degree of overlap of home range and the different shapes of each dog's range tend to combine to cover most of the area within a 1.5km radius of a village, suggesting that any of this area could pose a transmission risk to the wolves or other wild carnivores.

Overall dog preference reflects the typical areas used where those where livestock grazed and habitat that was easily accessible from the village. Across all dogs, there was a greater than expected usage of drainage lines, most likely due to the ease of movement that these provide. This habitat type could be a hotspot of disease transmission particularly if infectious residue is left in it. The aversion to lava flows and shrublands could indicate that there are habitat types which would be of lower risk for disease transmission between dogs and. Lava flows and shrublands are areas with lower rodent density which may also mean lower availability of food which dogs forage for, which would explain why these habitats were not preferred. During the wet season, dogs showed only preference for drainage lines and grasslands; it is possible that some other habitat types become less suitable for occupancy in the wet season due to flooding and lack of foraging opportunities. The method for measuring habitat preference was simple and it is possible usage of more complex techniques such as resource selection functions (Boyce et al. 2002) would provide more accurate habitat preference measures. If the wolves in general have similar habitat usage to the dogs, then this pattern of wet season occupancy could indicate a higher risk of wolves encountering infected individuals. With the possibility of CDV in the environment (although the dynamics and duration of this is extremely understudied)(Park 2012), areas that wolves prefer could be infectious for a period after a dog has visited it. As the habitat selection of the domestic dogs

is partially driven by people and livestock this may be a target for behavioural change of people. If there are habitats which wolves have high preference for it may be possible to convince pastoralists to use these less for grazing and reduce the risk of transmission, but changing grazing regimes might be a difficult ask.

Dog behaviour has distinct temporal patterns of activity that could also pose risks to wolves (Proffitt, White, and Garrott 2010). The mornings may be a high risk time as dogs spend up to 50% of their time moving in some way in the mornings and while travelling the risk they pose is higher, due to increased probability of encounters (Robert, Garant, and Pelletier 2012). Foraging behaviours (Foraging and eating) peaked during the day where they are possibly leaving infectious material in the ground that can be picked up by other individuals. Activity peaks matched the peak of further distance from village, which suggests that dogs were more active when outside of the village and resting more when inside the village. The majority of time dogs were resting, even at times during the active peaks when they were likely to be in wolf habitat resting was as high as 35%. Nearly all resting behaviour was classified as lying down; however, the behavioural signals of lying and sitting or standing were so similar, and in disease transmission terms are likely to be equivalent, so that the total stationary time was key in further analyses. While resting may reduce the possible direct contact rate with other travelling dogs or wolves, it may increase the infectious material left in the environment at specific locations and could mean those locations have a higher risk of contact and transmission making them a possible target for management.

These dogs may be archetypal in terms of free roaming dogs that are posing a haz-

ard to threatened wildlife. In many systems domestic dogs are seen as a threat to humans and are vaccinated accordingly, but these tend to be either urban or semi-urban populations (Davlin and VonVille 2012). In systems where dogs threaten wildlife it is more likely that they will be working dogs, which serve some form of community role but encounter wildlife on a regular basis. Habitat usage is the main parameter that will vary between systems and would need independent analysis. However, the principle of a core usage area around villages and times when the dogs are most active outside the villages are most likely to be universal for domestic dog-wildlife disease systems. Other dog-wildlife systems, such as with the Serengeti lions and African wild dogs (*Lycaon pictus*), where management authorities and practitioners also run dog vaccination campaigns (Cleaveland 2009; Kaare et al. 2009; Beineke, Baumgärtner, and Wohlsein 2015; Czupryna et al. 2016), could adopt methods used here to survey the relative dog populations and adapt recommendations accordingly. With similar analyses performed, it may be possible to develop a generalised model of dog behaviour for the purposes of disease transmission.

With this work it is important to be aware that there are some limitations, some coming from the usage of a machine learning framework. Complex and rare behaviours, such as specific mating behaviours, would be missed due to the inability of the deep learning algorithm to differentiate them without a large dataset. This leads to diminishing returns as the time required to collect enough validation data in the form of videos would reduce the usefulness of the automated data collection. Rabies as a disease causes behavioural modifications within the host, particularly extreme aggression leading to enhanced transmission, so these behaviours may

not apply to a final stage rabid animal and an infected individual may exhibit entirely different spatio-temporal patterns of behaviour. However, the collection of behavioural data of rabid animals would be extremely difficult, dangerous and possibly unethical. The data collection window in this study was short, which was a trade off with between covering more behavioural variation and the intensity of data collection. Other resolutions of data may be able to give insights into different behaviours and further study of the long-term trends in domestic dog behaviour globally should become a conservation priority.

3.5.1 Conclusions

Understanding the temporal and spatial patterns of behaviour of any disease host is becoming increasingly easy with access to cheaper and better tracking methods as well as new techniques custom made for individual species. With this increased understanding, we can design and implement more effective disease management techniques to help improve the health and well-being of people and animals globally. In the specifics of domestic dogs as a source of disease for the Ethiopian wolf, the understanding of spatial patterns can help identify target locations to place bait for oral vaccinations; the temporal component allows to know when the opportune time is to put out the bait. Increased knowledge of how much the animals are moving it providing evidence in support of strategies that limit movement of domestic dogs to reduce transmission risks.

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Chapter 4

Spatial and temporal overlap of Ethiopian wolves and domestic dogs: implications for disease transmission and management.



4.1 Abstract

A primary driving force for communicable disease transmission is contact rate between hosts. Contact rate is itself an emergent property of the spatial and temporal patterns of behaviour disease hosts have. Domestic dogs are the primary source of disease for Ethiopian wolves, a rare Afroalpine endemic, whose most immediate threat is viral diseases, critically rabies and canine distemper. Further understanding of the behaviour of the two species and how they overlap in space and time can inform management strategies for controlling contact rates and disease transmission. Using data on the behaviour of 26 free-roaming dogs, collected by GPS loggers recording over 10 days, and long-term records of wolf behaviour in the Bale Mountains National Park, I determined the home range, habitat preference, movements and behaviour of both species and then quantified their spatial and temporal overlap. The species showed a high level of overlap, with individual dog ranges encroaching into wolf habitat on average 47%. Both had preference for grassland habitat, and 75% of diurnal overlap. High levels of overlap indicates high disease transmission risk in the Bale Mountains. The areas closest to the village present the highest risk due to spatial overlap, reducing the distance that dogs travel into wolf habitat can reduce this risk considerably.

4.2 Introduction

Rapid human population growth has resulted in the expansion of human-dominated habitats. When humans encroach wilderness areas, this is often to the detriment of wildlife (IPBES 2019). In particular, the increasing prevalence of diseases in endangered species (Gulland 2010). This threat is bound to increase with climate change as much of the world's human and wildlife populations shift their ranges to adapt to changing habitats. This displacement could lead to a surge in diseases threatening endangered species in ways conservation practitioners are not yet dealing with (Reiter 2001; Jones et al. 2008).

Diseases are a particular threat to wildlife species whose population numbers are low and with restricted ranges (Gulland 2010). A single disease outbreak can cause a rapid population decline, becoming a serious risk when compounded with other long-term threats such as habitat loss, hunting or illegal wildlife trade (Heard et al. 2013). Diseases are becoming more of a pressing conservation concern, with well documented cases of disease threatening endangered species globally. This has been a known problem as far back as the 1980s with Canine Distemper Virus (CDV) in black footed ferrets (*Mustella nigripes*)(Williams et al. 1988). Due to the abilities of multiple strains to combine and the virus to jump and become multi-host diseases, carnivores are particularly susceptible to CDV and there have even been calls to rename the disease to Carnivore Distemper Virus (Terio and Craft 2013). Recent outbreaks of CDV have been recorded in lions (*Panthera leo*)(Cleaveland et al. 2000), leopards (*Panthera pardus*)(Sulikhan et al. 2018), tigers (*Panthera tigris*) (Nagao et al. 2012) and caspian seals (*Pusa*

caspica)(Kuiken et al. 2006), raising concerns about the threat it poses on endangered species. Rabies is another zoonotic disease highly detrimental to populations of endangered species. Outbreaks of rabies have devastated Ethiopian wolf (*Canis simensis*)(Randall et al. 2004) and African wild dog (*Lycaon pictus*)(Gascoyne et al. 1993) populations in East Africa. When combined, rabies and CDV can cause severe declines (Gordon et al. 2015), driving local populations of Ethiopian wolves to the brink of extinction (Marino et al. 2017).

Disease transmission is driven by the dynamics of the hosts involved. When the complete disease system is not well understood, management strategies are limited to only direct medical interventions of infected or susceptible individuals. Disease hosts, with their own unique behaviours, ranges and ecological preferences, create a particular spatio-temporal distribution of disease risk (Lloyd and Jansen 2004). In order to build up a full picture of disease risk, behavioural data are required for all the species involved, to understand where disease transmission occurs, between individuals of the same species or across species in areas where they overlap. Area of overlap is critical to understanding risk of disease transfer (Proffitt, White, and Garrott 2010; Robert, Garant, and Pelletier 2012) and to determine where management is most needed or effective.

The Ethiopian wolf is the most threatened carnivore in Africa and the rarest canid in the world (see Introduction). The most immediate threat it faces comes from rabies and CDV passed on from domestic dogs (Laurenson et al. 1998; Gordon et al. 2015). Ethiopian wolves live in small pockets of Afroalpine habitat in the highlands of Ethiopia, a country with a human population of 100 million, the high-

est rates of livestock ownership in the world (Asresie 2015) and among the highest incidences of rabies in the world (Aga, Hurisa, and Urga 2016). Under increasing need for space, people and livestock encroach into the Afroalpine habitat where Ethiopian wolves occur, bringing with them domestic dogs that then transmit diseases to the wolves (Laurenson et al. 1998). Domestic dogs are traditionally used to guard livestock and often go out into wolf habitat with livestock or on their own (Atickem, Bekele, and Williams 2009), where disease transfer can potentially occur. Diseases in Ethiopian wolves are currently managed through long-running dog vaccination campaigns and reactive vaccination of the wolves during outbreaks (Randall et al. 2006). After successful trials of an oral rabies vaccine (Sillero-Zubiri et al. 2016) there is the option to manage disease through proactive wolf vaccination; the trails of a parenteral CDV vaccine in wolves is ongoing.

By determining the species use of space and quantifying their overlap, we can predict when and where disease management interventions would be most effectively applied for the protection of Ethiopian wolves, a species of high conservation concern. Understanding the entire disease system will also allow managing diseases in domestic dog populations more completely, with benefits for people and their livestock with a "one health" approach (American Veterinary Medical Association 2008).

Wolves and dogs in the Bale Mountains have been studied previously and are constantly monitored. Perry, Marino, and Sillero Zubiri (2018) investigated the behaviour of domestic dogs through direct observation while in wolf habitat while Atickem, Bekele, and Williams (2009) looked at diet and general behaviour; nu-

merous studies have investigated the behaviour and ecology of Ethiopian wolves (Sillero-Zubiri and Macdonald 2004). With this wealth of knowledge and further quantification of dog behaviour, it is possible to better understand disease transmission as a function of the overlap between the two species as well as other impacts this overlap could have on Ethiopian wolves.

4.3 Methods

4.3.1 Study area

Data was collected in the Bale Mountains National Park (BMNP), South-east Ethiopia. The park covers 2400 km^2, ranging from 1500m to over 4000m above sea level. Within the park, wolves occupy around 1,200 km^2 of Afroalpine habitat, but concentrated in two optimal areas in the Web valley and the Sanneti plateau (Gottelli and Sillero-Zubiri 1992). Data was collected in both these areas and combined with a vegetation map (Tallents and Macdonald 2011) of the Bale Mountains described in Chapter 3.

4.3.2 Dog behaviour

Dog behaviour was studied using custom built tracking devices placed on domestic dogs living next to the two optimal wolf habitats in the Bale Mountains National Park (Chapters 2 3, Chapter 3 Table 1). Data were collected using a custom-built GPS and accelerometer logger (described in Chapter 2) deployed on 26 domestic dogs in BMNP in June and July during the wet season (April – September), and

between January and February during the dry season (October - March) of 2018. The devices collected GPS locations at a frequency of approximately 10 per hour, dependent on fix acquisition time, and tri-axial accelerometer at 10hz.

Location data were analysed to determine home range, habitat preferences and movement patterns (details in Chapter 3) in R (R Development Core Team, 2011). To avoid heavy bias towards the time dogs spend near the village where they come from, the data within 100m from the village was excluded for habitat preference and home range calculations. Home range size was calculated using autocorrelated 90% kernel density estimates (AKDE) (Fleming et al. 2015), package ctmm (Fleming et al. 2020). To assess habitat preferences an existing habitat map was used (Tallents and Macdonald 2011), based on a Landsat image and classified using ground truther data. For each location, habitat type was extracted from this map. For each dog, the location data were compared against an equal number of random points generated from within the minimum convex polygon of its home range as well as from the area of occupancy of all collared dogs (Aarts et al. 2008). The distance between each location and the previous location of an individual, was used to calculate speed of travel; distance of each point from the household the dog belongs to was used to measure extent of movement away from the home village. These measurements were calculated for each individual and then averaged for the calculation of home range, and travel extent and pooled for proportion of locations in village and proportions within 1.2km, pooled data of proportions is mathematically identical to averaged proportions, so pooled for ease. 1.2km was chosen as it is the area which showed core usage. This 1.2km core usage area was used for a simple descriptive calculation of the impact of park policy to restrict the

movements of dogs to within 200m of the village. This calculation was the % area remaining after reducing the 1.2km core area down to 200m. Habitat preference was calculated for each dog within its respective home range and then an overall dog preference was calculated using all dog locations within the total extent of all dogs. These generalisations were made for later comparison against the equivalent wolf data.

Deep learning methods (Saleh, Hossny, and Nahavandi 2018), constructed in Julia (Bezanson et al. 2017), were used to classify each dog's accelerometer data into behaviours, throughout the study period, as specified in Chapter 3. Videos of collared dogs performing different behaviours were located and compared against the respective sections data to label accelerometer patterns. A training dataset of 2,400 fully classified behavioural data series across the 26 domestic dogs were used to train a neural network allowing for robust activity estimations (overall accuracy of 97%). Full description of this methodology is found in Chapter 3.

4.3.3 Wolf behaviour

Data on Ethiopian wolf behaviour were derived from two datasets. One includes intense behavioural follows recorded originally by Sillero-Zubiri (1994) between 1988 and 1992, involving 46 wolves from 8 packs. During behavioural follows, several specific behaviours were recorded (Table 4.1) at three-minute intervals. Wolves were followed for as long as possible recording constantly. For the purpose of this analysis, follows shorter than 30 minutes were excluded, as they would not be representative of an hour interval, selected to analyse daily temporal patterns. This left 231 follows accounting for 520 hours of detailed wolf observations

(Sandoval-Seres 2018).

Table 4.1: Description of categories of behaviours recorded during the behavioural follows of Ethiopian wolves between 1988 and 1992 in the Bale Mountains (based on Sillero-Zubiri, 1994).

General Behaviour	Specific Behaviour	Description
Foraging	Drinking	Gulping Down Water
	Foraging	Searching for food
	Eating	Ingesting the food
	Standing	Upright position vigilant for food
Resting	Lying	In horizontal position
	Sitting	Upright with rear on ground
Patrol-Marking	Walking - Marking	Moving at slow pace while excreting urine, scratching, rolling, sniffing
	Trotting Marking	Moderate pace movement as above
	Standing Marking	As above in one place
Moving	Trotting	Moderate paced movement
	Running	Rapid paced movement
	Walking	Slow paced movement
Socialising	Socialising	Mating, playing, marking one another, behaving aggressively, greeting or grooming

For comparative purposes, these behaviours were grouped into the categories used to describe domestic dogs: Moving (combining all movement behaviours except foraging), Forage (combining all foraging behaviours), and Resting (combining sitting and lying down). Socialising behaviours were included in the total number of behaviours for each hour for deriving proportions of each specific behaviour but not used for an overlap comparison as they had no equivalent domestic dog data. The behavioural follows were used to produce a breakdown of the hourly time allocation of wolves to each behaviour was determined by taking all follows over 30 minutes in duration (n = 231) and categorising the proportion of each of the main behaviours (Resting, Moving, Foraging and Socialising) that were performed per hour. A direct measure of distance travelled between each data point was also recorded in the follows and this was used to determine a distribution of travel speeds for the wolves. Both analyses performed in R (R Development Core Team 2011).

The second dataset is from long-term monitoring of packs in the Bale Mountains by the Ethiopian Wolf Conservation Programme for the past 30 years; this includes sightings of dogs and wolves during intensive pack observations (Marino, Sillero-Zubiri, and Macdonald 2006). I analysed data between 2007 and 2019 to achieve a good generalisation of the range of variation in the behaviour of Ethiopian wolves, across many packs over the years (Table 4.2), both during wet and dry seasons. More data have been collected in the dry season which coincides with the breeding period. The wolf or wolves in each sighting are usually are recognise as belonging to a specific pack; sex and age is usually identified but individual recognition is not always possible.

Table 4.2: Breakdown of the available data from pack observations of Ethiopian wolves between 2007 and 2019 Dry season Oct-Mar, wet Apr-Sept

Season	No sightings	Average no packs per year
Wet	4371	25.5(14-49)
Dry	6204	23.8 (13-37)

The monitoring data consists of 10,577 sightings of one or more wolves including a GPS location, habitat they were in, behaviour they were performing and the pack or individual ID of the wolves if known. Over the time period packs fluctuate as some go extinct so the total observed number of packs is. The GPS locations from each year for each pack were used to construct 90% kernel density estimates of home range in the 'adehabitatHR' package in R (Calenge 2006). GPS locations were also used to determine habitat preference of the wolves, using the same base map, as opposed to the habitat data associated to each observation to allow for direct comparison against dogs' habitat preferences. Points randomly generated within the area of occupancy of all Web Valley packs were compared against all locations to compare use versus habitat availability using z-tests of proportions (Lawley 1938).

4.3.4 Overlap analysis

Due to the bias in the data, overlap was calculated only for the dry season. Spatial overlap between dogs and wolves was calculated from kernel density estimate distributions, using the overlapping package (Pastore 2019) within R (R Development Core Team 2011). This quantified the overlap of each dogs' home range into overall wolf occupancy area during the corresponding year as each dog's home range may extend into the territory of multiple different packs. The overlap of behaviours

and habitat preference was performed through area under curve analysis. The proportion that each behaviour accounted for out of the total behaviours in each hour were summarised as numerical distributions in the form of histograms, this provides a single numerical value for each behaviour at each hour in the day. Habitat preference was derived as the ratio of recorded locations within each habitat type, of either the dogs or wolves, to the available habitat, as calculated previously, a distribution of these values across all the habitat types was similarly constructed.

The data in these constructed distributions were interpolated, using linear interpolation, between each hour or habitat type; to create continuous distributions which can be plotted as graphical curves and then points of intersection between the curve for wolves and the curve for dogs were found. Overlap between the distribution for the wolves and the distribution for the dogs was calculated by mathematical integration of the respective distributions to calculate graphical area under the curves using the package flux in R (Jurasinski et al. 2014). By sequentially running through both, the wolf and dog curves by hour or habitat type, and checking which has the greater or lower value, two separate curves were created to describe the minimum and maximum combined curves of the two species. The % overlap was then the ratio of the minimum combined curve area to the maximum combined curve area * 100. In this way, overlap was calculated for activities at time of day (Active, Forage, Moving, Resting), habitat preference and spatial usage (home range). Ethiopian wolf data were bounded to daytime hours, between 06:00h and 18:00h (outside of these times they are mostly sleeping (Sillero-Zubiri 1994); data from the domestic dogs was also clipped to this range; dogs are almost always in their village (94% of fixes at night in village) at these times so discounting overlap

at these times does not impact direct overlap.

4.4 Results

4.4.1 Domestic dog behaviour

Across all dogs they spent 72% (dry season) and 64% (wet season) of the time within 100m of their respective household. When the dogs were outside of the village, 90% of fixes fell within 1.2km of the home village, regardless of season, at overall mean distance of 727m (range 346m - 1457m). Dogs remained stationary (no movement) between 70% and 62% of the time in the dry and wet season respectively (Figure 3.2). Between each fix (∼every 6 minutes) generally there was low distance travelled, with 90% of data falling into less than 300m, with a mean of 122m between each fix (Figure 3.4) representing approximately 1.2km/h travel speed. The dogs were out of the village mostly during the day between 09:00h and 15:00h, however few dogs would sporadically briefly leave the village during the night, these were rare events with less than 6% of fixes being beyond 100m between 19:00 and 07:00h. Reducing the 1.2km 90% usage area down to 200m shows that this policy would lead to a reduction of 83% in terms of are around the village no longer being occupied. Refer to Chapter 3 for a further break-down of domestic dog behaviour.

Habitat preferences within home range varied between dogs, due to the difference of available habitat within individual home ranges. When preference was calculated against all dog occupation area, there was a preference for drainage lines,

wetlands and Erica moorland during the dry season, and avoidance of lava flows and shrubland (Figure 3.5). The only seasonal difference was that dogs no longer preferred Erica moorlands during the wet season.

The mean dog home range was 3km^2 using the 90% kernel ($\pm$0.626km^2). KDE was highly variable depending on the individual and the surrounding terrain. With a mean wet season estimate of 2.9km^2 ($\pm$0.584km^2)(Chapter 3).

Hourly time allocations for major activities (Figure 3.6) showed two peaks: one 07:00h until 10:00h during the dry season, followed by a smaller peak at 14:00h - 18:00h. In the wet season this pattern was reversed, with the larger peak at 14:00h and a smaller peak beginning at 07:00h. Dogs spent most of their time resting; up to 80% time lying down at night time in the village, and up to 30% of the time within out of village times of 09:00-15:00h.

4.4.2 Ethiopian wolf behaviour

Ethiopian wolf packs had larger home ranges than dogs with a mean range of 10km^2 ($\pm$0.975km^2) (90% kernel) across all years, individual pack areas ranging from 4.8km^2 to 20.1km^2 (59 packs across 13 years) (Figure 4.1). Wolves had a distinct habitat preference for grassland areas ($z = 614.95$, $df = 1$, $p < 0.0001$), had no preference for drainage lines, bare soil and herbs or Helichrysum ($p = 0.33$, $p = 0.71$, $p = 0.51$) and avoided Erica moorland ($z = 187.97$, $df = 1$, $p < 0.0001$), wetlands ($z = 124.79$, $df = 1$, $p < 0.0001$), lava flows and shrubland ($z = 65.76$, $df = 1$, $p < 0.0001$) (Figure 4.2). Wolves had a mean movement speed of 1.1 km/h

and 55% of all speeds were less than 1km/h. The maximum distance travelled in an hour was 4.6km (Figure 4.3b).

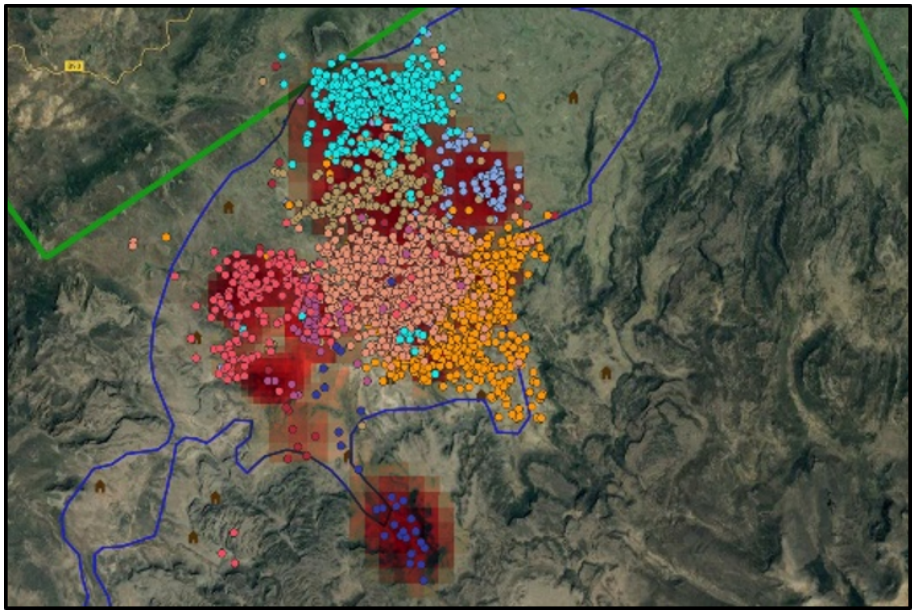

Figure 4.1: 90% Kernel density estimate of wolf home ranges with GPS locations overlaid for wolf packs in the Web Valley of Bale Mountains National Park, Ethiopia. n = 10571 observations of wolves.

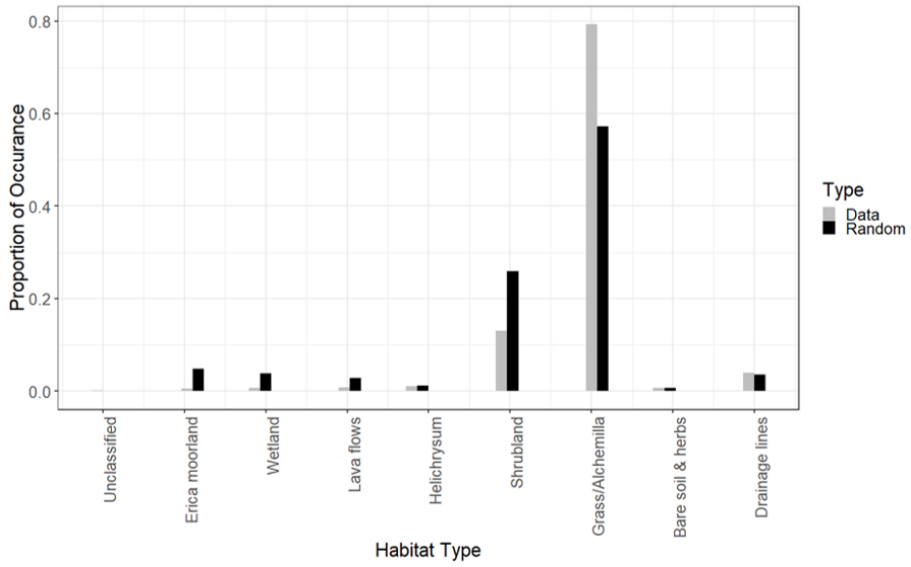

Figure 4.2: Habitat preference of Ethiopian wolves in the Web Valley, Bale Mountains National Park; Grey indicates selected from GPS locations; in black is the proportion that habitat makes up in the entire area within wolf territory to represent availability from n – 10571 observations.

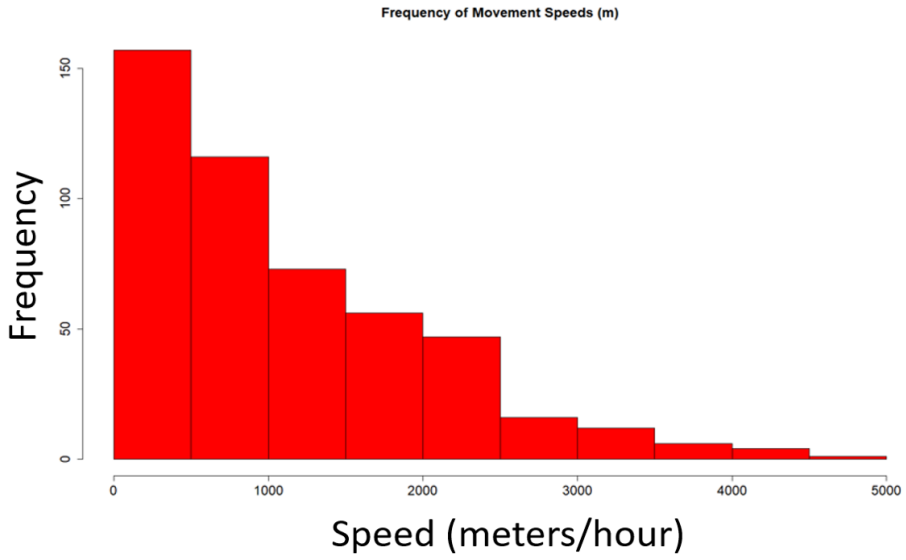

Figure 4.3: Ethiopian Wolf movement speeds from follows in meters per hour from 520 hours of observation.

4.4.3 Overlap analysis

Each dog's home range overlapped into wolf habitat by 48%. Dogs and wolves had a habitat preference overlap of 44.7% (Figure 4.4).

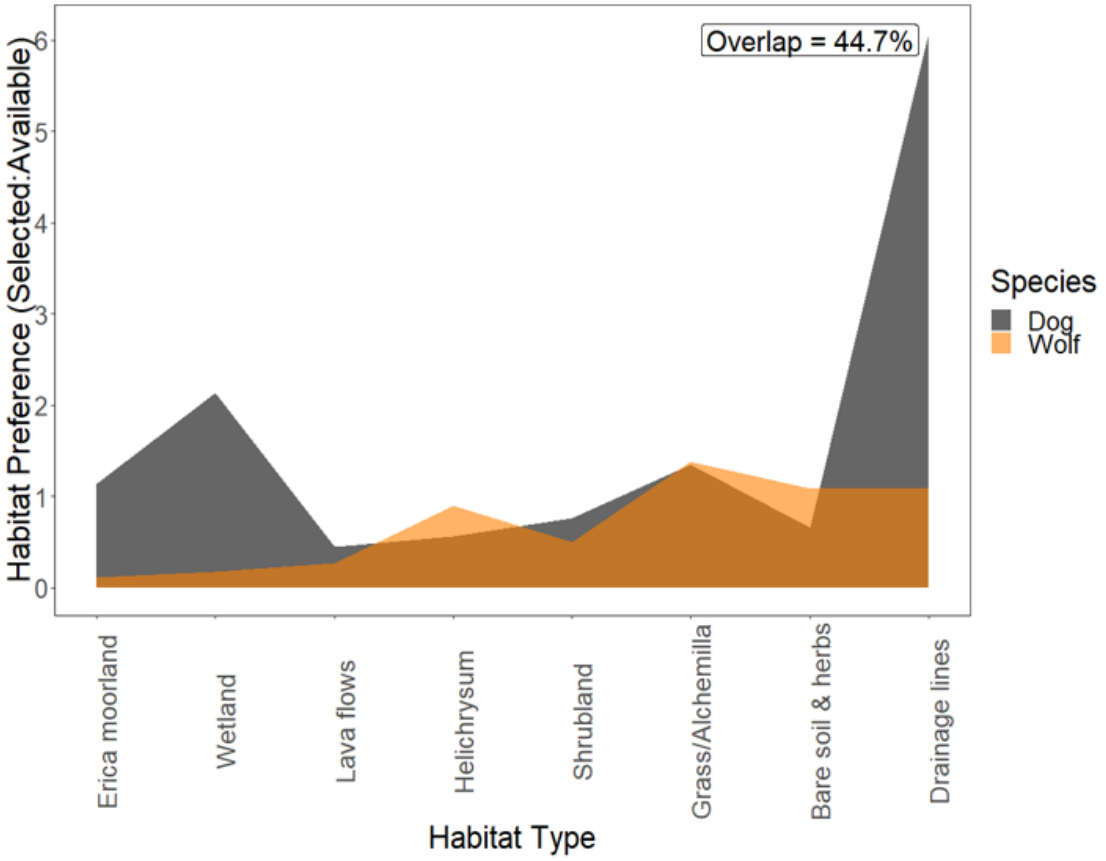

Figure 4.4: Overlap of habitat preference between domestic dogs and Ethiopian wolves. Distributions constructed using linear interpolation between preference for each habitat type. Overlap % calculated by working out the area under the curve of the combined area against the total area.

There was a 75% level of overlap for periods of activity (defined as all active behaviours) between dogs and wolves, but with different peaks (Figure 4.5a). There was a 67% overlap for foraging times (Figure 4.5b), 51% overlap for moving times (Figure 4.5c) and 77% overlap for resting (Figure 4.5d).

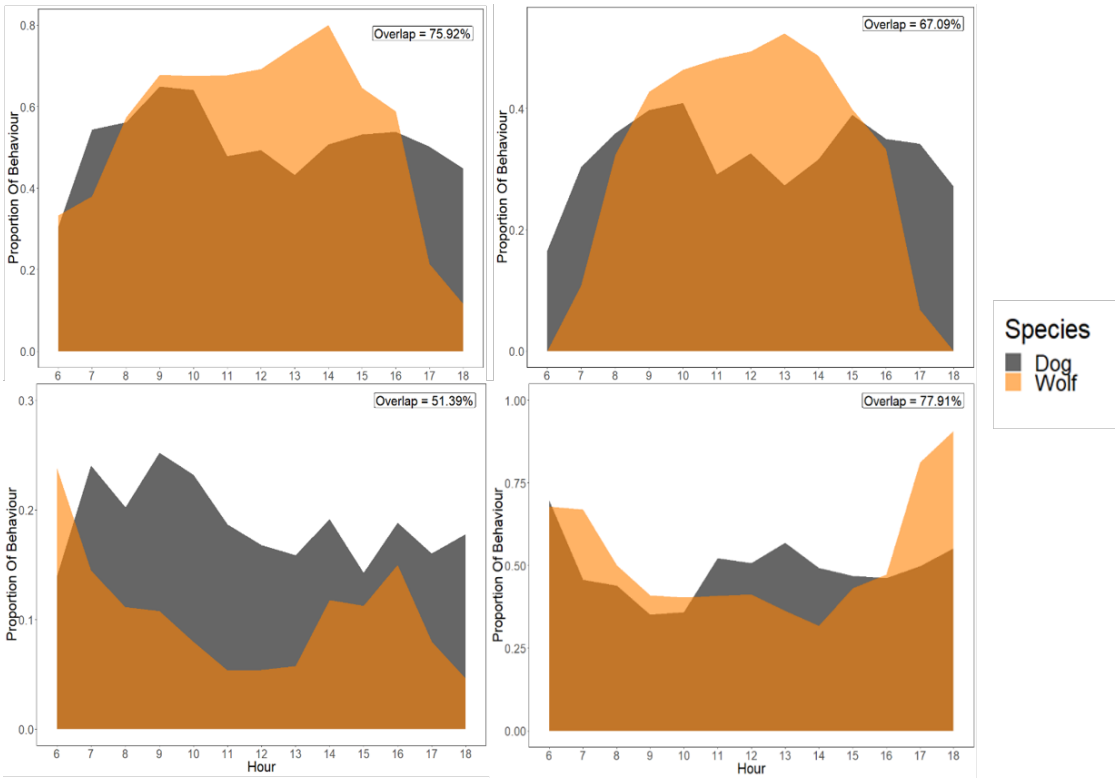

Figure 4.5: Overlap between domestic dogs and Ethiopian wolves of behaviours at each time of the day. a) All active behaviours; b) Foraging behaviours; c) Moving behaviours; d) Resting behaviours. Distributions constructed using linear interpolation between the proportion of each behaviour in each hour. Overlap % calculated by working out the area under the curve of the combined area against the total area.

4.5 Discussion

4.5.1 Implications of behaviour and overlap on disease management

We can safely assume that domestic dog behaviour, as the primary source of disease, will be the greatest individual contributor to disease transmission dynamics. The areas around the villages, particularly the 1.2km area where the dogs spend

the majority of their out of village time, would naturally provide the highest risk for disease transmission. In the Bale Mountains National Park, recent park policy is that dogs movement should be restricted to within 200m from the village (Ethiopian Wildlife Conservation Authority. 2017).If this policy was effectively enforced, it would reduce the high risk area by 1km or an overall reduction of 83%, which could reduce the risk of disease transmission drastically if the risk scaled with total occupied area. Domestic dogs in Bale are kept for livestock guarding and often accompany livestock when they are put out to graze (Atickem et al. 2010). Any policy aimed at shifting pastoralist behaviour to avoid grazing livestock on Alchemilla grasslands may help to dramatically reduce overlap and the potential for transmission events.

There was clear overlap in the Bale mountains between domestic dogs and wolves in their use of space, habitat preferences and activity timings. Dog lives were centered around their village, with the village being the point from which they starter their forages and and returned to. As dogs spill-out further away from villages, they begin to overlap with the wolves and thus can pose a disease transmission risk. The areas that would pose the highest risk would be the 50% of dog home ranges that are within wolf range; this risk would be particularly acute within a 1.2km radius of the village, where the dogs spend most of their time. The interspecific overlap in habitat preference could mean that, when outside of their village, the dogs will experience an increased chance of encountering wolves in those habitat types. This will be particularly true for grasslands, the only areas actively selected for by both wolves and dogs, possibly due to dogs accompanying livestock when grazing in these grasslands. However, some areas of preference ay be selected or

avoided by either species to reduce the chance of encounters.The areas that are used by the wolves represent prime targets for oral vaccination. After successful trails of oral rabies vaccination for the Ethiopian wolf (Sillero-Zubiri et al. 2016) this can now be applied for management but there is a chance that bait uptake by the wolf would be reduced if dogs are also consuming the bait. With dogs being almost entirely restricted to villages over night the ideal time to deploy baits oral vaccination would be in the evening or at night when there is no overlap, however dogs may not be the only non-target species that will consume bait.

There is an even greater level of temporal overlap between wolves and dogs. This increases the risk of disease transfer in the areas which are already high risk, as they will be performing similar activities at the same time and in the same location. Activity patterns were similar between dogs and wolves, with the highest overlap at around 10:00h when both were equally active, which correlates with a sharp increase in giant mole rat (*Tachyoryctes macrocephalus*)(a primary prey source for the wolves) and Ethiopian wolf activity (Sillero-Zubiri and Gottelli 1995; Sillero-Zubiri, Tattersall, and Macdonald 1995). Both dogs and wolves foraged at similar times, except for the middle of the day when the dogs were likely to be resting but wolves continue to forage as this is the peak of mole-rat activity. This was similar to Perry, Marino, and Sillero Zubiri (2018) which showed that foraging was a greater proportion of the time in the morning and afternoon. Dogs in general spent a higher proportion of their time moving than did wolves, and the overlap suggests that during the times that the wolves were moving, the dogs were also moving. An increase of movement would lead to an increased area covered, which again presents more opportunity for a contact event. Resting had the highest

overlap for behaviours but as it is higher than the habitat preference overlap there is an indication that they are likely resting in different locations. Areas that are highly used for resting could themselves be high transmission areas particularly for CDV.

CDV is transmitted by direct contact but can be left in and picked up through the environment (Appel and Gillespie 1972), viral particles are contained in bodily fluid particularly in mucus or urine and if consumed or inhaled by an uninfected individual can lead to infection taking hold, which means that a larger spatial overlap and particularly area travelled over could increase the risk of CDV as a greater area was left contaminated. The preferred areas could also be high risk areas even without direct contact as areas preferred by dogs may have a higher chance of having infectious residue left in them. Rabies requires direct contact for transmission however it commonly modifies the behaviour of infected individuals (Shuangshoti et al. 2016) which may mean that behavioural overlap is less critical but the spatial overlap, particularly the proximity of wolf territories to villages, becomes key.

4.5.2 Impacts of overlap outside transmission

The overlap could pose a risk to the wolves beyond just disease transmission, as it suggests the potential for competitive exclusion even if they may not be foraging directly for the same resources (Atickem, Bekele, and Williams 2009). The mere presence of dogs has been shown to impact wolf activity. Aggressive interactions occur between the wolves and dogs and this can lead to displacement of the wolves

from their foraging locations (Perry, Marino, and Sillero Zubiri 2018). Aggressive interactions with domestic dogs are just a part of the disturbance that occurs due to the presence of humans. An unintended consequence of human disturbance is that many carnivore species shift activity periods or habitat utilisation. Under disturbance cheetahs have shifted behavioural patterns to adapt to human management (Bissett et al. 2015) and polar bears have shifted their ranges and foraging patterns in response to reducing sea ice (Derocher, Lunn, and Stirling 2004). However, these often have negative consequences such as reduced offspring survival to this from moving into lower quality habitats or maladaptaive niches (Kokko and Sutherland 2001; Wong and Candolin 2015). Wolf packs with larger home ranges may begin to exhibit spatial displacement avoiding the parts of their territory that are used more by dogs. With close proximity between the packs. Sillero-Zubiri and Gottelli (1995) showed that pack home ranges while discrete formed a tight tessellated mosaic; if wolves responded to disturbance by avoiding areas that dogs use it would likely mean negative impacts due to less foraging area, foraging area size has been shown to impact group size and structure (Marino et al. 2012). This would only be compounded as habitat loss increases in the Afroalpine range. There are indications that Ethiopian wolves in the Northern populations have shifted their peak time of activity later in the day and into the night (Yalden and Largen 1992)(Gebeyehu Pers Comm). This time shift could be to reduce the temporal overlap with the domestic dogs or people, either due to threats of disease or just competitive interactions.

4.5.3 Future considerations for studying disease transmission

Overlap between threatened wildlife species and infectious disease hosts is only going to increase as the human footprint increases. Direct quantification of this overlap can help understand the dynamics of these diseases as they become more common (Robert, Garant, and Pelletier 2012). There are ongoing trials of disease management in endangered species, but it is important that these are applied with full understanding of the disease host or hosts involved. This methodology can be applied to not just a domestic dog disease system but any disease system where the behaviour of the involved species can be quantified. Overlap between hosts has been used to understand disease and management in other systems previously. Overlap between buffalo (*Syncerus caffer*) and domestic cattle (*Bos taurus*) was quantified to better understand the transmission risk of Foot and Mouth Disease (Kaszta et al. 2018). Barasona et al. (2014) quantified spatiotemporal overlap of GPS collared cattle and wild boar (*Sus scrofa*) and found there were particular habitat types with high overlap and these correlated with increased risk of Tuburculosis transmission. Technologies such as GPS are making are critical in collecting data on the overlap of species.

Novel technology and statistical methods are making it easier to observe and collect behavioural data from species (Brown et al. 2012; Fischer et al. 2018). New methods such as optical tracking of mosquitoes in a room using 3d sensors (Kröner et al. 2019) are revealing increasing dimensions of behaviour that can lead to better understanding of disease dynamics and disease management. It is important to

maintain studies of behaviour of disease hosts over time as well, mosquitoes have behaviourally adapted to malaria prevention methods by shifting feeding times to before people apply repellents or use bed nets (Hoi and Roitberg 2014). Monitoring of host behaviour allows for an adaptive management strategy that could prove to be more effective and prevents the return of outbreaks after control methods.

This work has focused on specific time windows of overlap as that is when the data is available. It may be that there are periods that have a extremely high risk that are not encapsulated here such as the full timing of the wolf breeding season. Wolves show synchronicity of breeding where neighbouring packs all breed at the same time which could be a period where density is particularly high and disease transmission would be severe (Sillero-Zubiri, Johnson, and Macdonald 1998). Further work should maintain a long term behavioural study of the overlap to make sure it is known over all periods and to monitor if it is changing over time. As more and more people and dogs move into wolf habitat there is a possibility that wolves will respond with behavioural change and the effect this has on overlap and the resulting disease dynamics and management would need to be quantified. Quantification of direct contact between dogs and wolves and the behavioural dynamics of them would also be useful but has proven difficult in the past due to the low number of observations of such occasions. As a dataset builds up of these contacts it may be possible to expand on the risks, including non-disease related risks such as competitions, that the overlap causes.

4.5.4 Conclusions

The high level of overlap between Ethiopian wolves and domestic dogs, the primary source for rabies and CDV in the Bale Mountains, presents a constant and very real risk for disease transfer. Understanding the overlap gives us the opportunity to predict areas and times that are at high risk of disease transmission. Focusing management on overlap times or areas can lead to a more targeted or more effective approach to reduce disease transmission. There is still a need to understand the underlying drivers of this overlap and whether modifications in animal husbandry may be one of the most suitable areas for targeted management or behavioural change of the dog owners. This framework of characterising overlap between host species could be more broadly used in a number of disease systems where information can be collected on the behaviour of the species. Behavioural classification and overlap measurement can then be used on a number of modelling frameworks to quantify the threat diseases pose and to trial targeted management scenarios to evaluate their possible effectiveness.

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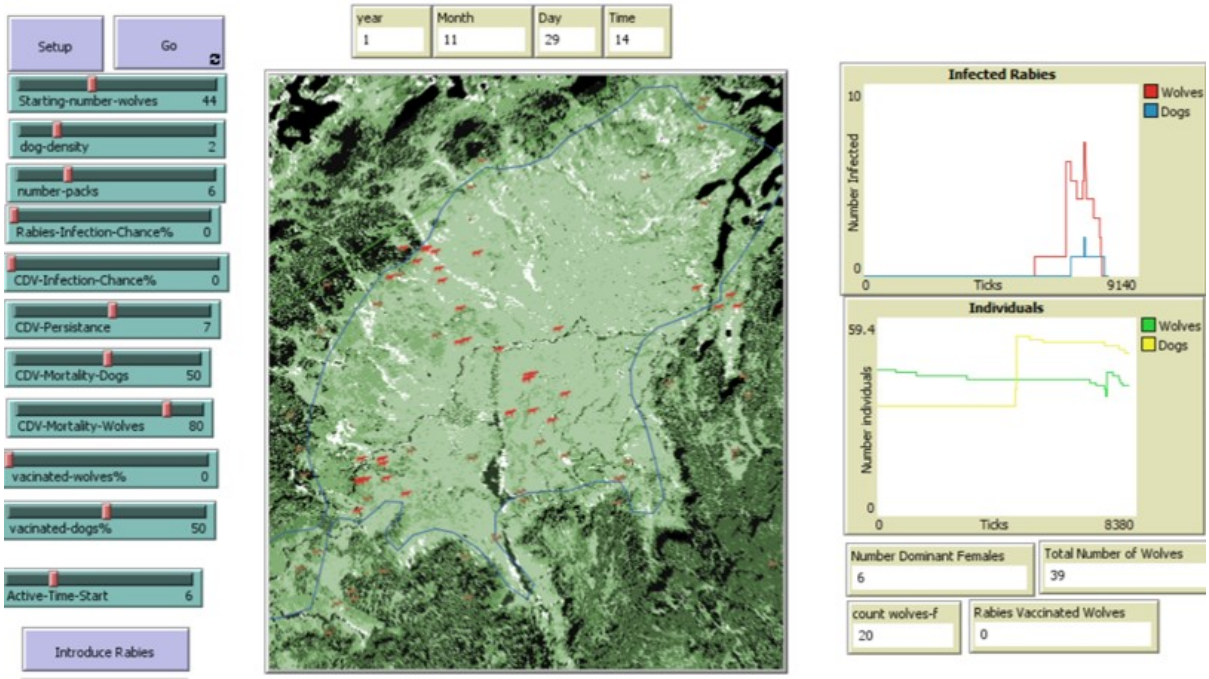
Chapter 5

A scalable agent-based model of viral diseases in Ethiopian wolves and the primary host, domestic dogs.



5.1 Abstract

Disease transmission from domestic animals to endangered wildlife is becoming a pressing conservation concern. The Ethiopian wolves, a rare pack living Afroalpine specialist, living in the highlands of Ethiopia, threatened by rabies and canine distemper virus transmitted from domestic dogs. This is partly mitigated through vaccination of domestic dogs, reactive vaccination of wolves and, recently, via preventive oral vaccination of wolves. Information on required vaccination thresholds and associated costs is required to develop an integrated disease management strategy for Ethiopian wolves. Modelling frameworks can help inform the dynamics of disease as well as the impacts of management through simulated trials. Agent-based modelling, where individuals within the population have their own set of parameters and behaviours, excels at simulating potential disease transmission and the outcomes of interventions. With this purpose in mind, I used detailed behavioural observations of Ethiopian wolves and free-ranging dogs in the Bale Mountains of southern Ethiopia to build a highly parameterised agent-based model. The model was constructed over a detailed habitat map of Bale Mountains, with wolves and dogs following a set of behaviours defined as model procedures, such as movement or rest. At each time-step, these were based on conditions such as infection status, season and time of day, based on data from real world behaviours and demography. When compared to real epizootic data, the resulting model was able to accurately predict population and disease parameters with 95% confidence and low root mean squared error of 3.74, a measure of the difference of actual Ethiopian wolves to the population size predicted in the model. The model showed low general sensitivity to variations in input parameters (less than 0. 1

linear sensitivity), with all parameters being within the same order of magnitude of sensitivity on the model but dog density and the number of wolf packs having the highest sensitivity. This model can be applied to assess disease dynamics in the Bale Mountains Ethiopian wolf system and to simulate current and future vaccination intervention scenarios. This study demonstrates the power of agent-based models to inform control of diseases affecting wildlife Moreover, by reducing or increasing complexity, the model generalisation or predictive accuracy could be improved and provide a framework for other systems at the domestic animal – livestock interface.

5.2 Introduction

Epidemiological modelling provides a framework for the estimation of various disease parameters which can subsequently be manipulated to quantify impacts on the system (Garner and Hamilton 2011). Traditional disease modelling uses matrices or differential equations to represent the susceptible-infected-resistant-removed (SIRR) components (Schneckenreither et al. 2008) of a population, based on a fairly coarse parameterisation. Agent-based modelling are increasingly used in epidemiological work as greater resolutions of data become available (Ajelli et al. 2010). Agent-based models (ABMs) allow for complete parameterisation of every individual within the model with (Grimm et al. 2010a). These individuals then behave or perform actions following a policy which is set by the model builder. Agents can also represent environmental parameters, allowing the creation of a spatial world within a model. Non environmental agents then move around this space interacting with each other and the environment. ABMs can simulate micro-scale features of a system and the properties of the system emerge from within it (Coates and Schmid 1998). The decision of what to monitor is entirely up to the model user and can be specified; this is one of the powers of ABMs in that specified monitoring parameters do not need to directly interact with the underlying mathematics of the model which is not possible in differential equation series without including them as an equation (Schneckenreither et al. 2008). This bottom up approach, where understanding the ecology or behaviour of individuals in a system allows for understanding and prediction of a complex dynamic systems, is becoming more popular (McLane et al. 2011). Recent epidemiological work has focused on the inclusion of a specific or adaptive behaviour to see how this might

impact transmission (Fenichel et al. 2011) or including social dynamics, or other network structures, to more accurately represent transmission within a population, as opposed to stochastic transmission between individuals (Amouroux, Desvaux, and Drogoul 2008; El-Sayed et al. 2012). Species which have complex behaviours and social dynamics, such as canids, impacted by disease are particularly ideal for ABMs.

The Ethiopian wolf (*Canis simensis*) is a pack-living canid occurring at high density in the rodent-rich Afroalpine ecosystem of Ethiopia. The wolves live in packs ranging from two to eighteen individuals with packs in high quality areas between three and thirteen with a mean of six and low quality areas living mostly as pairs (Zubiri and Gottelli 1995; Marino et al. 2012; Marino et al. 2013). With fewer than 500 remaining, the species is listed as endangered (Marino 2003; Marino and Sillero-Zubiri 2011). The most immediate threat to the wolves comes from diseases spread by free ranging dogs (*Canis familiaris*) brought into wolf habitat by pastoralists grazing their livestock (Laurenson et al. 1998), this is particularly compounded by range restriction from habitat loss. Dogs reside in small villages where they are used for livestock protection (Atickem et al. 2010) but during the day often go out into wolf habitat with the livestock or people where they pose a threat to the wolves (Atickem, Bekele, and Williams 2009). When out in wolf habitat they can come into contact with wolves that can lead to transmission of disease primarily rabies and canine distemper virus (CDV) which are transmitted through direct contact or CDV can also be left in the environment (Appel and Gillespie 1972; Appel and Summers 1999)

There are periodic outbreaks of rabies (Sillero-Zubiri, Gottelli, and Macdonald 1996; Randall et al. 2004; Johnson et al. 2010) and CDV (Gordon et al. 2015; Marino et al. 2017) that have caused and continue to effect large scale oscillations in the wolf populations, as recorded during 30 years of monitoring in the Bale Mountains. To try and reduce the chance and severity of such outbreaks rabies and CDV vaccination campaigns have targeted domestic dogs for many years (Ethiopian Wildlife Conservation Authority. 2017). When outbreaks occur, wolves are targeted with reactive vaccination, with wolf pack around the infected pack captured and vaccinated to halt or mitigate an outbreak (Haydon et al. 2006; Randall et al. 2006). An oral vaccine for rabies has been successfully trialled and is being implemented (Sillero-Zubiri et al. 2016) and a CDV vaccine is currently being trialled (Ethiopian Wolf Conservation Programme 2019). There are also official park policy management actions that focus on the dogs such as reduction of dog density and the restriction of dog movements to close to villages (Nelson 2011). Any interventions requiring capture are intrusive and come with an inherent risk (Dennis and Shah 2012; Ludynia et al. 2012) and can incur high costs. It is vital that any such health management intervention be informed by understanding of the underlying disease dynamics and the impacts that management would have in Ethiopian wolves. Modelling can be used to help inform understanding and management. Previous modelling work on the Ethiopian wolf – domestic dog disease system predicted that small populations were at greater risk of extinction and that even a low level of vaccination of the wolves can help prevent outbreaks (Haydon, Laurenson, and Sillero-Zubiri 2002; Haydon et al. 2006). This modelling was done on a population scale and with less information on the ecology of free-roaming dogs, the primary disease host.

ABMs can provide greater levels of understanding than traditional modelling, provided the relevant data is available. The spatial world is an explicitly defined part of the model making it possible to track the disease locations providing spatial hotspots of infections. Classic disease parameters such as rate of spread. R_0 or R_e become an emergent property of individual behaviour and can be quantified directly from the model rather than needing to be specified beforehand. The power of agent-based modelling lies in its dynamic parameterisation, resulting in understanding of individual decision-making by species and the risks of interaction between the species (Perez and Dragicevic 2009; Bonnell et al. 2010; Pais et al. 2017). Models can be readily evaluated, and parameter exploration can be used to determine better management strategies (Morrison et al. 2008; Liu et al. 2015). In this chapter I built an ABM of an Ethiopian wolf-domestic dog system to inform not just the disease dynamics but also the effectiveness of different disease management scenarios and cost effectiveness by including costs of the vaccination process such as logistics, vaccine and human resources.

5.3 Methods

Here I present an overview of a model described using the Overview, design concepts and details (ODD) framework (Grimm et al. 2010b).

5.3.1 Overview

5.3.1.1 Purpose

I constructed a model of disease (Rabies and Canine Distemper Virus) transmission in a wolf-dog system and various vaccination management scenarios using Netlogo 6.0.4 (Tisue and Wilensky 2004), and the GIS plugin. Netlogo is a purpose-built agent based modelling language with inbuilt graphical user interfaces. It was built using GPS locations and behavioural data collected on dogs and wolves (Chapter 3 and 4) and then validated and tuned using historical population size data during epizootic (Marino, Sillero-Zubiri, and Macdonald 2006; Marino et al. 2013)). Disease parameters were estimated using published or available veterinary data and then tuned using parameter estimation. A full table of parameters with descriptions and ranges is available in the appendix.

5.3.1.2 State Parameters and Scales

The model is constructed on four hierarchical scales starting with the lowest level of agents which are the individual wolves or dogs, the pack or village level comprising the smaller groups, the population scale which consists of all individuals of either species and then the model world which is the background environment and time scale. Disease related variables are sub parameters of individuals or the world.

Agent Parameters: All individual dogs or wolves within the model had an age and sex as basic demographic parameters and stored a list of all patches within their territory or home range broken down by habitat type for efficient processing of movement. Habitat preference determined the movement of individuals to habitat

types and the map stayed constant throughout the run assuming no form of habitat change. In addition, all individuals had a series of disease-related parameters to track their infected and resistant state for the two viruses. On each time step every individual performs an action or series of actions based on conditions of the model. Individuals can be performing specific behaviours such as reproducing, or a standard behaviour such as moving, foraging or resting.

Wolf parameters: Wolf paramaters were based on empirical data collected by the Ethiopian Wolf Conservation Programme over the course of his long-term monitoring project, and analysed in Chapter 4 and previously published ecology of the wolves (Zubiri and Gottelli 1995; Sillero-Zubiri, Gottelli, and Macdonald 1996; Marino, Sillero-Zubiri, and Macdonald 2006; Marino et al. 2012; Marino et al. 2013). Wolves were assigned to a pack, representing other individuals they socialise with and share a territory. Individuals from the same pack also shared the location of their den while they are reproductively active (denning period). Wolf territory sizes were estimated from wolf observations and averaged 10 km^2 (Chapter 4). Wolves only move within their territories following the behaviour and habitat preference from real data. The world is made up of a finite number of territories and these are filled by wolves when available. Within each pack there is a dominant female and a dominant male, only the dominant female breeds within each pack and if either of the dominant individuals die the oldest of the subordinates of that sex becomes the dominant. Pack reproduction is mediated by the number of individuals within the pack, the larger the pack the less pups the dominant female will give birth to. Non dominant individuals may disperse and form a new pack if there is an empty territory available, a subordinate male and a

subordinate female from a different pack will move to inhabit the empty territory and then begin breeding at the next breeding season.

Dog parameters: Dog parameters are also derived from empirical dog data presented in Chapter 3. Dog home range size was derived from home range estimation from GPS collars and averaged 3 km2. Dogs did not have a pack or den, but had the location of their village as an additional parameter. New dogs can enter the system in two ways, either they are born from female dogs or they are brought in during the wet season as a proxy for the seasonal movement of people in the area.

Disease Parameters: Diseases in the model were not their own agents but exist as variable parameters within all components (agents and patches). Both diseases had an incubation time (the time between initial infection and becoming infectious), an infectious time (the time between the start of infectious period and end of the infection) and a total duration time. These parameters came from Jackson (2002) for rabies and Appel and Gillespie (1972) and Takenaka et al. (2016) for CDV. These timings are distributions, so each infected individual will have a variable incubation and infectious time. CDV has a mortality risk of 80% in wolves (Gordon et al. 2015) and 50% in domestic dogs (Deem et al. 2000; Miller and Hurley 2009) while rabies was assumed to have 100% mortality (Jackson 2002). CDV also has environmental persistence - which is the rate at which it decays out of the environment (Appel and Gillespie 1972; Miller and Hurley 2009). Rabies has a ratio of dumb to furious rabies (Shuangshoti et al. 2016) which determines the behaviour of infected individuals, furious individuals will move randomly rather than follow standard procedures . Both diseases had true/false values for infected

or resistant that are stored for each agent. Disease is not a constant presence in the model but is introduced into the system when new dogs are brought into the model. This has a random chance to occur each time new dogs are brought in but is at a rate to work out to approximately every 3 years, which is based on the outbreak history of the wolves (Marino et al. 2013). Disease transmission between individuals occurs when they have come into contact with each other at an 80% chance of transmission during a contact event, this was tuned during the sensitivity analysis with parameter tuning.

Model World:The model world is made up of 404,004 patches based on a Landsat map of 30m x 30m pixels classified into habitat types from the Bale Mountains (Tallents and Macdonald 2011). The map includes seven main habitat types in the Bale highlands above 3,000m asl: Erica moorlands, wetlands, lava flows, Helichrysum, shrubland (*Artemesia*), grass, bare soil and herbs, and drainage lines. Each patch then contained its habitat classification as a variable. Patches also had disease and monitoring parameters. The patches have their own set of procedures; villages are allowed to incorporate new dogs and all patches store a true/false of whether CDV is present within them and can thus infect agents or have the CDV expire.

5.3.1.3 Process overview and scheduling

The resulting model works on a 1-hour timestep and progresses 24 hours a day 30 days a month for 12 months in a year; it can be run for as many time steps as desired. Agents and patches (unique cells) have procedures that are called at each time step. Currently the model can run 100,000 steps (approximately 12 years) in 390 seconds (6.5 minutes) with over 400,000 patches, based on a real world GIS

constructed map, that made up the model world and 265 agents, but the model is capable of scaling up with less than linear speed reductions (Railsback et al. 2017). The underlying procedure policy is for each individual to first check their infection status, then to check the time, and then iteratively choose procedures such as specific behaviours based on conditions and underlying probability distributions from real data (Figure 5.1). The primary condition within the model is infection status, which can switch an individual's behaviour completely in the case of rabies and also causes other behaviours such as infecting others. The other conditions were primarily timing based: time of day decides many generalised behaviours, season determines denning behaviour and specific times can cause specific behaviour such as reproduction.

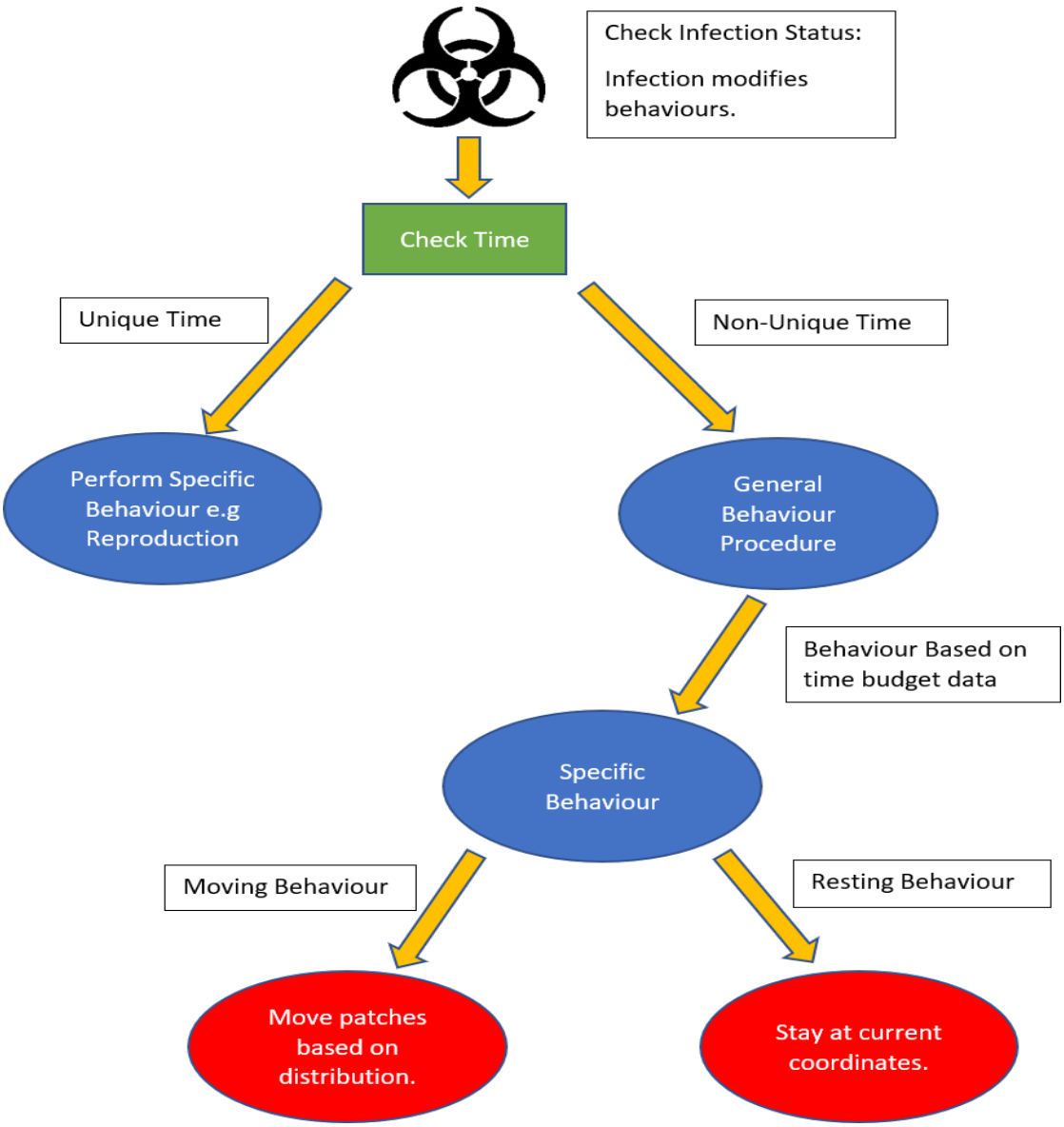


Figure 5.1: An example of procedure policy that an agent may follow at any given time step. The two major conditions that determine procedures are infection status and time. There were a total of 4 unique time specific behaviours, a general behaviour procedure with four behaviours with it and eight disease specific procedures. A single timestep can involve a combination of up to eight procedures called by one agent.

5.3.2 Design Concepts

Emergence: The disease transmission emerges from the individual behaviours and dynamics, based on the underlying assumption that contacts between individuals will transmit the disease.

Stochasticity: nearly all non-input parameters in the model were based on distributions rather than fixed values and when used are drawn from these probability distributions. Meaning there is stochasticity in each type step. This is important to include the demographic and behavioural noise and is accounted for by running multiple simulations.

Monitoring: The model tracked and stored parameters, termed monitors, during each run to help inform the user about model progress and outputs in addition to standard parameters that are stored by Netlogo. It also had many parameters that are used by the simulation itself for conditional procedures. The principal monitors were the number of epizootics and the cost of vaccination interventions, both of which were allocated to each species. The model also tracked the individuals infected with each disease, the number of introductions of each disease and the number of cases of CDV picked up from the environment. Each agent in the model stored the number of other individuals that they have infected, in the event they are themselves infected. All patches stored a count of the number of infections that have occurred in them and the number of individuals of either species that have visited that patch; this allows for finding hotspots of infection and usage.

5.3.3 Details

5.3.3.1 Initialisation

The model is initialised with 20 wolf packs across the entire area each with varying territory and pack sizes based on the real world distributions. Each pack has a dominant male and a dominant female and the rest of the pack members are subordinantes. All individuals within the pack are aged 1 – 8 with no pups. Dogs are initialised in villages with between 1 – 5 dogs per village randomly assigned. The model begins on January 1st at midnight and carries on from then. There is no disease in the system at the start of the model.

5.3.3.2 Inputs

The model required several user-specified inputs for each run. The starting number of wolves, number of packs, maximum pack size and domestic dog density all decide the starting and maximum number of agents. There were a number of predefined disease parameters that need to be set by the user, the percentage chance that a disease will enter the system on any given year, the persistence of CDV in the environment and the mortality of, separately, wolves and dogs due to CDV. The final inputs were management scenario inputs, including the proportion of dogs or wolves vaccinated and restriction of dog movements via protected area enforcement.

5.3.3.3 Submodels

There are two parameters that rely on underlying models. Survival is based on age, at each tick there is a random chance based on the age that an individual

will die. For wolves, mortality is high for pups over 6 months until 1 year (Marino et al. 2012) and then stable until over 8 years old where it increases the older they get. Dogs have a constant mortality risk related with age until 8 years where it again increases as they get older. Reproduction is density dependent to prevent constant population growth, mimicking the effect of a carrying capacity. As wolves approach the upper range of pack sized that have been observed (18 individuals) their reproduction is slowed (Marino et al. 2013). Domestic dog populations are monitored by EWCP and the number of dogs in villages counted and as villages approach the upper end of this range fewer new dogs are brought into the village.

5.4 Results

5.4.1 Sensitivity analysis

Sensitivity analysis was performed on the input parameters of the model (Hamby 1995) in R (R Development Core Team 2011); 10 runs were performed for a series of values of each input parameter, keeping all others fixed. Variability range for each input parameter was different but based on a range that was biologically feasible, full ranges are presented in Appendix 2.1.7. This resulted in 70 runs in total. The differences in model output, including the population sizes of both species, the number of epizootics and number of infected individuals, were then used in linear models to determine the linear sensitivity of each parameter on each output. These were then averaged to obtain the sensitivity of a parameter as a whole. In general, all the input parameters had a low sensitivity (less than 0.1 mean gradient of the regression lines (Kleijnen 1992)) with dog density and

number of packs the most sensitive parameters (Figure 5.2).

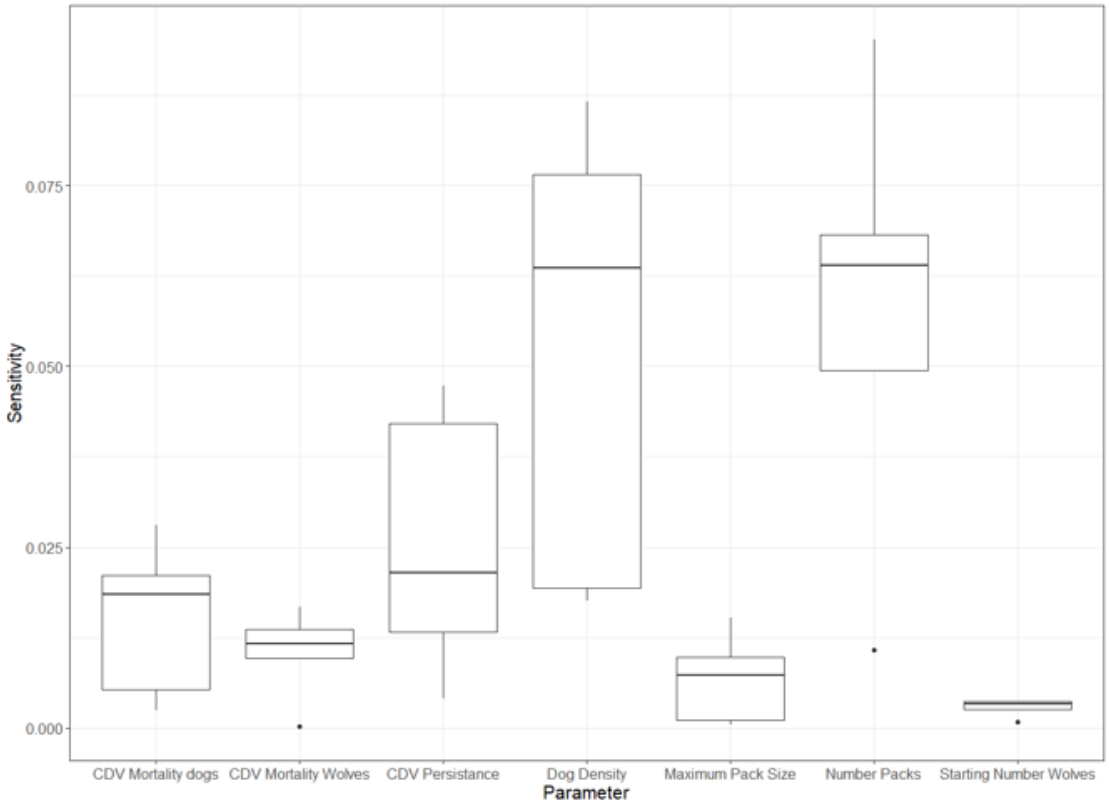


Figure 5.2: Linear sensitivity, calculated through linear regression of model outputs, of the Ethiopian wolf – domestic dog disease agent-based model to the various input

5.4.2 Validation

The model was validated using historical epizootic and population data in the Web Valley wolf population. During 2008 to 2012, there were sequential outbreaks of rabies and then CDV (Marino and Sillero-Zubiri 2011) and represented an ideal time period to test the accuracy of disease and population dynamics in the model. The model was restricted to the area of the Web valley population, then provided with nothing but the number of wolves that were recorded in 2008 and pre-programmed

to have outbreaks, by infecting a single wolf, at the time when they were recorded in the data, while standard introduction of the disease was removed. The wolf population was assumed to be naive to the diseases at the start but there may have been some residual resistance from previous vaccination. The model then was allowed to run for 100 runs and the resulting population of wolves at each time step was compared to available data. The real data were within the 95% confidence interval of predictions for 3 of the 4 years and overall a low root mean squared error (Chai and Draxler 2014) of 3.47 (Figure 5.3) a measure of the difference of observed Ethiopian wolf population size to the population size predicted in the model.

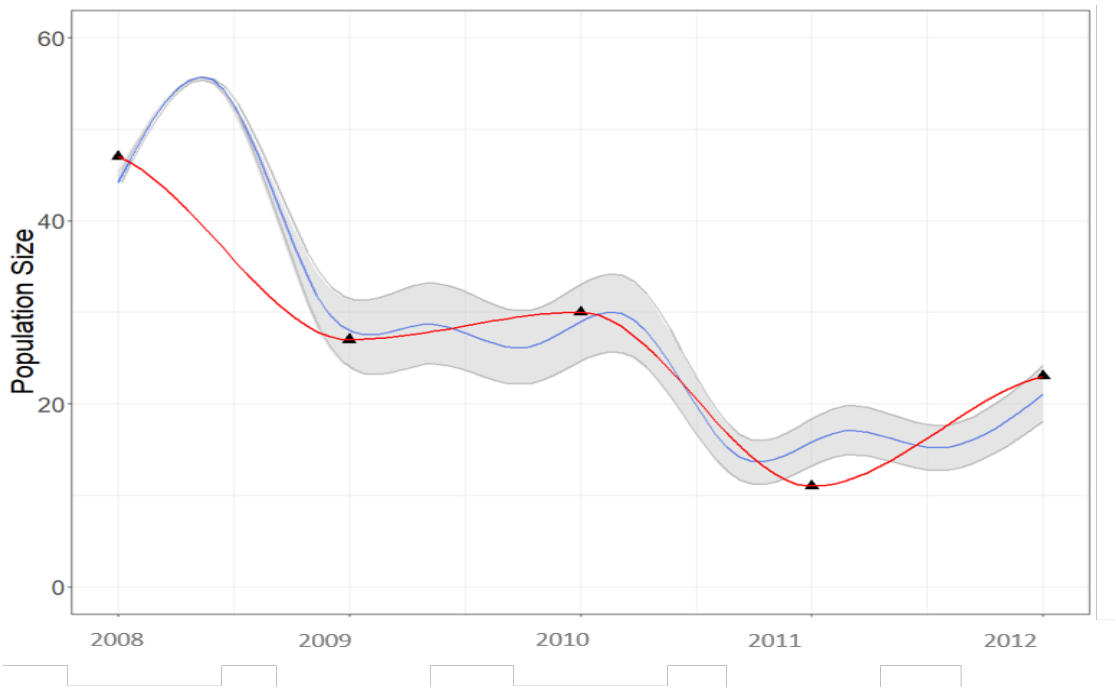


Figure 5.3: The mean Ethiopian wolf population size across 100 runs of Ethiopian wolf – domestic dog disease agent-based model set for validation of parameters in blue with standard errors against the real data that it was attempting to replicate in red. A rabies outbreak occurred in 2008 and a CDV outbreak in 2010.

Due to stochasticity each simulation will predict different levels of decline and population growth rates across the 100 runs. Population change, calculated as the change in number of individuals (either increase or decrease) in the population from the previous year, during epizootics and recovery years were compared to 30 years of recorded data encompassing five large epizootic declines. There was no significant difference between the simulated and the real data for epizootic declines (t test, t = -0.21, df = 4.85 p = 0.84) or for population growth (t test, t = -1.52, df = 19.04, p = 0.15) (Figure 5.4).



Figure 5.4: Simulated epizootic declines from Ethiopian wolf – domestic dog disease agent-based model runs against observed epizootic declines (red) and simulated population growths against observed population growths (green).

5.5 Discussion

The model was found to be robust to parameter variation, and accurately predicted the decline and subsequent recovery a local Ethiopian wolf population in historical outbreaks with a 3.47 RMS error. The model constructed here performs well in predictive ability while having a large range of usages beyond just prediction of population declines. The accuracy in predicting population and epizootic processes in the Bale Mountains provide confidence in the robustness of simulation of other scenarios such as vaccination strategies or behavioural changes. The predicted declines showed more variation than those observed, possible the result of small outbreaks, where only one or few individuals are infected, which may often be missed by observers and the mortality recorded as from unknown sources. Simulated epizootics are capable of being larger, with more individuals experiencing mortality, than the observed data. This may be due to efforts of management being intensified during outbreaks in the real world; as more mortality is recorded it is likely that that management is adapted and applied even more intensively such as increasing the reactive vaccination level. This is not currently in the model, but an adaptive management strategy is something that could be added as mortality can be tracked. While all input parameters had a low level of sensitivity, the parameters that determined biological agent number, dog density or number of wolf packs, had the highest sensitivities. This is logical and should be of little concern as many of the output parameters of the model are in some way directly related to the number of agents. The more susceptible individuals are available to be infected, the more likely there is to be an outbreak, or the higher number of infected individuals there will be. The population dynamic parameters should be

considered carefully at initialisation to ensure the robustness of the model, and if necessary, a variety trialled to determine valid starting points.

Construction of the model required a large amount of specific data to parameterise it at a level useful to developing disease management strategies. It would, however, be possible to construct a model with less detailed data and to make less accurate but still informed predictions from it. This model was built at a very fine scale time-step of 1 hour, in order to encapsulate the role that specific behaviours such as travelling or resting might have on disease transmission, requiring a large number of steps to simulate over longer periods and computational time. To simplify procedures and computational effort, it may be possible to use a larger time-step. The model world was constructed over a habitat-classified map and individuals had a habitat preference stored which determines their movement, but a simpler model could be tested with a world without direct habitat classification if the data did not exist. A simpler world made up of coarse resolution occupancy could be used in its place; this would also have the benefit of requiring less computer memory for faster model setup. The model was also built with strict social structures in the wolves that represent the real social dynamics of packs, however these dynamics are most likely strong contributors to the final output of the model. Sociality and cooperative breeding shapes the population dynamics and contact networks of these species (Bateman et al., 2013) which in turn will, at least partially, determine which individuals will become infected (Drewe, 2010; Patterson et al., 2017). The social dynamics of infection have been shown to be important in canid species (Sterner and Smith, 2006). Testing the impacts of removing the social dynamics from the model would demonstrate how sensitive the model is to these dynamics and could reveal the relative importance that social dynamics has on infection in

Ethiopian wolves.

ABMs have a growing role in epidemiology for their ability to simulate different scenarios easily once the base model has been built (Venkatramanan et al. 2017). A particularly powerful application of ABMs is the trial of different management strategies to inform policy in the real world. Disease control has been simulated in wildlife using an ABM, a model of Indian foxes (*Vulpes bengalensis*) found that domestic dog vaccination was not sufficient to protect the foxes while direct fox vaccination is highly effective (Belsare and Gompper 2015). More generally within epidemiology ABMs have been used to explore the cost-effectiveness of Johne's disease control in dairy herds using different disease diagnostic methods, leading to management recommendations and reduced costs (Robins et al. 2015). An ABM of measles eradication prospects in urban Canada predicted a requirement for very high vaccination coverage amongst under 18s, but this was still only successful dependent on the behaviour of parents, the level of association among vaccinated individuals and contact rates (Perez and Dragicevic 2009).

ABMs do have some caveats, particularly the large amount of data required to construct them and the trade-of between realism and simplicity (Tracy, Cerdá, and Keyes 2018). In any attempt to model reality some generalisations are required and when trying to model an individual it is possible for an individual to perform many different behaviours at different times. This leads to either the omission of behaviours from the model or to what is often termed, stylised facts; where behaviours without data are created and then tuned until they approximate reality (Beikirch et al. 2018). ABMs have also been criticised for their inability to determine causal relationships (Grüne-Yanoff 2009), yet they can simulate coun-

terfactual outcomes to estimate causality, an increasingly common methodology (Marshall and Galea 2015).

Stored agent parameters allowed me to construct complex behaviours in the form of policies of conditional procedures but took up considerable computer memory and time. The trade-off between agent complexity, computational efficiency and complex procedures needs to be taken into account (Railsback et al. 2017). For example, this model did not treat diseases as individual agents to allow for more efficient computation, with transmission done through the other agents. With specific disease agents, however, it is possible to simulate virus adaptation and evolution (Yilmaz 2013), of particular relevance for antibiotic or antiviral resistance (Handel, Longini, and Antia 2009). Inputs of the model can also be expanded to include more behavioural parameters and simulate behavioural change, such as shifts in habitat preference or activity times and how that would impact disease transmission. Shifts of mosquito feeding times earlier in response to bed nets lead to increased transmission (Carrasco et al. 2019), similar effects could be incorporated into ABMs easily.

Where agent-based models shine is in spatially explicit worlds; it is easy to incorporate spatial data into a model and define levels of interaction between the spatial world and the agents (Brown et al. 2005; Ostfeld, Glass, and Keesing 2005). In traditional models spatial features are incorporated as constants or partial differential equations integrating across space and time, dramatically increasing model complexity (Keeling 1999). Within epidemiological modelling there have been efforts to create hybrid models that combine an ABM at the small scale with population

models, once infections reach a large size (Bobashev et al. 2007). This allows for understanding the spatial and behavioural dynamics when they are important but also not reduce computational efficiency in large populations. This has already been trialled in mosquito borne diseases (Mniszewski et al. 2014) and could be applicable in a large number of wildlife diseases.

5.5.1 Conclusions

The model I built performed well during validation and can now be used to help inform management and policy in a real-world scenario. By manipulating Ethiopian wolf and domestic dog vaccination inputs, the model can inform the ongoing and future vaccination interventions implemented by conservation organisations and governments. The validation demonstrates the applicability and power of models such as this, which are only going to increase in number and power as more and better data becomes available across numerous disease systems, and computational power increases. With this will come better understanding of disease systems and hopefully more effective management of disease in many systems.

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Chapter 6

Recommendations from in-silico trials for integrated disease management for Ethiopian wolf protection.



6.1 Abstract

Vaccination interventions to protect threatened wildlife from disease have remained a controversial topic for many years despite growing evidence of effective conservation outcomes. Rabies and Canine Distemper Virus (CDV) transmitted by free-roaming dogs threaten the remaining populations of the endangered Ethiopian wolf, a rare canid endemic to the highlands of Ethiopia. To mitigate their impact, widespread vaccinations of domestic dogs for rabies have been implemented for over two decades, and more recently against CDV, but periodic disease outbreaks among wolves still occur. A recent disease mitigation approach has involved emergency vaccination of the wolves themselves, but this carries high costs and involves animal handling. There have been successful trials of oral rabies vaccination and ongoing trials of a CDV vaccine for the wolves. Current management to protect wolves from disease in the Bale Mountains National Park (business as usual) involves large-scale domestic dog vaccination campaigns and the emergency vaccination of wolves. There is a need for a better-informed disease management approach that weigh in the effectiveness of different approaches. With this aim I used a highly parameterised agent-based model to simulate possible disease management scenarios and determine their cost effectiveness. The model predicted a 17% chance for the wolves in the Bale Mountains to go extinct due to disease in the next 30 years under business as usual. This risk increased to 57% if all disease management activities were halted; suggesting that past management has had a positive impact in reducing the chance of the wolf population going extinct. Restriction of dog movements or density would be effective additional measures, both methods reduce extinction risk to 0% and number of disease outbreaks by

50%. When trialling combinations of vaccination thresholds vaccination of wolves was more effective and cost effective, in reducing the number of predicted epizootics than vaccination of dogs. Wolf vaccination reduced the extinction risk to 0% and can decrease number of epizootics linearly to 0 at high thresholds, while dog vaccination reduced the frequency of epizootics but plateaued before removing disease altogether. Based on these results I recommend that preventive wolf vaccination should be deployed immediately even at low coverage levels with coverage as low as 10% reducing epizootic frequency by 30% and 40% coverage reducing the frequency to < 1. The cost of providing equivalent or better protection to the wolves is lower using preventive wolf vaccination than dog vaccination with the most cost-effective strategy being 70% preventive wolf vaccination with 0% dog vaccination, this prediction indicates that dog vaccination can be scaled back as wolf vaccination increases saving money on disease management. When modelling treatment of wolves with preventive oral rabies vaccine but no CDV vaccination, dog vaccination was still required to provide protection from CDV, while oral rabies vaccination in wolves helped reduce epizootics. Management effectiveness varied with wolf population density and wolf range size. High density populations and populations in small isolated ranges had a higher extinction risk and experienced more frequent epizootics than low density and populations in large ranges, suggesting that more intensive management strategies would be required for high-density populations or smaller wolf ranges.

6.2 Introduction

Management of diseases through vaccination of domestic or wild animals has been an effective health measure worldwide (Beran and Frith 1988; Cross, Buddle, and Aldwell 2007).Many diseases are controlled through the vaccination of host species, to reduce the chance of a target species (often humans) contacting an infected individual (Gortazar et al. 2015). This provides a level of herd immunity, not just for the vaccinated species but also the target species. This approach is common in the control of food-related pathogens for humans such as salmonella in chickens, which are vaccinated as chicks to prevent infection of humans (Cooper et al. 1990). Wild species have also been vaccinated to control disease in human or domestic animal populations such as vaccinating Eurasian badgers (*Meles meles*) for bovine tuberculosis to provide immunity to cattle (Chambers et al. 2014). Across Europe vast oral vaccination campaigns targeting wild carnivores, such as red foxes (*Vulpes vulpes*) and raccoon dogs (*Nyctereutes procyonoides*), helped prevent outbreaks of rabies (Blancou et al. 1986). This landscape approach has been successful in reducing rabies cases in humans in Europe from 3,748 to 215 in 10 years, with twenty-three of thirty reporting European countries being declared rabies free (da Fontoura Budaszewski et al. 2016; Scientific Panel on Animal Health and Welfare 2016). Similar declines have been reported in the United States with an oral vaccination programme focusing on northern raccoons (*Procyon lotor*), grey foxes (*Urocyon cinereoargenteus*) and coyotes (*Canis latrans*) that has led to the incidence rate of one to three human cases annually (Ma et al. 2018). There have also been attempts to prevent disease in endangered wildlife through the vaccination of domestic animals. For instance, vaccination of domestic dogs has been used in

the Serengeti ecosystem, to prevent outbreaks of rabies and canine distemper virus (CDV) in lions (*Panthera leo*) and African wild dogs (*Lycaon pictus*) (Cleaveland et al. 2003; Lembo et al. 2008; Czupryna et al. 2016). Despite these intensive interventions, disease still poses a risk to these species with periodic outbreaks; this failure may be related to the unfeasibility of attaining sufficient coverage of the dog population (Prager et al. 2012; Woodroffe et al. 2012; Nikolin et al. 2017). The World Health Organisation sets up a an 80% dog vaccination coverage threshold to prevent rabies in people (World Health Organisation 2013), but reaching this target can be difficult when there is high population turn over in the dog population or costs are high and cannot be sustained. Where coverage of vaccination programmes breaks down, outbreaks may still occur, and this may result in enhancing local extinction risks for some endangered species, such as the African wild dog (Ginsberg, Mace, and Albon 1995). In some cases, this has led to trialling direct vaccination of the affected threatened species.

Increasingly, vaccination interventions to protect wildlife from infectious disease have been considered, and some limited interventions have been trialled or implemented. For instance, the California condor (*Gymnogyps californianus*) was pre-emptively vaccinated against the West-Nile virus in both captive and wild populations, successfully protecting individuals during an outbreak in 2004 (Chang et al. 2007). Vaccination of wild canids was successful to protect the Santa Catalina island fox (*Urocyon littoralis*)(Kohlmann, Schmidt, and Garcelon 2005) after severe declines in the population due to canine distemper (Timm et al. 2009). Other species that would benefit from vaccination are great apes to protect them from Ebola virus (Leendertz et al. 2017) and black-tail prairie dogs (*Cynomys ludovi-*

cianus) against sylvatic plague (Rocke et al. 2008).

Vaccinating endangered species remains controversial, despite evidence that it could offer an effective disease management tool. Much controversy arose from a rabies vaccination intervention in African wild dogs, where all individuals within a pack disappeared after capture, immobilisation and vaccination (Gascoyne et al. 1993; Kat et al. 1996). Woodroffe (2001) concluded it was extremely unlikely that vaccination was responsible, but that it was possible that the single dose of vaccination did not provide sufficient protection from the virus. Jackson et al. (2019) found no evidence for handling and vaccination to be responsible for the Serengeti wild dog mortality, attributing it instead to interspecific competition with growing lion and spotted hyaena (*Crocuta crocuta*) populations; both experienced approximately 150% growth during the wild dog decline. Modelling work has suggested that even a low vaccination coverage would improve wild dog population persistence (Prager et al. 2011). Similarly, Haydon et al. (2006) suggested based on 4 models of different coverage levels that low coverage vaccination would help prevent outbreaks in the rare Ethiopian wolf (*Canis simensis*).

The Ethiopian wolf, listed as Endangered by the IUCN (Marino and Sillero-Zubiri 2011) is a pack-living canid only found in the Afroalpine ecosystem of Ethiopia, where fewer than 500 individuals remain in six isolated, unconnected mountain enclaves (Marino 2003). The most immediate threats to the wolves are rabies and CDV, transmitted from free-roaming domestic dogs (Laurenson et al. 1998). Domestic dogs living in villages within or around protected areas go out into wolf habitat to provide protection to livestock, which also represents foraging opportu-

nities for the dogs (Atickem, Bekele, and Williams 2009; Atickem et al. 2010). This can lead to contact with or risk of disease transmission to the wolves. The wolves in the Bale Mountains, where over half of the global wolf population lives, have been exposed to periodic disease outbreaks over the last 30 years (Sillero-Zubiri, Gottelli, and Macdonald 1996; Marino, Sillero-Zubiri, and Macdonald 2006; Marino et al. 2013; Gordon et al. 2015). Vaccination of the domestic dogs as a preventive measure has been ongoing in Bale for over two decades, but despite this, outbreaks of diseases in the wolves persist. To counter this threat, reactive rabies vaccination of the wolves was introduced in 2003; when 69 wolves across 12 packs were captured and vaccinated around infected packs (Randall et al. 2006), limiting the spread of the outbreak. Similar interventions followed subsequent rabies outbreaks (Marino and Sillero-Zubiri 2011). Despite monitoring and management across areas, outbreaks are still occurring, such as in 2016 where a small population in the Northern Highlands of Ethiopia led to a local functional extinction (Marino et al. 2017). The National Action Plan for Ethiopian wolf conservation (Ethiopian Wildlife Conservation Authority. 2017) included proactive, as opposed to reactive, wolf vaccination as part of an integrated disease management approach. After successful trials (Sillero-Zubiri et al. 2016), an oral rabies vaccine is now being used as an intervention and trials of a parenteral vaccination for CDV are ongoing (Ethiopian Wolf Conservation Programme 2016). Haydon et al. (2006), simulated preventive vaccination of the wolves in Bale with target coverage from 10% up to 40%, which suggested that even low coverage vaccination would significantly reduce outbreak severity and improve population persistence and 30% and 40% coverage removing almost all outbreaks. In order to refine such a vaccination toolkit there is a need to understand how vaccinations can most effectively be de-

ployed, assess their feasibility and outcomes and assess whether these interventions are cost-effective.

Management plans require understanding the dynamics of the disease to be controlled and the impacts of any proposed interventions, such as the impact of capture, handling, post-handling stress and adverse effects of vaccine (Dennis and Shah 2012; Ludynia et al. 2012) would have on the species involved. Handling and vaccination of Ethiopian wolves do not seem to have any negative impacts, in the short or long term (Sillero-Zubiri 1996; Randall et al. 2006). Vaccination also requires large effort and expense in the form of research such as vaccination development, vaccine trials, and designing and testing vaccination campaigns prior to its full implementation. Until sufficient data has been collected on the efficacy of vaccination, hosts or reservoirs and chances of success, management should be applied cautiously. To inform such decision-making, modelling can enhance understanding of the pathogen epidemiology and provide recommendations. A good example of this concerned rabies in Indian foxes (*Vulpes bengalensis*) where modelling showed that direct vaccination of foxes was more effective than dog vaccination (Belsare and Gompper 2015). Models allow trial manipulations of the system that would take place as part of future disease management and assess the costs involved (Robins et al. 2015).

In this chapter I apply an agent-based (Janssen 2005) model of Ethiopian wolf populations (see chapter 5) to explore disease dynamics and a range of vaccination strategies. Understanding disease dynamics such as R_e under the current state of management can highlight where shortfalls currently are. The impact of mod-

ifications to domestic dog behaviour or density can also be explored with these models. Full examination of different vaccination thresholds can determine optimal strategies for vaccinating domestic dogs, wolves or some combination of both. An estimate of the costs involved will help to identify the most cost-effective strategy. These model outputs will inform disease management strategies and whether these strategies change effectiveness under different population structures.

6.3 Methods

I used an agent-based model of rabies and CDV in Ethiopian wolves and free-roaming domestic dogs in the Bale Mountains of southern Ethiopia. For a detailed exploration of the construction of this model see Chapter 5. Exploration of model outputs was performed in R (R Development Core Team 2011).

The model was run to determine current epidemiological properties of the system, effective reproduction number R_e, the number of secondary infections each individual causes in the model), for the viruses in both species, and various management scenarios to determine their effectiveness in reducing the number of epizootics. As an ideal goal would be to entirely prevent outbreaks of disease the number of epizootics (both rabies and CDV) in the wolf population was used as an easily quantifiable measure of management success. An epizootic was deemed to have occurred when 5% of the population became infected, this threshold is higher than in human diseases but representative of the low population size of the wolves (Green et al. 2002). As avoiding extinction of this rare canid is the ultimate target, the extinction risk (% of runs in which wolves went extinct) was also measured. As

most forms of management reduced extinction risk due to disease to 0 it does not provide a general measure of success to compare between all management options but for certain scenarios it can be an informative measure. The costs of each scenario were recorded to determine cost-effectiveness. All scenarios were run for 30 years or 260,000 time steps with 100 replicates to account for stochasticity in the model. The running of all models totalled over 340 billion hours (40 million years) of simulations, making it one of the largest agent-based models of wildlife when compared to similar research (Miller et al. 2014; Tracey et al. 2014; Carter et al. 2015; Loraamm 2019).

To determine the prospects of the wolf populations if current management (business as usual) continues and how things would progress in the absence of any interventions, a series of null scenarios were run. These scenarios were:

- No management - where all current vaccination interventions were interrupted.
- No reactive vaccination - A scenario without emergency reactive wolf vaccination during outbreaks, but dog vaccination ongoing.
- "Business as usual scenario" - with dog vaccination at current rates (80-90% target vaccination, reduced to approximately 60% after population turnover is taken into account) plus reactive wolf vaccination, where 50% of the individuals within the surrounding packs are vaccinated.

The Bale Mountains National Park has a policy to the effect that domestic dogs should be restricted in movement to within 200m of their village (Nelson 2011). To trial the effect of actively enforcing the regulation on the frequency of, restriction of

dog movements to within 400m and 200m of the village was trialled and compared to a standard business as usual model. There have been efforts to try and limit the scale of dog ownership inside the park, and to trial the effects of this proposal, the carrying capacity of dogs in each village who go into wolf habitat was reduced in steps of 25% down to 25%. Both of these were run within the "business as usual" scenario. In addition to the above, I performed a parameter sweep of the impact of various levels of dog and preventive wolf vaccination, including reactive wolf vaccination, in the situation where it is possible to vaccinate for both rabies and CDV in wolves and dogs. Each year, a proportion of individuals were made resistant to diseases in relation to the specific vaccination coverage tested; this did not mean that the coverage % was the number of resistant individuals, as the population will change over time as new individuals are added by births and imports. Resistance decays over time so individuals will need to be repeatedly vaccinated over their lifetime. The parameter sweep trialled vaccination levels from 0 to 100 percentage coverage at intervals of 10% (e.g. vaccination of dogs at 10% and vaccination of wolves at 10%, etc) for a total of 1,200 different combinations. Cost of management was included in the model as a simple per unit of vaccination cost where each individual made resistant is added to the total cost of the model run. This quantifies the direct cost of vaccination but will not include the other necessary operating costs of management such as staff salaries, implementation or monitoring. Cost-effectiveness of management was calculated under equation 6.1:

$$\frac{\frac{1}{exp(Epidemics)}}{Cost} \tag{6.1}$$

Using 1/ the number of epizootics generated higher scores for lower numbers of

epizootics and taking the exponential of epizootics removed some of the bias of scenarios producing 0 epizootics. Regarding preventive vaccination, the only currently approved option is vaccination of wolves for rabies using oral vaccines. Select coverage levels ("business as usual", dog 60% wolf 30%, dog 60% wolf 60%, dog 0% wolf 30%, dog 0% wolf 70%) from the parameter sweep were re-evaluated under these constraints to test whether this would still reduce epizootics.

To simulate the effects of varying population densities and wolf range size (area) on management outcomes select vaccination coverage levels were trialled under four different constraints:

- High density large area – running on the full model area with the maximum group size of the wolf packs set to top of its distribution.
- Low density large area – running on the full model area but the maximum group size of wolf packs halved in comparison to the mean from the distribution.
- High density small area - taking a small part of the original model world and isolating it (less overall packs can fit in this area and there is reduced spatial isolation between packs) but with the maximum group size of the wolf packs set to top of its distribution.
- Low density small area: Taking a small part of the original model world and isolating it, but maximum group size of wolf packs halved in comparison to the mean from the distribution.

6.4 Results

6.4.1 Epidemiological properties

The respective R_e of rabies and CDV in each species and the range of values are presented in Table 1. Both diseases had R_es below 1 which indicated that there cannot be an endemic background level of the infection. CDV had a higher R_e than rabies indicating that it is more infectious than rabies. There was large variation in R_e across individuals indicating that in the model most individuals did not infect others and that there were some *super infectors* (Table 6.1).

Table 6.1: Reproductive numbers (R_e) of Rabies and Canine Distemper Virus (CDV) in both Ethiopian wolves and domestic dogs from the agent-based model simulations of disease transmission in the Bale Mountains.

	Rabies in Wolves	Rabies in Dogs	CDV in Wolves	CDV in Dogs
R_e	0.41	0.45	0.60	0.51
range	0 - 14	0 - 9	0 - 10	0 - 6

6.4.2 Null Scenarios

All pre-defined null scenarios predicted some risk of wolves becoming extinct within 30 years. The no management scenario had the highest extinction risk at 58% (Figure 6.1a) and highest number of epizootics (Figure 6.1b). Vaccinating domestic dogs reduced the extinction risk from 58% down to 27% and the number of epizootics from 5 to 2.8. Adding in reactive wolf vaccination (business as usual) did not reduce the number of epizootics, but the extinction risk declined to 17%.

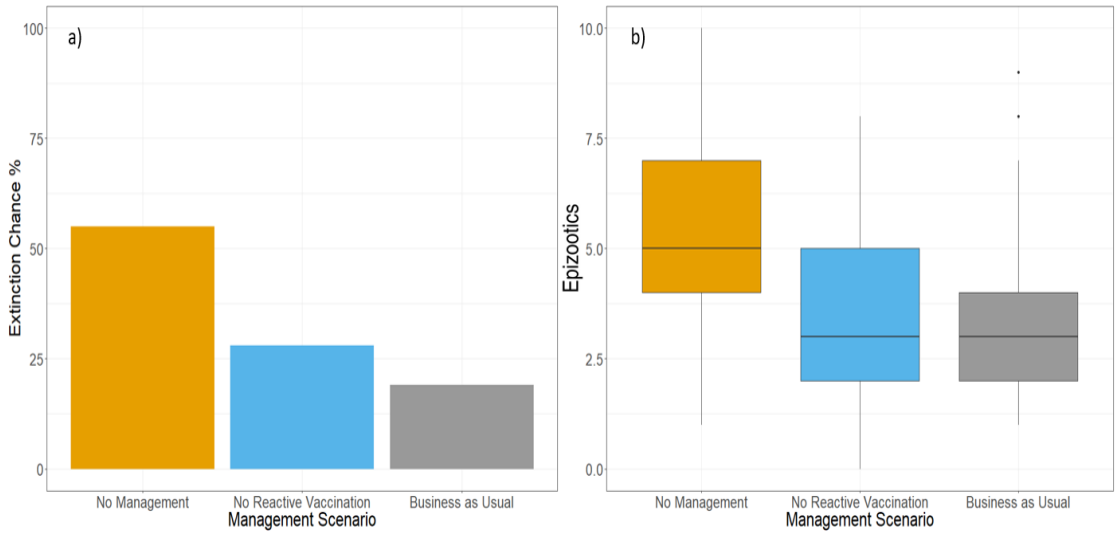

Figure 6.1: Disease management scenarios simulated by the Ethiopian wolf – domestic dog disease agent-based model against a) extinction risk chance (% of simulations where Ethiopian wolves went extinct in 30 years) in three different management scenarios; b) the number of epizootics that occurred in those scenarios.

6.4.3 Dog husbandry scenarios

Models with restriction of dog movements to either 400m or 200m, in addition to current disease control management, predicted a reduction in extinction risk of wolves to zero (Figure 6.2a) and fewer epizootics compared to business as usual (Figure 6.2b). However, there was no difference in number of epizootics with dog restriction of 400m or 200m.

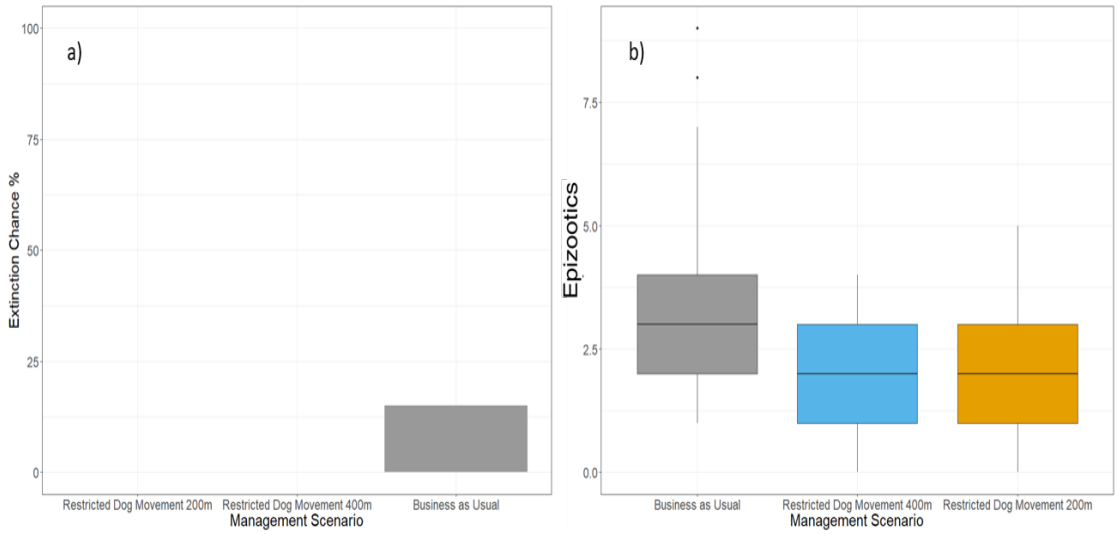

Figure 6.2: Restricted dog movement scenarios simulated in the Ethiopian wolf – domestic dog disease agent-based model against: a) extinction risk chance (% of simulations Ethiopian wolves went extinct in 30 years) in the three different levels of dog movement restriction; b) number of epizootics that occurred in those scenarios.

Predictions under reduced domestic dog density, while maintaining current disease control management, also had low extinction risks to less than 1% and, in similar fashion to the restriction of dog movements (Figure 6.3a), slightly reduced the prevalence of epizootics. Epizootics were still occurring in the models with the mean number for each scenario between 2.3 and 2.6 epizootics per 30 years (Figure 6.3b).

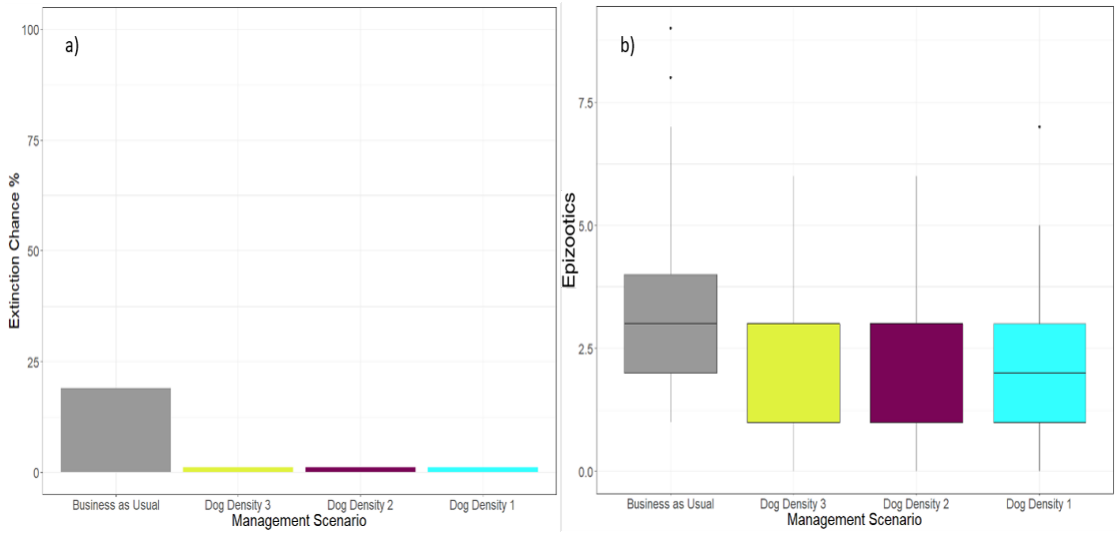

Figure 6.3: Dog density management scenarios simulated in the Ethiopian wolf – domestic dog disease agent-based model against a) extinction risk chance (% of simulations Ethiopian wolves went extinct in 30 years) in the three different levels of dog density restriction where each is a carrying capacity representing the target population of free roaming dog per village. b) the number of epizootics that occurred in those scenarios.

6.4.4 Parameter sweep of vaccination thresholds

The comparisons among predictions provided the following results:

- vaccination of only dogs (with no preventive wolf vaccination) was not effective at preventing outbreaks in the wolves, even at high levels.

- Across low wolf vaccination levels, reduced dog vaccination coverage predicted the same number of epizootics in wolves as under scenarios of high dog vaccination, leading to savings in costs.

- Preventive wolf vaccination reduced the number of epizootics at even low levels of coverage (40% preventive wolf vaccination reduced numbers of epizootics to <1 in 30 years) but without dog vaccination outbreaks still occurred in the dog pop-

ulation.

- Preventive wolf vaccination at high levels totally prevented outbreaks (number of wolf epizootics approached 0 by 70% coverage); outbreaks still occurred in dogs.
- The effectiveness of increasing preventive wolf vaccination plateaued at approximately 70% of the population; above that level epizootics were functionally absent regardless of the level of dog vaccination (Figure 6.4a).

In summary, vaccination of dogs alone did not appear to effectively reduce the frequency of epizootics in wolves at any level. Due to the large number of dogs and the high turnover within the population, it was almost always more cost-efficient to preventively vaccinate wolves even though this activity is considerably more expensive per dose than that for dogs (Figure 6.4b). The optimal cost-effective strategy predicted by the model was vaccination of 70% of wolves and 0% of dogs which produced an average of 0.33 epizootics in 30 years at a cost of £140,000 for vaccine over the 30 years (Figure 6.4c).

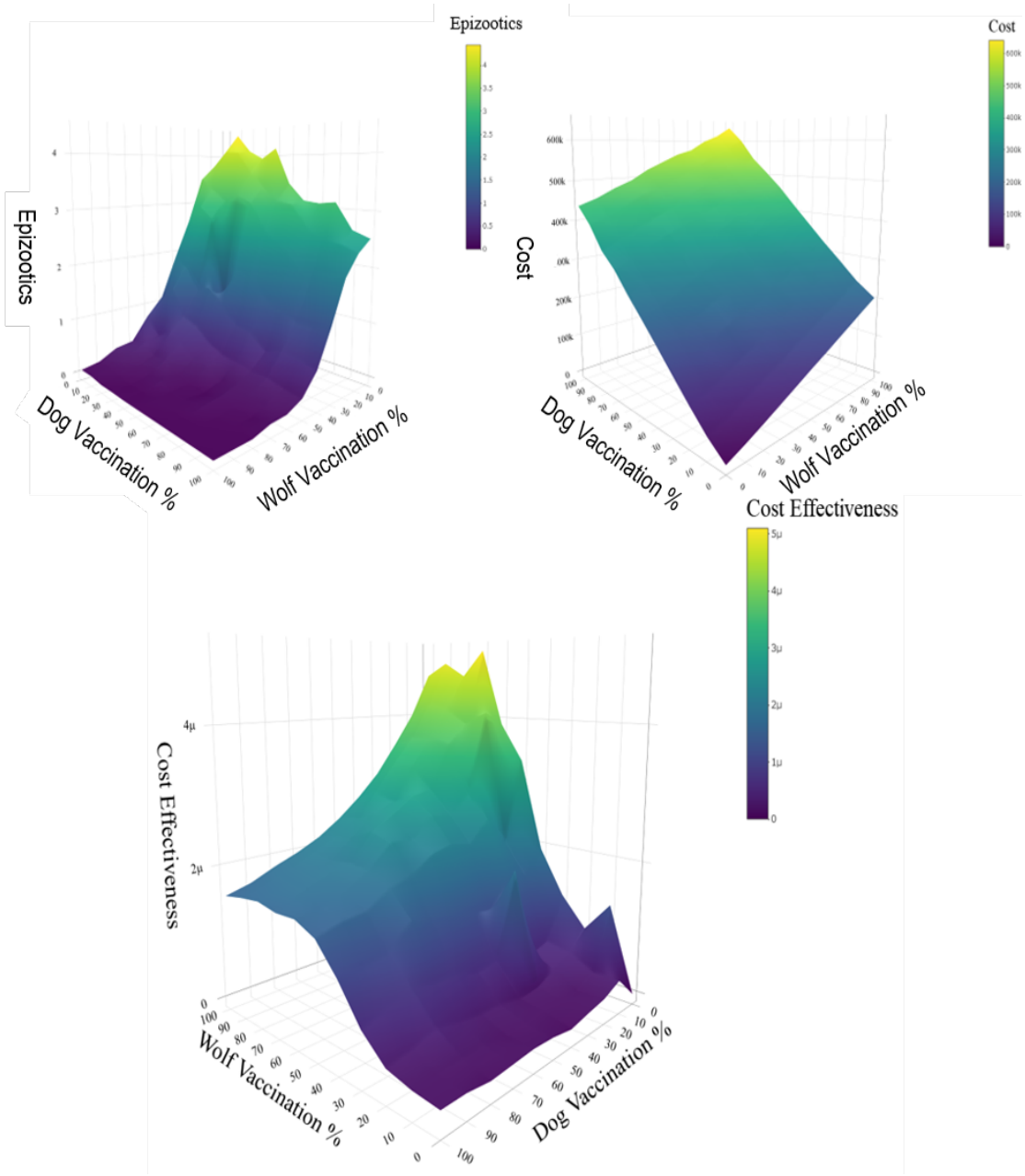

Figure 6.4: Outputs of the Ethiopian wolf – domestic dog disease agent-based model parameter sweep combining range of vaccination coverages against a) the average number of epizootics after 30 years of each combination of vaccination coverage levels (lower is better); b) The average cost of management of each combination of vaccination coverage levels; c) average cost effectiveness of each combination of vaccination coverage levels. $\mu = \text{x}10^{-6}$

6.4.5 Oral rabies vaccination

When wolves were only preventively vaccinated for rabies but not for CDV, the effectiveness of vaccination was considerably reduced. Removing dog vaccination lead to an increase in wolf epizootics unless wolf vaccination coverage was high, and even then, no improvement was predicted over current high-level dog coverage and reactive vaccination (mean of 3.43). Adding in preventive wolf vaccination to current management in the models did not help reduce the number of outbreaks; only with high wolf vaccination coverage the number dropped to a mean of 1.8 at 60% dog vaccination and 60% wolf vaccination which is half the frequency of epizootics with respect to current management predictions (Figure 6.5).

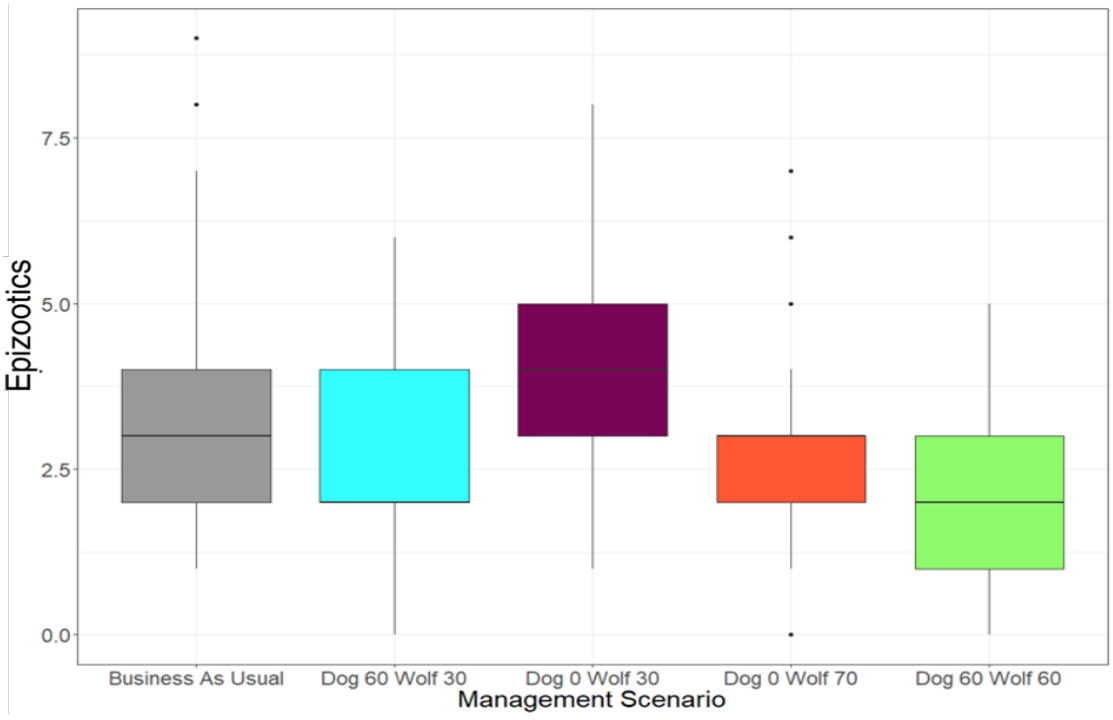

Figure 6.5: Outputs of Ethiopian wolf – domestic dog disease agent-based model from different vaccination scenarios where only rabies is vaccinated for against: The number of epizootics that occurred in each scenario when wolves were only preventively vaccinated for rabies.

6.4.6 Wolf density and area size

Smaller wolf ranges (areas) have a higher risk of extinction from disease than larger ranges with more geographic separation between packs, and higher densities also have a higher risk of extinction than low density populations (Figure 6.6).

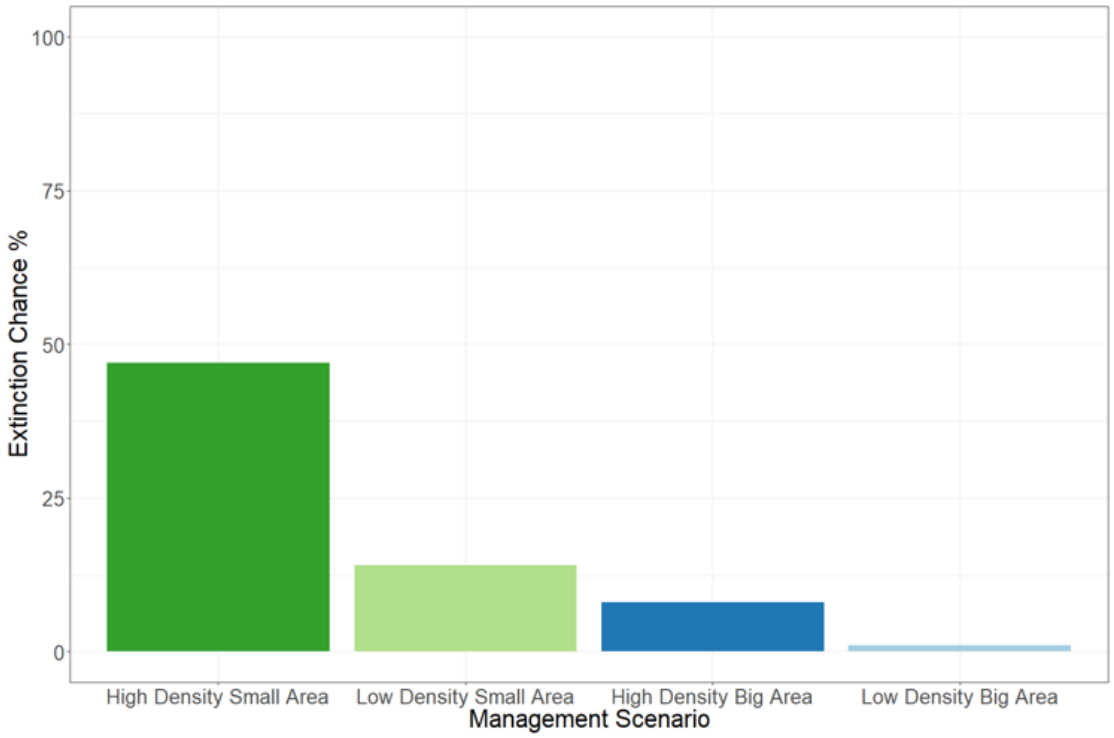

Figure 6.6: Extinction chance from the Ethiopian wolf – domestic dog disease agent-based model in each scenario when trialling different combinations of wolf range size (area) and wolf density (maximum number of wolves per pack). The small area was modeled by taking a small section of the model world and running it separately. Preventive wolf vaccination removed all extinction risk, so results are from business as usual scenarios.

When assessing the effectiveness of different management scenarios there was no real effect of area size on the number of epizootics, however reduced density, when compared within a given area, did reduce the number of epizootics (Table 6.2).

Table 6.2: Average number of epizootics over 100 runs of the Ethiopian wolf – domestic dog disease agent-based model for each management scenario in different wolf densities and area sizes.

	Large Area			Small Area		
Scenario	Business as usual	Dog 60% Wolf 30%	Dog 0% Wolf 70%	Business as usual	Dog 60% Wolf 30%	Dog 0% Wolf 70%
High Density	3.1	1.42	0.7	3.04	1.68	0.42
Low Density	2.76	1.01	0.17	2.96	0.94	0.05

Table 6.3: Average cost effectiveness over 100 runs of the Ethiopian wolf – domestic dog disease agent-based model for each management scenario in different wolf densities and wolf range (area) sizes. μ = x10^6 due to low number of epizootics in respect to overall cost, cost-effectiveness ended up as a small number, higher cost-effectiveness is better

	Large Area			Small Area		
Scenario	Business as usual	Dog 60% Wolf 30%	Dog 0% Wolf 70%	Business as usual	Dog 60% Wolf 30%	Dog 0% Wolf 70%
High Density	0.185μ	0.78μ	4.18μ	0.54μ	1.35μ	5.65μ
Low Density	0.25μ	1.25μ	8.29μ	0.58μ	2.98μ	9.19μ

6.5 Discussion

The model presented here demonstrated the power that agent-based models can have to understand the fundamental epidemiology of diseases and to trial management interventions. The low R_e (less than 1) of the diseases in both species indicated that there is no background level of the two key diseases in the population of wolves and dogs, as each case on average does not cause a second case so it cannot be maintained. This matches historical records with the wolves where

outbreaks among wolves were highly lethal but brief, and disease-related mortality is not observed constantly during non-outbreak times, or at least not detected (Ethiopian Wildlife Conservation Authority., 2017). For both diseases, wolves had a larger range of individuals infected by a single diseased individual than dogs. This suggests that wolves may be more prone to become super spreaders, where a small proportion of individuals are responsible for most of the infections (Stein, 2011). This has been explained due to the social nature of packs (Haydon, Laurenson, and Sillero-Zubiri 2002; Randall et al. 2006; Haydon et al. 2006; Sterner and Smith 2006): once a single individual is infected, they are likely to spread it to many of the other individuals within their pack and then those other individuals will have a lower infectivity, as other individuals within the pack are already infected, but high morbidity unless they introduce it to a new pack. The Re of dogs would most likely be higher than predicted in the model, as the model only includes the free-roaming dogs that go into wolf range as agents, while village dogs are stored as a numeric parameter for calculating cost. Most dogs within a village stay only in the village, so while they do not present a risk to the wolves directly, it is likely that an infected village dog would still infect other dogs in the village and have a higher true R_e. It is also possible that a rabid village dog may leave the village due to rabies-mediated behavioural change (Hueffer et al. 2017), even if not typically free-roaming. The higher R_e of CDV compared to that of rabies is different to results for red foxes populations (Nouvellet et al. 2013), probably because in Ethiopian wolves rabies infection is driven by wolf pack dynamics. The low res here, less than required for a self-sustaining disease, may make vaccination an even more effective tool, but the dynamics of the super spreader individuals may need further study to fully control disease.

The predicted extinction risk of ending current management to the wolf population in Bale Mountains was extremely high, at 57% within 30 years. The introduction of reactive wolf vaccination helped reduce the risk of extinction in the model by 10%, but it did not reduce the overall number of epizootics that occurred. Such an effect is likely to result from the delay between the beginning of the outbreak and reactive vaccination, so logically reactive vaccination is merely limiting the extent of the outbreak not preventing it. There is still a 13% extinction risk to the wolves under the current management (business as usual including reactive vaccination) strategies. For small populations, such as the wolf population in Bale (around 300 wolves at full carrying capacity), which are particularly vulnerable to stochasticity this level may itself be a success. Yet there is still a pressing need to improve management of disease in some way to help conserve such an iconic species, when also considering that total area and therefore population size, continue to decline due to habitat conversion to agriculture and new settlements within the park, and the potential effects of climate change affecting maximum population size.

Restriction of dog movements (to within 200m of villages) could eliminate the extinction risk due to disease of the wolves in Bale. In principle, the official national park policy of movement restriction (Nelson 2011) could be effective if enforced, and that rabies-mediated behavioural changes can be also be controlled for. The positive effects would still occur when dogs are restricted to within 400m, so even some level of restriction could be effective and is probably more palatable to the dog owners. Even though a reduction in the number of epizootics is expected as a result of restricting dogs, it is still insufficient to remove the risk entirely, likely

due to chance encounters of dogs and wolves very close to villages, that are known to occur (Atickem et al. 2010). However, there is no difference in increased cost of vaccination associated with dog restriction, meaning it could be a cost-effective strategy to reduce epizootics; but there may be associated costs with greater enforcement through park scouts or incentives to owners. Reducing the number of dogs that range into the wolf habitat (and into sympatry with wolves), rather than the distance that they are roaming out to, also removed extinction risk and slightly reduced frequency of infections, but like dog restriction, the chance that one of the remaining dogs get infected can lead to outbreaks in the wolves. A strategy of restricting dogs from roaming into the national park could also be effective at least as part of a larger strategy. This will require cooperation from all stakeholders and depend on the willingness of dog owners to restrict their movements, limit dog breeding and the number of dogs they own. Dogs are used in the area for livestock protection (Atickem et al. 2010), mainly against predation by hyenas at night time near the houses but presumably also against wolf predation when livestock is taken to best pasture which from the village. Keeping dogs at home may require restriction of livestock movements within the national park, or increased costs of human guarding. Such management practices, which depend on changing human behaviours, will require great effort but could also bring significant benefits for Ethiopian wolf conservation.

The preventive vaccination of the wolves may be a much more achievable method in the short term. When combined with concurrent vaccination of the dogs, it has One Health benefits of both protecting dogs and livestock, thus improving the livelihoods and impact on the health of local people. Dog vaccination is compar-

atively more costly than preventive wolf vaccination because of the numbers of dogs even though the cost per animal is lower. The model predicted that reducing dog vaccination in favour of wolf vaccination was will be more effective and lower cost. If current dog vaccination was continued combined with low-level preventive coverage of the wolves (40%) is predicted to reduce the number of epizootics to approximately 0.29 in 30 years. Moreover, it would be possible to increase wolf coverage to 50% while dog vaccination drops to 20% and the model still predicts less than one epidemic in 30 years and have reduced costs across the 30 years. The same would be achieved through vaccination of the wolves alone, the most cost-effective strategy was to vaccinate 70% of wolves with no vaccination of dogs, which provides strong evidence not just for the vaccination of wild animals but the cost effectiveness of these measures.

Oral vaccination for rabies has now been authorised and is currently being deployed throughout wolf populations; trials of CDV are in their final stages, so the model can be used to predict how disease should be managed in the interim. The model suggested that reducing dog vaccination as wolf vaccination is implemented will not provide sufficient protection from epizootics as there is no protection for the wolves against CDV. Vaccination of both species is the only way to provide high levels of protection, but the small number of unvaccinated dogs will still in the long term introduce epizootics. Until the CDV vaccination can be appropriately determined effective and safe, effective rabies control is paramount. The model was also applied to investigate more general applications of disease management in scenarios when wolf densities might increase above current model thresholds and when the area occupied by a population is smaller than in the Bale Mountains. The predicted

higher risk of population extinction at high densities, when the area of the model is maintained constant, is most likely due to the increased risk of transmission between wolves when they are living at high density. Not only would contact rates be higher due to the larger number of pack members, there is an increased likelihood that wolves from neighbouring packs would encounter and interact with each other (often aggressively (Sillero-Zubiri, Johnson, and Macdonald 1998)). Smaller wolf ranges, with equivalent pack size, also have a higher risk of local extinction; most likely due to the lack of spatially separated packs that might avoid infection during an outbreak and that may eventually repopulate the now empty territories. Once preventive wolf vaccination was introduced extinction risk became 0 so frequency of epizootics was again determined. Wolf range (area) size does not influence management in terms of number of epizootics; however lower densities did have reduced epizootics again likely as a result of the reduced contact rate rather than any benefits of management. Where the model predicts there is an important effect is in the cost effectiveness of management. Managing disease in smaller wolf ranges, or areas with lower wolf densities provided a higher cost effectiveness. This is due to fewer wolves needing to be vaccinated, thus lowering the costs, to achieve an equivalent reduction in disease. This means that small low density populations are ideal targets for direct vaccination of the wolves. Full management recommendations based on the model predictions will combine all these results.

6.5.1 Management Recommendations

- Preventive wolf vaccination should begin as soon as possible to reduce the frequency of epizootics and improve population persistence across the species range.
- Domestic dog vaccination against CDV in Bale should be continued until trails of the CDV vaccine on wolves are complete. CDV vaccination of dogs could then scale back to help shift funds towards other management methods
- Rabies vaccination of dogs in Bale could be reduced once preventive wolf rabies vaccination is brought in and increases.
- Stakeholder engagement and awareness should be raised including among dog owners in Bale to encourage the restriction of dog ownership and movements as per current regulation. While human behavioural changes are extremely difficult to achieve, this is worth attempting as a very effective management option to compliment other approaches.
- Management interventions should be intensified when the wolves are living at high densities or in areas with limited range.

The results of this model support the increasingly popular proposition of vaccination of wild animals for disease control (Cleaveland 2009). These results also suggest that control of disease is best through the target species rather than through alternative hosts where possible. There are of course risks involved in any management plan varying from direct risk of animal handling to ineffective management; but these risks, particularly in Ethiopian wolves, have been proved to be minimal while the potential conservation outputs are significant. There are suggestions that the handling of animals, stress of capture or vaccine side effects may have

deleterious effects but evidence against the use of wild animal vaccination is weak with almost no known cases of confirmed negative effects. The only known case is short-term negative effects in young rabbits of myxomatosis vaccine (Calvete et al. 2004). In contrast, this study adds to the growing evidence in favour of vaccination of susceptible wild species from empirical-based modelling. Much of the current evidence focuses on whether vaccines are effective measures from a purely immunological point of view without looking at the level of control and delivery strategies that are necessary. Level of control and delivery strategies are aspects of management in which full knowledge is needed in order to identify the best methods and tools, how to apply them, and their cost-effectiveness to achieve a predetermined goal.

The generalisation of this model across other species may be limited by the dynamics of the specific system particularly the numbers of the non-target hosts and ease of vaccination of the target species. If the primary host is less numerous than the target species, it may be just as if not more expensive to vaccinate the target. If vaccinating the target species is extremely costly from e.g. high cost of animal capture in highly elusive, mobile or volant species, it may be more cost effective to vaccinate the non-target host. It would be advisable for any management authority to develop a model to test effectiveness in their system. Any model will of course generalise and therefore might miss something that is happening in the real world but over-parameterising to specific conditions would reduce the applicability to other systems or situations. This model focused on the applications of different thresholds of domestic dog and wolf vaccination but there are other situations not trialled with potential applications such as seasonal application of management

or targeting individuals. Modifying wolf behaviour to reduce disease transmission might be much harder to achieve as a management strategy than changing movement of domestic dogs for example, but many species have naturally adapted their behaviour to avoid infections such as grooming in mammals to remove parasites that can carry pathogens and licking behaviours to clean wounds (Hart, 1994; Hart and Hart, 2018). Further parameter sweeps can be performed to understand how a specific management plan should be applied. The timing at which it should be applied, or the habitat type that oral vaccination should be applied to could be informed by the model.

6.5.2 Conclusions

While local extinction risk for the Bale wolf population is currently quite high, the tools exist to help protect these populations at least with regards to disease risks. Among the management suggestions derived from the model, restriction of domestic dog to or close to the villages would be an effective measure for reducing disease transmission to wolves. However, if this is not feasible, preventive wolf vaccination would be an even more effective disease prevention measure almost entirely preventing rabies and CDV outbreaks in the wolves, with a reduction in costs in contrast to domestic dog vaccination. Understanding not just the effective measures but the relative cost effectiveness of these measures provides a baseline for modelling numerous other systems which rely on vaccination. It is common that the number of domestic dogs would far outweigh the number of any endangered animal thereby inflating the cost of their vaccination. This bolsters the evidence

for wild animal vaccination in any of those settings and can encourage conservation globally.

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Chapter 7

Discussions on the management of disease in Ethiopian wolves.

This thesis explored the process behind developing management recommendations for interventions to protect threatened wildlife from diseases including the tools, data and modelling required to do it. The system studied was that of the endangered Ethiopian wolf (*Canis simensis*), which faces a morbidity and mortality disease burden primarily due to contact with domestic dogs (*Canis familiaris*) iin the Afroalpine ranges of Ethiopia. With the pressing need for conservation actions to safeguard the Ethiopian wolf and other species threatened by disease globally, integrated management strategies are urgently required. To accomplish this, collection of in-depth real-world data and use of advanced modelling with those data are all needed. The development and improvement of management tools and analysis techniques comes down to improving access to or collecting more information about diseases and the hosts involved. Management decisions are best undertaken with full understanding of the system and a broad range of data. This thesis aimed

to provide new methodology for the monitoring of wildlife using custom build devices developed for use on dogs, but which could potentially be used on a plethora of species globally. These devices were used to describe the behaviour of domestic dogs that are the primary source of disease to the Ethiopian wolf and quantify the overlap between the two species. This knowledge allowed the development of a highly detailed and robust model of Ethiopian wolf disease. Modelling was done to trial management options and provide recommendations for future action on conservation of the Ethiopian wolf.

7.0.1 Custom-built Monitoring Devices

I designed and built a cost-effective open source device to monitor domestic dog movement that can effectively be used to monitor wild species (Chapter 2). These devises were able to accurately and reliably collect data and, in some respects, can be competitive with commercial devices (Matthews et al. 2013). Open source data collection devices represent one important tool in the future of behavioural data collection and wildlife monitoring. It is possible to construct devices to exactly match the specifications required and make a considerable saving in terms of cost, with little engineering experience. The most common open source platforms have instructions and code available for almost any device one could conceive of and the components can be acquired easily and cheaply. This opens up the option of collecting very fine scale data or novel data types that may be specific to a research question (Thompson et al. 2012). These devices could be fitted with any number of specific components, even collecting video from the point of view of an animal. Accelerometers, magnetometers and audio recorders are being used to classify

animal behaviour on a fine scale and this ability is rapidly increasing (Wijers et al. 2018; Studd et al. 2019). The customisable nature of the devices also makes them suitable for a variety of environments depending on housing, from aerial use on birds to monitoring aquatic species. The other major benefit of this self-built approach is the reduction in cost. For the price of a single commercial GPS collar it is possible to build several devices, with complete control over their design and specifications. There is also growing evidence for the unreliability of commercial devices with several performance reviews been recently published (Matthews et al. 2013; Jung and Kuba 2015). While performance of custom-built devices might not outperform those of commercial devices (Jung et al. 2018), a judgement has to be made on whether the increase in cost becomes effective as the performance gap closes. Besides, the ability to deploy many more devices for the same budget opens the opportunity to collect a wider array of data or track a larger and more representative sample of the population (Bastille-Rousseau and Wittemyer 2019). To adequately represent the behaviours of a target species, a sufficient sample size is needed which is often limited by funding and other constraints such as ethical considerations and inherent risks from capture interventions (Dennis and Shah 2012). For that reason, many studies have focused on particular individuals or aimed for a single device per group in social species (Boult et al. 2019). Many research projects are limited in funds, particularly those that operate in developing countries. These contexts would benefit the most from having access to more devices and can expand monitoring of species, particularly in developing countries which also have the highest biodiversity and harbour many of the most threatened species (Myers et al. 2000). Being able to track a greater number of individuals or species could play a key role in anti-poaching and monitoring measures in the

future. Being able to deploy devices that can monitor an animal's movement and alert to mortalities or abnormal behaviour on more animals could drastically reduce poaching (O'Donoghue and Rutz 2016). With carnivore species that prey on livestock or raid human settlements for food, there are often hostile interactions between people and wildlife such as the spearing of lions and persecution of crop raiding elephants (Nyhus, Tilson, and Sumianto 2000; Hazzah, Borgerhoff Mulder, and Frank 2009). Monitoring devices can create a form of GPS fence that can alert people to animals coming into their area and proactively manage livestock or deter the individual (Weise et al. 2019).

7.0.2 Domestic Dog and Ethiopian Wolf Behaviour and Overlap

Like most wolf-like canids (*Canis* genus), domestic dogs and Ethiopian wolves have similar patterns of ecology and behaviour, for instance in the establishment of territories or home ranges, foraging, moving and resting behaviours (Sillero-Zubiri and Macdonald 2004; Danchin, Giraldeau, and Cézilly 2008). Understanding dog behaviour in one setting may inform similar settings where dogs are impacting other wild species of conservation concern. As individual behaviours can contribute to disease transmission (Bansal, Grenfell, and Meyers 2007; Liu et al. 2015), knowing what behaviours a species is exhibiting, and when, are crucial and underperformed steps in epidemiology. The overlap between wolves and dogs represents a clear risk for transmission of disease and even the persistence of wolf populations. Having both spatial and temporal overlap can further increases risk, as there is no chance of temporal niche separation in areas of spatial overlap. Being able to

directly quantify overlap is a pivotal step in understanding disease transmission. The higher the overlap between individuals or species the greater the chances of encounter and pathogen transmission (Robert, Garant, and Pelletier 2012). For other studies where animals are the primary source of infection, such as domestic dogs in the Serengeti (Craft et al. 2015) or Eurasian badgers (*Meles meles*) and cattle with bovine tuberculosis (Chambers et al. 2014), quantifying overlap may be a missing feature of understanding transmission dynamics. Transmission of foot and mouth disease between African buffalos (*Syncerus caffer*) and cattle has been related to the overlap between the species and, as overlap increased seasonally, so did disease risk (Kaszta et al. 2018). But further understanding of behaviour from real data is the critical component to disease transmission that is often lacking. For diseases transmitted via hosts, rather than natural and environmental processes, the behaviour of hosts is the underlying driver of infection (Hoi and Roitberg 2014). With advances in machine learning and artificial intelligence (AI) there is a rising applicability in the study of animal behaviour (Valletta et al. 2017). Behavioural studies have often focused on following individuals and categorising their behaviour, however this is labour and time intensive (Danchin, Giraldeau, and Cézilly 2008). AI methods can automatically classify behaviours when provided with a dataset of observational data and with the increasing use of sensor technology such as accelerometers, GPS and satellite imagery it may be possible to collect and classify large quantities of behavioural data which could drastically change behavioural ecology. This was clearly modelled and demonstrated in Chapter 3, where a deep learning algorithm was able to classify millions of data points into windows of behaviour at an extremely high accuracy (97%). Behavioural ecology should play a larger role in epidemiology than it currently

does. Most epidemiological studies leverage modelling focusing on transmission at a population level which misses the dynamics caused by host behaviour entirely (Bobashev et al. 2007; Auchincloss and Diez Roux 2008; Rahmandad and Sterman 2008; Ajelli et al. 2010). Models that determine transmission from a bottom-up approach, starting at host behaviour, may prove to be more realistic as this aspect is a crucial driver of infection (Venkatramanan et al. 2017).

7.0.3 Modelling of Disease Management Interventions

The agent-based model (ABM) described in Chapters 5 and 6 used host behaviour to understand disease transmission between wolves and dogs. The model was extremely complex when fully parameterised, pushing the boundaries of what has previously been achieved using Netlogo, yet it was still achieving reasonable speeds despite this complexity (Railsback et al. 2017). Being able to accurately predict a disease system based on behaviours is an achievement on its own, but extracting the disease dynamics of the system from behaviour is a powerful tool that is currently underutilised in epidemiology (Dougherty et al. 2018). The use of behaviour as the primary source of parameterisation meant that the model had low sensitivity to the input parameters that were primarily density or disease related. The impact of host behaviour on disease transmission has become a focus of study in mosquitos which exhibit behavioural adaptations leading to increased transmission of malaria (Carrasco et al. 2019); further, mosquitoes have distinct host preferences which also impact transmission (Bakker et al. 2019). Behavioural drivers of disease are most likely to be an extremely common phenomenon. ABMs that focus specifically on the role that behaviour plays in disease transmission could be an

exploratory methodology more commonly applied in the field (Marshall and Galea 2015). Beyond these potentials, the model here developed was able to directly inform disease management strategies involving both wolves and dogs. The modelled scenarios showed that vaccination of domestic dogs is a costly and less effective measure than direct vaccination of the wolves. Even if vaccination of the wolves is difficult, low-level coverage would still reduce the required dog vaccination coverage to get equivalent results at reduced costs. There is merit in maintaining some level of dog vaccination under a One Health system (American Veterinary Medical Association 2008). Dog vaccination can reduce the incidence of disease affecting people and livestock, with associated improvements in the health and livelihoods of local people. The models of oral rabies-only vaccination also indicated that at least in the short term it was important to maintain dog vaccination for CDV, to provide some protection to the wolves while the use of a CDV vaccine in wolves is being trialled. Initiatives for maintaining wolf population viability in the long-term through conservation translocations are planned (Ethiopian Wildlife Conservation Authority. 2017), but due to the more immediate high threat of disease these kinds of long-term actions tend to be of lower priority and attract less funding. Funds freed up through a reduction of dog vaccination could be invested in these complementary strategies for wolf range expansion.

Additionally, being able to suggest a starting point for disease management interventions as a result of building the interactive model avoids the need for expensive and time intensive field trials. This model provides a framework for other disease systems worldwide, particularly ones with domestic dogs as the primary source of infection. Many large carnivores worldwide are impacted by diseases from domes-

tic dogs (Hughes and Macdonald 2013) and these charismatic species often have long running research projects or a large wealth of data associated with them. Using behavioural data collected over many years, ABMs can be effectively parameterised and taken further. In developed countries the focus tends to be more on how wild animals can transmit diseases to domestic animals, such as badgers with bovine tuberculosis (Chambers et al. 2014; Thomas 2019) or helminth parasites transmitted from urban foxes (Mackenstedt, Jenkins, and Romig 2015), but both these systems could still employ this form of modelling. What may be required in many of these systems is further study of the domestic dogs as their impacts on wildlife are only going to increase (Bonacic, Almuna, and Ibarra 2019). A programme to monitor dogs and implement interventions that can mitigate the negative impacts on wildlife is or likely will soon be needed in many wilderness areas in a similar manner they are used in urban population centres to control rabies. Simple projects to determine the relative behaviour of dogs in different settings could help inform their own ABMs.

7.0.4 Limitations and Future Research

While innovations in technology and modelling open up new possibilities for the advancement of research, with added complexity comes greater room for error. Any self-made device will only be as good as its construction, even though open source platforms remove much of the difficulty from building and programming devices, they will still require a large amount of trials and validation. Environments vary hugely and the standards of the devices will vary with them, in stable environments or on sedentary species a custom-built device might work immediately

but considerable adaptations would need to be made for extreme environments or species with strenuous or cryptic behaviours such as burrowing or aquatic species. Any handling of wild animals carries a risk, to them or to human observers, and these must be taken into account (Dennis and Shah 2012; Ludynia et al. 2012). The devices also have the capability to produce enormous amounts of complex data and more complex analytical techniques will be required.

Machine learning methods need a large amount of data and even though with behavioural classification they are achieving extremely high accuracy, they are still limited in the complexity of their classification (Lockhart and Weiss 2014). Behavioural data collected will always be incomplete in some way, be it due to uncaptured seasonal variation or even unusual individuals; one simply cannot collar or observe every individual in a population. Without robust long-term monitoring, it is impossible to completely determine the behaviour of any species so behavioural data will always have error and assumptions. Errors can then compound upwards if these data are used in other analysis or modelling. The modelling done here is currently limited in its scope particularly as it specific to the Bale Mountains National Park. This is home to the largest population of wolves, and the one best studied, but the much-needed applicability of the outputs of the model to other wolf ranges may be somewhat limited if differences in the behaviour of wolves and dogs in those areas depart significantly form that observed in the Web Valley. Using small subsections of the Bale Mountains model, or different wolf parameters such as density as a proxy for other conditions in other populations, gave us an indication of how these smaller wolf populations may be impacted by disease management interventions. In the future, the best approach will be to feed the model

the appropriate data from the relevant population. Within the model, disease is only coming from domestic dogs, widely assumed to be the case for Ethiopian wolves (Laurenson et al. 1998). It would be prudent to study if any other carnivore species might also be acting as a reservoir or carrying disease in the Afroalpine ecosystem. CDV is an extremely complex disease that, despite its prevalence and impact on pets and wildlife, little is known about it. The ability for CDV to persist in the environment has not been quantified directly with suggestions for persistence varying from hours to days depending on the environment. This persistence could be very important in viral transmission and even management with certain periods being higher risk based on the weather (Appel and Gillespie 1972; Park 2012). Similarly, little work has been done on the immune response post-infection or post-vaccination in wild animals, whether exposure is enough to produce immunity and the time that vaccination decays in its protective effects are both important for disease management (Miller and Hurley 2009). These parameters are very likely to be highly variable depending on the setting, so areas affected by CDV may need independent studies of the virus in their respective settings. The model presented here could be easily adapted to answer these questions, once data from other wolf populations is parameterised, viral dynamics determined or if the model is simplified to rely on less complex behaviours for movement or habitat preference.

There is still much that can be done to help understand disease management strategies, and the threats posed by domestic dogs to Ethiopian wolves. There is a wealth of options that the model can provide to investigate further the minute detail of disease management. Further exploration of the methods to which it is

applied could be incorporated, as for example effectiveness may increase in different seasons or by targeting particular individuals. This could lead to further reduction of costs if the required management intervention is reduced whilst increasing its effectiveness. One such area of interest would be to provide a dynamic environment to the model, to take into account changes due to habitat loss and climate change, and to see how this would affect management or wolf populations in the future. A management intervention may be effective in the current setting, but it might need to be changed or adapted as the environment changes. As new data become available, the model could be updated to provide rolling management recommendations. However, the principle behind the reduction of dog vaccination interventions in favour of wolf vaccinations is expected to hold, regardless of the exact vaccination level even as the model is updated. If disease management is improved with the use of these recommendations, there are still other threats to the wolves, particularly habitat loss (Marino 2003; Marino, Sillero-Zubiri, and Macdonald 2006) but also persecution, hybridisation and possibly genetic depression from repeated population bottlenecks (Gottelli et al. 1994; Randall et al. 2010). Further studies are needed to explore the impacts these threats will have on the wolf populations in the future and how they can be mitigated. Domestic dogs pose other threats to the wolves not just the disease, including direct aggression and competitive effects such as suppression of prey abundance, disruption of foraging, disturbance of denning sites (Gottelli and Sillero-Zubiri 1992; Atickem, Bekele, and Williams 2009) and even hybridisation (Gottelli et al. 1994). As the number of dogs in wolf habitat increases, these factors may become important threats that will need further investigation. A study of the social and cultural aspects underlying dog ownership may be able to help unravel the motivations and ways

to promote change in people's behaviour with regard to keeping dogs and their perceived role in preventing livestock predation by wild carnivores.

7.0.5 General Conclusions

This thesis endeavours to make informed management recommendations to help protect Ethiopian wolves from canid related disease. Data that quantifies dog and wolf behaviour and the level of overlap between them can be leveraged to make informed decisions for management interventions. The individual results have wider applicability in their various areas, particularly from a methodological perspective. Within the Ethiopian wolf system there is a pressing need for management, and this should be acted upon now, particularly in relation to preventive vaccination of wolves. While reduction of dog vaccination, or any changes in dog ranging behaviour or dog density, may be highly effective and reduce costs, they will no doubt require time, debate and further studies as well as cooperation from dog owners living inside and around protected areas. Nevertheless, I am confident that the approach and evidence presented here should provide a platform to initiating preventive low-level vaccination of Ethiopian wolves, with the long-term goal of a reduction in dog vaccination and the shifting of available funding into other wolf conservation priorities.

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Appendix A

Supplementary Materials

A.1 Chapter 2 Supplementary Materials

Full instructions including links on where the components were purchased from and all the code is available at https://github.com/JF717/GPS-Collars .

A.2 Chapter 5 Supplementary Materials

A.2.1 Model Parameters

A.2.1.1 Globals

Variable	Description	Range
Year		1 on-wards
Month		1-12
Day		1-30
Time	These are used to determine when events happen and behaviours performed.	0-23
Starting Number of Wolves	The initial density of wolves at the start	0-200
Starting Dog Density	The initial density of dogs per village that go into the park at the start	0-10
Number of Packs	User controlled determines the number of available territories for wolves to inhabit or expand into	1 - 20
Maximum Pack Size	The carrying capacity of the average pack, reproduction slows as it gets closer to this number	1 - 18

A.2.1.2 Disease Parameters

Variable	Description	Range
Introduced Infection chance rabies	The chance that rabies will appear	0 - 100%
Introduced Infection chance CDV	The chance that CDV will appear	0 - 100%
Vaccination % of Dogs	The % of the dog population to vaccinate each year	0 -1 00%
Vaccination % of wolves	The % of the wolf population to vaccinate each year	0 -1 00%
Rabies Incubation Time	Number of days before rabies kills the infected individual	0-30
CDV Incubation Time	Number of days before CDV kills or is cleared from the infected individual	0-30
CDV Persistance	The number of days that CDV persists in the environment	0 - 14

A.2.1.3 Wolf Parameters

Variable	Description	Range
Territory Size	The size in patches of the wolf pack's territory. Drawn from distribution of pack sizes	3.9 - 18.6 km^2
Infected Rabies	A true of false value for each individual to indicate infection with rabies	True / False (T/F)
Infected CDV	A true of false value for each individual to indicate infection with CDV	T/F
Furious	Whether the individual has furious or dumb rabies	T/F
Age	An integer that is used to determine non disease related mortality	0 - 8
Sex		Male/Female
Pack	Each individual maintains a record of which pack they belong to and the associated territory	Numeric ID
Den Site	The x y location of the den during the breeding season	X Y coordinates
Dominant	Each individual maintains a record of whether they are dominant or not, only one dominant male and one female per pack	T/F
Resistant Rabies	Whether the individual has been vaccinated for rabies	T/F
Resistant CDV	Whether the individual has been vaccinated for CDV	T/F
Behaviours	Based on the time allocation of behaviours at each hour they draw a behaviour from a distribution.	% chance of each behaviour in each hour from time allocations (chapter 4)

A.2.1.4 Dog Parameters

Variable	Description	Range
Village	The location of the village they live in to return to	Village Location x,y
Home Range	The Distance outside of the village the dog will travel	1.6 – 11.3 km^2
Infected Rabies	A true of false value for each individual to indicate infection with rabies	T/F
Infected CDV	A true of false value for each individual to indicate infection with CDV	T/F
Furious	Whether the individual has furious or dumb rabies	T/F
Age	An integer that is used to determine non disease related mortality	0 - 8
Sex		Male/Female
Pack	Each individual maintains a record of which pack they belong to and the associated territory	Numeric ID
Den Site	The x y location of the den during the breeding season	X Y coordinates
Dominant	Each individual maintains a record of whether they are dominant or not, only one dominant male and one female per pack	T/F
Resistant Rabies	Whether the individual has been vaccinated for rabies	T/F
Resistant CDV	Whether the individual has been vaccinated for CDV	T/F
Behaviours	Based on the time allocation of behaviours at each hour they draw a behaviour from a distribution.	% chance of each behaviour in each hour from time allocations (chapter 4)

A.2.1.5 Environmental Parameters

Variable	Description	Range
Habitat	What kind of habitat is in this square	1 - 9
Wolf Range	Whether this square is within the high quality wolf habitat	T/F
Village	Whether there is a village on this square	T/F
Infections	a counter for each square that counts the number of infections that have occurred on it.	0 On-wards
CDV	Whether this patch contains CDV in the environment.	T/F

A.2.1.6 Monitoring Parameters

Variable	Description	Range
Number of rabies introductions	Counts the number of times rabies has been introduced	0 On-wards
Rabies in System	Counts the total number of individuals with rabies at any time	0 On-wards
Number of CDV introductions	Counts the number of times CDV has been introduced	0 On-wards
CDV in System	Counts the total number of individuals with CDV at any time	0 On-wards
Epidemics	A running tally of how many times there has been an epidemic level outbreak in either	0 On-wards
Epidemics Dogs	A running tally of how many times there has been an epidemic level outbreak in the dogs.	0 On-wards
Epidemics Wolves	A running tally of how many times there has been an epidemic level outbreak in the wolves.	0 On-wards
Environmental CDV	Counts the number of environmental squares that currently have CDV in them	0 On-wards
Number of CDV infection from the environment	Running tally of how many infections of CDV have occurred from the environment.	0 On-wards
Total Cost	The total cost of management	0 On-wards
Wolf Cost	The cost of management in the wolves only	0 On-wards
Dog Cost	The cost of management in the dogs only	0 On-wards
Rabies in System	Whether there is currently rabies in the system	T/F
CDV in System	Whether there is currently CDV in the system	T/F

A.2.1.7 Sensitivity Analysis Input

Input Parameter	Range Trialled
Dog Density	0 - 10
Number Wolf Packs	1 - 10
Maximum Pack Size	0 - 18 by 2
Starting Number Wolves	10 – 100 by 10
CDV Mortality Wolves	10 – 100 by 10
CDV Mortality Dogs	10 – 100 by 10
CDV Persistance	0-14