ENVIRONMENTAL AND SOCIAL DETERMINANTS OF TICK-BORNE ZOONOSES IN THE SOUTH OKANAGAN

by

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ABSTRACT

Zoonoses (i.e., diseases transmitted from wild and domestic animals to humans) are health challenges with environmental and social determinants. For my thesis, I examined the environmental and social determinants of zoonoses transmitted by ticks, an obligate arthropod ecto-parasite, in the South Okanagan—a region with a potentially increasing risk of infection to tick-borne zoonoses. I first reviewed proximate (e.g., pathogens) and distal (e.g., land use) determinants of tick-borne zoonoses, and the management options to address them. This resulted in the description of an interdisciplinary approach to manage and prevent the diseases. In the remaining of my thesis, I contributed to this approach by examining two environmental determinants (prevalence of tick-borne zoonoses; and ecological dynamics of ticks and host species diversity) and two social determinants (impacts of land use practices on tick densities; and reasons for the adoption of protective practices).

For the environmental determinants, the prevalence of tick-borne zoonoses was found to be low in the South Okanagan. As well, in contrast to previous works, host species diversity only reduced tick densities when there were specific changes in host species composition that affected tick-host dynamics. For the social determinants, tick densities were found to be better predicted by the type of land use practice, rather than the patch size of suitable habitat. Finally, adoption of protective practices was not related to knowledge of ticks and tick-borne diseases, but to the level of experience with ticks.

These results help determine the prevalence of tick-borne zoonoses, and thus the infection risk of those diseases in the South Okanagan. They also help predict how various human activities at small ecological and large landscape scales may increase or decrease tick densities, and thus human exposure to ticks and their diseases. As well, these results can be used to develop risk communication strategies encouraging the adoption of protective practices, and reduce social concern regarding tick-borne zoonoses.

Given that the prevalence of tick-borne zoonoses in the South Okanagan is low, adopting management options against ticks or tick-borne zoonoses may not be necessary. Instead, promoting personal protective practices against ticks may be cost-effective in reducing the infection risk of tick-borne zoonoses.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

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DEDICATION

My family deserves many many thanks for having long-suffered my inexplicable hippie-granolaness, weird habits (What? You don't eat meat every day?), and for very likely still not understanding what it is that I do, and why it is that, after all this, I'm still not a "real" doctor.

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CO-AUTHORSHIP STATEMENT

All the manuscripts (Chapters 2-6) were co-authored, and the following outlines each of the authors' contributions, as well as the doctoral candidate, Jack Teng:

Chapter 2: Jack Teng identified and designed the research program, performed the research, analyzed the data, and prepared the manuscript. Karen Bartlett, Brian Klinkenberg and Muhammad Morshed aided in the preparation of the manuscripts with comments, edits and advice on content.

Chapter 3: Jack Teng identified and designed the research program, performed the bulk of research (collection of ticks and deer mice), analyzed the results, and prepared the manuscript. Robbin Lindsay, Muhammad Morshed, Antonia Dibernardo and Heidi Wood conducted the laboratory analysis on the ticks and deer mice to identify the presence of pathogens. Robbin Lindsay, Karen Bartlett, Brian Klinkenberg aided in the preparation of the manuscripts with comments, edits and advice on content.

Chapter 4: Jack Teng identified and designed the research program, performed most of the research (mathematical simulations), analyzed most of the data, and prepared the manuscript. Christina Cobbold conducted some of the mathematical simulations in the chapter. Christina Cobbold and James Muldowney performed the mathematical derivation (analytical analysis of the mathematical model). Christina Cobbold aided in the preparation of the manuscripts with comments, edits and advice on content.

Chapter 5: Jack Teng identified and designed the research program, performed the research, analyzed the data, and prepared the manuscript. Karen Bartlett and Brian Klinkenberg aided in the preparation of the manuscripts with comments, edits and advice on content.

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CHAPTER 1: Introduction

Maintaining human health is an interdisciplinary challenge that involves not only the expertise of medical practitioners and epidemiologists, but numerous other disciplines, including ecology and the social sciences (3, 6). Beyond the most proximate aspects of the disease itself (e.g., the disease-causing pathogen or agent), human health is influenced by a combination of environmental and social determinants (e.g., the ecological context of the pathogen; the human behavioural causes that lead to exposure), which cannot be addressed by a single discipline (7, 11, 12). As such, to develop prevention and mitigation strategies to maintain human health, an interdisciplinary understanding of these complex health challenges must be gained.

A prime example of a human health challenge that involves environmental and social determinants is the emergence of zoonoses, that is, diseases that reside in wild and domestic animals but that can be transmitted to humans (e.g., West Nile virus, avian influenza) (4, 9, 13). Zoonoses are especially challenging, as they are often new threats (e.g., highly pathogenic H1N1 influenza, Severe Acute Respiratory Syndrome), and, as such, are poorly characterized and lack strategies to address them. In addition, the threats of zoonoses are only increasing as human populations continue to encroach on wildlife areas (4); indeed, zoonoses represent >60% of emerging infectious diseases (14).

Zoonoses have environmental determinants, which include epidemiological and ecological determinants. Causative pathogens of zoonoses originate in wild and domestic animals, and their prevalence in the environment is maintained by their interaction with their disease vectors and reservoirs (e.g., ticks, mosquitoes, rodents, corvids) (5). Further, populations of the disease vectors and reservoirs are influenced by their ecological interactions with other species and the habitat they reside in—which determine their density and likelihood of spreading to areas inhabited by human populations (8).

Zoonoses also have social determinants: human populations are exposed to the causative pathogens zoonoses as a result of human activities and behaviour, such as land use practices (e.g., housing and agriculture) and the adoption of personal protective practices. Land use practices not only bring humans into proximity with wildlife, but cause disruptions in ecosystems, such that populations of disease vectors and reservoirs could proliferate (10). Human behaviour also affects an individual's exposure to disease vectors and pathogens, such as through the perception of risk, which determines the adoption of personal protective practices (1).

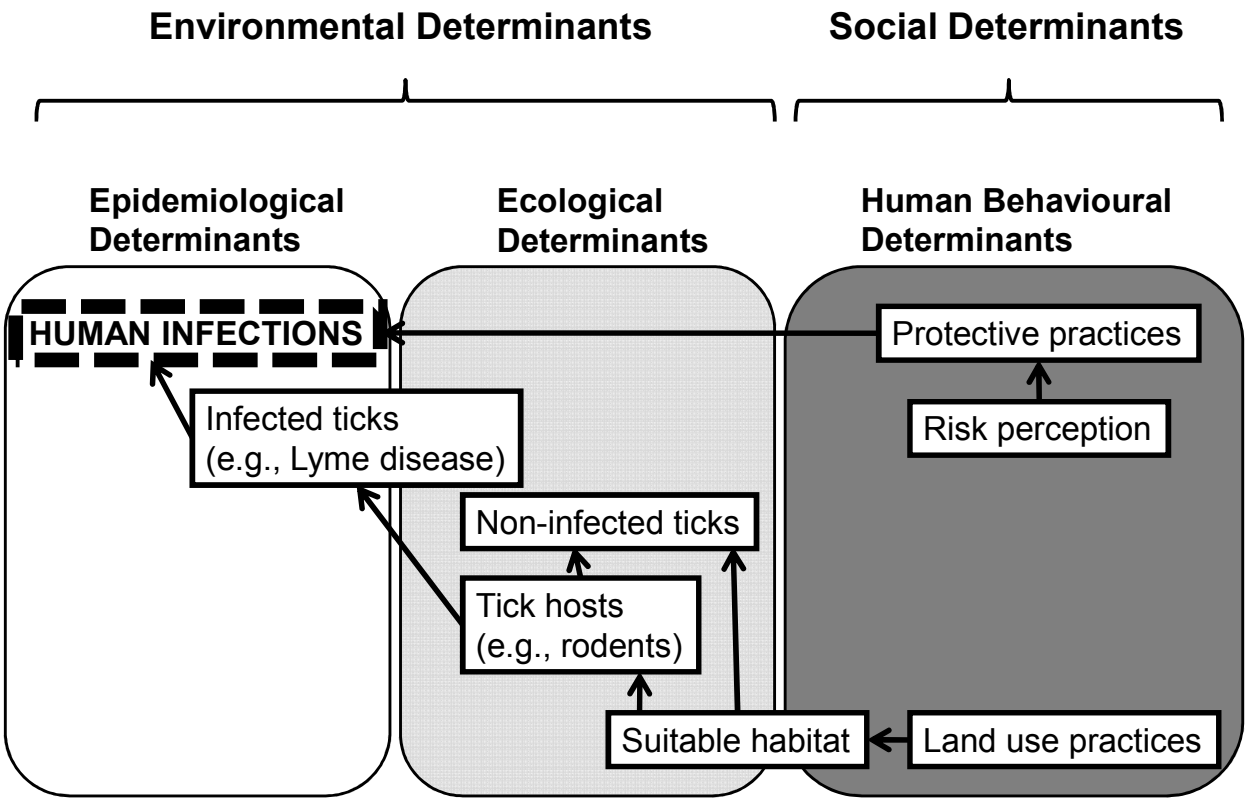
To help further the understanding of zoonoses and ultimately prevent and mitigate their health impacts, I examined the environmental and social determinants of zoonoses transmitted by ticks, an obligate arthropod ecto-parasite, in the South Okanagan. The South Okanagan is a rural region in the province of British Columbia (BC), Canada, which is changing with increasing human population and economic growth (2). As a result of these changes, human populations are becoming more active in the wildlife-human population interface, where the risk of encountering zoonoses, such as tick-borne zoonoses (e.g., Lyme disease, Rocky Mountain Spotted Fever), is higher (4).

For my thesis, I began by developing an understanding of the environmental and social determinants of tick-borne zoonoses and the management options to prevent them; this resulted in the description of an interdisciplinary approach that may be used to manage and prevent tick-borne zoonoses (Chapter 2). To then take the first steps of this approach, I examined the following environmental and social determinants (Figure 1.1): for the environmental determinants, I examined the prevalence of tick-borne zoonoses (Chapter 3) and the ecological dynamics of ticks and host species diversity (Chapter 4); for the social determinants, I examined the impact of land use practices on tick densities (Chapter 5), and the reasons for the adoption of personal protective practices against ticks and tick-borne zoonoses (Chapter 6). Hence, for my thesis, I adopted an interdisciplinary approach and employed quantitative and qualitative empirical methods, as well as theoretical mathematical modeling. As a result of this approach, however, I examined a wide breadth of determinants and approaches, but, to do so, did not pursue in the same depth as required for a thesis focussing on a narrower range of determinants and approaches. The chapters are summarized below:

-In Chapter 2, "Proximate and Distal Determinants of Tick-Borne Zoonoses and the Management Options to Prevent their Outbreak and Spread," I conducted a systematic review of the determinants of tick-borne zoonoses and the management options to address them. I first reviewed the determinants of tick-borne zoonoses from the most proximate to the most distal. I then described the management options of three disciplines that tackle tick-borne zoonoses: infectious disease epidemiology, pest management and conservation management. To integrate the approaches of the three disciplines, I described an integrated assessment approach, and discussed how it may be applied to the South Okanagan.

Figure 1.1. Conceptual flow diagram of the environmental and social determinants of tick-borne zoonoses

The environmental and social determinants leading to human cases of tick-borne zoonose infections—in the dashed box—are indicated. Environmental determinants include both epidemiological and ecological determinants, while social determinants include human behavioural determinants. This illustration is not comprehensive, and only indicates the determinants examined in this thesis. Note how certain determinants (e.g., infected ticks, suitable habitats) fall under two categories of determinants. In Chapter 3, I examined the prevalence of infected ticks. In Chapter 4, I examined the interaction between tick hosts and ticks (infected and non-infected). In Chapter 5, I examined the relation between land use and suitable habitat. In Chapter 6, I examined the relationship between risk perception and protective practices.



-In Chapter 3, “Prevalence of Tick-Borne Zoonoses and Hantavirus in the South Okanagan, British Columbia: Active surveillance of ticks (*Dermacentor andersoni*) and deer mice (*Peromyscus maniculatus*),” I examined an epidemiological determinant of tick-borne zoonoses: the prevalence of tick-borne zoonoses in the South Okanagan. I employed a quantitative empirical research approach, using an active survey of ticks (*Dermacentor andersoni*) and the main disease reservoir, deer mice (*Peromyscus maniculatus*). I found that the prevalence of tick-borne zoonoses is low in the South Okanagan. Given the availability of deer mouse serum samples, I also found that the prevalence of Hantavirus, a rodent-borne zoonose, is low.

-In Chapter 4, “The Influence of Host Competition and Predation on Tick Densities and Management Implications,” I examined an ecological determinant of tick-borne zoonoses: the dynamics of tick densities as a result of changes in host species diversity that affect host competition and predation. I employed a mathematical modeling approach, developing a stage-structured tick-host model. I examined the influence of specific changes in host diversity that modify the competition among and the predation on small and large host populations. I found that increasing host diversity will not necessarily reduce tick populations, but depends on changes in host species composition affecting the degree and type of competition among hosts, and also on changes in host species composition affecting the host dynamics with the tick life-stages.

-In Chapter 5, “The Influence of Agricultural Practices on Tick Densities,” I examined a social determinant of tick borne-zoonoses: the influence of agricultural land use practices on tick densities. I employed a quantitative empirical research approach to examine the influence of two agricultural practices common in the wildlife-human population interface in the South Okanagan: grazing (GA) (e.g., grazing pastures) and non-grazing (NGA) (e.g., orchards) agricultural practices. I found that tick densities were higher in smaller patches of suitable habitat areas and in landscape contexts formed by NGA and GA practices, in comparison to low human impact (LH) areas.

-In Chapter 6, “Mental Models and the Adoption of Protective Practices Against Ticks and Tick-Borne Diseases in the South Okanagan,” I examined another social determinant

of tick-borne zoonoses: the reasons for the adoption of personal protective practices against ticks and tick-borne diseases. In this chapter, I employed a qualitative research approach to determine how risk perception influences the reasons for the adoption of personal protective practices against ticks and tick-borne zoonoses. I found that adoption was not directly related to knowledge of ticks and tick-borne diseases, but was better explained by differences in the amount of experience with ticks: participants with greater experience had increased adoption and knowledge of personal protective practices.

As further described in the following chapters, the results of my thesis help provide a comprehensive understanding of tick-borne zoonoses by examining both their environmental and social determinants. This understanding may be used to better manage tick-borne zoonoses and prevent their potential outbreak and spread into human populations. As well, the approach taken in my thesis may also be applied to other zoonoses, particularly vector-borne zoonoses, such as West Nile virus or avian influenza.

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CHAPTER 2: Proximate and Distal Determinants of Tick-Borne Zoonoses and the Management Options to Prevent their Outbreak and Spread[1]

2.1 INTRODUCTION

Ticks are obligate arthropod ecto-parasites, and are second only to mosquitoes in the number and diversity of diseases they can transmit to humans (64). These diseases are zoonoses, that is, they are diseases that are found in wild and domestic animals, but can be transmitted to humans by direct contact with vertebrate (e.g., rodents transmitting Hantavirus) or arthropod vectors (e.g., mosquitoes transmitting malaria; ticks transmitting Lyme disease). While tick-borne zoonoses are considered rare in human populations and limited to certain endemic regions, they are becoming more widespread, posing a threat to public health (80, 120). Indeed, many tick-borne zoonoses are emerging infectious diseases—previously unknown diseases that have recently been characterized or found in novel geographic regions, and for which management and preventative measures have not been developed (65, 172).

The emergence of infectious zoonoses, such as tick-borne zoonoses, has spurred much research into the determinants and factors that cause the spread and outbreak of zoonoses (37, 65, 187). Numerous determinants have been identified, resulting from environmental and social sources, such as climate change (e.g., 75), proximity of human activities to wildlife habitat (e.g., 38), and increasing global trade and travel (e.g., 171). These determinants not only differ in terms of their proximate or distal influence on the emergence of zoonoses, but can function on different spatial scales (e.g., climate change vs. pathogen prevalence) (50, 184) and can be interdependent (7, 30).

An understanding of how proximate and distal determinants originate from environmental and social sources and interact at different scales is necessary to predict future occurrences of zoonoses. More importantly, this understanding is also necessary for developing management options to prevent outbreaks of zoonoses. To this end, an interdisciplinary approach can contribute to a comprehensive understanding of zoonotic disease emergence; this would also assist with the management of the spread and outbreak of zoonoses, as the approach would

[1] A version of this chapter has been submitted for publication. Teng, J., Bartlett, K., Klinkenberg, B., Morshed, M.G. (2009) Proximate and Distal Determinants of Tick-Borne Zoonoses and the Management Options to Prevent their Outbreak and Spread.

integrate the disciplinary expertise gained from studying zoonoses from different perspectives (e.g., 30).

Indeed, infectious disease epidemiology, pest management and conservation management have complementary expertises and methods that can address zoonoses, such as tick-borne zoonoses, even though they have different frameworks from which they view zoonoses (50, 132). Infectious disease epidemiology focuses on primarily proximate determinants of zoonoses and at small scales, such as examining disease pathogens or the transmission pathways from wildlife to human populations (104, 187). Pest management focuses on more distal determinants and at larger scales, which tend to be delineated by the boundaries of a land use practice (e.g., agricultural areas or rangelands); the discipline examines mechanisms and measures—both ecological and anthropological—that affect populations of unwanted species (4, 59, 180). Conservation management focuses on distal determinants and at potentially very large scales, which can encompass a landscape containing several different land use practices; the discipline examines how land use practices and preservation measures can benefit endangered populations and potentially prevent unwanted species from proliferating (1, 36, 145). Integrating the management options of these three disciplines may then be effective in understanding and preventing the outbreak and spread of tick-borne zoonoses.

Thus, for this review, we integrate the knowledge and management expertises of three disciplines that have examined different proximate or distal determinants of tick-borne zoonoses: infectious disease epidemiology, pest management, and conservation management. To narrow the focus of this review, we focus on natural sciences disciplines. We also describe an interdisciplinary approach that comprehensively addresses tick-borne zoonoses and integrates the three disciplines. In section 2.2, we describe the methods employed to conduct this review. In section 2.3, we identify the proximate and distal determinants of tick-borne zoonoses by reviewing tick-borne zoonoses, tick life history, and their interaction with ecological and human processes. In section 2.4, we review the disciplinary approaches to addressing the determinants of tick-borne zoonoses from infectious disease epidemiology, pest management, and conservation management; we also describe an integrated assessment approach that could combine the three disciplines. In section 2.5, we discuss how an integrated assessment approach may be applied to tick-borne zoonoses in the South Okanagan, British Columbia (BC) in Canada. In section 2.6, we discuss the relevance of the integrated assessment approach to other vector-borne zoonoses.

2.2 METHODS

We conducted a systematic review of publications pertaining to ticks, tick-borne zoonoses and the management options available to address their outbreak and spread. We searched a variety of databases and indexes to find peer-reviewed scientific studies from journals and other resources, such as books and news articles. Our primary resources to locate scientific journals were the following subscription-based databases: PUBMED, which focuses on life sciences journals; ISI Web of Knowledge, which includes both natural and social sciences journals; Scopus; MEDLINE (OvidSP); and EMBASE (OvidSP). We also used open-access databases such as Google Scholar, and Scirus. Lastly, we also searched the TRIP database, EBM (Evidence-Based Medicine) Reviews, and Cochrane Database of Systematic Reviews for relevant reviews on zoonoses and zoonoses management.

When searching the databases, we used the following keywords and grouped them by the Boolean operators AND and OR: tick, disease, zoonotic, zoonoses, management, prevention, ecology, and epidemiology. As we read through the papers identified by these keywords, we identified further keywords that could be searched for more specific topics, such as the following: Borrelia, Lyme disease, Rickettsia, integrated pest management, conservation management, and spatial epidemiology. Reference lists of the identified studies were searched to locate further citations.

2.2.1 Selection criteria

We included articles and studies in this review if they met the following criteria: peer-reviewed study or article; and reviews or books on relevant topics, such as tick-borne zoonoses. Studies had to be relevant to the following topics: ticks, including their ecology and life-cycle involving other animal hosts; tick-borne zoonoses, including the pathogen itself, the transmission pathway, and its epidemiology; and management options from the disciplines of infectious disease epidemiology, pest management, and conservation management.

2.2.2 Compilation of review

The identified citations from the searches were reviewed to determine their relevance. We summarized the information found in the citations and organized the available information according to two categories: the determinants of tick-borne zoonoses and the management options to address them. We organized the determinants of tick-borne zoonoses from the most proximate (e.g., tick pathogen) to the most distal (e.g., habitat modification). Similarly, we organized the management options according to whether they addressed proximate determinants (e.g., vaccines) or distal determinants (e.g., tick host management). Finally, we summarized the management options available and described how they could be applied to the region of the South Okanagan in British Columbia, and included relevant information regarding the geography, land use development, and ecology of the area.

2.3 DETERMINANTS OF TICK-BORNE ZOONOSES

The emergence of tick-borne zoonoses results from proximate and distal determinants that derive from biological, physiological, environmental, and social sources (Figure 2.1). We review these determinants from the most proximate to the most distal, and describe how they influence the emergence of tick-borne zoonoses. We begin by reviewing tick-borne zoonoses and the pathogens. We then describe the conditions that determine the maintenance of disease pathogens in the environment. Following this, we review the biological and physiological determinants of tick survival in the environment. We then describe tick interactions with other species and review the relationships of ticks with their hosts and predators. Finally, we review the influence of human activities and behaviour on tick populations and tick habitat conditions.

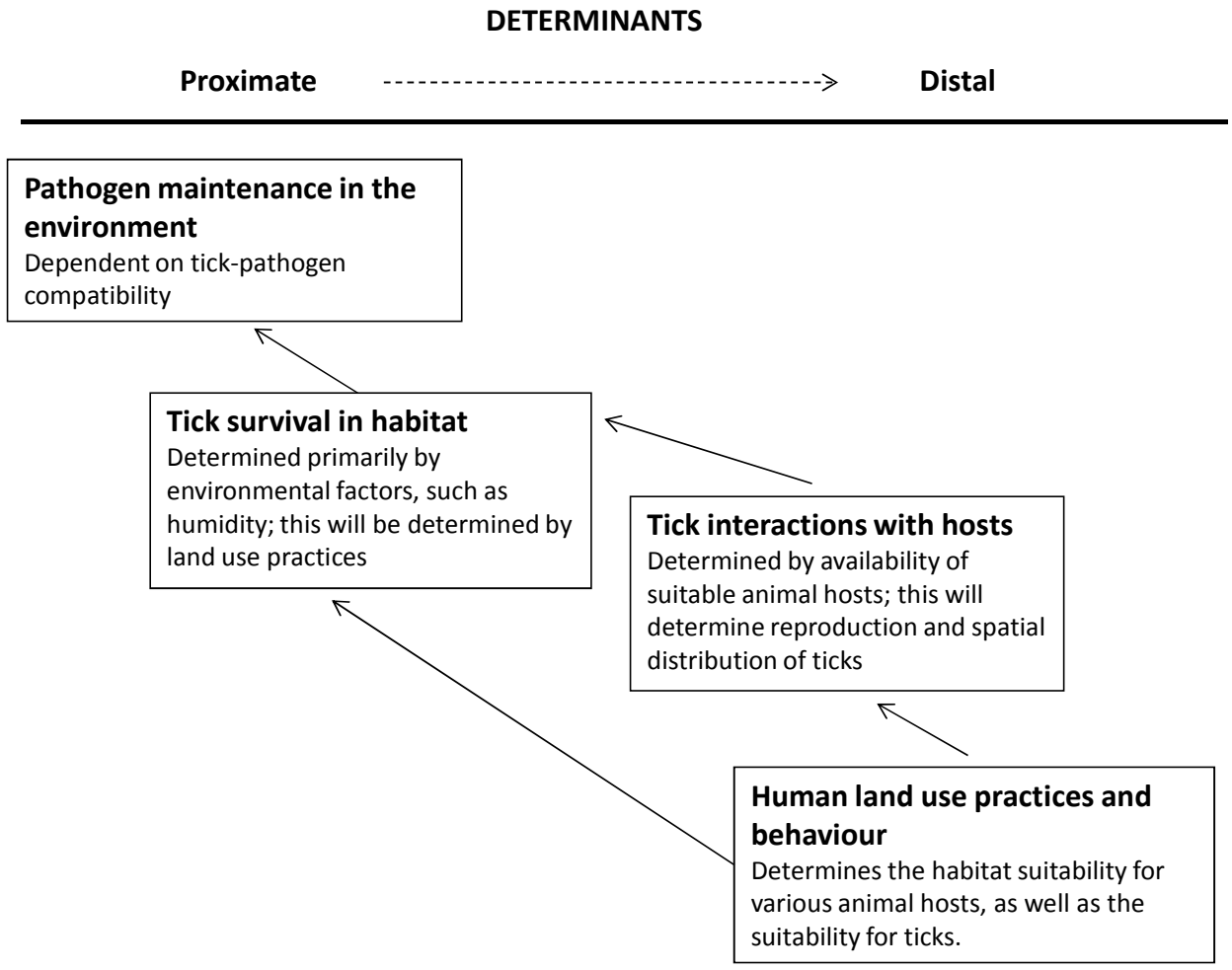
2.3.1 Tick-borne zoonoses

A multitude of tick-borne zoonoses have been identified that affect both human and wildlife populations. The causative agents of the zoonoses are diverse and may be protozoans, viruses, or bacteria (64). While humans can contract tick-borne zoonoses after being bitten by an infected tick, humans are accidental and dead-end hosts (i.e., the pathogen is not transmitted to additional hosts). The intended host is usually a small or large vertebrate animal (e.g., rodent, lizard, bird, sheep, deer) that is associated to the tick life cycle in which the disease is maintained (123, 163, 165). We provide a brief overview of tick-borne zoonoses to illustrate their diversity.

Protozoans and viruses cause a number of diseases in humans and animals. Ticks can transmit protozoans that are responsible for causing diseases such as Babesiosis, which is caused by *Babesia microti.* (15); these are intracerythrocytic parasites that infect red blood cells in a similar manner as malaria. Protozoans are often found in livestock and companion animals, such as dogs and cats, but can infect human populations (32, 174). Viruses are also transmitted to humans by ticks, but research on them is preliminary (85, 114). Tick Borne Encephalitis (TBE), caused by *Flaviviruses,* is a disease found in Eastern Europe, and many regions in North America (69). Other diseases caused by *Flaviviruses* include Powassan Encephalitis and Kyaranur Forest Disease. In Western North America, *Coltiviruses* are the causative pathogens of Colorado Tick Fever. Crimean-Congo Hemorrhagic Fever is common in certain areas of Europe and Africa, and is caused by a *Bunyaviridae* (64).

Figure 2.1: Proximate and distal determinants of tick-borne zoonoses

This diagram describes the determinants influencing the emergence of tick-borne zoonoses, which can originate from environmental and social sources. This is a simplified diagram, where a more complete diagram would include other factors such as climate change, medical practices, media, and risk perception.



Bacterial pathogens cause a large variety of tick-borne diseases. They are the causative pathogens of some of the most well-known diseases, such as Lyme disease, or Lyme borreliosis (10, 11, 24), whose causative pathogen is the spirochaete, *Borrelia burgdorferi sensu stricto*. There are also a number of different strains in Europe and Asia, which cause similar symptoms; thus, to avoid confusion, *Borrelia burdorferi sensu latto* is used to refer to the family of spirochaetes that cause Lyme disease-like symptoms (39, 67, 143). Other spirochaetes also cause other diseases, such as relapsing fever, which can be caused by *B. hermsii*, *B. duttonii* or *B. garinii*; these diseases span the globe from North America to Africa (45). *Rickettsia* and *Ehrlichia* are two other large genera of bacteria that contain a number of pathogenic species, such as *Rickettsia rickettsii* and *Anaplasma phagocytophilum*. Much like spirochaetes, numerous species of either genus are known to cause diseases, and new species are continually being discovered (13, 28, 57, 192). There are also the bacteria that cause Tularemia and Q fever, *Francisella tularenis* and *Coxiella burnetti* respectively; these bacteria are distinct in that they have free-living forms and can be contracted in the absence of a tick bite, while the other diseases are transmitted by a tick bite.

Being bitten by a tick can also cause tick-paralysis, which is caused by toxic substances in the tick saliva (98). These toxic substances can also cause non-paralytic toxicoses (e.g., hyperaestasia in guinea pigs). The toxic substances in tick saliva have yet to be identified, and the mechanisms by which they act are still poorly understood. However, most types of ticks have the potential to cause tick-paralysis (e.g., *Dermacentor andersoni* and *D. occidentalis* in North America; *Argas africolumbae* and *A. arboreus* in Africa). All potential hosts appear susceptible to tick paralysis (e.g., cattle, humans), but smaller animals and young children may have stronger reactions to them (e.g., rabbits, dogs). While tick paralysis is not typically life threatening, an affected animal can die from secondary causes (e.g., dehydration) if not treated promptly; fortunately, the condition is easily treated by simply removing the tick.

Clearly, a plethora of different diseases may be transmitted from ticks to humans. However, pathogens are only maintained in particular tick and host species. This plays a role in determining the prevalence of the pathogen in the environment.

2.3.2 Determinants of pathogen maintenance in the environment

Tick pathogens are maintained in wildlife populations through the interaction between ticks and animal hosts that are competent disease vectors and reservoirs (162, 165). Animal disease reservoirs carry the disease pathogen in their bloodstream. Ticks then acquire the pathogen when it obtains a blood meal from the animal. Following this, the tick may retransmit the pathogen to another animal host that is a competent disease reservoir—thus maintaining the pathogen in the environment. But, not all ticks, nor all animal hosts are competent carriers of disease pathogens: some may have successful immune responses that eliminate the pathogen, or others may die before transferring the disease to another carrier. In order for the pathogens to be maintained in the environment, there must be both competent ticks and animal hosts to be disease carriers. The competence of these carriers is determined by complex adaptations and factors further described below.

Tick-borne pathogens are not generalists that can be carried and transmitted by any given tick. Instead, these pathogens tend to be associated to certain tick genus to which they have adapted. For instance, the causative agent of Lyme disease, *Borrelia burgdorferi s.l.,* is only effectively transmitted by *Ixodid* ticks, such as *I. scapularis* (in Eastern North America), *I. pacificus* (in Western North America), and *I. ricinus* (in Europe) (67, 159). Similarly, the causative agent of Rocky Mountain Spotted Fever, *Rickettsia rickettsii*, is only effectively transmitted by *Dermacentor spp.* ticks, such as *D. andersoni* and *D. variabilis* (95). Hence, even though *Ixodes* and *Dermacentor* distributions can overlap, they will not transmit the same diseases. It is important to note that co-infections can occur, and more than one pathogen may be found in a tick; however, recent work suggest that co-infections may be rare, as the microbial competition among pathogens can prevent the introduction of further pathogens, such as with *R. peacockii* found as an endosymbiont in *Dermacentor spp.*, which can prevent the establishment of other Rickettsial agents (78, 179).

The tick-pathogen specificity has to do with the pathogen's adaptation to survive in two very different environments: the vertebrate host and the tick host. This adaptation is necessary as the pathogen must be present in both vertebrates and ticks for it to persist in the environment. The mammal and tick environments differ drastically in terms of temperature, salinity, and pH (19). The tick environment is especially variable, changing whenever the tick obtains a blood meal or undergoes physiological changes, such as moulting or reproduction. To survive in ticks

and mammals, pathogens have developed morphological diversity that allow them to assume forms with different outer membranes specialized to the varying conditions; in fact, some pathogens have adapted take advantage of the physiological changes in ticks, using them as cues to transition from one morphological state to another (19, 117). This has been observed in tick-borne *Ehrlichias* found in humans, cattle and dogs—respectively, *E. chaffeensis*, *E. ruminantium,* and *E. canis*; this can cause persistent infections that are difficult to diagnose, as different isolates from the same species can present different sizes and numbers of bands on Western blots (110).

The pathogen must also be able to be coexist with, if not overcome, the immune responses of both the tick and mammal hosts. To do so, pathogens have evolved closely with ticks, such that pathogens can take advantage of the pharmacologically active components in the tick saliva to enter into the mammal host blood stream and evade the new host's immune response (168, 186). Ticks have an immune system, albeit a primitive one, that relies on peptides to attack unwanted pathogens (163). When the tick acquires the pathogen from its blood meal, the ticks can suppress pathogens to a certain extent. As such, many pathogens have evolved to be relatively harmless to the tick to avoid inducing an immune response. Indeed, since there is often a long gap in between the times when the tick feeds on the next mammal host, the pathogen must be well adapted to survive in the tick, and not have many deleterious effects on the tick. This, though, is not always the case, as some pathogens can be highly virulent to the tick, infecting its reproductive organs, or disrupting its organ function: *R. rickettsii* can cause high mortality rates in *Dermacentor spp.* through vertical transmission, that is transmission of the pathogen from the adult ticks to the larvae; *B. burgdorferi* can disrupt oogenesis and reduce fecundity in *Ixodes spp.* (86, 164). However, such highly virulent pathogens have a low likelihood of being maintained in the environment.

The pathogen must survive in the animal host as well. In the case of an unsuitable disease host, the pathogen is either eliminated from the blood stream by the unsuitable host's immune system, or the pathogen may cause the host's death; in either case, the pathogen is removed from the environment. A unique example of this is the interaction of *I. pacificus* with one of its hosts, the western fence lizard (*Sceloporus occidentalis*), whose blood contains an anti-bacterial agent that effectively eliminates *Borrelia burgdorferi s.l.* from its blood stream (88). In contrast, an example of an ideal disease host is the white-footed mouse, *Permomyscus leucopus*, which is fed upon by the tick, *Ixodes scapularis*. White-footed mice lack histamine-containing basophils,

which allows a complement-inactivating enzyme in the tick saliva to prevent the development of natural immunity in white-footed mice; this is, in turn, allows the pathogen to enter into mouse's bloodstream and proliferate, thus forming a perfect vector-disease reservoir system (148).

While other tick hosts are not suitable disease hosts, many species have been found to maintain the pathogen at lower levels; there can indeed be numerous other secondary disease reservoir hosts, which can pose a challenge in identifying all possible disease reservoir hosts (76). For instance, large mammals (e.g., cattle, horses) are thought to be unsuitable pathogen hosts (131, 149), but recent work has found that certain pathogens can be found in wild ungulates, such as mule deer (5, 16, 191). Companion animals, such as dogs or cats, have been found to harbour diseases (14, 101). Avians, from migratory birds to pheasants, have also been found to maintain the pathogen at low levels (31, 62, 84). In these moderately suitable disease reservoirs, the pathogen is not completely eliminated from their bloodstream, and can still pass on the pathogen to ticks in lower levels (62, 92, 99). Thus, while many conditions need to be met for a suitable disease host, they may be met more often than not. Indeed, recent work suggests that there may be more suitable disease hosts for *Borrelia burgdorferi s.l.* than previously thought (18).

Nevertheless, transmission of tick-borne pathogens is not a given whenever a tick bites a new mammal host. Even given a proper tick host and disease reservoir, maintenance of the pathogen will be dependent on whether the tick itself manages to survive in the environment, which will be determined by both abiotic and biotic factors.

2.3.3 Determinants of tick survival in the environment

Although ticks are highly resilient, they have physiological restrictions that determine their survival in the environment. These restrictions are mainly governed by environmental conditions, since ticks spend almost 90% of their life off-host (112). The main environmental condition that ticks are sensitive to is humidity. Ticks must maintain an equilibrium between its body and the environment, known as the critical equilibrium humidity threshold, below which the tick will continuously lose water and rapidly die from desiccation; modifying the relative humidity of the environment in laboratory conditions can change the tick survival period from several months to just a few days (34). To retain their moisture, ticks have evolved behavioural and physical adaptations, such as being active only in favourable seasons (i.e., spring and

autumn), and becoming dormant in very hot or cold periods (48, 118). In addition to their seasonal activity, there are two main types of adaptations, which have been developed by two families of ticks that have evolved different survival strategies: the Ixodidae family of ticks, also known as "hard" ticks; and, the Argasidae family of ticks, also known as "soft" ticks (123, 165).

Ixodid ticks are diurnal feeders, and are mainly opportunistic ambush hunters. To find a host, they climb to the branches of shrubs or grasses, and wait until an animal comes close enough for it to latch on to. To limit their exposure, they climb up branches in the early hours of the day, and return to the ground before the heat becomes too elevated. Ixodid ticks have also evolved a distinctive hard, shell-like structure, a scutum, on its dorsal area; this waxy surface helps the tick retain its moisture. In extreme conditions, some Ixodid ticks can excrete a salty, highly hygroscopic solution on its mouth parts. Water then condenses on the mouth parts, and the tick can reabsorb the solution along with the water; however, this strategy is energetically costly, and becomes more difficult when ticks are older or are unfed for long periods of time.

Argasid ticks have adapted to be nidiculous, that is, they remain in the nests or burrows of their hosts, or they remain in dark, humid areas, such as cracks in stone walls or cellars. They are mainly nocturnal feeders, and are able to move quickly to locate a host, and then feed very quickly and multiple times (i.e., less than 1 hour); in contrast, Ixodid ticks feed once per life-stage, and can take 24 hours to properly attach and begin feeding. Argasid ticks' ease in movement is facilitated by their lack of a scutum; their dorsal area is covered only by cuticle, making them appear leathery and "soft." Yet, despite the "softness," they still have high survivability, due to their habitat selection, reduced energy investment given the lack of a scutum, and ability to remain dormant for long periods of time.

Thus, the sensitivity of ticks to humidity determines both their survivability and activity. These, in turn, determine periods and habitat areas with higher probabilities of encountering ticks and thus tick-borne pathogens. But, the presence of ticks will also be dependent on their hosts, as they require animal hosts to both reproduce and complete their development.

2.3.4 Determinants of tick ecology: interactions with other species

Ticks are obligate ecto-parasites that depend on other species to develop and reproduce, and are thus dependent on other species to be their hosts. These host species will influence tick population abundances and distributions, as they determine tick reproduction and dispersal, and

even survivorship through predation. Tick ecological interactions are thus important in determining the presence of ticks and tick-borne pathogens in the environment.

Tick life history begins in spring with larvae that quest for a host to obtain their first and only blood meal, usually from a small animal such as a rodent. Following this, the tick falls off to moult into the next stage, a nymph. The nymph overwinters, and, next spring, begins questing for a host, another small animal, to take a blood meal. It then falls off to moult into the third and final stage, an adult. During that same summer and fall, the adult quests for a host, usually a large animal host, such as deer, for another blood meal. With this third and final meal, the tick finds a mate, after which the female lays eggs (3-6,000 eggs) that will hatch into larvae the following spring. This two-year life cycle with only three blood meals on two or three different hosts is common to most hard ticks; there can be some variation around it, where some species may feed only a single type of host, rather than two or three. Soft-ticks have the most significant departure as they have adapted to avoid the high investment of taking one meal per host, and can instead feed several times on the same or different hosts until it obtains enough blood to moult to the next stage.

The availability of hosts is thus critical to tick survival. But, despite their dependence on hosts and their opportunistic feeding strategy, ticks exhibit some host-specificity, preferring to feed on a limited number of vertebrate hosts (123, 164). This preference is in part explained by the complex tick-pathogen interactions previously described: just as pathogens have evolved to persist in tick systems, ticks have also evolved to feed on a select variety of hosts. Tick saliva is replete with a number of pharmacologically active substances that act to facilitate tick feeding by preventing blood-clotting and also host immune responses (19, 117). And yet, it is important to note that though ticks have preferred hosts, the tick's opportunistic feeding strategy often puts them into contact with another host on which it is forced to feed given its constrained life history requirements.

Given the limited number of hosts that are suitable disease reservoirs, some recent works have proposed that increased species diversity could play a role in preventing the spread of tick-borne zoonoses (128, 155). The principle of this is that increased species diversity would make ticks encounter more unsuitable hosts, thus decreasing the reproductive rate of ticks and also removing tick pathogens from the environment (i.e., the dilution effect); this is based on the intuitive assumption that most species are not competent disease reservoirs. This appears to be the case with some animals and diseases, such as with birds and WNV (e.g., 56, 156).

As well, increased species diversity may also involve ecological interactions among tick hosts that could have an impact on ticks and their survival. Competition among the hosts for limited resources, such as among rodents or other small animals, could limit the abundance of ideal disease reservoirs, thus potentially reducing the pathogen abundance in the environment. Similarly, predation on the hosts could also potentially control populations of rodents and deer, and prevent the proliferation of tick populations (127). As such, ecosystems with a more diverse species assemblage may contain species that can control tick hosts through competition or predation, which, in turn can regulate tick densities.

Direct predation on ticks have been also been suggested to have an impact on tick populations. Indeed, ticks have a number of arthropod predators, such as ants, spiders and parasitoids—which have also been proposed to be used as bio-control agents (153). For instance, "fire ants" (*Solenopsis invecta)*, are thought to have reduced populations of the tick *Amblyomma americanum* in southern US, while spiders are thought to have reduced populations of the tick *Rhipicephalus sanguineus* in Corsica (190). There is also evidence that vertebrate predators such as lizards (e.g., skinks) or birds (e.g., chickens, egrets, oxpeckers) prey on ticks (123). However, the effectiveness of these different predators on ticks remains unstudied.

Finally, tick interactions with other species also determine the geographic distribution of ticks. Since ticks are not vagile and cannot travel large distances, they are dependent on other species to disperse. Migratory birds may allow for the most extreme dispersal, where some ticks have been shown to cross continents (109, 157). On smaller scales, other hosts, such as rodents or deer, also contribute to tick dispersal. By attaching themselves to rodents or deer, ticks can disperse to areas that are within the host's range. Indeed, recent research has found that tick distributions are effectively a subset of deer distributions (129).

Tick ecological interactions and those of their hosts will thus influence the abundances and distribution of ticks. These ecological interactions will depend on the species that are present in the environment, which in turn are influenced by human activities, such as land use practices.

2.3.5 Determinants of tick-borne zoonoses from human activities

Human activities are important determinants of the emergence of tick-borne zoonoses, as both proximate and distal determinants. In the most straight-forward sense, human behaviour is a proximate determinant of tick-borne zoonoses. Human behaviour determines the likelihood of

being exposed to ticks, and thus tick-borne pathogens. Working or recreating in tick-infested areas will increase the likelihood of being bitten by ticks; similarly, the adoption of protective practices, such as regular tick-checks or the use of pest repellent, will decrease the likelihood of encountering ticks and being bitten by one. Hence, determining the risk of different occupations and activities to tick-borne zoonoses is important in understanding how these diseases may arise (89, 181).

On a more distal sense, human activities, such as land use practices, can modify the landscape, affecting ecosystems and thus the habitat suitability for ticks and their hosts. Different human land use practices can increase habitat suitability for ticks, by creating areas that retain moisture or offer shelter to ticks (22, 79). Even such simple practices such as adding mulch on garden edges can increase tick densities (58). Other activities will decrease tick densities, such as the application of pesticides in agricultural areas or controlled burnings in conservation areas (167). However, neither pesticides nor burnings have been shown to permanently eliminate tick densities, as ticks can develop resistance to pesticides, and tick populations can return to burned areas two or three years later (136, 189). As well, human activities affect tick hosts, and can be an influential distal determinant on tick-borne zoonoses emergence. There has been much research demonstrating that land use practices will influence the species diversity in the area, such as with agricultural, ranching, logging, and exurban areas (42, 100). In some cases, the land use practice could decrease species diversity and lead to greater abundances of disease-carrying host populations (17, 56). As such, recent research have suggested that certain land use practices can lead to the emergence of infectious diseases (133, 171, 178). Land use can modify the habitat suitability of a landscape, such that many species will be unable to persist, leaving other species to thrive in the modified habitats, but which happen to be potential disease hosts (e.g., deer mice) (90, 178). Indeed, previous works have suggested that historic land use practices contributed the emergence of Lyme disease (10, 87, 129).

Finally, on the most distal end of determinants, climate change has been suggested to allow tick populations to thrive and become established in areas that had previously been unsuitable. Although the future impact of climate change on tick-borne zoonoses is still being debated (94, 119, 125), its effects on other vector-borne diseases have been well-documented, and thus deserve to be considered.

2.4 MANAGEMENT OPTIONS FOR ADDRESSING TICK-BORNE ZOONOSES

Infectious disease epidemiology, pest management and conservation management have distinct but complementary management options to address tick-borne zoonoses. These management options differ in that they address different proximate or distal determinants of disease emergence (Figure 2.2). We first describe the management options taken from the three disciplines. We then describe an integrated assessment approach that can combine all three disciplines.

2.4.1 Infectious disease epidemiology

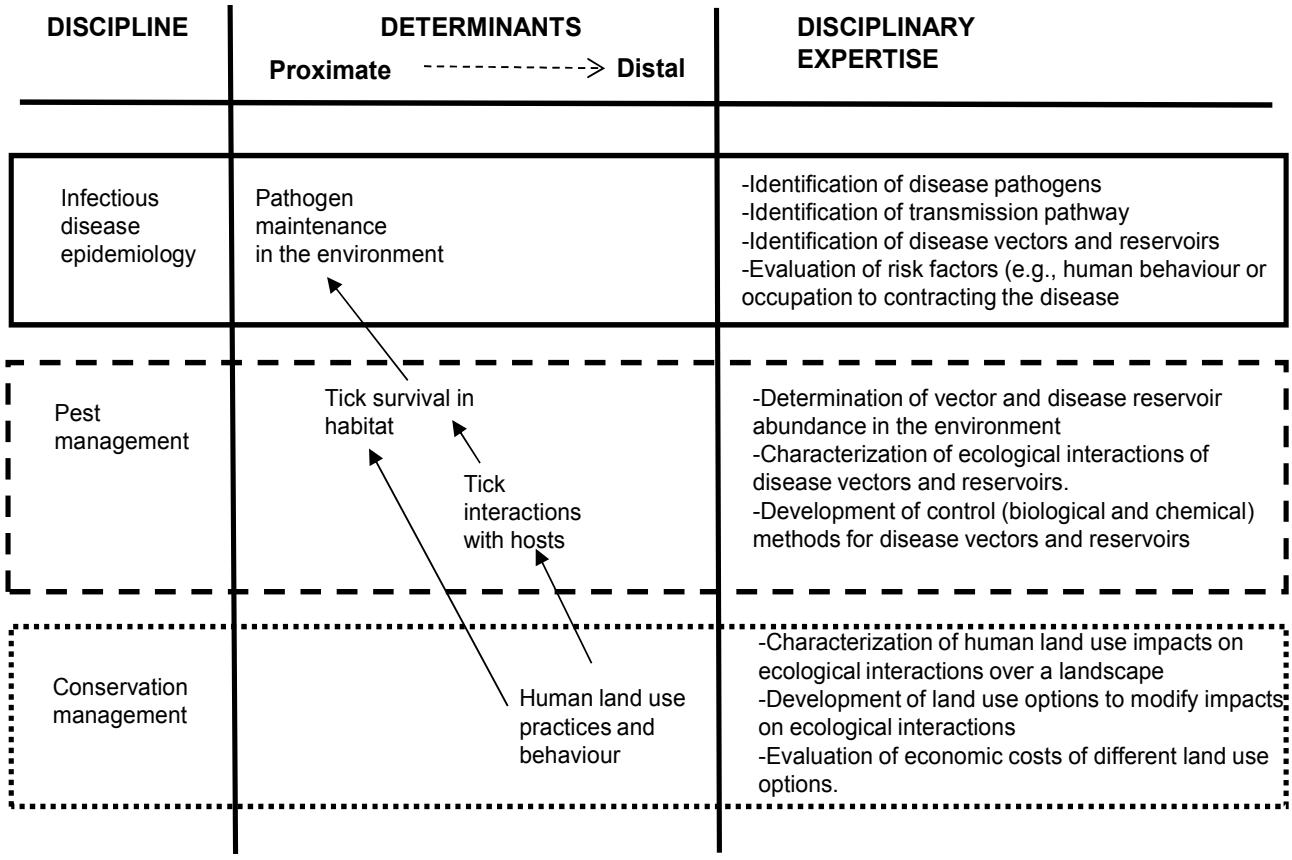
Infectious disease epidemiology helps determine the distribution and the causal agents of diseases that affect human populations. The discipline studies proximate determinants of infectious diseases, and is a necessary first step in understanding the fundamental biology of diseases. When these diseases affect human populations, epidemiologists employ analytical and experimental methods to do the following: identify the pathogen causing the disease; determine the prevalence of the pathogen in the environment; characterize the transmission pathway to human populations at risk; and, in the case of infectious zoonoses, identify the disease reservoirs and the possible disease vectors. With this knowledge, epidemiologists are then able to identify populations at risk to certain diseases, and provide recommendations on how to prevent their outbreak or limit their spread.

Using epidemiological studies, epidemiologists identify the conditions and factors that lead to diseases, following which the disease pathogen may be isolated using microbiological tools, such as microscopy, culturing of bacteria, and molecular tools (e.g., enzyme immunoassay; fluorescent antibody techniques). For instance, Lyme disease was first identified in 1975 by Steere, in Old Lyme, Connecticut, after an unusual cluster of children with juvenile rheumatoid arthritis was reported; the disease pathogen, *Borrelia burgdorferi*, was later isolated in 1982 by Burdorfer from ticks that had been collected from the area (24). Other works have identified emerging tick-borne zoonoses, such as Colorado tick fever in 1940 and Human granulocytic ehrlichiosis in 1994 (172).

After the isolation and characterization of the disease pathogen, effort is then invested into identifying the transmission pathway of the pathogen and the disease reservoirs. The

Figure 2.2: The disciplinary expertises of infectious disease epidemiology, pest management, conservation management with respect to the determinants of tick-borne zoonoses

This diagram describes the proximate and distal determinants of tick-borne zoonoses. Note how the combined expertises can address tick-borne zoonoses as a whole.



transmission pathways are often more complex and require careful study, as other species are involved, such as the disease reservoir and vector (83, 91); although many researchers are actively trying to identify tick disease reservoirs, the factors that determine a suitable disease host for tick-borne zoonoses are still poorly understood (76).

With the identification of the pathogen, the transmission pathway, and the disease reservoirs, epidemiologists can determine which human populations are more at risk to infectious diseases. Determining the risk of infection for different populations is done by estimating the likelihood of being exposed to an environment with a high prevalence of diseases (46). The exposure of different populations is dependent on not only biotic or abiotic factors (e.g., prevalence of the disease in the environment or seasonality), but also on human behaviour (e.g., occupations or adoption of protective measures) (130, 142). Hence, obtaining information on exposure is challenging, and can render calculation of infection risk coarse (e.g., 89, 181). For instance, estimating the infection risk of tick-borne diseases requires knowledge of not only the distribution of ticks in the environment, but also the prevalence of diseases within them—both of which can be difficult to obtain. Significantly too, calculations of infection risk often do not take into account distal determinants of diseases, such as ecological interactions or human modification of the landscape.

Despite these challenges and the uncertainty associated to estimating infection risk, the estimations are essential to policy makers to determine when and what kind of intervention measures should be employed. Depending on the level of infection risk, policy makers may suggest measures to address the diseases, such as funding vaccine development or simply suggesting people adopt personal protective practices and avoiding high-risk areas (33, 175). For instance, the infection risk of tick-borne zoonoses is not considered to be very high except in certain endemic areas, so people are generally recommended to avoid tick-infested areas, and to adopt personal protective practices when they must be in those areas (35, 66).

In addition, the estimation of infection risk is necessary for medical practitioners to accurately diagnose diseases in humans. Without an accurate understanding of infection risk, medical practitioners may not know to be vigilant for certain diseases, and end up not diagnosing them when they appear (113). This can be a problem with emerging diseases, such as tick-borne zoonoses, whose distributions are not well known. In locations that have not yet been identified as being endemic for tick-borne zoonoses, medical practitioners may fail to diagnose infected patients, thus causing a self-fulfilling prophecy that the area will not have cases of tick-borne

zoonoses (120). Hence, the information that infectious disease epidemiology provides is important not only to policy-makers, but to medical practitioners as well.

Infectious disease epidemiology has thus developed methods that can be used to address proximate determinants of tick-borne zoonoses. These methods not only provide knowledge in identifying the disease itself, the transmission pathway, the disease reservoirs, but they also help identify populations at risk and provide information that is necessary for decision making. Yet, these methods do not address more distal determinants of disease emergence, such as the ecological interactions that affect tick and host populations, as well as the human practices that affect ecosystems and ultimately tick and host populations.

2.4.2 Pest management

Pest management helps suppress and control pest species; "pests" are generally defined as species that decrease the economic value of agricultural crops and livestock, and is thus a label that is motivated by human, economic interests. The discipline has developed methods that directly suppress pests using pesticides, or indirectly by managing ecological interactions (e.g., biological control methods). These methods can be used to address proximate and distal determinants of emerging infectious diseases, particularly those transmitted by arthropod vectors.

While pesticides are often employed against pests, and adopted worldwide, they have negative impacts on the environment and humans. Over 3 million people are poisoned by pesticides each year, causing 20,000 deaths—three quarters of which occur in developing countries due to the absence of protective equipment for workers (106). As well, with increased usage, the effectiveness of pesticides have been shown to decrease with the appearance of pesticide-resistant species (e.g., 61).

As such, the limitations of pesticides lead to the development of chemical-free pest control methods, where there was a shift from a strategy aiming to eradicate pests, to one aiming to manage pests instead (111). To this end, integrated pest management (IPM) was introduced in the 1970s. IPM employs methods that integrate biological approaches that account for, and take advantage of ecological interactions (e.g., host-plant resistance, natural pest predators) (81). The main approach of IPM is to manage pests by using methods that influence the ecological interactions that are present in the agroecosystem, that is, the ecosystem formed by agricultural

area. This can involve using biological control methods or habitat management (3, 23). Pesticides can also be employed, but IPM aims to limit their use as much as possible, and ultimately to not rely on them at all (74, 77).

Biological control methods involve introducing another species that can control pest populations through predation or competition (103, 177). For instance, a common method is the introduction of predators, which is often employed with invasive species (e.g., the use of parasitoid wasps to control populations spruce budworm, or the use of gall flies to control knapweed; 124). However, these methods are not perfect as ecological interactions may not occur as predicted, such as predators that do not target the correct pest species, or habitat modification that subsidize pest populations (115).

IPM has been used to manage tick populations. The tick *Boophilius microplus* can cause cattle to contract babesiosis, which significantly decreases the cattle's vigor and can slow weight gain (15, 116, 185). A combination of using vaccines and tick-resistant cattle successfully reduced populations of ticks, and also limited the use of tick-specific pesticides (i.e., acaricides) (61, 135). Other tick-management approaches have targeted tick hosts, such as reducing deer populations with deer exclosures or vaccinating rodents, but these methods have not proven to be reliable (63). Biological tick control methods using parasitoids or nematodes have been proposed, but they have not yet been tested (152-154).

Pest management has thus developed a number of methods that may be applied to directly control tick populations by chemical methods, or indirectly by modifying ecological interactions. Pest management can thus address both proximate and distal determinants of tick-borne zoonoses. However, these methods are focused on species that are relevant to human populations, and could be missing important species that play a role in the transmission of tick-borne zoonoses. As well, pest management methods are largely focused on limited spatial scales, and do not consider the distal effects of landscape changes, which can be accounted for with conservation management methods.

2.4.3 Conservation management

Conservation management helps protect endangered species and maintain species diversity in response to human modification of landscapes that contain wildlife habitat. Conservation management has developed methods to determine the influence of landscape

changes on species and to predict species distributions across landscapes. These methods can be used to address both the distal determinants of the emergence of tick-borne zoonoses that affect the ecological interactions influencing tick populations, and the proximate determinants that affect the habitat suitability for ticks and their hosts.

Habitat loss is an inevitable consequence of human modification of landscapes for human use (e.g., housing developments, vineyards). The impact of landscape change on species will depend on not only the biological requirements of the species (e.g., habitat range size, resource availability), but also the ecological changes that result from modified species interactions within the ecosystem (e.g., presence or absence of predators and competitors). For instance, smaller bird species can be very sensitive to landscape changes as they require specialized habitat areas to obtain resources and to find shelter from predators; this may contrast with larger or migratory bird species, which may more readily adapt to landscape changes, as they would be able to find other suitable resources and habitat (8, 160). On the other hand, the same landscape changes could benefit certain species (e.g., rodents, deer) that are adapted to the new types of habitats that are created by human modification, and that also benefit from the disappearance of certain species that prey on or compete with them (e.g., 2, 90, 188).

Thus, human land use practices will modify landscapes, but their effect on species and ecological interactions will not be the same. Certain land use practices will affect species more than others, as some involve drastic modifications (e.g., urban areas) while others have much lower impacts and can support diverse species populations (e.g., agricultural areas). For instance, agricultural areas tend to reduce large mammal species diversity (i.e., by excluding them with fences), while playing an important role in subsidizing diverse small mammal species, such as rodent populations, with human food sources (3, 102, 144).

To predict the effects of these land use practices, conservation managers have developed predictive species distribution models that can be used to identify habitat areas for endangered species and areas with high levels of species diversity (51, 71, 137). Predictive species distributions modeling, or ecological niche modeling, use wildlife-habitat relationships derived from field survey data to determine suitable habitats, or niches, for a given species and, based on this, to predict species distributions on a given landscape (12, 51, 52, 108, 158). These models provide an important basis upon which conservation managers try to design conservation strategies. In fact, these models have been used to identify habitats for tick populations (54, 96).

Significantly, given its success in addressing conservation concerns, this approach has been employed for other purposes, such as predicting distributions of pest species (e.g., agricultural pests and invasive species; 138, 139), and also distributions of infectious diseases (e.g., 97, 140, 141). Using these models, conservation managers can also design land use plans or reserves to account for wildlife diseases (1). These diseases can be a major concern, as they could put certain wildlife populations at risk of becoming extinct (134). Thus, it would be possible to adapt these conservation decision-making methods to determine optimal land use management strategies to reduce the spread of tick populations and the infection risk of tick-borne diseases.

Conservation management thus has management options that can be used to address distal determinants of the emergence of tick-borne zoonoses. These conservation management approaches could be integrated with pest management and infectious disease epidemiology methods to gain a better understanding of the emergence of tick-borne zoonoses.

2.4.3 Integrated assessment approach

Integrated assessment is a structured approach that tackles complex problems requiring the expertise of different scientific disciplines (6, 40, 47, 151). Integrated assessments explicitly take into account not only environmental concerns, but economic and social ones, in order to provide decision-makers with a comprehensive understanding of the problem (6, 40). Integrated assessments can be a complex process, but the approach can be simplified into two main components: first, describing the problem within its social-ecological context; and second, modeling the problem and developing management options.

Describing the social-ecological context of a problem is an initial step to developing strategies or polices to address it. This can be challenging, as the problem is often novel, and its effects are unclear. However, based on available research from relevant disciplines, a working understanding of the extent and severity of the problem can be established. Importantly, this does not preclude future research from being included; indeed, describing the problem will make clear knowledge gaps and future avenues of research. This is because the determinants of the problem likely result from multiple factors that intersect seemingly independent spheres of influence, such as social factors (e.g., economic development), abiotic environmental factors (e.g., climate change), or ecological ones (e.g., species diversity changes) (72).

Having described the problem within its social-ecological context, solutions can be developed to address it. This can be undertaken using a process which involves the following two components: a modeling process; and, the development of management options. Again, with knowledge obtained from experts from various fields, a model of the social-ecological context from which the problem originates can be constructed by the researchers. This modeling process would help understand how the problem is influenced within its context; in particular, this modeling is necessary to understand the dynamics of the problem, and how it may be influenced by different management options or by different scenarios. With an understanding of the problem from the modeling process, management options can be developed. Given complex problems with varied and interdependent determinants, researchers from numerous disciplines will play an important role in describing the social-ecological context and in helping identify different management options, and highlighting the costs and benefits of the options.

An integrated assessment approach could then be effective in addressing tick-borne zoonoses, as they have numerous proximate and distal determinants that influence their emergence and result from environmental and social sources. This will require the expertise of infectious disease epidemiologists, pest managers, conservation managers, and other experts as other determinants of disease emergence are identified. The following section describes how an integrated assessment approach may be applied to tick-borne zoonoses in the South-Okanagan Similkameen.

2.5 INTEGRATED ASSESSMENT OF TICK-BORNE ZOONOSES IN THE SOUTH OKANAGAN

The South Okanagan (SO) is a rapidly changing rural area where tick-borne zoonoses have been increasingly becoming a public health concern (26, 27). We outline an integrated assessment approach for tick-borne zoonoses (Figure 2.3). We first describe the problem of tick-borne zoonoses, and outline its social-ecological context, as well as the knowledge gaps and avenues for future research. We then describe a possible process of modeling the problem within its social-ecological context, and the development of management options that integrate the disciplinary expertises of infectious disease epidemiololgy, pest management and conservation management.

2.5.1 Description of tick-borne zoonoses within its social-ecological context

2.5.1.2 Social-ecological context of the SO

The SO encompasses environmentally diverse habitats, from desert-like alpine areas to low elevation river valleys. This region has one of the highest species diversity in Canada—many of which are species at risk; 30% of the provincial red listed vertebrate species and over 300 rare invertebrates are located in the area (93). As well, the area is a mountainous region with many valleys, lakes, and habitats that are unique to Canada. As a result, the habitat distribution of the region is highly heterogeneous. For the purposes of this thesis, we examined SO habitats that are on the valley bottom, where human activity and potential exposure to ticks is highest. In particular, we examined habitats that contained shrubs and grasses (i.e., Bunchgrass habitat), that contained large sagebrush (*Artemisia tridentata*) and antelope brush (*Purshia tridentate*).

Unfortunately, many of the endangered species prefer the dry grassland habitats of the Okanagan valleys, which are also the ideal locations for human land use, such as agriculture, ranching, housing, and tourism. As such, most of the untouched habitats are fragmented and increasingly encroached upon by human developments. In 1990, less than 9% of the pristine grasslands in the valley were undisturbed by human activity (25). Indeed, the population has been growing very rapidly in the region, and is projected to grow from 70,000 in 1996 to

110,000 in 2013 (53). This will inevitably require further landscape modification to accommodate the new residents.

The current population and development trends have raised concerns about the sustainability of different land use practices. Partly as a result of these concerns and also of increasing awareness of potentially negative impacts of unregulated development, the Regional District of the Okanagan-Similkameen (RDOS) has begun to develop strategies to sustainably maintain economic growth, while limiting its potential environmental impact (53). As well, environmental non-governmental organizations (e.g., Western Canada Wilderness Committee) and local, concerned citizen-groups (e.g., South Okanagan Similkameen Conservation Program) have been applying pressure on decision-makers to adopt more sustainable practices that would preserve existing habitat and increase protected areas

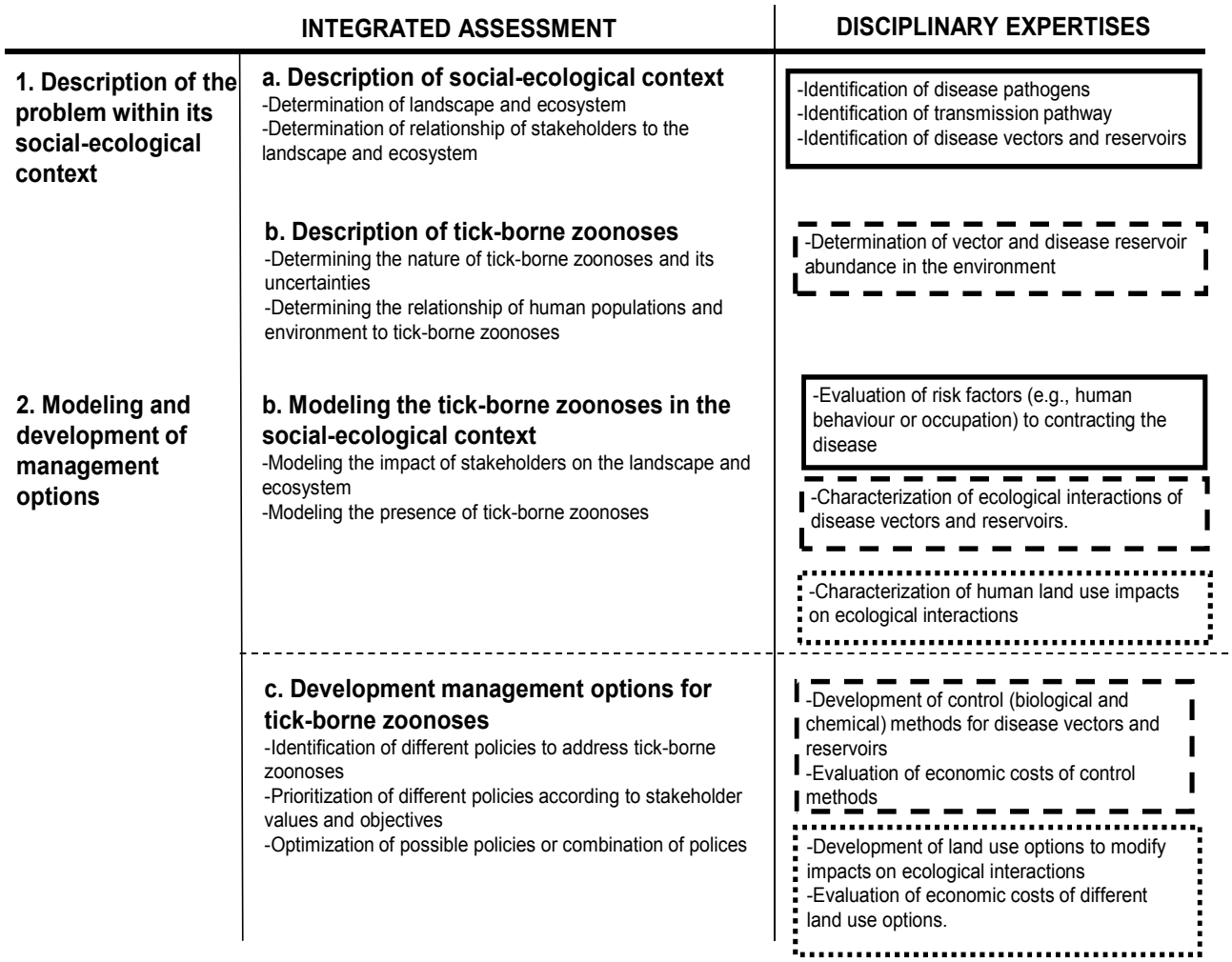
2.5.1.2 Tick-borne zoonoses in the SO

While the impacts of the landscape modifications in the SO on ecosystems and species diversity are being actively investigated (e.g., 82, 183), the human health impacts of these modifications are unknown. This is the case with tick-borne zoonoses, which have been a growing public concern, as well as a source of controversy (73). Currently available research about tick-borne zoonoses suggests that they are rare in the region (120), while advocacy groups believe that they are more prevalent, and that human cases are under-diagnosed (26). Ticks are certainly known to be in the area (68, 161), but there is much that is unclear about where the different species are distributed and in what abundance, let alone the prevalence of the zoonoses within them.

Tick-borne zoonoses are a growing concern in Canada, of which the most well-known is Lyme disease. There are about 70 cases of Lyme disease identified in Canada each year that originate in Canada (i.e., the patient did not contract it when abroad), most of which occurred in the eastern Canada, and especially Ontario. Between 1996-2006, 39 cases have originated in British Columbia—mainly on the Sunshine coast and Vancouver Island, but there have been a limited number (<5) of cases in the SO, such as in Oliver and Kelowna (9). The difference in disease incidence between the east and west of Canada, which is also found in the U.S., is likely due to the differences in pathogen transmission competency of the ticks in the area, where *Ixodes pacificus* in the west is considered a less efficient transmitter than *I. scapularis* in the east.

Figure 2.3: Integrated assessment for tick-borne zoonoses

This diagram describes an integrated assessment for tick-borne zoonose, with disciplinary expertises indicated at each step: infectious disease epidemiology with solid boxes, pest management with dashed boxes, and conservation management with dotted boxes.



Although the number of identified cases in Canada appears low (i.e., because an average of 20,000 new cases are reported a year in the U.S.), the population density in Canada and U.S. differ, where the density in the U.S. is ten times higher. When population density is factored in, the incidence rates in both countries are similar: a crude incidence rate of 0.3 cases per 100,000 person years in western coastal U.S., compared to a crude incidence rate of 0.1 cases per 100,000 person years in BC (120). Yet, underreporting likely occur in both Canada and U.S., and there may be more cases of Lyme disease than currently known. In addition, despite the heavy focus and public interest in Lyme disease, it is not the only tick-borne zoonoses in the area, and certainly not the most dangerous: Rocky Mountain Spotted Fever and tick-borne relapsing fever are all known to be present in western Canada. Hence, the prevalence of tick-borne zoonoses in the SO needs to be clarified.

Tick densities and distributions are also not well known in the region: due to budgetary cutbacks, the BC Ministry of Forests and Range have not conducted active surveys since 1970 (*pers. comm.* Phillip, Hugh). Instead, the British Columbia Center for Disease Control (BCCDC) has conducted passive and limited active tick surveys, specifically looking for the presence of *Borrelia burgdorferi*. Passive surveys involve asking medical practitioners and veterinarians to collect and send ticks to the BCCDC to be identified and studied for the presence of the disease; these have resulted in 5801 *I. pacificus* samples, from 327 locations, and 1151 *I. angustus* samples from 152 locations across BC between 1993 and 2006. The BCCDC has also performed limited active tick surveys in 2004 at 11 sites across BC—though excluding the SO—, which involves a combination of sampling the area for ticks by dragging a cloth on the ground (i.e., flagging), as well as trapping for deer mice, *Peromyscus maniculatus*, to examine the presence of anti-bodies to pathogens in their blood. Of the ticks collected, approximately 80 have been found to harbour the pathogen, while 66 of the 218 deer mice caught tested positive for antibodies, but no pathogens were isolated from their tissues—suggesting that the transmission of the pathogen was not effective, as is consistent with the understanding of *I. pacificus* (120).

However, though previous surveys have provided an invaluable picture of the distribution of ticks and tick-borne zoonoses, they did not encompass a number of areas due to the limitations of active surveys and the passive surveys. On the one hand, the areas examined by active surveys are often separated from each other by large distances. On the other hand, the ticks sent by veterinarians and private citizens for passive surveys are often sent only in small numbers that can be collected from pets, and thus do not represent an accurate survey of the

areas they were collected from. Thus, the prevalence and abundance of tick-borne zoonoses and ticks in many areas remain unclear in the SO. As well, the distribution of different tick species themselves is also not clear. Knowing the distributions of different tick species is important, as different species transmit different diseases; in western North America, *I. pacificus* is thought to transmit Lyme borreliosis, while *Dermacentor andersoni* is thought to transmit Rocky Mountain spotted fever.

In addition, the disease reservoirs of tick-borne zoonoses in the region have not been conclusively identified. Most research on reservoir competency has been undertaken in the United States, where the vertebrate tick hosts are quite different: in eastern U.S., *B. burgdorferi* is transmitted by a different *Ixodes* species, *I. scapularis*, and is maintained in deer mice, *Peromyscus leucopus*, and other recently identified species (126); in western U.S. (California, Oregon), the same tick species is present as in the SO, *I. pacificus*, but, while some hosts are the same (e.g., deer mice, *Peromyscus maniculatus*), other hosts are quite different (e.g., lizards, wood rats) (49). Though the main tick hosts in the SO are thought to be deer mice and mule deer, there are a number of different hosts available, such as Montane voles, chipmunks, pocket mice, red squirrels, and especially the many cattle from ranching. It is unknown whether these species can be competent disease reservoirs, or maintain tick populations. Thus, both the maintenance of pathogens in the environment and the ecological interactions with the tick hosts remain to be studied in the SO.

Finally, the effects of the land use changes in the SO on the habitats of ticks and their hosts are not understood. The effects of different land use changes may differ depending on the human practices in the area that may increase or decrease the suitability for ticks, such as irrigation practices or the use of pesticides in agricultural areas. Agricultural areas could have higher densities of rodents, but would have much lower densities of large vertebrates due to deer exclosures. In contrast, ranching areas may have much larger amounts of large vertebrates, due to the presence of cattle. In the same vein, the influence of climate change is also not known; climate change is thought to affect tick populations and increase their range (105, 121), but some works disagree with this (146, 150).

There are thus many uncertainties about tick-borne zoonoses in the SO, which need to be clarified by further research. When coupled with the knowledge that the SO is rapidly changing and potentially modifying ecological interactions, it is important to determine whether these changes may be facilitating the spread of ticks and tick-borne zoonoses.

2.5.2 Modeling and development of management options

Clearly, from the description of the social-ecological context of tick-borne zoonoses, there are many unknowns that need to be resolved with further research. However, despite certain gaps in knowledge, and given the importance of the problem, it is still possible to proceed with the modeling and the development of management options—which could later be refined based on the results of future research. The following are possible modeling approaches and management options that may be initially employed as a first step to address tick-borne zoonoses in the SO.

2.5.2.1 Modeling tick-borne zoonoses in the social-ecological context

Understanding the dynamics of tick-borne zoonoses within its social-ecological context is an important component for decision-makers to develop effective policies in the SO. A model could be developed to estimate the infection risk of tick-borne zoonoses across the SO landscape; this involves determining the distribution of ticks and of the different species of ticks, and the prevalence of tick-borne zoonoses among the ticks. Modeling will then provide a better understanding of how human activities can affect the emergence of tick-borne zoonoses and can be used to develop better policies to prevent them.

Using conservation management approaches, predictive species distribution models would be effective in determining the distribution of ticks, based on information regarding their habitat requirements (21, 54, 55, 70). In order to obtain accurate predictions, these models will depend on the passive and active survey data gained by the BCCDC; but, it will also require a comprehensive survey that relates tick-abundances to the different land use practices in the SO. As well, these models will depend on detailed maps of the SO, which would include abiotic information, such as soil type and climate.

Yet, predictive species distribution models generally only examine single species (96). Since ticks are dependent on their small and large vertebrate hosts for both reproduction, development and migration, other species and their interactions will have to be included in the model. Consequently, survey information regarding these tick host species' distributions and preferences for different habitats will have to be included. This information may be obtained by

collaborating with researchers who have collected data on bird species, lagomorphs, and rodents (e.g., 82, 169, 170); provincial researchers have also collected data on deer distributions from hunting reports, while provincial range managers have data on the number of cattle in different areas and at various times of the year.

Using infectious disease epidemiology and pest management approaches, the prevalence of tick-borne zoonoses among the ticks may be determined by examining the presence of diseases from the ticks collected from a comprehensive tick survey in the SO. This information can be complemented by studying the serum of tick hosts, such as deer mice, for the presence of antibodies to diseases (20, 176). Serum studies may also be available from veterinarians who can test for certain tick-borne zoonoses in dogs, such as Lyme disease (44). Indeed, dogs have been suggested as surveillance species, as their traveling habits are more easily determined than humans (43, 44). Using these studies, the prevalence of tick-borne zoonoses may be estimated in ticks. Estimates of disease prevalence from other studies in different regions may also be used (122), but must be considered carefully as the tick species and the hosts examined will be different. Combining the information of tick distributions and the prevalence of diseases in ticks would allow species distributions models to also predict the infection risk of tick-borne zoonoses in the SO.

However, examining distributions of ticks and the prevalence of diseases among them will only measure the infection risk within the environment. Human behaviour will also determine infection risk, where the decision to go in certain areas or adopt personal protective practices will affect the probability of encountering an infected tick. In the same vein, different occupations will have different risks, where occupations that require a great deal of outdoor activity will lead to higher probability of being exposed to ticks and diseases. Hence, studies on behaviour and occupations need to be conducted in order to determine how human behaviour affects infection risk (89, 181).

2.5.2.2 Development of management options for tick-borne zoonoses

A wide range of management options can be implemented to control ticks and prevent tick-borne zoonoses, from issuing warnings, to conducting acaricide sprays. Researchers from various disciplines can determine different policy options that may be effective for proximate

and distal determinants of tick-borne zoonoses. The following is a description of the management options available to address tick-borne zoonoses in the SO.

To address the most proximate determinants, the simplest and most inexpensive policy would be to issue warnings and advise people to adopt protective practices when going into wilderness areas that have high tick populations. This can be effective, since there are many conditions that need to be met for a tick to transmit a pathogen to humans: not only does a tick have to be a suitable vector for the pathogen, it takes almost 24 hrs for a tick to properly attach itself, and then to finally feed and to transmit the pathogen into the bloodstream (164). As well, tick activity tends to be restricted to certain times the year (i.e., typically spring and fall), so that the infection risk is seasonal. Hence, regular tick checks after outdoor activities, and taking precautions, such as covering exposed skin and using pest-repellent, could prevent the contraction of tick-borne zoonoses.

To make the adoption of personal protective practices effective, public awareness needs to be increased regarding the risks of tick-borne zoonoses. This may perhaps be achieved through awareness campaigns, or adding signage in tick-infested areas (e.g., a common practice in many areas in Eastern Europe). In addition, the awareness of medical practitioners needs to be raised regarding these diseases in order to be able to properly diagnose tick-borne zoonoses when they do occur—which has proven to be a controversial issue (26). Yet, increasing public awareness has been the practice in the U.S., and there are still over 20,000 new cases of Lyme borreliosis reported each year, suggesting that other more direct policies should also play a role (120).

The development of vaccines is another option that directly addresses the pathogen. Vaccines for certain diseases have been developed: in Eastern Europe, a vaccine for tick-borne encephalitis is provided to affected populations (69). This, however, can be an expensive solution that may not be economically viable: a Lyme disease vaccine was developed in the U.S., but was removed from the market, when the company did not consider it to be financially viable (107). As well, the effectiveness of vaccines are limited as they would only be able to provide immunity to a single disease, and not be able to protect against the large number of tick-borne zoonoses that can be transmitted. Another promising approach with vaccines has been to develop a vaccine against the tick itself, which would target components in the tick saliva and prevent the tick from properly feeding (60). Vaccinating the tick hosts is also possible (175), but this has not proven to be cost-effective.

Regarding more distal determinants, direct policies could target the tick populations themselves. This may be achieved by the application of acaricides, which would not be popular with many stakeholders who wish to limit negative environmental impacts. Other methods may employ bio-control methods, such as using nematodes, fungi, or releasing tick-predators. These methods are still being researched and have not yet been successfully implemented (152-154, 189); they can be difficult to implement as the release of fungi or nematodes can fail if applied at incorrect times of the day, while tick-predators may not successfully control, or even target, tick populations. Alternatively, modifying potential tick habitat areas can be effective, such as simply eliminating areas where ticks might find refuge, such as wood piles or mulch (58).

Tick populations may also be controlled by targeting their hosts. Deer exclosures were initially thought to be effective (166), but later research demonstrated that tick populations did not significantly decrease (63). Excluding large mammal hosts would be especially difficult in the SO given the presence of livestock (e.g., cattle). As well, controlling small mammal populations would be extremely difficult given their ubiquity, and the presence of small mammals that are endangered, which could make targeted approaches more difficult. However, instead of preventing the hosts from encountering ticks, acaricides may be directly applied to hosts so that the ticks die when encountering them: specially constructed devices which attract deer and harmlessly apply acaricides as they feed have been used with some success, while providing acaricide-soaked cotton bedding for rodents have been used as well (162, 165). Cattle-dipping with acaricides has also been used in Africa (61). These methods have showed some promise, but can be difficult, as they must be sustained over long periods of time.

On the most distal end of determinants, one option may be to implement land use policies that affect tick populations. These policies may be unpopular, as they would restrict certain areas from being used or modify existing practices that increase tick densities. However, specific measures could adapted to these land use practices, and could include any of the previously described methods. For instance, if cattle are found to be suitable hosts for ticks, then to decrease tick populations, acaricides may be used on the cattle; or, they may be put to pasture at times when ticks are not active. As well, if exurban areas are found to have higher infection risk due to the residents' proximity to disease-carrying rodents or ticks, then residents may be advised to remove suitable habitat areas for ticks, and to limit rodent populations through a combination of trapping and limiting access to human food sources.

Hence, a combination of different management options may have to be employed to be effective on all proximate and distal determinants of tick-borne zoonoses. This may in turn require more research and modeling to account for new or modified concerns, as well as the development and optimization of different policies.

2.6 CONCLUSION

The emergence of tick-borne zoonoses is governed by interdependent proximate and distal determinants originating from environmental and social sources. Infectious disease epidemiology, pest management, and conservation management have studied these determinants and developed complementary management options to address them. An integrated assessment approach combining these three disciplines can be used to help prevent the outbreak and spread of tick-borne zoonoses. This approach has been found to be effective for complex problems where there are many stakeholders who have differing and potentially conflicting interests (41, 182). In particular, this approach could be of use in the SO, where tick-borne zoonoses have been an increasing public health concern.

Importantly, the integrated assessment approach described in this review for tick-borne zoonoses can include other disciplines than those reviewed here. Although we have focused on natural sciences disciplines, social sciences methods could play an important role in the integrated assessment approach. Social sciences have developed methods to communicate and interact with stakeholders in an unbiased manner (147). Social sciences researchers could help ensure that the values and goals of all the stakeholders are clearly and fairly accounted for. This would be highly relevant to the SO, where there are numerous different stakeholders from ranchers to First Nation bands, who have different values and preferences on how they should relate to the environment and address tick-borne zoonoses.

As well, our proposed integrated assessment approach can be applied to other vector-borne zoonoses. Although other vector-borne zoonoses are different from tick-borne zoonoses, the general approach of comprehensively addressing the proximate to distal determinants using an interdisciplinary approach would be appropriate. Other considerations will, of course, have to be taken into account, especially the mobility of the other vectors. In contrast to ticks, most other vectors are mobile and transmit their own complement of zoonotic diseases, such as with mosquitoes (e.g., dengue, malaria; 178), birds (e.g., avian flu; 173), or rodents (e.g., Hantavirus; 29). However, given that tick-borne zoonoses are unique in that ticks are relatively immobile, tick-borne zoonoses could be a baseline scenario where vector dispersal is a minor issue. Future research on the dynamics of tick-borne zoonoses could then serve as a foundation on which other vector-borne zoonoses can build on by studying vectors with the capacity to disperse.

In sum, given the complexity of the determinants governing the emergence of zoonoses, an integrated assessment approach integrating infectious disease epidemiology, pest management and conservation management could be effective in addressing tick-borne zoonoses. This approach can potentially be applied to other vector-borne zoonoses, as well as other health challenges influenced by complex environmental and social determinants. Indeed, the remaining chapters of this thesis represent the first steps of an integrated assessment approach for tick-borne zoonoses in the SO, by examining the proximate determinants, such as the prevalence of pathogens in ticks (Chapter 3), or the more distal determinants, such as the ecological interactions of ticks and their hosts (Chapter 4) and their relation to human land use activities (Chapter 5) and risk perception (Chapter 6).

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CHAPTER 3: Prevalence of Tick-Borne Zoonoses and Hantavirus in the South Okanagan, British Columbia: Active surveillance of ticks (*Dermacentor andersoni*) and deer mice (*Peromyscus maniculatus*)[2]

3.1 BACKGROUND

Zoonoses (i.e., diseases transmitted to humans from wild or domestic animals) are human health challenges whose prevalence are potentially increasing (8). Several species of ticks—obligate arthropod ecto-parasites, such as *Ixodes pacificus* and *I. scapularis*—are involved in the transmission of the most frequently contracted zoonoses in North America (37). Lyme disease, perhaps the most well-known tick-borne zoonose and caused by the pathogen *Borrelia burgdorferi s.s.*, is contracted in over 20,000 patients in the United States and 70 patients in Canada every year (12, 26). Ticks can also transmit other pathogens that can cause human infections including human granulocytic anaplasmosis, human babesiosis and Powassan encephalitis virus (14, 37).These diseases can have devastating consequences if not diagnosed and treated in a timely manner (28, 31).

To address tick-borne zoonoses, the prevalence of disease-causing pathogens needs to be determined, particularly in regions where human populations are increasing, such as the South Okanagan in British Columbia (BC). Current understanding of tick-borne zoonoses is that they are rare. For instance, Lyme disease is believed to have an incidence rate of <0.1/100,000 within human populations in BC, based on reports of patient cases (1, 13). This low prevalence is supported by passive tick surveys, that is, health practitioners and private citizens sending ticks for analysis to the British Columbia Center for Disease Control (BCCDC). These surveys have resulted in 5,801 *Ixodes pacificus* samples, from 327 locations, and 1,151 *I. angustus* samples from 152 locations across BC between 1993 and 2006; of the ticks collected, approximately 80 have been found to harbour *B. burgdorferi s.s.*from coastal regions in BC (19). *Dermacentor spp.* ticks were also submitted, but they were not examined as *Ixodes spp.* ticks were the focus of the study, as they are vectors for *B. burgdorferi s.s.*.

While passive surveys provide an idea of the distribution tick-borne zoonoses (i.e., presence or absence), they are indirect methods that provide an incomplete understanding of infection risk. In particular, the tick-borne zoonoses that are tested for are those that are of public

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concern (i.e., *B. burdorferi s.s.*), and not necessarily those that are present in the region. As well, passive surveys do not reveal the prevalence of pathogens within tick populations, and thus the risk of contracting a pathogen with each tick bite. As such, current understanding of the prevalence of tick-borne zoonoses may be under- or over-estimated.

Active surveys can help further clarify the prevalence of tick-borne pathogens, by directly examining ticks and their main disease host for the presence of pathogens. In BC, tick-borne pathogens are maintained in the environment by the interaction between ticks and the main disease host, deer mice (*Peromyscus maniculatus*; *P. leucopus* in the eastern North America) (27). Hence, examining ticks and deer mice provides an understanding of the prevalence of the pathogens in the environment: examining ticks estimates the current prevalence of pathogens, while examining deer mice can confirm the prevalence found in ticks, as well as suggest past exposures to pathogens from antibodies in the serum. As well, different species of ticks transmit different pathogens (e.g., *Dermacentor andersoni* transmit *Rickettsia rickettsii*; *Ixodes pacificus* transmit *B. burdorferi s.s.* and *A. phagocytophilum*), while earlier life-stages of ticks (e.g., the nymphal stage) are thought to be more dangerous, since they are smaller and more difficult to find attached and remove promptly than adult ticks (29). Thus, knowing the prevalence of the pathogens, the species present and the life-stages most frequently encountered, all inform infection risk.

Notably, while active surveys are a necessary component to understanding infection risk, they are also imperfect, as sustained and comprehensive surveys are limited to specific geographic areas—due to funding and time constraints. For instance, the BCCDC conducted limited active tick and deer mice surveys in 2004 at 11 sites to examine the presence of *Borrelia burgdorferi s.s.*: 66 of the 218 deer mice caught tested positive, but no pathogens were isolated from their tissues; while the ticks tested had the same results as the passive surveys. However, these surveys were located in areas very distant from each other, and were not conducted over a sustained period of time (i.e., they were opportunistic)—thus also providing only a limited understanding of prevalence. Further, active surveys can only examine the main disease reservoir, deer mice, and not examine other species in the area, because they tend to be species at risk (e.g., Great basin pocket mice), which could not be collected and analyzed.

Active surveillance for zoonotic pathogens was conducted in the South Okanagan, a rural region in British Columbia, which is undergoing extensive human population and economic growth (3). Ticks and deer mice were collected from April to August in 2007, 2008 and 2009.

Ticks and serum samples from deer mice were analyzed for pathogens (ticks only) or antibodies to pathogens (deer mice serum) that are suspected to be in the region and that are of public concern: *Borrelia burdorferi s.s.*; *Rickettsia rickettsii,* the causative pathogen of Rocky Mountain Spotted Fever; *Analplasma phagocytophilum*; and, *Bartonella henselae*. Our focus was on hard ticks (e.g., *Dermacentor spp., Ixodes spp.*) and not soft ticks (e.g., *Ornithodores spp.*). Deer mice serum samples were also tested for antibodies against Sin Nombre virus (SNV), a species of hantavirus. Deer mice are the known reservoir and vectors for SNV, where human exposure to SNV can lead to respiratory failure and death (15, 16).

3.2 METHODS

3.2.1 Collection of ticks

Ticks were collected from April 1-30, 2008 and April 1-June 30, 2009; this sampling period was chosen as it is the time when human populations increase their recreational and occupational activities in wildlife areas, and is thus the period when human exposure to ticks is high. Tick collections were undertaken in sites with suitable tick habitat (i.e., areas with shrubs and grasses and evidence of animal activity). A total of 11 sites were selected in the study region (Figure 3.1), and were visited on a weekly basis for a period of one hour. All sites were located within the South Okanagan (lat. 49 28.41 N, long. 119 35.43 W), in an area that spanned from Kaleden in the north to Osoyoos in the south (~500km^2).

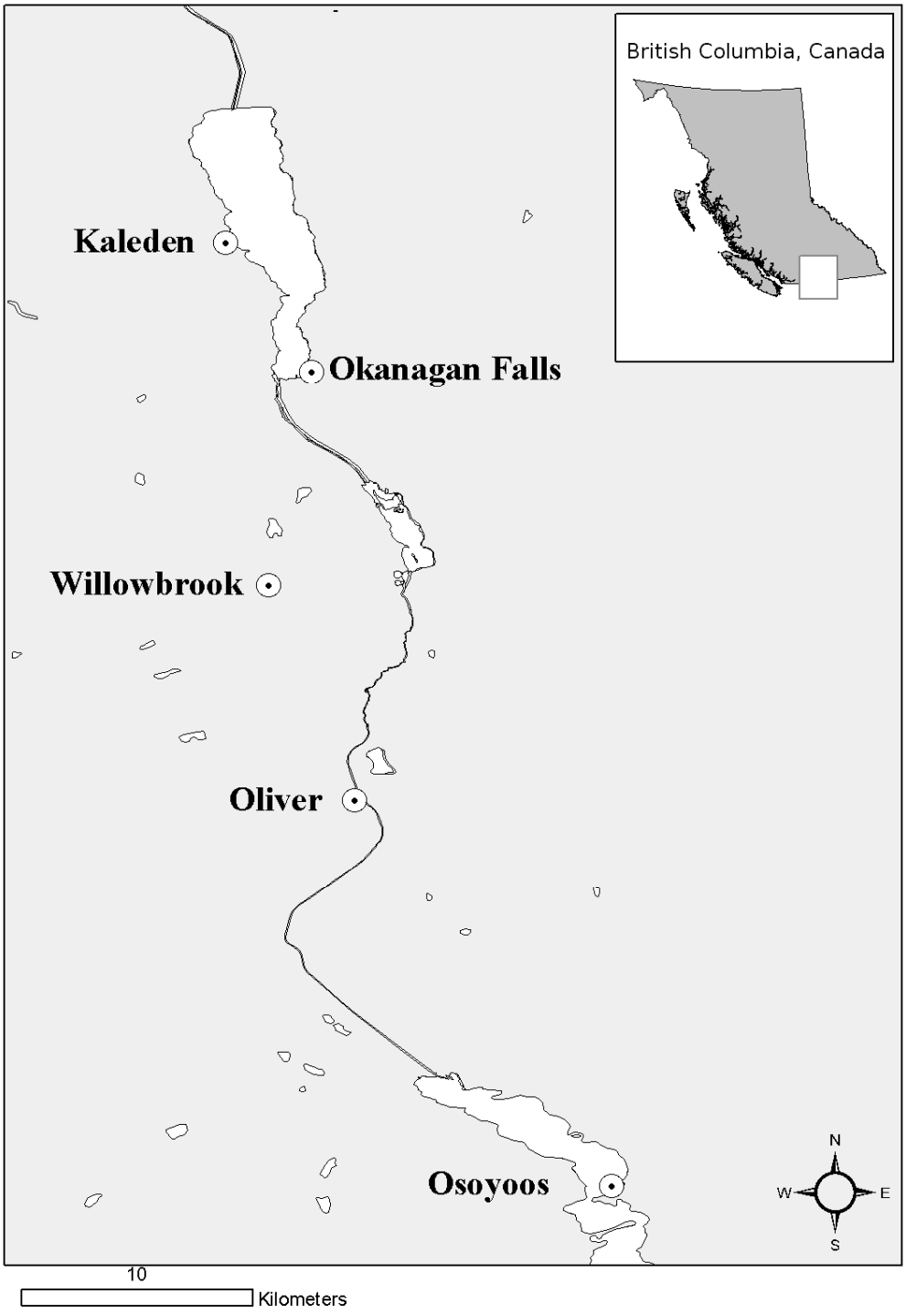
Ticks were collected using the "flagging" method (7), which involves dragging a 1m^2 flannel cloth on the ground and through or over the vegetation (e.g., grasses, shrubs). At five minute intervals, the flannel cloth was examined, and ticks found attached were collected in a sealable bag for subsequent identification to species and life-stage (10). The sites were visited between the hours of 6-10am, when tick host-seeking activity was greatest.

3.2.2 Collection of small mammals

Deer mice were trapped from May 1-30 and August 1-31, 2007 and April 1-30, 2008. Mouse-collection sites were suitable habitat for both deer mice and ticks (i.e., areas with mixed vegetational structure (35)), to ensure that deer mice may have encountered ticks and tick-borne pathogens. A total of 10 sites were selected in the study region, and were visited every two weeks. At each site, 36 Longworth live traps were placed at 16m intervals in a 1 ha 6x6 sampling grid (20). All animal handling and treatment was done in accordance with the University of British Columbia Animal Care Protocol (approval #: A08-0711).

The sex and weight of all captured deer mice was determined and these animals were also examined for ticks. Other types of rodents (e.g., chipmunks, *Tamias townsendii*) were examined for ticks and released without further processing as per animal care guidelines. Deer mice were euthanized by inhalation of isoflurane and blood samples (0.5 to 0.8 ml) were

Figure 3.1: Study area location within the South Okanagan.



collected via cardiac puncture. Sera was separated from cells by centrifugation and serum samples were temporarily stored -20ºC prior to further analysis.

3.2.3 Testing for pathogens in host-seeking ticks

For each pathogen (*B. burgdorferi s.s.*, *A. phagocytophilum, B. henselae*, and *R. rickettsii*), 11 subsamples of 10 adult *D. andersoni* ticks (110 ticks in total), representing ticks from each of the different sampling sites were tested. Although *D. andersoni* is not believed to be a competent vector for *B. burgdorferi s.s.* and *A. phagocytophilum,* the ticks were examined for the presence of those pathogens, as the diseases they cause—particularly Lyme disease—are of public concern in the SO. Testing of *B. burgdorferi s.s.* was conducted at the BCCDC on one series of 110 ticks, while all other testing was conducted on a separate series of 110 ticks at the National Microbiology Laboratory (NML) in Winnipeg. The midguts of the 10 ticks in each subsample were collected in an eppendorf tube and pooled as one sample; at the NML, the subsamples were further separated into pools of 5 ticks. DNA was extracted from the 11 subsamples of ticks using Qiagen commercial extraction kits as described in Cockwill et al. 2009 (5).

At the BCCDC, tick samples were screened for *Borrelia burgordferi s.s.* DNA as previously described (21). Briefly, PCR targeted amplicons of borrelial DNA, and amplified a portion of the variable spacer region between two conserved structures, the 3' end of the 5S rRNA (*rrf*) and the 5' end of the 23S rRNA. The PCR was performed using a GE illustra PuReTaq Ready-To-Go PCR Beads on Stratagene Robocycler. Amplification was carried out using negative and positive controls for all PCR reactions. The negative control was sterile water, and the positive control used purified *B.burgdorferi s.s.* strain B31. Amplification products were analyzed by electrophoresis in 2.0 % agarose gels followed by staining with ethidium bromide and ultraviolet light illumination on Biorad Geldoc system.

At the NML, tick samples were screened for *A. phagocytophilum, B. henselae* and *R. rickettsii* using PCR. The primers and probes for *A. phagocytophilum* were directed towards the *msp2* gene (6), while the primers for *B. henselae* were against *321s* and *H495as* segments (18) using the following real time probe (5' FAM-CCA CCG TGG GCT TTG AAA AAC GCT-DBHQ10). After DNA extracts were screened for *A. phagocytophilum* and *B. henselae*, they were screened for the presence of spotted fever rickettsial species as previously described (34).

All reactions were performed using Taqman Fast Universal PCR Master Mix (Applied Biosystems). Each reaction contained a final concentration of 0.3 μM of each primer and a final concentration of 0.1 μM of the probe. Five μl of tick DNA was used in each reaction. For determination of the rickettsial species in positive ticks, DNA was PCR amplified with Rr190.70 and Rr190.701 primers for the primary step and Rr190.70 and Rr109.602 for the seminested step as described previously (30). All reactions were performed using the HotStar Taq Master Mix kit (Qiagen) following the manufacturer's instructions. Five μl of tick DNA was used for the primary PCR reactions, and two μl of the primary PCR product was used for seminested PCR. All amplicons were purified using the QIAquick PCR Purification kit (Qiagen) and sequenced by the Genomics Core Facility at the NML in Winnipeg. The sequences were analyzed using DNASTAR Lasergene 7 software. Homologous sequences were detected using the National Center for Biotechnology Information (NCBI) search engine.

3.2.4 Serological assays on deer mouse sera

Serological assays were performed to detect antibodies against *B. burgdorferi s.s.*, *A. phagocytophilum, R. rickettsii*, and SNV in deer mouse serum samples. All serological assays were conducted at the NML.

The methods used to detect *B. burgdorferi s.s.* antibodies in rodent serum samples have been described previously (25). Briefly, a two-tiered approach was employed such that serum samples were initially screened using a enzyme-linked immunosorbent assay (ELISA) and reactive or positive samples were confirmed using a western blot assay (MarDx).

Serum samples were screened for antibodies against *A. phagocytophilum* using an indirect immunofluorescence assay (IFA) similar to that described by Nieto and Foley 2008 (24). However, in our assays, samples were diluted to 1:64 in FTA (Hemagglutination) buffer, slides were obtained from a commercial source (Fuller Laboratories, CA) and conjugate was diluted in Evan's Blue rather than iriochrome black to reduce background fluorescence. Samples that were positive in the IFA were confirmed using an IgG western blot assay similar to that described by Walder et al. 2006 (36); however, goat anti-*Peromyscus* conjugate was substituted for anti-human conjugate.

Serum samples were also screened for antibodies to *R. rickettsii* using an IFA. The diagnostic protocol was similar to the National Centre for Infectious Diseases CDC publication

(22) though modified for use with rodent sera. Briefly, serum samples were applied to slides pre-coated with *R. rickettsii* (provided by CDC Viral and Rickettsial Zoonoses Branch) at a screening dilution of 1:64 and performed as per the *A. phagocytophilum* IFA above. Reactive samples were further titrated and samples with titres of ≥1:64 were considered positive for this study.

Lastly, serum samples were tested for evidence of infection with SNV using the same protocol as previously described (15). The only modification to this protocol was that Black Creek Canal virus was used in the ELISA rather than recombinant antigen during the initial screening.

3.3 RESULTS

3.3.1 Tick and small mammal collection

A total of 5,557 ticks were collected. Although other species are known to be present in the area (e.g., *Ixodes angustus*, *Ixodes pacificus*) (32), *D. andersoni* was the only species collected and >99% of these were adult males and females. Only 37 *D. andersoni* nymphs and 0 larvae were collected, of which 17 nymphs were collected from the small mammals. A total of 276 deer mice were captured, and serum samples were collected from 219 animals. The deer mice collected were mainly adults (262/276; 95%), and the rest were juveniles.

3.3.2 Pathogens detected in ticks

DNA of *B. burgdorferi s.s*, *A. phagocytophilum*, *B. henselae*, and *R. rickettsii* was not detected in any of the tick pools tested by PCR. However, *R. peacockii* was present in the ticks (i.e., all pooled tick subsamples were positive), and *R. rhipicephali* was present in 4 tick pools. Only the 2008 ticks were tested, as the testing did not reveal the presence of pathogens, and did not warrant the testing of the 2009 ticks.

3.3.3 Antibodies in deer mouse sera

From the deer mouse sera tested, the results confirmed those found with the ticks: 0% (0/219) positives for *Borellia burgdorferi s.s.*, 0.46% (1/219) positives for *A. phagocytophilum,* and 12.3% (27/219) positives of *R. rickettsii*.. The single positive for *A. phagocytophilum* suggests that the pathogen is present; but, given the absence of *Ixodes spp.* collected, it is at a low prevalence in the environment. Similarly, the positives for *R. rickettsii* confirm the low prevalence found among the ticks. However, because *R. rhipicephali* was present in the ticks at our study sites, but not *R. rickettsii*, the seropositivity may be due to cross-reactions in the IFA(9). Finally, 4.1% of the deer mice had evidence of infection with SNV.

3.4 CONCLUSIONS

The prevalence of tick-borne zoonoses and hantavirus was low in the South Okanagan. From the ticks tested, there was 0% *Borrelia burgdorferi s.s.*, 0% *A. phagocytophilum*, and 0% *Bartonella henselae*, and 0% *R. rickettsii*. As an endosymbiont of *Dermacentor andersoni*, it was not surprising that *R. peacockii*, a non-pathogenic Rickettsial agent, was present in all ticks tested. *R. rhipicephali* was found in 3.6% of ticks tested and is of unknown pathogenicity. These results were confirmed with the deer mouse sera tested: 0% *B. burgdorferi s.s.*, 0.4% *A. phagocytophilum*, and 12.3% possible positives for *R. rickettsii*. The positive *R. rickettsii* in the deer mouse sera are questionable, given that they were found at low titres (≥1:64) and may be cross-reactions with *R. rhipicephali* or other Rickettsial agents. In addition, only *D. andersoni* ticks were collected, suggesting that pathogens transmitted by those ticks (i.e., *R. rickettsii*) are likely more present in the region and of more concern, rather than those transmitted by *Ixodes spp.* (i.e., *B. burgdorferi s.s.*). Finally, 3.1% of the samples were positive for Hantavirus, representing a low infection risk.

The tick results are in accordance with reports of patient cases and passive surveys in the region (1, 9). However, our results differ from the BCCDC surveys of deer mice, where 66 of the 218 deer mice caught tested positive for *B. burgdorferi s.s.*. This difference is due to the fact that the deer mice collected by the BCCDC were collected in regions of BC that had populations *Ixodes spp.* present, rather than *Dermacentor spp.*. The absence of *B. burdorferi s.s.* in our results, in either the ticks or the deer mice, is in accordance with the rarity of *Ixodes spp.* in the region, and that *D. andersoni* is not a competent vector for the pathogen, but is competent for Rickettsial agents, such as *R. peacockii* (9).

However, we only examined deer mice, as we did not have permits to collect other species (e.g., shrews, chipmunks), since some were considered species at risk. As such, other tick-borne pathogens that could be harboured by other hosts may have been overlooked; but, as other species are imperfect disease reservoirs (2), the prevalence of tick-borne pathogens among them would be similarly low as in deer mice or lower. In addition, the presence of the endosymbiont *R. peacockii* within the *D. andersoni* ticks could prevent other pathogens from being established in the tick population through microbial competition within ticks—which may explain the absence of the pathogenic *R. rickettsii* among the ticks examined (9). Thus, the low prevalence of tick-borne pathogens determined by the analysis of ticks and deer mice in this

study would not be greatly changed by studying other mammals. Notably, as *Ixodes spp.* were not collected, we could not conclusively determine the presence or absence of *B. burgdorferi* and *A. phagocytophilum* in the SO; though, the results of the deer mouse serum do suggest that their presence would still be low.

Our collecting only *D. andersoni* and mainly adult ticks may be due to the sampling period (April-June) and times (6-10am), which were chosen to gain a representative understanding of the ticks that humans would most likely be exposed to. Other species of ticks (e.g., *Ixodes spp.*; soft ticks that are nocturnal) and life stages of ticks (*D. andersoni* nymphs) are known to be present in the region (11, 32), but do not appear to have a high probability of being encountered by human populations during the period and times we sampled. Those ticks are likely more active in cooler months (e.g., January-March), at earlier hours in the day (e.g., 4-6am); this is in part because the SO is an arid and hot region, where the temperatures can be in excess of 30^{o}C from May-August and precipitation is rare. In these conditions, only the hardiest ticks will be active: *Ixodes spp.* are more sensitive to heat than *D. andersoni*, contributing to the former's rarity (23, 33); similarly, being smaller, nymphs are more sensitive to heat and desiccation than adults (23). Indeed, recent predictive modeling of *I. pacificus* and *I. angustus* distributions in BC suggest they are mainly located along the coast of B.C (19).

As well, our collecting *D. andersoni* may be due to our only examining habitats that contained vegetation such as shrubs and grasses. These habitat areas are known to be suitable for ticks, but *Ixodes spp.* and nymphs may prefer to quest for hosts on leaf litter rather than vegetation, thus again making them unavailable for collection in this study. The SO is not a region with homogeneous habitats, but rather contains a wide-range of habitats (e.g., Douglas Fir, English Spruce habitats) that may harbour populations of *Ixodes spp.*. Given the size of the SO region, our study was necessarily limited to habitats with shrubs and grasses. Future research should thus examine other habitat regions, particularly cooler habitats which could contain other species of ticks.

Finally, our results may have been affected by fluctuations in the density of ticks and deer mice; that is, it may have been an unusually high or low year for their populations due to other factors such as resource availability and climate. Though these factors are inevitably impossible to control, the results from both the ticks and deer mice represent a longer range of time than they were examined, due to their life span, and could account for potential variations in the population: the adult ticks examined would have been exposed to two years of potential

pathogens; while, adult deer mice would have been exposed to two to three years of pathogens. Hence, our results are robust in the sense that they do not constitute an isolated "snap-shot" of the pathogens in the region. As well, we examined deer mice from 2007-2008 and ticks from 2008-2009, so that there was potential overlap between the populations, where deer mice from 2007 may have been exposed to larval ticks in 2007 that would have become adults in 2008. Thus, the consistency between the deer mouse and tick results strengthens our finding a low prevalence of pathogens.

Given the low prevalence of tick-borne zoonoses and hantavirus in the South Okanagan, strategies aimed at the pathogens or the ticks and deer mice (e.g., vaccine development or tick pesticides) may not be warranted. However, as suggested by local media coverage (4, 17), public concern regarding ticks and tick-borne zoonoses may still be present. Thus, though not a medical issue, tick-borne zoonoses remain a social issue that may be addressed through risk communication, which would aid the public in managing their risk of infection to tick-borne zoonoses. This can be achieved by raising public awareness and promoting personal protective practices (e.g., performing self-checks for ticks; tucking pants into socks; application of repellent) (13, 38). Another possibility may be to erect signs with information on protective practices in front of access points of locations with high numbers of ticks. In fact, sites where large amounts of ticks were collected were easily accessible and frequently used for recreational and occupational purposes (e.g., parks), and were thus areas where the risk of tick-human encounters remains high. As such, Chapters 4 and 5 repsectively examine the tick-host and the tick-land use relationships to determine whether the risk of encountering ticks may be increasing.

In conclusion, the prevalence of tick-borne zoonoses and hantavirus was found to be low in the South Okanagan, but merits vigilance and increased public messaging. Medical practitioners should be aware of these diseases, and particularly be familiar with their clinical presentation and exposure pathways to ticks and tick-borne zoonoses. However, focus should be placed on raising public awareness of ticks, tick-borne zoonoses and hantavirus, and promoting the adoption of personal protective practices. To aid this, Chapter 6 examines the risk perception of SO residents regarding ticks and tick-borne zoonoses.

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CHAPTER 4: The Influence of Host Competition and Predation on Tick Densities and Management Implications[3]

4.1 INTRODUCTION

Recent studies suggest that ecosystems with higher biodiversity (i.e., ecosystems with a more diverse species assemblage) can prevent the emergence and spread of zoonoses (45, 46); zoonoses are diseases present in wild and domestic animals, but can be transmitted to humans. Higher biodiversity—specifically with respect to higher number of species that may interact with hosts or vectors— has been suggested to be able to lower the abundance of pathogens in the environment, or lower the densities of disease vectors and hosts (25). In this paper, we describe a stage-structured model of vector-host dynamics that examines the influence of modifying host diversity (i.e., higher or lower numbers of host species) on the densities of a disease vector: ticks, an obligate arthropod ecto-parasite. We use the model to examine the influence of specific changes in host diversity that affect competition among and predation on tick populations' small and large hosts.

Ticks can transmit numerous zoonoses (17, 18, 24), of which Lyme disease is perhaps the most well-known. Lyme disease, caused by the spirochete *Borrelia burgdorferi s.l.* and present in North America, Europe and Asia (2, 42), is a debilitating disease with over 20,000 new cases reported per year in the United States (19). However, ticks are also the vectors of many other diseases such as Rocky Mountain spotted fever, Babesiosis, Ehrlichiosis, Tick-Borne Encephalitis (27, 60). Here, we focus on hard ticks (e.g., *Ixodes spp.*, *Dermacentor spp*.), rather than soft ticks (e.g., *Argas spp.*, *Alveonasus spp.*); hard ticks are diurnal and non-nidiculous, that is, they search for hosts in the environment, while soft ticks are nocturnal and search for hosts in their nests or burrows (39, 44).

Tick-borne zoonoses are transmitted to humans when a tick has a blood meal on humans, and transfers the disease-causing pathogen (e.g., *Borrelia burgdorferi s.l.*) into the blood stream (58). Humans are not the usual hosts ticks feed on: depending on its life-stage, ticks normally feed on either small hosts (e.g., deer mice, *Peromyscus maniculatus*, or chipmunks, *Tamias townsendii*) during the larval and nymphal life-stages, and, large hosts (e.g., deer, *Odocoileus hemionus*) during the adult life-stage. However, tick-human encounters still occur, because ticks are opportunistic feeders that attempt to feed on any animal they encounter.

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While ticks can feed on a variety of hosts, it is commonly believed that pathogens are associated with a particular host that acts as a disease reservoir that maintains the pathogen in the environment (50). For instance, the spirochete *Borrelia burgdorferi s.l.* is maintained mainly in deer mice: the spirochete is transferred to the tick when it feeds on an infected deer mouse; after which, the infected tick can transfer the disease to a human, causing Lyme disease, or to another deer mouse—thus maintaining the disease in the environment. If the tick feeds on an alternate small or large host that is not a disease reservoir (e.g., pocket mice, rabbits, humans), the pathogen will either be eliminated by the immune system, or lead to the death of the host, or not be transferred to another host; in all cases, effectively acting as a dead end that removes the pathogen from the environment.

Consequently, the species composition of the host population can be important in determining tick densities and the presence of the pathogen in the environment. As such, previous works suggest that higher diversity of hosts can mitigate the emergence and spread of tick-borne zoonoses by two pathways: 1. the presence of unsuitable disease vectors or hosts that cannot maintain the pathogen in the environment; 2. the presence of other species that regulate populations of disease vectors and hosts through ecological processes, such as competition or predation. For the first pathway, the presence of unsuitable disease hosts and vectors leads to a decreased probability that a vector will encounter a suitable host that can act as a disease reservoir; as a result, the pathogen would be "diluted" and maintained in the environment at a lower abundance (55). For the second pathway, the presence of other species could regulate the disease hosts and vectors through competition, predation or other ecological processes—thus decreasing the abundances of disease hosts and vectors and the risk of encountering them (45, 46). Though these two pathways can overlap, they are distinct in that the first affects the abundance of the pathogen, and not necessarily the densities of the disease host or vectors, while the second affects the opposite.

Most empirical and theoretical studies on the effects of host diversity on tick-borne diseases have examined the pathway where the pathogen can be diluted through unsuitable hosts and vectors. These works have examined the transmission dynamics of tick-borne zoonoses using host-parasite models (7, 37, 51, 52, 59). These models take an epidemiological approach focussing on the transmission of the pathogen from the vectors to susceptible hosts, which become infected, and which can later recover; these models are otherwise known as susceptible-infected-recovered (SIR) epidemiological models of the disease. Using these host-parasite

models and evaluations of the reproductive ratio (Ro), previous works have determined conditions where the pathogen may persist at equilibrium within the host population (Ro =1), or proliferate to cause epidemics (Ro > 1), or disappear from the population (Ro < 1). As well, these studies have gained insights on how transmission dynamics are affected by factors such as climate and seasonality (4, 13, 43) or metapopulation and spatial dynamics (8, 12). Notably, however, they did not take an ecological approach and examine the population dynamics of the host and parasite populations as they relate to the ecosystem within which they interact. While some works have examined the dilution effect in multi-host systems (11, 40, 55), they were interested in the abundance of pathogens, and did not include predation, nor did they distinguish between the different hosts of the tick life-stages (i.e., small hosts vs. large hosts; but see (41) for the influence of only predation, though without host competition).

We build on the findings of previous works by examining how host diversity may mitigate tick-borne zoonoses by the pathway of having increased species that can regulate tick densities through ecological processes. We examine changes in host diversity that affect two ecological processes: 1. changes in host diversity that affect the influence of competition among hosts for each life-stage (i.e., small mammals at the larval and nymph stages, and large mammals at the adult stage); 2. changes in host diversity that affect the influence of predation on the different hosts (e.g., coyote predation on small mammals, such as mice; wolf predation on large mammals, such as deer). Here, we are concerned with how total tick densities are influenced by host competition and predation, rather than the densities of infected ticks. As such, we do not use an SIR approach, but instead develop a stage-structured model of the tick-host system.

4.2 MODEL

We develop a stage-structured model of the tick-host system (Figure 4.1), using field data from previous works (8, 12, 14, 32, 41, 49). We begin by accounting for the questing life-stages of the tick that are dependent on obtaining a host blood meal: larva (x_1), nymph (x_2), and adult (x_3). Questing ticks are not attached to a host, but are dormant or searching for one to attach to (39). As our focus is on hard ticks (e.g., *Ixodes spp.*, *Dermacentor spp.*), we model ticks such that they require only a single blood meal to moult to the next stage (58). To include the hosts, we make the assumption that tick larvae and nymphs can parasitize either their most common small host, H_1 (i.e., deer mice or white-footed mice), or an alternative small host, H_2 (e.g., chipmunks, birds). Similarly, adult ticks can either parasitize their most common host H_3 (i.e., deer), or an alternate large host, H_4 (e.g., raccoons, cattle, horses). We also assume that each of the hosts, H_n, has a predator P_n.

The tick-host system can be described by a system of ordinary differential equations, where we do not include either the host or predator as a state variable, but as constants or a function that models predation pressure. We make the simplifying assumption that the H_n-P_n predator-prey dynamics are decoupled from tick dynamics; this though will not be applicable in domestic host populations (e.g., cattle), which we discuss later. We describe the tick-host system with three ordinary differential equations corresponding to the three tick life-stages:

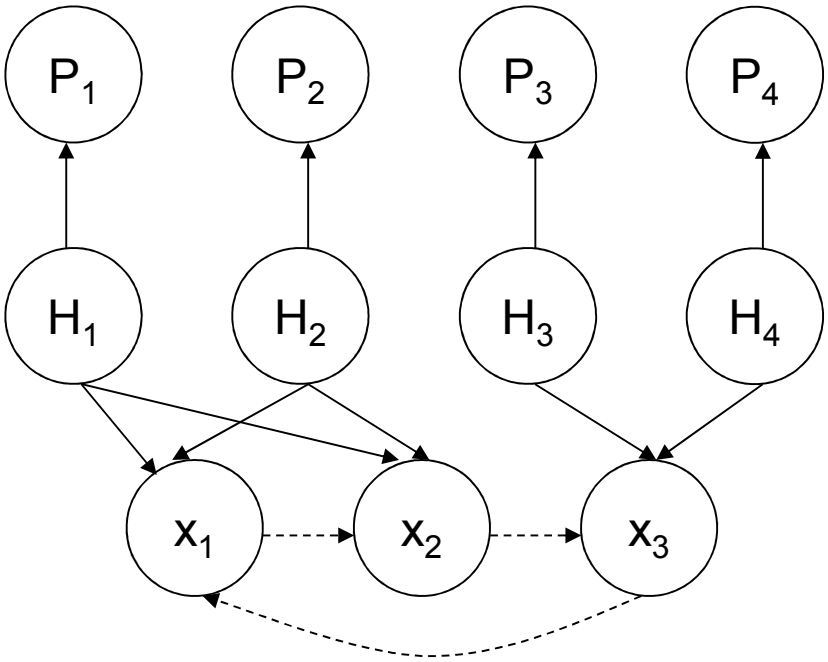
$$\frac{dx_1}{dt} = \overbrace{-\mu_1 x_1}^{\text{natural death}} + \overbrace{\beta_1(\sigma_3(p_L)H_3(t)\lambda_{3,3} + \sigma_4(1-p_L)H_4(t)\lambda_{3,4})\frac{x_3}{a_3+x_3}}^{\text{tick larvae produced by adults}} - \overbrace{(\sigma_1(p_s)H_1(t)\lambda_{1,1} + \sigma_2(1-p_s)H_2(t)\lambda_{1,2})\frac{x_1}{a_1+x_1}}^{\text{tick nymphs produced by larvae}}, \tag{1}$$

$$\frac{dx_2}{dt} = \overbrace{-\mu_2 x_2}^{\text{natural death}} + \overbrace{\beta_2(\sigma_1(p_s)H_1(t)\lambda_{1,1} + \sigma_2(1-p_s)H_2(t)\lambda_{1,2})\frac{x_1}{a_1+x_1}}^{\text{tick nymphs produced by larvae}} - \overbrace{(\sigma_1(p_s)H_1(t)\lambda_{2,1} + \sigma_2(1-p_s)H_(t)\lambda_{2,2})\frac{x_2}{a_2+x_2}}^{\text{tick adults produced by nymphs}}, \tag{2}$$

$$\frac{dx_3}{dt} = \overbrace{-\mu_3 x_3}^{\text{natural death}} + \overbrace{\beta_3(\sigma_1(p_s)H_1(t)\lambda_{2,1} + \sigma_2(1-p_s)H_2(t)\lambda_{2,2})\frac{x_2}{a_2+x_2}}^{\text{tick adults produced by nymphs}} - \overbrace{(\sigma_3(p_L)H_3(t)\lambda_{3,3} + \sigma_4(1-p_L)H_4(t)\lambda_{3,4})\frac{x_3}{a_3+x_3}}^{\text{tick larvae produced by adults}}. \tag{3}$$

Figure 4.1: Flow diagram of the tick-host system

We let x_1 denote the larvae, x_2 the nymphs, and x_3 the adult tick life-stages. Hosts are denoted by H_n, where H_1 and H_2 are small hosts and H_3 and H_4 are the large hosts. P_n are the predators of the tick hosts. The solid lines represent energetic flows between the species. The dashed lines represent the development of the ticks from one life-stage to the next.



The three tick stages undergo natural mortality at rate μ_i. After each blood meal, a new tick stage is produced: β_i is the maximum number of stage i ticks produced by one tick from the previous stage (i.e., number of eggs produced by one adult to form larvae; one larvae to moult to one nymph; one nymph to moult to one adult). The transition from a larvae to nymph and nymph to adult produce at most a single new stage, while the adult is the only stage that can produce eggs and hence multiple larvae; hence, β_2 and β_3 are ≤ 1. Each tick stage i obtains its blood meal from its preferred or alternate host, H_n, where a host can carry an average of $\lambda_{i,n}$ stage i ticks per time unit. Since each host can carry a maximum number of ticks (5), the production terms saturate with a type II functional response in tick density, where a_i is half the maximum number of stage i ticks per hectare. The full list of parameters and their values are summarized in Table 4.1.. These parameters refer to empirical data estimated for *Ixodes scapularis*. However, given that many of these parameters are estimates with a significant uncertainty, as further described in numerical simulations, we examined the parameters over a wide range (e.g., μ_i, Figure 4.3) to ensure that the results are robust over a biological meaningful range; we effectively conducted targeted Monte Carlo simulations for selected parameters that had greater uncertainty and that had a stronger influence on tick-host dynamics.

To include host competition, we employ the probability that larvae find and feed on their preferred small host, H_i, which is given by $\sigma_1(p_s)$, where $p_s=H_1/(H_1+H_2)$ is the proportion of small hosts that are of type H_1. Models in the literature often make the simplifying assumption that $\sigma_1(p_s)$ is a constant (40, 54). We, however, include the effects of host competition by relaxing this assumption and allowing the feeding probability to depend on the relative abundance of a given host, p_s. By varying the relative abundance of either host and keeping the total number of hosts fixed, we simulate the effects of competition: the presence of only one host implies no competition (p_s =1 or 0); different proportions of either host ($0< p_s <1$) implies the presence of competition. When $p_s >0.5$, there are more H_1, and when $p_s <0.5$, there are more H_2. We let $\sigma_2(1-p_s)$ be the probability that larvae feed on the alternative small host, H_2; we assume no difference in the larval and nymph host finding and feeding probabilities; we also assume that $\sigma_2(\cdot)$ and $\sigma_1(\cdot)$ have the same functional form. Similarly, we denote $p_L =H_3/(H_3+H_4)$, the proportion of large hosts of type H_3, and $\sigma_3(p_L)$ and $\sigma_4(1-p_L)$ the corresponding probabilities of finding and feeding on host H_3 and H_4 respectively.

As well, the functional form of $\sigma_1(p_s)$, and $\sigma_i(\cdot)$ in general, can capture differences in host competition, which affect host behavioural responses that can modify host encounter rates. When

Table 4.1: Description of parameter values used in numerical simulations

The data refers to *Ixodes scapularis* ticks. Average tick loads $\lambda_{i,n}$ account for successful moulting of the tick which is typically 50% (32). In the absence of data on alternative large hosts (H_4), we used raccoon data, a common tick host with large tick burdens. We convert ticks per host into ticks produced per host per year by multiplying by the reciprocal of the average duration of the tick stage. We estimated tick mortality assuming that larvae are the most sensitive stage.

Parameter	Description (units)	Value
$\mu_1{}^{*}$	Natural mortality of larvae (yr^{-1})	1.1
$\mu_2{}^{*}$	Natural mortality of nymph (yr^{-1})	0.73
$\mu_3{}^{*}$	Natural mortality of adult (yr^{-1})	0.037
$\beta_1{}^{**}$	Number of eggs laid by an adult (ticks/ha)	350
$\beta_2{}^{**}$	Number of nymphs produced by a larvae (ticks/ha)	1
$\beta_3{}^{**}$	Number of adults produced by a nymph (ticks/ha)	1
$\lambda_{1,1}{}^{***}$	Average tick load of larvae on H_1 (ticks/deer mice/yr)	28.95
$\lambda_{1,2}{}^{***}$	Average tick load of larvae on H_2 (ticks/chipmunk (birds)/yr)	12.57 (3)
$\lambda_{2,1}{}^{***}$	Average tick load of nymphs on H_1 (ticks/deer mice/yr)	0.68
$\lambda_{2,2}{}^{***}$	Average tick load of nymphs on H_2 (ticks/chipmunk (bird)/yr)	4.90 (9.67)
$\lambda_{3,3}{}^{****}$	Average tick load of adults on H_3 (ticks/deer/yr)	201.84
$\lambda_{3,4}{}^{****}$	Average tick load of adults on H_4 (ticks/racoon/yr)	69.54
$a_i{}^{*****}$	Half the maximum number of stage i ticks per hectare	650
$H_1{}^{****}$	Number of mice per hectare	0-100
$H_2{}^{****}$	Number of chipmunks (birds) per hectare	0-50 (31)
$H_3{}^{****}$	Number of deer per hectare	0.075-0.4
$H_4{}^{****}$	Number of raccoon per hectare	0.2
p_s	Proportion of small hosts of type H_1	$\frac{H_1}{H_1+H_2}$
p_L	Proportion of large hosts of type H_2	$\frac{H_3}{H_3+H_4}$

*(41)

**(12)

***(14)

****(32)

*****(49)

$\sigma_1(p_s)$ is a constant, the hosts do not affect each other's behaviour, and only compete for resources; this implies indirect competition, such that the differences in abundance between the hosts reflect their ability to forage and the relative abundances of the hosts (63). In this case, the ticks' encounter rate with the host is not affected by the composition of the host community; even though there may be few hosts of type H_2, this does not affect the ticks' encounter rate with those hosts.

As further described below, another choice for $\sigma_i(\cdot)$ is $\sigma_1(p_s)=\phi_1 p_s/(\phi_1 p_s + (1-\phi_1)(1-p_s))$, where ϕ_1 is the probability of encountering H_1. By doing so, tick-host encounter rates can depend on the relative abundance of the hosts in a non-linear manner. When more hosts of one type are present, the probability of encountering the other host may be much lower or higher than predicted by relative abundance alone, since the behaviour of one host may change in the presence of the more abundant competitor. Differences in the hosts' relative abundances would then lead to a non-linear relationship in the ticks' host-finding probability, similar to the relationship proposed by (52). This implies direct competition, since the hosts' behaviour and ability to forage for resources is affected by the presence or absence of the other host and competitor. Other abiotic and biotic factors will lead to similar effects, such as spatial heterogeneity, migratory behaviour, and seasonal fluctuations in resource availability; but, in our paper, we focus only on the potential effect of competition, while later research with spatially explicity models can disaggregate other factors.

To include the effects of predation on the tick hosts, we account for the presence of predators through the dynamics of the host term $H_n(t)$. Since we assume Lotka-Voltera predator-prey interactions, and, since we consider that H_n - P_n predator-prey dynamics as being decoupled from tick dynamics, we model host population, $H_n(t)$, as a constant or a periodic function depending on the predator, prey species, and the environment we wish to describe. When predation pressure is low, the host population is constant. When predation pressure is high, the host population is assumed to be oscillating, where the amplitude of the oscillations reflect the intensity of predation. For this, we use a cosine function, in order to approximate the life history variations of small and large hosts. Our use of Lotka-Voltera cycles is necessarily a coarse approximation of predator-prey dynamics, as those interactions will be modified effects that may dampen or modulate the dynamics, such as prey defensive behaviours or predators switching to another prey once a preferred prey becomes rare. Our study is an initial examination that can be expanded to include more realistic predator-prey dynamics.

4.3 ANALYTICAL RESULTS

Before examining the effect of host diversity changes, it is instructive to analytically examine the general conditions that are required for tick population persistence and cyclic dynamics. These both have management implications that can be expanded and further examined in our numerical analysis: persistence criteria can be used to identify conditions where ticks may be eradicated, while criteria for cyclic behaviour can be used to identify conditions where tick population dynamics are unstable and potentially vulnerable to interventions. To analyze the model we introduce some simplifying notation. Let the coefficients in front of the second term of equation (1)-(3) be denoted by α_i and the coefficients in front of the third term be denoted by γ_i. Thus equations (1)-(3) can be rewritten as:

$$\dot{x_1} = -\mu_1 x_1 + \frac{\alpha_1 x_3}{a_3 + x_3} - \frac{\gamma_1 x_1}{a_1 + x_1} \tag{4}$$

$$\dot{x_2} = -\mu_2 x_2 + \frac{\alpha_2 x_1}{a_1 + x_1} - \frac{\gamma_2 x_2}{a_2 + x_2} \tag{5}$$

$$\dot{x_3} = -\mu_3 x_3 + \frac{\alpha_3 x_2}{a_2 + x_2} - \frac{\gamma_3 x_3}{a_3 + x_3}\,. \tag{6}$$

We note that

$$\gamma_1 = \alpha_2/\beta_2 \geq \alpha_2 \text{ and } \gamma_2 = \alpha_3/\beta_3 \geq \alpha_3 \tag{7}$$

because the probability of survival from larvae to nymph and nymph to adult (β_2 and β_3 respectively) is less than or equal to 1. Similarly, $\gamma_3 = \alpha_1/\beta_1 \leq \alpha_1$ as each adult female successfully produces of the order of 350 female eggs.

4.3.1 Persistence criteria

As the model is stage-structured, it can be seen that the only axial equilibrium is the trivial (*0,0,0*) equilibrium. To examine the stability of this equilibrium and address the question of population persistence we consider the equation for the total tick population, $x=x_1+x_2+x_3$. Thus,

$$\dot{x} = -\mu_1 x_1 - \mu_2 x_2 - \mu_3 x_3 + (\alpha_2 - \gamma_1)\frac{x_1}{a_1 + x_1} + (\alpha_3 - \gamma_2)\frac{x_2}{a_2 + x_2} + (\alpha_1 - \gamma_3)\frac{x_3}{a_3 + x_3}\,. \tag{8}$$

All of the terms in (8) are negative except the final term, which saturates for sufficiently large x_3 thereby giving $\dot{x} < 0$. Thus, the population is bounded and the system is dissipative; in other words, tick populations are regulated by host density. The necessary condition for persistence is $\alpha_1 > \gamma_3$. This is equivalent to requiring that, on average, adult ticks produce more than one surviving offspring. The sufficient condition for persistence can be obtained from standard stability analysis. Persistence occurs if

$$(\mu_1 a_1 + \gamma_1)(\mu_2 a_2 + \gamma_2)(\mu_3 a_3 + \gamma_3) - \alpha_1 \alpha_2 \alpha_3 < 0\,. \tag{9}$$

This condition is obtained by applying the Routh-Hurwitz criteria (36), and is not very informative biologically because (9) involves all of the model in parameters and it is difficult to discern the relative importance of any particular process.

An alternative to the local stability result obtained from the Routh-Hurwitz criteria is a novel application of compound matrix theory and constructing Lyapunov functions (see 4.6 Analytical derivation) criteria can be found which establish when population persistence is not possible. In a similar manner, we can construct criteria for when the system does not exhibit periodic orbits. Table 4.2 summarizes these results.

Criteria A and B describe conditions for the persistence of tick populations. Criteria A can be re-expressed in the original parameters as $\mu_3 > \beta_1[\sigma_3(p_L)H_3\lambda_{3,3} + \sigma_4(1-p_L)H_4\lambda_{3,4}]/a_3$. From this, reducing numbers of large hosts (H_3 and H_4) can lead to tick eradication. However, the reduction would need to be of the order of a thousand fold reduction in deer density to around 0.0002 deer per hectare. On the other hand, from criteria B, ensuring $\mu_1 > \alpha_1/a_3$ is the most difficult inequality to satisfy due to the high larval production by adults (α_1). But, interestingly, if larval mortality is sufficiently high to prevent nymph production, and small host density is low, the three conditions that constitute criteria B can be satisfied and tick eradication is possible.

Criteria C and D give the conditions for when tick population cycles are absent and the dynamics are stable. As with criteria A, criteria C is difficult to satisfy and would require an extreme reduction in the number of large hosts. Criteria D describes more practical conditions where tick populations will not be cycling, which is achieved when either small hosts are reduced or by increasing larval and nymph mortality.

Table 4.2: Analytical criteria for tick eradication (A,B) and the absence of tick cycles (C,D)
Note that (A) and (B) are alternative criteria, only one of these needs to be satisfied and similarly for (C) and (D).

	Result	Criteria
(A)	(0,0,0) is globally asymptotically stable.	$\mu_3 > \frac{\alpha_1 - \gamma_3}{a_3}$.
(B)	(0,0,0) is globally asymptotically stable.	$\mu_1 > \frac{\alpha_1}{a_3}$, $\mu_2 > \frac{\alpha_2}{a_1}$ and $\mu_3 > \frac{\alpha_3}{a_2}$.
(C)	There exist no invariant closed curves & the omega limit set of any orbit is a single equilibrium.	$\mu_2 + \mu_3 > \frac{\alpha_1 - \gamma_3}{a_3}$.
(D)	There exist no invariant closed curves and the omega limit set of any orbit is a single equilibrium.	$\mu_1 + \mu_2 > \frac{\alpha_1}{a_3}$, $\mu_2 + \mu_3 > \frac{\alpha_2}{a_1}$ and $\mu_3 + \mu_1 > \frac{\alpha_3}{a_2}$.

In addition to the extinction equilibrium, the model has a coexistence equilibrium. However, it is not possible to derive an explicit analytical expression for this equilibrium; it can be found by numerically solving an implicit equation. Thus, in the next section, we numerically examine the coexistence equilibrium and how it is impacted by changes in competition and predation.

4.4 NUMERICAL RESULTS

We now examine the response of total tick density (x) to changes in host diversity that modify competition and predation among small and large hosts. We first study the impact of small and large host competition under low predation pressure, meaning that the host populations are at equilibrium (i.e., H_n is a constant). We consider competition, by examining the effects of p_s, the proportion of the small hosts that are of type H_1 (white-footed mice) versus hosts of type H_2, and p_L the proportion of large hosts that are of type H_3 (deer) versus hosts of type of H_4. Following this, we consider the effects of predation, by assuming that host populations are undergoing Lotka-Voltera cyclic behaviour (i.e., H_n is cycling).

4.4.1 The influence of host competition

We examine the influence of small host competition by varying p_s and $\sigma_1(p_s)$, while fixing the composition of the large host population at equal host densities (p_L=0.5). We examine $\sigma_1(p_s)$ as a constant (σ_1=1), representing indirect competition and when tick densities are only dependent on relative densities of hosts, p_s ($\sigma_1(p_s) = p_s$). We then explore a functional form of σ_1 dependent on p_s, which modifies the probabilities of tick-host encounters, and represents the effect of different types of competition and host behavioural responses. We consider the general form for $\sigma_1(p_s)$ given by,

$$\sigma_1(p_s) = \frac{\phi_1 p_s}{\phi_1 p_s + (1-\phi_1)(1-p_s)}, \tag{10}$$

where ϕ_1 describes the probability of ticks encountering H_1 versus H_2, which may be reflected as behavioural or environmental differences (e.g., deer that move around frequently, versus cattle that are stationary for long periods). The probability of finding H_1 and H_2 is now affected by the relative abundance of the hosts in a non-linear manner; depending on the value of ϕ_1, the tick encounter rates for the different hosts may be different even when their populations are equal (e.g., due to the hosts' behaviours affecting their encounter probabilities with ticks). When ϕ_1= 0.5, there is an equal probability of the ticks encountering either host and $\sigma_1(p_s)= p_s$. When ϕ_1>0.5 tick larvae have a higher probability of encountering H_1 than would be suggested by relative abundance alone; with a value of ϕ_1<0.5 ticks have a higher probability of encountering H_2.

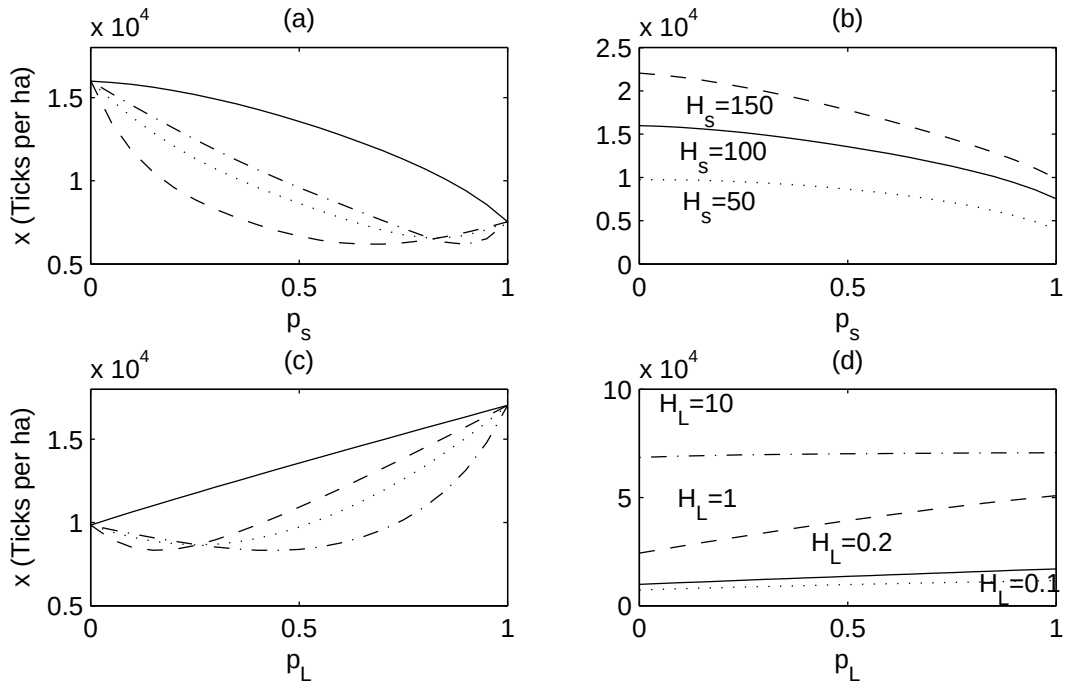
In Figure 4.2a, we explore how p_s affects total tick density while fixing the total number of small hosts to H_s, thus $H_1 = p_s H_s$ and $H_1 = (1 - p_s)H_s$. When $\sigma_1(p_s) = 1$, the case of indirect competition, tick host-finding probability is independent of the relative host abundance, we find the equilibrium total tick density depends on p_s in a monotonic fashion, decreasing with higher densities of H_1, ($p_s \rightarrow 1$). H_1 is a less suitable host for nymphs, but more suitable for larvae. However, since the parameters in the production terms in the nymph equation are smaller than that in the larval equations, the nymph production determines the rate of total tick production. Consequently, as host H_2 can support the highest number of nymphs (compare λ_{21} and λ_{22} in Table 4.1), maximizing the number of H_2 hosts maximizes tick densities and hence we see tick densities in Figure 4.2a are maximized when $p_s = 0$ and minimized when $p_s = 1$. Hence, in the case of indirect competition, maximizing host diversity in small hosts ($p_s = 0.5$) does not reduce tick densities; instead, reducing or completely eliminating the abundance of the less suitable host (H_2) would most effectively reduce tick densities.

For the influence of direct competition, we examined $\sigma_1(p_s)$ with $\phi_1 = 0.5$, 0.8 and 0.2. We now find that host diversity in small hosts can lower tick densities, such that there is a minima at an intermediate value of p_s. In accordance to the previously described role of nymphs, when $\phi_1 = 0.5$, the minimum lies closer to the H_1 host, which is less suitable to the nymphs; however, this minima can shift closer to H_2 or H_1, when ticks have a respectively higher probability of encountering host H_1 or H_2 ($\phi_1 = 0.8$ or 0.2). These results hold for a range of values of values of H_s, total small host densities (see Figure 4.2b). We can estimate the location of the minima since γ_2 determines that rate nymphs become adults. Taking $\phi_1 = 0.5$ so $\sigma_1(p_s) = p_s$ and $\phi_2(1 - p_s) = 1 - p_s$ we have, $\gamma_2 = p_s H_1 \lambda_{2,1} + (1 - p_s) H_2 \lambda_{2,2}$. Thus with $H_1 = H_s p_s$ and $H_2 = H_s (1 - p_s)$, then γ_2 is minimized, with respect to p_s, when $2 p_s H_s \lambda_{2,1} - 2(1 - p_s) H_s \lambda_{2,2} = 0$, that is, when $p_s = \lambda_{2,2}/(\lambda_{2,1} + \lambda_{2,2}) = 0.88$. The minimum of the dotted curve for $\phi_1 = 0.5$ in Figure 4.2a is located at $p_s \approx 0.85$, in good agreement with our estimate.

We next examine the influence of large host competition by varying p_L, $\sigma_3(p_L)$ and $\sigma_4(1 - p_L)$ while fixing $p_s = 0.5$ and keeping the functional forms for $\sigma_3(\cdot)$ and $\sigma_4(\cdot)$ the same (Figure 4.2c-d). We again examined the influence of indirect and direct competition, when $\sigma_3(p_L) = 1$, and when the expression for $\sigma_3(p_L)$ is analogous to equation (10) with ϕ_3 at values 0.5, 0.8, and 0.2. We find that the trends are similar to when p_s is varied. In Figure 4.2c, we again see that, with indirect competition, increasing host diversity (i.e., $0 < p_L < 1$) in large hosts does not decrease

Figure 4.2: Total tick density plotted as a function of p_s and p_L

(a) Illustrates the effect of varying the functional form of $\sigma_1(p_s)$ and $\sigma_2(1- p_s)$, where the solid line is indirect competition; the remaining lines represent direct competition, where the dotted line represents no preference (ϕ_1=0.5), the dashed line represents preference for H_1 (ϕ_1=0.8), and the dash-dot line represents preference for H_2 (ϕ_1=0.2). (b) We fix $\sigma_1=\sigma_2=1$ and vary the total small host density, H_s. (c) Illustrates the effect of direct competition, where the solid line is indirect competition as a reference; the dotted line represents no preference (ϕ_3=0.5), the dashed line represents preference for H_3 (ϕ_3=0.8), and the dash-dot line represents preference for H_4 (ϕ_3=0.2). (d) We fix $\sigma_3=\sigma_4=1$ and vary the total large host density, H_L. Unless otherwise stated parameters are a given in Table 4.1 and $H_s = H_1 + H_2$=100, $H_L = H_3 + H_4$=0.2, σ_i=1 and $p_s = p_L$ =0.5.



tick densities since the minima occurs when there is only one species (H_4, p_L =0). Tick densities are maximized when there are only large hosts of type H_3 (p_L =1); this is because H_3 hosts can carry the largest burden of adult ticks, and only the adult tick feeds on the large hosts, so that conditions that increase adults would determine tick production.

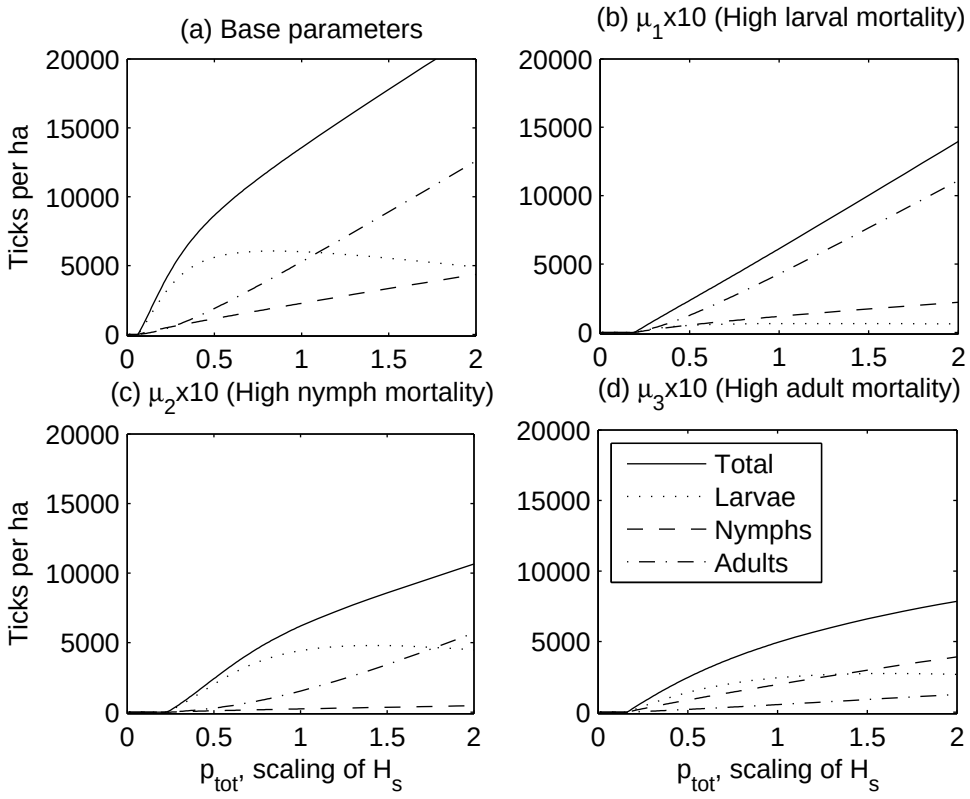
On the other hand, with direct competition, minima in tick densities occur when there is higher host diversity among the large hosts, that is, at intermediate values of p_L. When the ticks have no host preference (ϕ_3=0.5), the minimum is located to the left, that is when there is a larger population of H_4, which is less suitable for the adults. When there is a preference for H_3 (e.g. ϕ_3=0.8) or H_4 (e.g. ϕ_3=0.2), the minima shifts to the right or left respectively. Since $\sigma_3(p_L)$ is non-constant, tick densities are minimized when γ_3, that is, the rate adults produce larvae, is minimized. In an analogous calculation to the small host case, we ask what value of p_L is this rate minimized in the case that ϕ_3=0.5: this gives $p_L = \lambda_{3,4}/(\lambda_{3,3}+ \lambda_{3,4})$=0.26, which is a good approximation to the minimum in Figure 4.2c.

These results hold for a range of values for H_L, total large host density, (see Figure 4.2d). However, we find that, when large host densities are very high (H_L=10), changing p_L has little effect on the equilibrium tick density and there is no longer a minimum. In other words, there is only an effect when large hosts are at low densities, that is, at ecologically relevant levels for deer and other wildlife (e.g., ~20 deer per 100 ha); while, in the presence of high densities of large hosts (e.g. cattle farms), changing host diversity will have a minimal effect. This occurs since the availability of large hosts no longer limits larval production. So, although increasing host diversity of large hosts lowers larval numbers slightly, larval densities are so high that $\gamma_1 x_1/(a_1+x_1) \approx \gamma_1$, and we thus see virtually no effect from a change in the host diversity of large hosts.

Now, returning to the analytical results, criteria A and B found that reducing large hosts and nymph populations could eradicate ticks, suggesting that there is a difference between the roles of the hosts and ticks stages in controlling tick populations. So, to understand the relationship between the small and large hosts on tick densities, we examine changes in host diversity that affect the composition of hosts, where we study changes in the proportion of small and large hosts (Figure 4.3a). As small hosts are at a much higher density than large hosts, it is not meaningful to directly consider the proportion of hosts that are small or large; similarly, we encounter the same problem if we try to consider the proportion of tick meals that are on small or

Figure 4.3: Total tick density, and its break down into larval, nymph and adult tick densities

Total tick density is plotted as a function of the scaling of small host numbers away from H_s =100, i.e. a scaling of p_{tot}=1.5 implies H_s =150, while H_L remains fixed. (a) Illustrates the base parameters as given in Table 4.1. (b), (c) and (d) illustrate the effects of a 10-fold increase in μ_1, μ_2 and μ_3 respectively. Unless otherwise stated σ_i=1, $p_s = p_L$ =0.5 and H_3=0.1, H_4=0.1.



large hosts. We thus begin by examining the effects of scaling the ratio of small to large hosts H_s / H_L. For example, a scaling of 2 reflects a doubling of H_s from base parameters; in other words, a scaling factor p_{tot}<<1 reflects a decrease in small hosts, where the host population is mainly large hosts, and a scaling factor p_{tot} >> 1 reflects an increase in small hosts. To focus the study, we fix σ_i=1 and $p_s = p_L$ =0.5.

We find a biphasic pattern in the influence of large and small hosts on tick densities: when the host population is mainly large hosts (p_{tot} <<1), tick densities are low and increase rapidly with small additions of small hosts; while, when the population of small hosts is high (p_{tot} >>1), increases in tick production is low. This pattern occurs because, when populations of small hosts are low (p_{tot} <<1), they act as a rate limiting step, such that small increases of small hosts lead to rapid increases in tick densities; in contrast, when populations of small hosts become large (p_{tot} >>1), they are no longer rate limiting, and further increases in small hosts have little effect. We see this pattern confirmed when we look at the breakdown of the tick densities into the different life-stages: small increases in small hosts when they are low leads to increases larval densities initially, but a further increase reduces the rate of larval density production, which matches the biphasic graph of total tick density. The decrease in the rate of production of larval densities is because larval production from adults is a saturating function of adult tick densities, while the rate at which larvae become nymphs (γ_1) is a linear function of H_s. In other words, even though numbers of adult ticks are increasing as H_s is increased, there is little change in the rate larval ticks are produced, but the rate larval ticks transition into nymphs increases with H_s because of the linear dependence.

While these results suggest that small hosts play a strong role in tick production, the biphasic pattern is also present when we examine the effects of scaling the ratio of large to small animals (data not shown). In this case, we vary 1/ p_{tot}, but changing H_L while keeping H_s fixed; a scaling factor 1/ p_{tot} <<1 reflects a decrease in large hosts, where the host population is mainly small hosts, and a scaling factor 1/ p_{tot} >>1 reflects an increase in large hosts. Again, when densities of large hosts are low and there are mainly small hosts, tick densities are low, and small increases in large hosts cause large increases in tick densities; when densities of large hosts are high, changes in large hosts make little difference in tick production. Much like with small hosts, when their relative populations are low, large hosts can cause rate limiting steps to occur in tick populations: larval densities increase when increasing large hosts and cause adult ticks to

produce larvae; however, in this case, because of the fixed population of small hosts, the rate of nymph production saturates.

As the previous results suggest that changes in the production of different tick life-stages influence total tick populations, we also examine the relative roles of the tick life-stages. We do so by further exploring the effects of tick mortality by looking at increasing mortality in each stage of tick development (Figure 4.3b-d). We see that increasing adult mortality leads to the largest reduction in tick numbers, followed by nymph mortality leading to the next largest reduction. This is an unsurprising result, as adult ticks are responsible for a very large production of larvae (i.e., ~350), while larvae and nymph individuals produce at most one other individual. Increasing adult mortality should then have a large impact on total tick production.

As well, to help further clarify the relative roles of the tick life-stages and hosts, we explore changing the average tick loads on a host, $\lambda_{i,n}$. We find that reducing nymph loads on H_2 leads to the biggest reduction in tick densities, while changing larval loads had little effect (Figure 4.4a). Similarly, increasing the nymph loads on H_2 leads to one of the largest increases in total tick densities. However, for intermediate densities of small hosts increasing adult tick loads on hosts led to a slightly larger increase in tick numbers (Figure 4.4b). Significantly, the influence of nymphs hold when the density of large hosts was high (Figure 4.4c), while changes in adult tick loads had little effect. Generally, changes to nymph tick loads caused significant change in tick densities, and was most noticeable at high small host densities (Figure 4.4c).

These results are consistent with the criteria A and B, as we find that low densities of either small or large hosts, or higher mortality of nymphs and adults can cause sharp declines in tick populations. Our numerical results, however, suggest reasons why these patterns occur. While it is true that reducing large and small hosts can decrease tick densities, the importance of the small or large hosts is dependent on their relative abundance and contribution to tick production; in other words, when either host acts to cause a rate limiting step, then it will strongly influence tick production. We also find that, in addition to adult ticks, nymph ticks have a strong influence on tick densities, such that they are sensitive to changes in nymph tick loads; this is again due to the transition from the nymph to adult stage acting as a rate limiting step in total tick production since the tick loads on its hosts are smaller than the other tick stages.

4.4.2 The influence of host predation

We now examine the influence of predation by assuming that predation is at a sufficiently high level that it leads to Lotka-Volterra oscillations in the host populations. We introduce this by allowing periodic temporal cycling in the small and large hosts by using a cosine function. Cycling in the small hosts, $H_1(t)$, is given by $p_s H_s(1+A \cos(2\pi t/10))$, where the average density is $p_s H_s$, and where A is the amplitude, with increasing A analogous to increased predation pressure on $H_1(t)$, and similarly for $H_2(t)$. Similarly, cycling in large hosts, $H_3(t)$, is given by $p_L H_L(1+A \cos(2\pi t/10))$ where the average density is $p_L H_L$, and where A is the amplitude, or predation pressure on $H_3(t)$, likewise for $H_4(t)$.

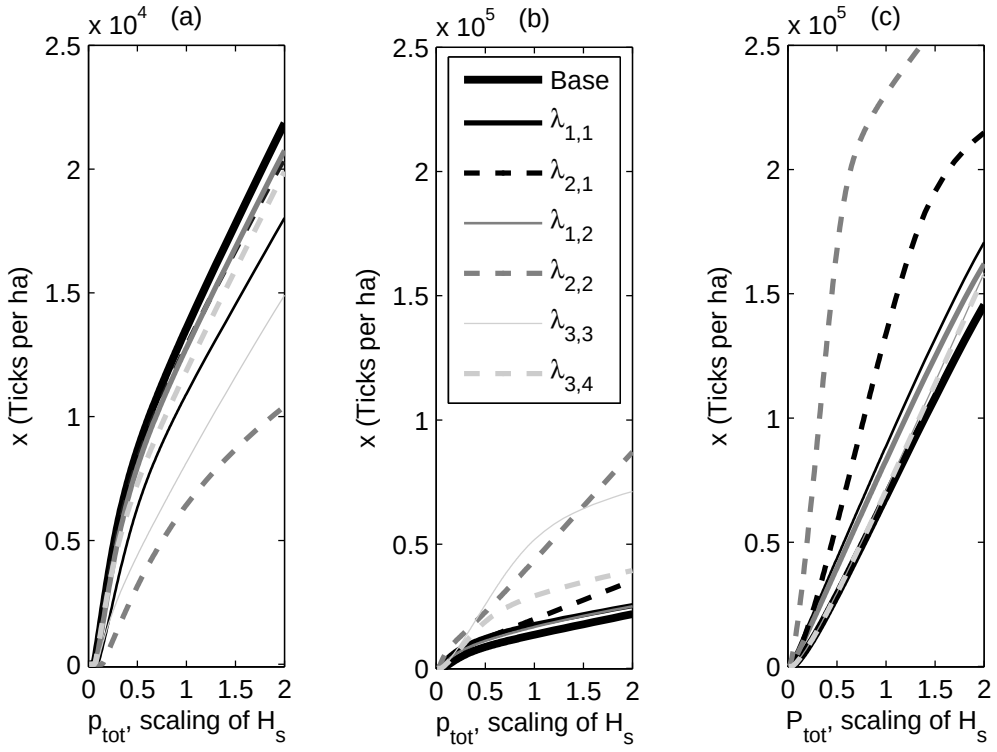
As in section 4.4.1, we examine the change in tick densities as a function of small and large host diversity (p_s and p_L), where, at each value of p_s or p_L, we simulate the tick population dynamics. However, given that the tick populations can be oscillating, we calculate the average tick densities after the dynamics have reached an attractor. We also calculate the maximum and minimum tick densities reached on the attractor. By then comparing the average, maximum and minimum of the cycling tick densities under different predator pressures (corresponding to changing the amplitude of $H_n(t)$), we systematically examine the influence of predation on small or large hosts. (Figure 4.5).

We begin by examining the influence of predation in H_1 across changing proportions of small hosts (p_s) and large hosts (p_L) (Figure 4.5a and c). We find that predation has little effect on average tick densities, such that there is almost no difference between the influence of predation on small hosts at low or high predation pressure. Predation on the large host H_3 under changes in p_s and p_L also has limited impact on average tick densities; although tick densities decrease at higher predation intensities, the magnitude of the influence on the average is negligible (Figure 4.5b and d).

When we examined the tick population dynamics across time, we found that the effects of predation are dampened by the nymph and larvae dynamics: while larvae and nymph oscillations have the same period as the host, they are out of phase with one another (data not shown). When $H_1(t)$ is high, there is a large flow out of the larval class, and the flow out of the larval class oscillates with $H_1(t)$. We thus see a minimum in larval density when $H_1(t)$ is at its peak and a maximum in larval density when $H_1(t)$ is at a minimum. Similarly, nymphs have a flow in and out of the nymph class that oscillate with $H_1(t)$, but the flow in is greater because

Figure 4.4: Total tick density plotted as a function of the scaling of small host numbers from H_s=100

(a) Illustrates the effect of decreasing host tick loads, $\lambda_{i,n}$, with large host densities set at typical levels, H_L =0.2. The $\lambda_{i,n}$ line corresponds to a 90\% reduction in this parameter. (b) and (c) illustrates the effect of increasing host tick loads, $\lambda_{i,n}$. The $\lambda_{i,n}$ line corresponds to a 10-fold increase in this parameter. The large host densities in (b) are at typical levels of H_L =0.2, while in (c) we consider high large host densities with H_L =5. Unless otherwise stated the parameters are as given in Table 4.1 and σ_i=1 and $p_s = p_L$ =0.5.



$H_1(t)$ hosts support more larvae. Hence, the lack of effect on ticks of small and large host predation is due to the out of phase oscillation of the nymph and larvae densities.

However, we find that the largest effect of predation is on the maximum and minimum tick densities achieved, that is the magnitude of the tick population oscillations. While, for small hosts, predation has a small effect on the maxima and minima of the oscillating tick densities (Figure 4.5a and c), for large hosts, predation has a pronounced effect on the maxima and minima of tick oscillations both as a function of p_s and p_L (Figure 4.5b and d). Even low predation on $H_3(t)$ leads to large changes in maximum and minimum tick densities, which are much larger than those observed with high predation on $H_1(t)$. High predation on $H_3(t)$ leads to large changes in maximum and minimum tick densities and unstable population dynamics.

Further, since predation may occur at different frequencies depending on the predator type and on seasonal fluctuations in resource availability, we also examine changes in the period of predation pressure on the host (Figure 4.6). We find that increasing the period increased the magnitude of oscillations in the total tick population. Again, cycling in tick densities were most sensitive to predation in large hosts, where the tick densities were more sensitive to the period of oscillations in H_2 hosts rather than H_1. This is due to the sensitivity of total tick numbers to the rate that nymphs become adults which is enhanced by increases in H_2 hosts. Hence, the effect of predation on tick densities is dependent not only on what host is being affected, but also on the period of the predation. These results hold when we examined predation on H_2 and H_4 individually, or with simultaneous (synchronous) predation on H_1 and H_2 or on H_3 and H_4.

However, as previously mentioned, since Lotka-Voltera interactions are rarely found in natural populations, we also examined cases where the predation on the small and large hosts may be modulated and more realistic. We studied the cases where predation can be occurring asynchronously on the small or large hosts. In accordance to some work (21), we find that asynchronous predation on small hosts can increase average tick densities, but the effect is very limited (data not shown). Similarly, asynchronous predation on both large hosts may decrease tick densities, but again, the magnitude of the effect is negligible. We have also examined situations where one of the small or large hosts has higher predation levels than the other, as well as cases where both the small and large hosts are being predated on, but the results do not differ from the previous cases (data not shown). Finally, these results are consistent with criteria C and D from the analytical results, which found that cycles would be present with high densities of large hosts, and that there would be limited cycles with predation on small hosts.

Figure 4.5: Total tick density plotted as a function of p_s and p_L in the presence of predation The solid lines in all the plots correspond to the average tick density over the period of the attractor and the dashed lines correspond to the maximum and minimum tick densities over the period of the attractor. (a) and (b) illustrate total tick density plotted as a function of p_s. (a) Illustrates the effect of different predation pressures on $H_1(t)$, while (b) illustrates the effect of different predation pressures on $H_3(t)$. The bold lines corresponds to A=1, 100% fluctuation in $H_1(t)$ or $H_3(t)$ around the average, while the lighter lines correspond to A=0.1, a 10% fluctuation in about the average.(c) and (d) illustrate total tick density plotted as a function of p_L. (c) Illustrates the effect of different predation pressures on $H_1(t)$, while (d) illustrates the effect of different predation pressures on $H_3(t)$. Again the bold lines corresponds to A=1 and the lighter lines correspond to A=0.1. Unless otherwise stated $H_s = H_1 + H_2$ is fixed at 100, $H_L = H_3 + H_4$=0.2, $p_s = p_L$ =0.5 and σ_i=1.

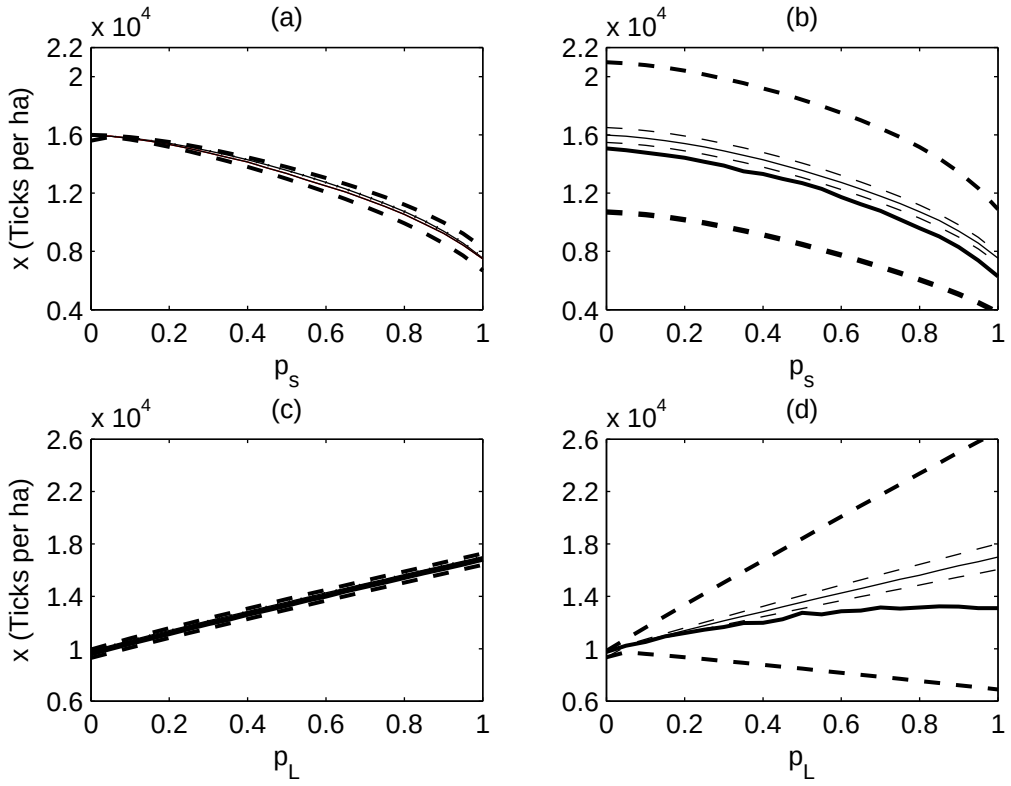
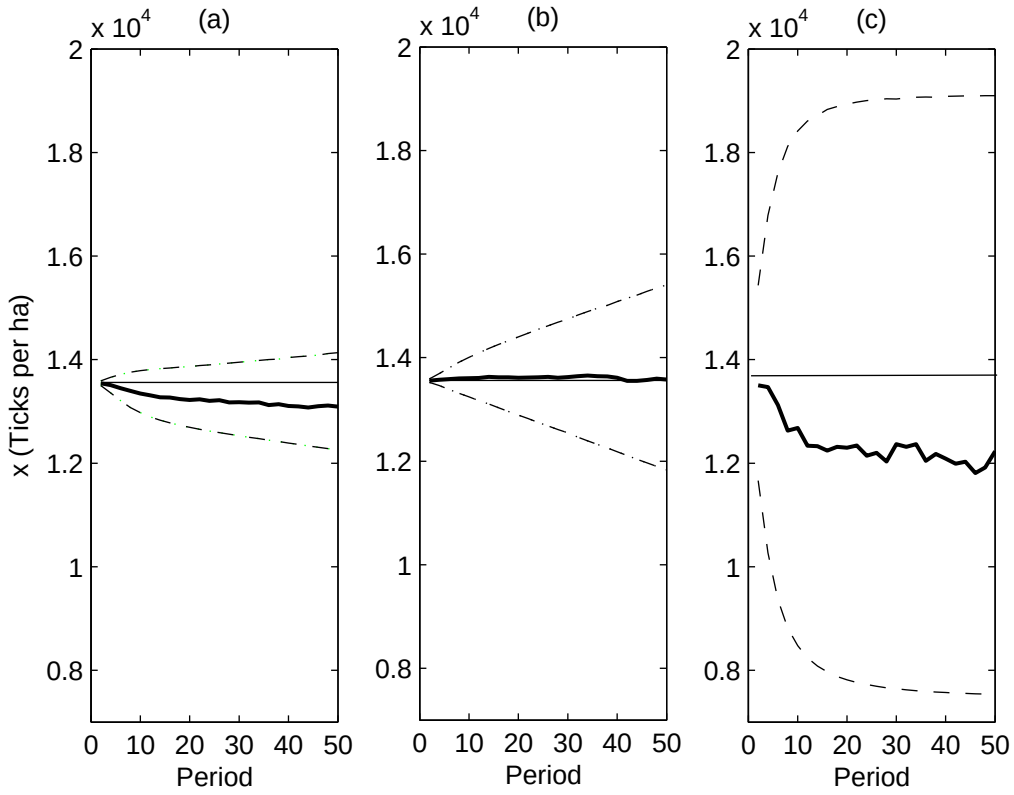


Figure 4.6: Total tick density plotted as a function of the period of small or large host oscillations

(a) Illustrates the effect of varying the period of oscillations in H_1, where $H_1(t)=50(1+cos(2\pi t/period))$. The solid line indicates case where H_1=50. When $H_1(t)$ oscillates, so does the equilibrium total tick density, and the bold solid line is the average tick density (averaged over the period of the attractor), the dashed line indicate the maximum and minimum tick densities over the period of the attractor. (b) Illustrates the effect of varying the period of oscillations in H_2, where $H_2(t)=50(1+cos(2\pi t/period))$, the lines are as described in (a). (c) Illustrates the effect of varying the period of oscillations in H_3, where $H_3(t)=0.1(1+cos(2\pi t/period))$, the lines are as described in (a). Unless otherwise stated H_1+H_2 is fixed at 100, H_3+H_4=0.2, $p_s = p_L$ =0.5 and σ_i=1.



4.5 DISCUSSION

By constructing a tick-host stage-structured model, we were able to determine how changes in host diversity that affect host competition and predation influence tick densities. In so doing, we numerically determined the conditions where host diversity may potentially regulate tick densities; we also found analytical conditions for persistence and cyclic behaviour that were in accordance with our numerical results. Our results show that, though increasing host diversity can have a regulating influence on tick densities, it is in itself too coarse of a measure to predict the magnitude and direction of the regulating effect. Instead, the effect can be better understood and predicted by examining the specific ecological dynamics affecting ticks and their hosts, such as the type of interaction among the hosts and the existence of rate limiting steps in tick-host dynamics.

4.5.1 Competition type and encounter rates

We found that increasing host diversity to include competition will not necessarily have a regulating effect. In order for host diversity to have an effect on tick populations, the competition among the hosts had to be direct, rather than indirect (Figure 4.2). With indirect competition, the presence of another competitor will not affect the hosts' ability to forage; while, with direct competition, the presence of a competitor affects the host's ability to forage (e.g., through changes in behaviour). This difference affects tick densities because, with indirect competition, the hosts do not modify their encounter rate with ticks, such that there is no benefit of increasing host diversity. In fact, it is even better to have a single species present that supports a lower tick load. In contrast, with direct competition, the hosts' encounter rate with ticks is modified in a non-linear manner, and results in decreased tick populations. This result suggests that the changes in tick-host encounter rates, which can often be associated to direct competition, are one of the fundamental ecological processes that determine whether increasing host diversity will regulate tick populations.

This result appears trivial, as host competition should commonly be direct competition, and thus will affect the host encounter rates. There is ample evidence that the presence of other small hosts greatly affect the behaviour of deer mice and other rodents, so that their encounter rate with ticks would necessarily be also modified (34, 64); for instance, deer mice have been found to change their foraging behaviour in the presence of other competitors (10). Similarly, the

behaviour of deer also change when other large hosts are present (20, 29). As well, recent work has shown that rodents may also change their behaviour in the presence of large hosts (35).

However, there may be cases when the assumption of indirect competition among the hosts may hold, and also when direct competition may lead to an increased encounter rate with ticks, rather than a decrease. In the simplest sense, the hosts themselves may have behaviour that facilitates tick encounters (e.g., contrast cattle grazing to wild ungulates rapidly moving in the bush), such that influence of competition or host diversity has less importance in comparison to the type and interaction of host species. In addition, the situation of indirect competition can also occur when the resources available are plentiful, and there is no need to compete directly (63). This may occur around spatially heterogeneous agricultural areas where there is often the presence of food subsidies, and also habitat regions that support small hosts (e.g., orchards or corn fields). Finally, direct competition may not necessarily lead to a decrease in encounter rates with ticks, but an increase. On the one hand, it is well documented that increased competition among rodents leads to an increased likelihood of staying in burrows, both of which would potentially lead to more exposure to ticks; on the other hand, increased competition could lead to higher aggression and lowered grooming rates (53, 56), which could lead to more tick attachment success.

4.5.2 Tick life-stages and rate limiting steps

We also determined the possible mechanisms behind the regulating influence of host diversity on tick populations. Our analytical results suggested that the tick life-stages and hosts had different impacts on tick production, so we examined the relative importance of the different tick life-stages and of the small and large hosts on total tick production. Our results suggest that the relative importance of the hosts and each tick life-stage depends on whether they cause rate limiting steps in the tick population: if the host densities are low, or if the transition rate of one life-stage is slower than the other stages, then the host or tick stage will cause a rate limiting step that effectively regulates the rate of total tick production. Notably, the particular rate limiting influence of nymphs is based on the parameterization derived from the *Ixodes scapularis* tick; in other tick species, the rate limiting step may be in another life-stage—highlighting the need to consider the specific ecological characteristics of the tick-host system.

In terms of the hosts, it is not surprising that a reduction in either the small or large hosts will cause decreases in tick production, given that at least one of the tick life-stages will be

lacking a food source. There will then always be an opportunity for tick eradication when either one of the host are targeted and culled. However, reducing populations of small or large hosts is often not feasible; it is very difficult to significantly reduce populations of small hosts (38), while there may be populations of large hosts that cannot be reduced either because they are domestic animals (e.g., cattle, horses), or because the public would be not be comfortable with it (e.g., deer) (26). In addition, in cases where large host densities are high (e.g., cattle grazing pastures), higher host diversity would have a limited impact on total tick densities (Figure 4.2d; Figure 4.4c). This is simply because the density of large hosts is such that larval production is very high, and neither the transition from adults and from larvae are a rate limiting step in the tick life cycle.

The role of the tick life-stages can have more practical relevance to tick management. In terms of the tick life-stages, we found that nymph and adult ticks play a significant role in tick-production, such that changes in nymph loads on hosts and increases in adult mortality can cause decreases in tick production. Looking at the relationship between the ticks and their hosts, we observe that the main reason for nymphs being the rate limiting step is the low tick loads of nymphs on their respective small hosts (Table 4.1). On the other hand, the effect of adult ticks on total tick densities is due to its high production of larval ticks, while the other life-stages only produce at most one next stage tick. However, while targeting both the nymphs and adults may be effective in reducing ticks, reducing nymph populations may have a stronger impact in situations where potentially high densities of large mammals lead to high larval production.

4.5.3 Predation and host population cycles

In contrast to competition, changing host diversity to include host predation had the least influence on tick populations: there was negligible change in total tick populations with predation on small hosts, while there was a relatively larger influence with predation on large hosts. In both cases, the average tick densities did not deviate significantly from the cases with no predation. However, the magnitude of the cycling in the tick populations increased with increasing predation pressure and the lengthening period of the predator oscillations (Figures 4.5 and 4.6). These results remained insensitive to various combinations of asynchronous predation and predation on small and large hosts. Thus, the influence of predation and host cyclic behaviour on tick populations is limited and approaches to regulate ticks with host predation may not be effective.

This is a counterintuitive result, as predation should decrease populations of tick hosts, which should lead to decreases in tick populations. Previous studies have suggested that predation could potentially be one of the processes of host diversity that controls the emergence of disease (e.g., (45), but see (21)). While we did find that, with predation on large hosts, there can be unstable population dynamics, predation on small hosts has a limited effect on tick populations. Even with large oscillations in the small host populations, these oscillations affect the tick populations only very moderately.

However, we also observed that the magnitude of the tick population oscillations could be greatly increased when the period of the host predation was increased (Figure 4.6). This is due to prolonged periods of high and low host densities, which, in turn, lead to prolonged periods of tick increases or declines. These changes in the period of the host predation may occur as a result of changes in the type or behaviour of the predators; but, the change in period may result from changes in the host dynamics themselves, which may be sensitive to resource availabilities (e.g., production of acorns during masting events) or climate variations (47). While these fluctuations in resource availability will certainly occur in wildlife situations, they are likely not observed in areas close to human land use, as there may be sufficient food subsidies to support stable populations of hosts.

4.5.4 Management implications

Promoting conditions that increase host diversity in general has numerous benefits, not the least of which would be the conservation of endangered species, but also potentially preventing the emergence of zoonoses (1). Previous works have suggested that conservation could play a role in controlling the infection risk of tick-borne diseases (15). However, as we found from our results, the implementation of such a management approach to control ticks by protecting or promoting host diversity is not guaranteed to be effective. The underlying ecological processes necessary to allow host diversity to act on ticks may not be present, while there may be ecological conditions that counteract them (e.g., there may be indirect competition, or the large host populations may be very high). As well, from a practical standpoint, increasing host diversity is mainly possible in conservation areas (e.g., parks, reserves); it is not practical in areas with numerous human land use activities, particularly agricultural areas. Areas with high human activity and land use often have restrictions (e.g., proximity to human habitations; inability to cull host populations due to public disfavour; existing land uses that will likely not

change, such as agricultural practices). This relationship between ticks and land use practices is further examined in Chapter 5.

Yet, areas with human land use or activity are particularly at risk for human encounters with emergent diseases, such as tick-borne diseases (9, 48), suggesting that more targeted tick management strategies are necessary. These targeted tick management strategies may be derived from the results we obtained from examining the ecological processes underlying host diversity that can regulate tick populations. Our results suggest that targeting the encounter rates or attachment of nymph and adult ticks could be effective in decreasing tick populations, as they would both modify the tick transition rates between life-stages. In fact, a common tick-management practice targets the adult ticks feeding on large hosts; the practice essentially attracts deer to a device that applies acaricides (i.e., tick specific pesticides) on the deer as it feeds (57).

While targeting large hosts approach has been shown to be effective, coupling the practice to a similar approach that targets nymphs and small hosts could increase the reduction of tick densities. One approach may be to cull small hosts, but this is impractical given their ubiquity and high density (38). Another promising method would be similar to that employed with deer, where small hosts could be given access to nest bedding that is imbibed with acaricides (23); in so doing, they would kill the ticks that have attached to the rodents when they return to their nest. Other innovative approaches may involve orally vaccinating small hosts against the tick bites, which has been shown to have some preliminary success (16).

4.5.5 Limitations of the results

For our analysis, we made a number of simplifying assumptions that had limitations. First, in terms of the ecology of ticks, tick-host dynamics are more complex than modeled. While research has suggested that tick-host dynamics can be at equilibrium in wild populations (6, 22, 28, 62), other studies have found that ticks can affect the behaviour as well as the fitness of domestic hosts (3, 61) and wild hosts (33). Similarly, while the tick stages do usually feed on small or large hosts as we described, it is possible for any stage of a tick to feed on any host, since they are opportunist feeders. As well, in our model we modeled tick attachment to be density dependent, that is, tick attachment saturates on a host; but, tick attachment may also be frequency dependent, which has previously been examined (11). The inclusion of these considerations would modify the dynamics of the tick-host system, as the ticks would then be

causing population fluctuations in the hosts, since they can influence host fitness, and likely also the potential for changes in tick-stage transition rates, since they may feed on small and large hosts. Future works may examine the influence of these considerations.

Notably, the parameters we used for our model were estimated for *I. scapularis*, and would likely differ for other species, such as *D. andersoni* ticks, which were examined for Chapter 3 and 5. However, since we examined the parameters over a wide range to account for their uncertainty, the general properties we found would be insensitive to changes in the parameters. Rather, our results suggest that it is more important to understand the relative values between the parameters such that rate limiting steps within the tick life-stages could be determined (e.g., transition of larvae to nymph with respect to that from nymph to adult). Similarly, understanding the relative changes in tick loads between the hosts would help determine the location of the rate limiting step and which tick life-stage is acting as a bottleneck. The trends of our results are thus robust to changes in parameters and the dynamics we identified would hold for a wide range of parameter values.

4.5.6 Conclusion

Our paper examined how changes in host diversity affecting host competition and predation can potentially regulate tick populations. While higher host diversity can regulate tick densities, this will depend more on the specific ecological characteristics determining the relationship between the ticks and their hosts, such as the type of interaction among the hosts and attachment rates of ticks on hosts. Significantly, these ecological characteristics may trump the predictions of host diversity alone, such that higher host diversity may have no or the opposite effect expected. Hence, though host diversity may be a good initial measure of whether disease emergence may occur, the ecological characteristics that govern the vector-host dynamics must be examined more closely.

4.6 ANALYTICAL DERIVATION

Consider a system of differential equations $dx/dt=f(x)$, where $x=(x_1,x_2,x_3) \in \mathbb{R}^3$ and $x(t,x_0)$ is a solution of the equations which satisfies $x(0,x_0)= x_0$. We use a generalisation, to higher dimensions, of a criteria of Bendixson for the non-existence of invariant closed curves such as periodic or homoclinic orbits. The theory was developed by Li and Muldowney (30, 31) and shows that oriented infinitesimal line segments, $y(t,y_0)$, evolve as solutions of

$$\frac{dy}{dt} = \frac{\partial f}{\partial x}(x(t, x_0))y \tag{11}$$

and oriented infinitesimal areas, $z(t,z_0)$ evolve as solutions of

$$\frac{dt}{=}\frac{\partial f}{\partial x}^{[2]}(x(t, x_0))z \tag{12}$$

where $\frac{\partial f}{\partial x}^{[2]}$ is the second additive compound matrix. For a general matrix A the corresponding second additive compound matrix is given by $A^{[2]}$ as follows,

$$A = \begin{bmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix}, \quad A^{[2]} = \begin{bmatrix} a_{11}+a_{22} & a_{23} & -a_{13} \\ a_{32} & a_{11}+a_{33} & a_{12} \\ -a_{31} & a_{21} & a_{22}+a_{33} \end{bmatrix}.$$

Thus for equations (4)-(6) the second additive compound matrix is

$$\left(\frac{\partial f}{\partial x}\right)^{[2]} = \begin{pmatrix} -\mu_1-\mu_2-\frac{\gamma_1 a_1}{(a_1+x_1)^2}-\frac{\gamma_2 a_2}{(a_2+x_2)^2} & 0 & -\frac{\alpha_1 a_3}{(a_3+x_3)^2} \\ -\frac{\alpha_3 a_2}{(a_2+x_2)^2} & -\mu_1-\mu_3-\frac{\gamma_1 a_1}{(a_1+x_1)^2}-\frac{\gamma_3 a_3}{(a_3+x_3)^2} & 0 \\ 0 & \frac{\alpha_2 a_1}{(a_1+x_1)^2} & -\mu_2-\mu_3-\frac{\gamma_2 a_2}{(a_2+x_2)^2}-\frac{\gamma_3 a_3}{(a_3+x_3)^2} \end{pmatrix}.$$

By Theorem 3.3 of Li and Muldowney (31) if for each $x_0 \in \mathbb{R}^3_+$ equation (11) and equation (12) are uniformly asymptotically stable then all line segments collapse to the origin and we have global stability of $(0,0,0)$ and there exists no invariant closed curves (periodic orbits, homoclinic or heteroclinic cycles) and the orbits converge to a single equilibrium.

Asymptotic stability of (11) and (12) is shown by constructing Lyapunov functions. Using the Lyapunov function $V(x_1,x_2,x_3)=|x_1|+|x_2|+|x_3|$ and together with equation (11) we have

$$\dot{V}(y) = (1,1,1) \cdot \frac{\partial f}{\partial x} = -\mu_1 + \frac{a_1(\alpha_2 - \gamma_1)}{(a_1 + x_1)^2} - \mu_2 + \frac{a_2(\alpha_3 - \gamma_2)}{(a_2 + x_2)^2} - \mu_3 + \frac{a_3(\alpha_1 - \gamma_3)}{(a_3 + x_3)^2}$$

If $\dot{V}(y) < 0$ we have global stability of the zero solution of (11). Since $\gamma_1 \geq \alpha_2$ and $\gamma_2 \geq \alpha_3$ then a sufficient condition for $\dot{V}(y) < 0$ is $\mu_3 > (\alpha_1 - \gamma_3)/a_3$, condition (A) in Table 4.2. Showing that $\dot{V}(y) = (1,1,1) \cdot \left(\frac{\partial f}{\partial x}\right)^{[2]} < 0$ guarantees asymptotic stability of (12) and gives condition (C).

Alternatively, using the Lyapunov function $V(x_1,x_2,x_3)=\sup\{|x_1|+|x_2|+|x_3|\}$ gives stronger results (conditions B and D in Table 4.2).

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CHAPTER 5: The Influence of Agricultural Practices on Tick Densities[4]

5.1 INTRODUCTION

Increasing land use and encroachment of wildlife areas by human populations raises the infection risk of zoonoses, that is, diseases that reside in wild and domestic animals, but can be transmitted to humans (e.g., West Nile virus, swine flu, avian influenza) (14, 26). The proximity of human populations to wildlife increases contact between the two and the transmission of previously unknown infectious zoonoses, which represent >60% of emerging diseases (89). However, the consequences of changing land use for human health remain unclear (65), although potentially severe (13, 42, 50, 59, 60, 78).

Land use can have significant impacts on ecosystems that affect habitat conditions for wildlife species (19, 43, 67). As a result, the species diversity and composition of ecosystems can be greatly modified, leading to higher densities of disease vectors and reservoirs, such as ticks, mosquitoes, and rodents, and thus higher risk of exposure to the pathogens they carry (40, 47, 60, 61, 71, 80, 81). This occurs as the species that ordinarily regulate the populations of disease-carrying species become rare or extirpated (21, 58, 62).

The impacts of land use result from various practices, such as forestry and agriculture, which affect ecosystems through activities, such as logging and pesticide application. While all land use practices will affect all ecosystems, the type and strength of the impacts from differing practices will not be identical, given that the activities associated with them are also different. Hence, the influence of land use on human health and the infection risk of zoonoses will depend on differences in land use practices. To predict and ultimately mitigate the negative impacts on human health that result from increasing land use, it is crucial to understand how different land use practices may influence the infection risk of zoonoses.

This paper focussed on zoonoses transmitted by ticks, an obligate arthropod ecto-parasite (e.g., *Dermacentor andersoni*), and examined how tick densities change in response to two agricultural land use practices that are common in rural areas and in the wildlife-human population interface: grazing agricultural practices (GA) (e.g., range grazing, pastures), and non-grazing agricultural (NGA) (e.g., orchards, vineyards, crop lands). We examined changes in tick densities that occur as these agricultural practices modify habitat suitability for ticks and their

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hosts in two ways: 1. fragmentation of suitable habitat into small patches; 2. the influence of the landscape context formed by GA and NGA practices on suitable habitat.

Tick-borne zoonoses (e.g., Lyme disease) are threats to not only human health but to agricultural livestock (34, 45, 86). Lyme disease, caused by the spirochete *Borrelia burgdorferi s.l.*, is perhaps the most well-known tick-borne zoonose, and is diagnosed on average in over 20,000 new patients per year in the United States and 70 new patients in Canada, and is endemic in the north-east of North America (32, 55); it is also present in Europe and Asia (34, 64). However, ticks can transmit a variety of other diseases that are caused by bacteria, viruses and protozoans (e.g., Rocky Mountain Spotted fever, Tick-Borne Encephalitis, Babesiosis) (38, 83). In fact, tick-borne zoonoses are the most commonly contracted zoonoses in North America.

Fortunately, tick-borne zoonoses occur because of inadvertent contact between ticks and humans or livestock. Ticks usually feed on wildlife hosts, such as deer and rodents, but, being opportunist ecto-parasites, they will attempt to feed on any animal they encounter (66). Unfortunately, the risk of infection to tick-borne zoonoses may be increasing as a result of human impacts on ecosystems, from not only land use practices, but also changes in bird migratory patterns and in climate, which could bring ticks to new areas or allow new areas to be suitable for ticks and their hosts (52, 56). Notably, though, we only examined hard ticks (e.g., *Dermacentor spp., Ixodes spp.*) and not soft ticks (e.g., *Ornithodores spp.*): hard ticks are diurnal and tend to be encountered in the open environment on bushes and in leaf-litter, while soft ticks are nocturnal and tend to be encountered in cellars or animal nests (53). As they have different behaviours and habitat preferences, hard ticks and soft ticks will be affected by land use practices differently.

Land use practices, such as agricultural practices, impact ticks and their hosts by affecting habitat suitability through fragmenting habitat into smaller patches, and through the influence of landscape contexts formed by the practices. The negative impact of smaller patch sizes is well documented (22, 23, 79): numerous species require large areas of continuous habitat for foraging or territorial purposes, and would no longer be able to persist in fragmented habitats; this is particularly the case with large animals and migratory birds (6, 11, 68).

As well, landscape context can negatively impact species: landscape context is the region that is influenced by land use practices through the activities associated with it (e.g., pesticide application, logging, ranching) (18, 31, 87). The effects of land use practices are not limited to where they are located, but can affect regions that are proximate to it—effectively forming a

landscape context influencing the ecosystems around the land use practice. Hence, while both fragmentation and landscape context are related, they are separate processes that can affect habitat suitability differently.

Studies have separately suggested that smaller patch sizes and human landscape contexts may increase the infection risk of zoonoses, such as those transmitted by ticks (2, 7, 16, 27, 33, 36, 59). Small habitat patches favour populations of tick hosts, such as rodents (e.g., deer mice, chipmunks) and ruminants (e.g., mule deer), who specialize in living in interface areas. Landscape contexts created by human habitation or agriculture can attract rodents and ruminants, due to the lack of predation and the unwillingness of inhabitants to cull charismatic tick hosts (i.e., deer) (35).

GA and NGA land use practices are known to impact ecosystems and can influence ticks and their hosts (4, 10, 14, 24, 39, 41, 76, 77), but their ultimate effects are unclear. On the one hand, GA and NGA landscape contexts can increase tick densities: GA practices introduce large numbers of livestock into the area (i.e., cattle) that can act as tick hosts and that can modify vegetational structure to the benefit of rodents and, by extension, ticks (10, 48, 85); NGA practices can exclude large mammals (i.e., with deer fences) further forcing them to aggregate in fragmented patches, where tick populations can proliferate (3, 39, 46). On the other hand, activities in GA and NGA landscape contexts can also decrease tick populations: livestock in GA practices are often treated for parasites and other diseases, which can also affect tick survivability (29); NGA practices can apply large amounts of pesticides that eliminate ticks as well as their targeted pest (28, 75).

Hence, to understand the influence of agricultural practices on tick populations and thus the infection risk of tick-borne zoonoses, we examined tick densities in study sites spanning a range of patch sizes and within GA and NGA landscape contexts. The influence of GA and NGA contexts were compared to low human impact (LH) landscape contexts (e.g., parks, wilderness areas). A better understanding of the influence of patch size and landscape context resulting from agricultural practices would help predict how future land use changes will affect tick populations and the infection risk of tick-borne zoonoses, as well as suggest a role for land use management strategies that could mitigate negative impacts on human health.

5.2 MATERIALS AND METHODS

5.2.1 Study area

We conducted our research in the South Okanagan, a region in the province of British Columbia (BC), Canada (lat. 49 28.41 N, long. 119 35.43 W). Our study sites ranged from the Town of Osoyoos in the south, to the Town of Kaleden in the north (Figure 1). The South Okanagan is a rapidly changing rural area, where growing human populations and economic development are leading to land use practices that encroach on wildlife areas (9, 69). The South Okanagan is located in a valley, through which the Okanagan River flows and serves as the irrigation source for most agricultural practices (i.e., orchards, vineyards, ranching). As a result, most of the arable and usable land is located in proximity to the river, leading to a high density of agricultural practices on both sides of the river.

Wildlife habitat areas (e.g., ecological reserves, provincial parks) are still present within these agricultural practice areas, and are intended to preserve rare and endangered flora and fauna (e.g., antelope brush, *Purshia tridentate*; bluebunch wheatgrass, *Pseudoroegneria spicata*; Great Basin pocket mice, *Perognathus parvus*; Western harvest mice, *Reithrodontomys megalotis*). These areas are bounded by agricultural practices and geographic features (e.g., lakes, mountain ranges). Only remote areas unsuitable for human habitation have unfragmented wildlife areas.

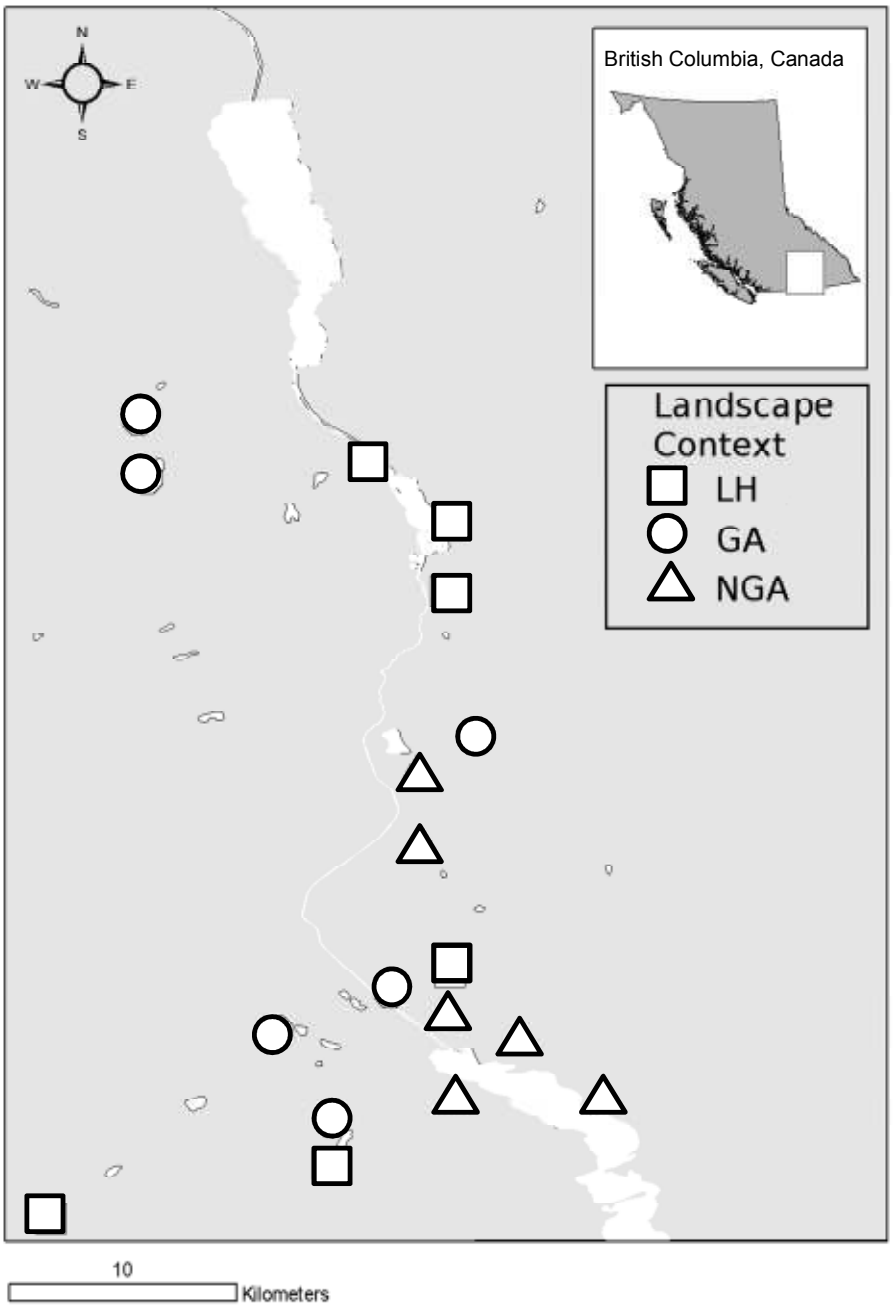
Although ticks are well-known to be in the area (70), their distribution and density are not known. Previous research in the area involved only passive surveys of ticks; that is, health practitioners and private citizens sending ticks to the British Columbia Center for Disease Control. This only provides a rough idea of the location of ticks, but not their density.

5.2.2 Study site selection

A total of 18 study sites were selected, representing a range of patch sizes and within landscape contexts formed by GA, NGA and LH (Figure 5.1): six sites within an NGA context (e.g., orchards, vineyards); six sites within a GA context (e.g., range pastures); and six sites within an LH context (e.g., remote areas or parks). Study sites were defined as patches of habitat areas that are suitable for ticks and their hosts (i.e., deer mice, *Peromyscus maniculatus*; and

Figure 5.1: Study site locations

All 18 sites were located in the South Okanagan in the province of British Columbia, Canada. Low human impact (LH) sites are indicated by boxes; grazing agricultural (GA) sites are indicated with circles; and, non-grazing agricultural (NGA) sites are indicated by triangles.



deer, *Odocoileus hemionus*), such as areas composed mainly of large sagebrush (*Artemisia tridentata*) and antelope brush (*Purshia tridentate*) (7, 57, 76, 82, 84). Notably, these habitats are not the only type in the SO. Indeed, the SO contains a wide range of habitats (e.g., Subalpine Fir zones), but were not all examined. The habitat chosen for this study are common mainly at lower altitudes, and were, significantly for human health, easily accessible and highly frequented.

To examine the influence of patch size, the six selected sites for GA, NGA and LH represented a range of patch sizes varying from 4.2 ha to 349.8 ha (Table 5.1). The size of the sites was determined using provincial land use practice delimitations and aerial photos, which were then adjusted by ground-truthing to account for geographic features (e.g., mountain ranges, valleys) (Figure 5.2). Sites were located a minimum of 500 m apart. Given the heavy agricultural activity in the region, the selection of the study sites with suitable habitat and within the appropriate landscape context was limited, resulting in study sites with patch sizes that were dominantly mid-sized (i.e., 20-50 ha) and large (i.e., >100 ha).

To examine the influence of landscape context, the six sites for GA and NGA were located in areas affected by the impacts of the agricultural practices, while LH sites were located in areas with limited human activity (Figure 5.2). A site was determined to be within the landscape context of the agricultural practice if it was directly adjacent to or within the agricultural practice; the landscape contexts were not further quantified, as the agricultural practices did not overlap and there was no uncertainty regarding the context the sites were in. GA and NGA differed in terms of where their agricultural practices occurred in relation to tick habitat: GA practices occurred within the study sites (i.e., areas for livestock grazing were also suitable tick habitat), while the NGA practices did not occur within the study sites, but around them (i.e., areas with orchards and vineyards were not suitable tick habitat). As such, the delimitation of the boundaries of the GA and NGA study sites differed: GA site boundaries were determined by geographic features (e.g., mountain ranges, cliffs, or large water bodies); while NGA site boundaries included at least one agricultural practice (e.g., orchard, vineyard) on one more of its sides and also geographic features. LH site boundaries were determined by geographic features.

5.2.3 Tick collection

Tick densities were measured at each study site by conducting active surveys for ticks using the "flagging" method (12). This involved dragging a 1 m^2 flannel cloth on the ground and the vegetation we encountered (e.g., grasses, shrubs). At each site, a series of standardized "drags" were conducted, consisting of 100 m transects of each site, and were random paths that were not repeated or crossed. This distance was chosen to represent the approximate distance that a human would travel and potentially encounter a tick, which then allows for an estimate of density (ticks·(100 m^{-2})) that is meaningful to human exposure to ticks. The 100 m distance was approximated by walking for five minutes at a pace previously determined to cover 100 m. At the end of each drag, the flannel cloth was examined, and the ticks found attached were collected in a sealable bag for identification of genus and age classes.

The number of drags were varied at each site to minimize over- and under-sampling sites of different patch sizes. Due to time and spatial constraints, the number of drags were not functionally dependent on patch size, but was determined iteratively during a pilot tick sampling week, when the study sites were visited at least twice. The number of drags per site were divided into four different categories: large sites (>200 ha) had 24 drags; mid-range sites (150-200 ha and 30-100 ha) had 22 and 16 drags; and, small sites (<5 ha) had 8 drags (Table 5.1). The number of ticks obtained for each drag at each site were averaged after each visit, obtaining an estimate of the density of ticks·(100 m^{-2}).

The sites were sampled on a weekly basis between April 1st and June 30th, 2009, such that each site had at least 12 measures of tick density (ticks·(100 m^{-2})). The sites were visited between 6-10 am, when ticks are most active and questing for hosts (72). Because of the high sensitivity of ticks to heat and humidity, where higher temperatures and lower humidity results in lower tick survival and thus lower tick activity (53), the temperature and relative humidity were also recorded. An analog device was used to coarsely estimate temperature and relative humidity; this device was placed on the ground to estimate the conditions experienced by ticks.

5.2.4 Statistical analyses

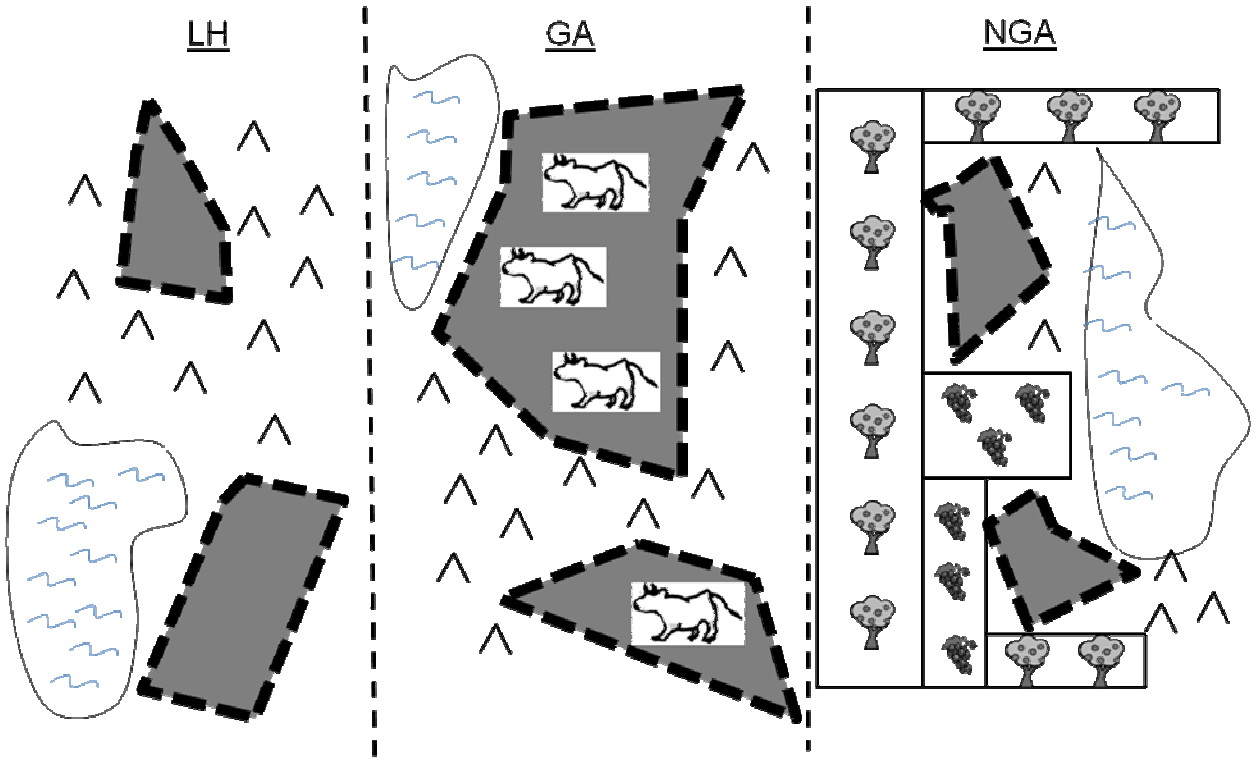
The influence of patch size and landscape context on tick densities was evaluated using the statistical package, SPSS Statistics 17.0 (74). Generalized Linear Models (GLM) were

Table 5.1: Description of the study sites

Site label, size (ha) and drags per site are indicated. Sites are grouped by landscape context: low human impact (LH); grazing agriculture practices (GA); and, non-grazing agriculture practices (NGA). The sites are ordered from smallest to largest.

Land Use Practice (site #)	Size (ha)	Drags per site
LH(1)	24.4	8
LH(2)	29.9	8
LH(3)	53.2	16
LH(4)	69.7	16
LH(5)	109.7	16
LH(6)	349.8	24
GA(1)	41.2	16
GA(2)	167.7	22
GA(3)	178.5	22
GA(4)	207.7	24
GA(5)	277.6	24
GA(6)	325.0	24
NGA(1)	4.2	8
NGA(2)	28.2	8
NGA(3)	35.0	8
NGA(4)	46.4	16
NGA(5)	55.2	16
NGA(6)	265.4	24

Figure 5.2: Conceptual illustration of study sites within different landscape contexts
The study sites are defined as patches of suitable habitat for ticks, indicated by the dark grey areas and outlined by a dashed line. The sites were located within the following landscape contexts: low human impact (LH); grazing agriculture (GA); and non-grazing agriculture (NGA). Geographic features (e.g., mountains, lakes) are indicated by triangles and water bodies are indicated by waved lines. Livestock grazing, indicated by cartoons of cows, are present within GA study sites. Non-grazing agricultural practices, indicated by cartoons of apple trees or grapes are located around NGA study sites.



constructed, since patch size is a continuous variable and landscape context (i.e., GA, NGA or LH) is a categorical variable, and also since tick densities were non-normally distributed (54). The GLM was analyzed using the Tweedie family of distributions at p=2 (for gamma distributions), due to the high number of zero estimates of tick densities, and the decrease of tick densities for all sites to zero over the sampling period (17). This approach allowed us to account for temperature, relative humidity, the effects of week and month (i.e., 1^{st} , 2^{nd} week of April; or, April, May, June). Using the Akaike Information Criterion (AIC) (1), a stepwise regression approach was adopted to determine which combination of variables form the best model describing tick densities, where lower values of AIC indicate a better model: different models were tested by systematically adding and removing the variables to see if they improved the model; previous research suggest that a difference >2 between the AIC of different models warrant the addition of a new variable (8, 25).

5.3 RESULTS

From the 18 sites, a total of 5243 ticks were collected. Although other species are known to be present in the area (e.g., *Ixodes angustus*) (70), only *Dermacentor andersoni* were collected, and were dominantly adults with <1% nymphs. Tick density varied from 0 ticks·(100 m^{-2}) to a high of 20.8 ticks·(100 m^{-2}). For all sites, tick densities were highest in April and decreased to 0 ticks·(100 m^{-2}) for all sites at the end of June, when the recorded temperatures reached >30 ˚C.

Tick density was characterized by a GLM consisting of patch size, landscape context, and temperature (˚C) (Table 5.2). All three variables were significantly correlated to tick density ($p<0.01$) (Table 5.3). Relative humidity, week, and month did not improve the model; week and month covaried with temperature and were thus not included; combinations of interaction terms (e.g., temperature x patch size, patch size x land use practice) were also tested, but did not significantly improve the model.

For the influence of the landscape context, NGA and GA practices had a positive effect on tick densities in comparison to LH. Interestingly, NGA sites had significantly higher average tick densities than GA sites: NGA contexts had an average tick density of 3.09 ticks·(100 m^{-2}) (95% CI ± 0.76), while GA contexts had an average tick density of 1.94 ticks·(100 m^{-2}) (95% CI ± 0.98).

This trend was confirmed when we examined the estimated marginal means of tick densities for the three landscape contexts. The estimated marginal means can evaluate the effect of landscape context independently from the other parameters, as they are calculated by holding temperature and patch size constant at their average values (i.e., temperature = 20.60 ˚C; patch size = 125.28 ha): LH = 0.133 ticks·(100 m^{-2}) (95% CI ± 0.09); GA = 0.92 ticks·(100 m^{-2}) (95% CI ± 0.61); NGA = 2.92 ticks·(100 m^{-2}) (95% CI ± 1.25) (Figure 5.3).

For the influence of patch size, there was a weak negative relation between patch size and tick density. However, the relation was weak: change of tick density for a change in patch size (ha) was -0.004 ticks·(100 m^{-2})·ha (95% CI ± 0.004). Finally, confirming the temperature sensitivity of ticks, temperature was negatively correlated to tick densities: the rate of change of tick densities for a positive change in temperature (˚C) was -0.15 ticks·(100 m^{-2})·˚C (95% CI ± 0.04).

Table 5.2: Akaike Information Criterion (AIC) of different generalized linear models using different combinations of variables

Lower values of AIC indicate models that better describe tick densities. The full model (i.e., combination of landscape context, patch size and temperature) best describes tick densities (ticks·(100 m^{-2})). Other models are ordered by increasing difference of the AIC values with the full model (Δ AIC).

Model	No. of parameters	Δ AIC	AIC
-Landscape context, patch size, temperature	3	0	692.15
-Landscape context, temperature	2	14.86	707.01
-Landscape context, patch size	2	44.26	736.41
-Landscpe context	1	63.19	755.34
-Patch size, temperature	2	91.98	784.13
-Temperature	1	110.54	802.69
-Patch size	1	118.37	810.52

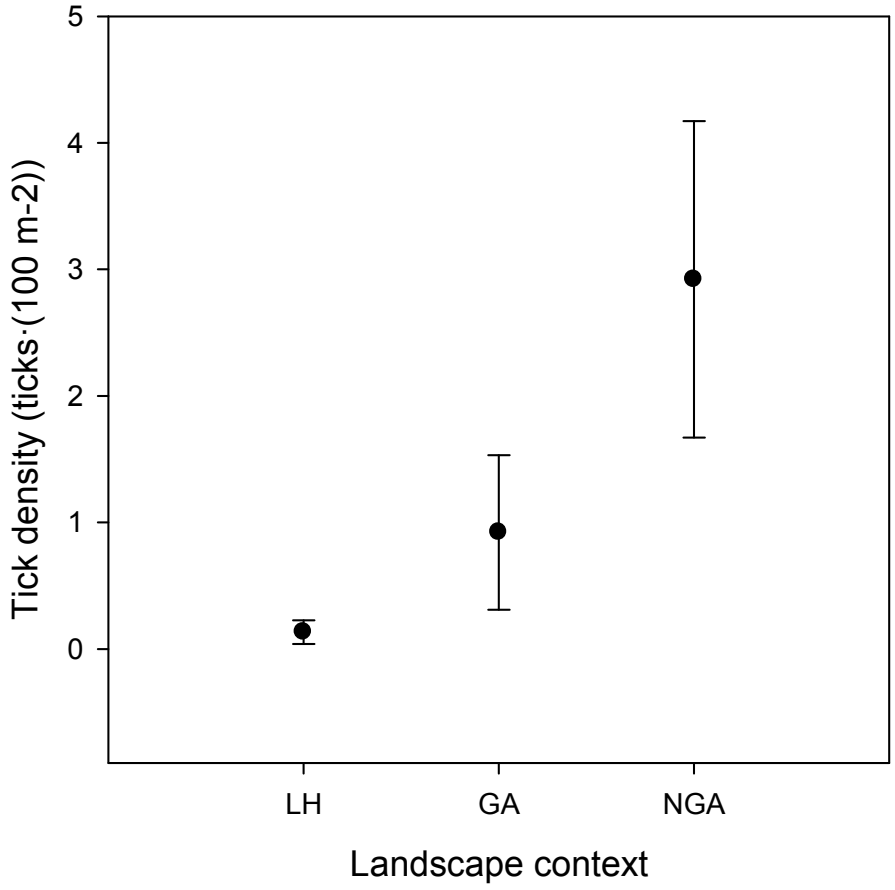
Table 5.3: Results of the full generalized linear model

The full generalized linear model of tick densities includes landscape context, patch size and temperature. For the landscape context parameters, B indicates the estimated mean tick densities (ticks·(100 m^{-2})): low human impact (LH), used as reference; grazing agriculture (GA); and, non-grazing agriculture (NGA). For the patch size and temperature parameters, B indicates the estimated rate of change of tick densities in relation to patch size or temperature. The 95% confidence intervals are indicated beside the parameter estimates, as well as the significance of the variable in the model (*p*).

Variable	B	*p*
Intercept	0.83 ± 0.90	0.069
Landscape context		
(LH as reference)		
GA	1.94 ± 0.98	<0.00
NGA	3.09 ± 0.76	<0.00
Patch size	-.004 ± 0.004	0.013
Temperature	-0.11 ± 0.04	<0.00

Figure 5.3: Estimated marginal means of tick densities

Tick densities (ticks·(100 m^{-2})) are measured in the landscape contexts (i.e., low human impact (LH); grazing agriculture (GA); and, non-grazing agriculture (NGA)). Marginal means are estimated for the agricultural practices when temperature and patch size are held constant at their average values: temperature = 20.60 °C; patch size = 125.2841 ha. The 95% confidence intervals are indicated.



5.4 DISCUSSION

Tick densities were higher in grazing agricultural (GA) (e.g., grazing pastures) and non-grazing agricultural (e.g., orchards, vineyards) (NGA) areas than in low human impact areas (LH). Smaller patches of habitat areas had higher tick densities, while landscape contexts formed by GA and NGA had higher tick densities than in LH contexts. As well, NGA contexts had higher densities than GA contexts (Table 5.3, 5.4). Ticks densities decreased with higher temperatures, reflecting the temperature sensitivity of ticks (20, 53, 73). Our results are consistent with previous research suggesting that smaller patch sizes and human-mediated landscape contexts may increase tick densities and pose a human health risk (2, 7, 59, 60).

However, in contrast to previous research, we examined the influence of patch size and landscape context together, which allowed us to distinguish their influence on tick densities. While patch size was significantly related to tick densities, it was a weak relation, where only large changes in patch size lead to differences in tick densities: a decrease in one hectare of a patch lead to a decrease of 0.004 ticks·(100 m^{-2}). In contrast, differences in landscape context had strong effects, such that a given land use practice could lead to significantly different tick densities in the area: NGA sites had on average tick densities three times higher than in GA sites, and >25 times higher than LH sites (Figure 5.3). Hence, our results suggest that the distribution of tick densities and thus the infection risk of tick-borne zoonoses may be predicted by both patch size and landscape context, but that the latter may have more predictive power.

Previous research also found that ticks densities were correlated to changes in patch size, but found a stronger relation than the one identified in this paper: Allan et al. (2003) found that small patches had up to three times more ticks than large patches. The comparatively weak relation of fragmentation with tick densities that we identified may be due to non-linear effects that occur at small patches as opposed to large patches. The range of patch sizes Allan et al. (2003) studied differed from our own: where their patches spanned 0.7 – 7.6 ha, ours spanned 4.2 – 253 ha; they also considered small patches to be those <1.2 ha. Due to the availability of study sites in the South Okanagan, we were not able to examine the same range of smaller patches: our study sites were dominantly mid-sized (i.e., 20-50 ha) and large (i.e., >100 ha), with only a few small patches. As a result, we did not capture the same relation over small patches as observed in previous works.

Instead, we found that landscape context had a strong influence at the larger spatial scale we examined. This may be because the effects of activities associated to land use practices (e.g., irrigation, food subsidies, pesticides, cattle grazing) are not restricted to their immediate location, and affect habitat suitability over a larger area. In contrast, the effects of patch size are more isolated, directly affecting tick and wildlife populations, and are also limited by the range of movement of the wildlife within them (e.g., rodents and deer). Hence, although patch size will influence tick densities, when examining large spatial scales (>50 ha), the influence of the landscape context of land use practices may be more effective in predicting the distribution of tick densities.

However, predicting the influence of a particular land use practice and its landscape context on tick densities may not be straightforward. Given the higher aggregation of potential tick hosts (e.g., deer mice, deer, cattle), it was not surprising that habitat patches within both GA and NGA contexts had higher tick densities than patches within the LH context. Yet, we found that patches within NGA contexts had higher tick densities than patches within GA contexts. This result was non-intuitive, because, although higher tick densities in NGA contexts could occur with the attraction of wildlife (e.g., deer) to those patches, the positive influence on tick densities could be counterbalanced by the application of pesticides and the presence of domestic predators (e.g., cats) on small mammals. In contrast, GA contexts have higher densities of livestock and thus more potential tick hosts, suggesting that tick populations would be higher in GA contexts than in NGA contexts.

The difference between habitat patches within GA and NGA sites may be understood by examining the specific characteristics of the sites themselves and the impacts on the wildlife within them. In particular, tick densities may be influenced by characteristics that do not influence them directly, but their potential hosts, such as the following: the proximity to water sources (e.g., lakes); the availability of food subsidies (e.g., grazing in orchards and vineyards); or the security from predators (e.g., coyotes). These characteristics may be positively correlated to densities of large mammals. Unfortunately, our study design could not effectively test the influence these characteristics due to the lack of sample size (i.e., only two of the field sites were close to large water bodies and had differing tick densities). However, our field observations suggest that they may be significant covariates that future research may examine systematically in relation to patch size and land use type.

Generally, we hypothesize that the influence of land uses on tick densities may be in part predicted by their influence on large mammals that can act tick hosts: land uses that attract higher densities of large mammals will likely have higher densities of ticks. Indeed, the region of the SO we examined has numerous feral horses within the NGA contexts—which appeared to be the result of the characteristics of the area; as a result, the density of large mammals in smaller NGA patches may have been much larger than would be observed with deer alone. As support to our hypothesized relationship of tick densities to the presence of large mammals, the highest tick numbers were encountered (e.g., a maximum number of 70 ticks after one drag) when walking around areas that were also clearly used by feral horses (i.e., there was evidence of horse dung and horse trails). In addition, most NGA contexts are located next to water bodies (i.e., Okanagan River and the lakes next to them); wildlife must cross the NGA contexts (and the habitat patches therein) in order to access the water. In contrast, GA contexts tend to be in areas where the main source of water is brought in for the livestock, and that water is not as much of an attractor for wildlife. Consequently, the net amount of potential hosts in NGA contexts is larger than in GA contexts, contributing to the larger tick densities.

Thus, the higher tick densities in NGA landscape contexts than in GA landscape contexts is likely a result of aspects of the South Okanagan based on its ecology and wildlife that we were not able to systematically test. Other regions will differ in what characteristic will have the greatest influence on tick densities. For instance, habitat suitability may play a larger role in tick densities than the net large mammal density: in residential areas, where, even though deer may be present, there is not suitable habitat for ticks. More specifically, there may be other covariates that we did not examine which may influence tick densities directly and have strong influence, such as the suitability of the microhabitat within the soil. As ticks spend over 90% of their life off-host, and much of that being dormant within the soil, their survival would highly depend on the abiotic and biotic features of the soil ecology, from the humidity (e.g., moisture retention of the soil) to the presence of arthropod predators (e.g., ants, spiders) (53); the influence of these features are poorly understood and need to be further investigated in future studies Hence, predicting the specific impact of a land use practice will thus be context-dependent and vary from region to region, and will have to be based on an understanding of the effects of the practice on ticks and the wildlife they depend on.

As discussed in more detail in Chapter 3, the sampling period and times chosen for this study may also explain why we collected only adult *Dermacentor andersoni* ticks in the SO. The

SO is a region that is very arid and hot—the temperatures can often be in excess of 30 ^{o}C and precipitation only rarely occurs. In these conditions, only the hardiest ticks will be active. *Ixodes spp.* are more sensitive to heat than *Dermacentor andersoni*, contributing to the former's rarity (53, 72); similarly, adult ticks are more able to withstand heat than nymph ticks. Certainly, *Ixodes spp.* and nymph ticks are present in the region (70); some works suggest that nymph tick populations are higher in smaller patches given the higher abundance of available hosts (2, but see 88). However, *Ixodes spp.* and nymphs are likely more active in cooler months (e.g., January-March) and at earlier hours in the day (e.g., 4-6 am), that is, when we were not flagging for ticks. As well, recent species modeling of *Ixodes spp.* in BC suggest that they are located mainly on the Pacific Coast of the province (44).

Importantly, even though we found mainly adult *Dermacentor andersoni* ticks, the infection risk of tick-borne zoonoses is still present. Nymph ticks are believed to be more dangerous than adult ticks, as they are smaller and harder to locate and remove if they become attached to a human (83). Similarly, it is also believed that Lyme disease is principally transmitted by *Ixodes spp.* Nonetheless, adult ticks still pose an infection risk of tick-borne zoonoses, as they are still competent in transmitting diseases (72); and, despite their larger size, they may still elude discovery, especially in children. As well, *Dermacentor andersoni* can transmit other diseases, such as *Rickettsia rickettsii*, which can be fatal. Past research in the South Okanagan have identified tick-borne pathogens in ticks that have been collected, such as *Anaplasma phagocytophilum, Rickettsia rickettsii*; however, as we found in Chapter 3, the prevalence of the diseases is low (i.e., <0.1% of ticks are infected) (5, 15, 51).

Our results have management implications for the control of ticks and the prevention of tick-borne zoonoses for humans and livestock. Notably, many of the study sites that had high densities of ticks were easily accessible areas that are used for recreational and occupational purposes. As a result, in those areas, there is a high probability of tick-human encounters and human exposure to tick-borne zoonoses. Predicting the locations of high-tick density areas from an understanding of habitat patch size and landscape context can help guide strategies to reduce tick densities. Strategies may include modifying or limiting land use practices that promote situations where there could be an aggregation of large hosts (e.g., relocating calving areas; controlled burns) (28). In a similar vein, increasing areas of unfragmented conserved habitat areas may also lower large mammal aggregation (30). These, however, require changes in existing land use practices and thus public acceptance, which may limit the strategies' feasibility.

Other targeted measures may be necessary to reduce tick densities (e.g., cattle dusting; application of pesticides on deer using specialized devices) and have been shown to be effective as part of an integrated pest management strategy (37, 49). Most importantly, increasing public awareness in high-tick regions may be effective (e.g., signs at trail heads and access points), as well as promoting personal protective measures (e.g., self-checks, tucking pants into socks) (63).

Thus, agricultural practices can increase tick densities and the infection risk of tick-borne zoonoses by fragmenting habitat into smaller patches and by creating landscape contexts that influence the ecosystems within them. Our results suggest that smaller habitat patches have a weak influence on tick densities, while differences in landscape context have a stronger influence on tick densities. However, these results may be applicable only at larger spatial scales (>50 ha), while at smaller spatial scales the effect of fragmentation and small patch sizes may be more salient. As well, we found that land use practices that increase the presence of large mammals in the area will increase tick densities due to the greater presence of potential hosts. Indeed, the results of Chapter 4 illustrate how large quantities of large hosts can result in much higher tick densities, such that measures that reduce nymph ticks and larvae may be effective in controlling overall tick densities. In our study area, higher tick densities was found in habitat patches located within non-grazing agricultural areas than within grazing agricultural areas, but this may be the result of specific characteristics of the South Okanagan. Nevertheless, our results demonstrate that, with an understanding of the effects of land use practices on ticks and their habitats, the distribution and density of ticks may be predicted and the infection risk of tick-borne zoonoses be managed for humans and livestock.

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CHAPTER 6: The Adoption of Protective Practices Against Ticks and Tick-Borne Diseases in the South Okanagan[5]

6.1 INTRODUCTION

Reducing the risk of infection to tick-borne diseases (e.g., Lyme disease) poses a risk communication challenge: though the risk can be lowered through the adoption of personal protective practices (20, 56), the general public does not regularly adopt these practices (37, 64), there continue to be cases of tick-borne diseases reported each year (35, 38), and public awareness and concern regarding the diseases is increasing (1, 15, 61, 75). This suggests that current risk communication strategies have not been effective. How, then, should information about ticks and tick-borne diseases be communicated to maximize public adoption and minimize concern? We present research that improves our understanding of the public's knowledge of and attitudes towards ticks, which suggest future avenues for risk communication strategies, as well as further in-depth risk perception studies.

Tick-borne diseases are among the most frequently contracted zoonoses in North America, that is, diseases that usually reside in wild or domestic animals but can be transmitted to humans (60, 78). They are transmitted by ticks, an obligate arthropod ecto-parasite. Lyme disease, caused by the spirochete *Borrelia burgdorferi s.l.*, is diagnosed on average in over 20,000 new patients per year in the United States and 70 new patients in Canada (35, 50). It is endemic in the north-east of North America, and is also present in Europe and Asia (38, 57). Though treatable, Lyme disease can have devastating effects if not diagnosed and treated in a timely manner (23). Ticks can also transmit a wide variety of other diseases such as Rocky Mountain Spotted Fever and Tick-borne encephalitis (31, 45). These diseases are usually associated with particular tick species (e.g., Lyme disease is principally associated with *Ixodes spp.)* that are located in specific geographic areas (52, 59). However, numerous species of ticks are widespread and they can be encountered nearly everywhere, including sub-Arctic locations (e.g., Alaska, Northern Russia) (31).

Given the wide variety of diseases ticks transmit and their ubiquity, tick-borne diseases pose a risk to human health. Indeed, recent research suggests that the incidence of tick-borne diseases will potentially increase as human populations continue to move into the interface between human and wildlife areas, where the likelihood of encountering ticks is higher (19, 53,

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73). This is due not only to increased recreation in wildlife areas (e.g., hiking), but also occupational practices (e.g., logging) that expose humans to ticks. Compounding the risk, human practices, climate change, and modification of the environment may be making more areas suitable for ticks, thus widening their distribution (12, 26, 33, 51, 74, 79). Hence, tick-borne diseases pose a growing risk to human populations living, working and recreating in rural and wilderness areas.

On a positive note, personal protective practices against ticks can effectively prevent ticks from becoming attached in the first place, thus reducing the risk of infection to tick-borne diseases. Preventing tick attachment simply involves tucking socks into pants, wearing repellent, and performing self-checks (20, 56). In contrast to mosquitoes, the transmission of diseases from ticks to humans is not immediate, but occurs some time after the tick has attached itself—up to 24 hours after encountering a tick (66). Thus, if an attached tick is found rapidly and removed correctly, transmission of disease could be prevented. Notably, these protective practices apply only to hard ticks (e.g., *Ixodes spp.*) and not soft ticks (e.g., *Argas spp.*): hard ticks are diurnal and tend to be encountered in the open environment on bushes and in leaf-litter, while soft ticks are nocturnal and tend to be encountered in cellars or animal nests; since they are able to attach themselves rapidly, soft ticks take only a few hours to feed and transmit diseases (49).

Despite the simplicity of personal protective practices, they are not regularly adopted—even though there is often a good understanding of the severity of tick-borne diseases (37, 64). Of note, tick-borne diseases, especially Lyme disease, figure prominently in public discourse, from movies (e.g., *Under Our Skin*) to television shows (e.g., *Joan of Arcadia*) to news reports (14, 15, 21, 76, 80), suggesting that tick-borne diseases are known to be a potential risk and a source of concern. So, why is there not more widespread adoption of personal protective practices? The mismatch between knowledge of the risk and adoption of protective practices is found in other risks, such as cigarette smoking and driving (67). Studies have found that the individuals' risk perception and protective behaviour is affected by psychological factors, such as personal acceptance and familiarity of the risk (43, 67, 69). Indeed, previous work on the adoption of protective practices against ticks have suggested that lack of adoption may result from the perceived ineffectiveness of such practices (36), while adoption is influenced by social norms, such as the expectation of being a responsible parent (22).

While previous studies provide an understanding of the public adoption of protective practices against ticks, they have not examined the differences between the knowledge and

motivations of adopters and non-adopters and how these differences may improve future risk communication strategies. These motivations may be complex, and can help explain the risk perception of ticks and tick-borne diseases. To help understand them, interviews can be used to gain insight and to fill in the knowledge gaps that surveys and observations are unable to obtain on their own (25). As such, we conducted interviews to understand the public's knowledge and motivations, using an approach based on a mental models analysis; this is a systematic method designed to guide the development of risk communication strategies (48). Mental models analysis has been used in consideration of varied risks, such as flash floods and landslides, radon, and red tides (4, 40, 77). The analysis is based on the theory that an individual has a "mental model," or a conceptual map of ideas and concepts of a situation or a risk, which plays a role in determining the individual's behavioural response to risks. These mental models can be analyzed to determine how certain beliefs or attitudes lead to behaviours, which in turn facilitates more targeted risk communication. Notably, our approach does not constitute an in-depth mental models analysis, but is instead a preliminary analysis to gain an understanding of the public's knowledge and motivations (i.e., a knowledge schema) regarding ticks and tick-borne zoonoses. However, the understanding obtained from our preliminary approach may then be used to design surveys in future mental model analyses.

To develop an understanding of the reasons for the adoption of protective practices against ticks, we conducted interviews to elicit the knowledge schema about ticks and tick-borne diseases from residents of the South Okanagan, a region in Canada where there is increasing awareness of tick-borne diseases. Though tick-borne diseases in Canada are considered rare and emerging diseases (50), their medical and social importance is rising. We evaluated these knowledge schemas using an expert knowledge schema developed from a literature review and our experience conducting research on ticks. Importantly, we also examined the interviews for emergent themes that are not included in the expert knowledge schema, but may explain the motivations behind the adoption of protective practices.

6.2 METHODS

6.2.1 Study region

We conducted our research in the South Okanagan, a region in the province of British Columbia, Canada, spanning from Osoyoos to Kelowna (lat. 49 28.41 N, long. 119 35.43 W). The South Okanagan is a rapidly changing agricultural region, where residential and commercial developments have stimulated the local economy, bringing tourism and creating employment opportunities (13). As a result, the population has grown with the influx of new residents moving there for jobs or for retirement, resulting in an increase of residents who are unfamiliar with the region's environmental risks, such as ticks.

Though ticks are common in the region, tick-borne pathogens that have been identified (e.g., *Anaplasma phagocytophilum, Rickettsia rickettsii*) are at a low prevalence (i.e., <0.1% of hard ticks are infected) (6). However, if these diseases are contracted and left undiagnosed, they can have devastating physical and neurological effects (31). The British Columbia Center for Disease Control (BCCDC) has made available online risk communication material on ticks and tick-borne diseases (10), but public concern still appears to be elevated. Indeed, recent local news reports have reported the risk of tick-borne diseases and their impacts, suggesting there is an increasing awareness of the risks in the region (14, 44). In addition, regional members of the Canadian Lyme Disease Association (CLDA) are active in raising awareness of tick-borne diseases; the CLDA is a non-governmental organization composed of Canadian citizens concerned about Lyme disease, including individuals suffering from symptoms they believe to be caused by Lyme and other tick-borne diseases. They are also active in lobbying the provincial and federal health authorities to recognize tick-borne diseases more widely and to change diagnosis and treatment guidelines (32).

The presence of new residents unfamiliar with ticks, but who may be aware and concerned of tick-borne diseases, highlights the need for effective risk communication in the region, in order to help the public manage their exposure to ticks and risk of infection to tick-borne diseases.

6.2.2 Study participants

We recruited residents to participate in the study (n=30) using the authors' pre-existing contacts in the region, whom were asked to recruit acquaintances (i.e., snowball technique) (42). The participants consisted of 18 women and 12 men, who were members of the lay public. Included among the participants were two groups of people who were expected to have higher levels of knowledge about ticks due to their profession or exposure to tick-borne diseases: 6 CLDA members, and 6 health practitioners (HP). The HP consisted of 3 nurses and 3 doctors. Though these two groups may have higher levels of knowledge of ticks and tick-borne diseases, they are not experts and still members of the lay public. As well, the two groups are more directly impacted by tick-borne diseases, and were thus included to represent the range of interests of the public.

The participants had differing levels of adoption of protective practices, and represented the wide range of activity and employment in the region, from retirees to park rangers, ranging in age between 20 and 65. Participants differed in the following attributes: concern regarding tick-borne diseases, length of residence in the area, and experience with ticks (Table 6.1). These attributes were examined as they may be related to adoption in the following ways: greater concern may encourage protective practices; longer residence in the region may raise awareness of local environmental hazards, as well as the protective practices against them; and, increased experience with ticks may result in more familiarity with ticks and knowledge of protective practices.

6.2.3 Study design

We constructed an expert knowledge schema of ticks and tick-borne diseases, which we used to evaluate the knowledge schemas of the participants. An expert knowledge schema is a model of the best scientific understanding of the process of exposure, infection, and protection for a given risk—in this case, ticks and tick-borne diseases (48). The model is used to evaluate the understanding of non-experts regarding a risk. We based the expert knowledge schema on a systematic literature review and our experience conducting field work on ticks (20, 52, 56, 59, 60, 78). Our model has three content areas relevant to the adoption of protective practices (Figure 6.1): tick ecology, tick-borne diseases, and protective practices and health care.

The tick ecology content area included the following concepts: tick hosts; season or time of tick activity; tick habitat; and, the means by which ticks come into contact with humans. Knowledge of tick hosts (e.g., deer, rodents) can be used to predict tick distributions: for example, if an individual is active in an area with many deer, an expectation of tick encounters should lead to the adoption of protective measures. Similarly, knowing when ticks tend to be active (i.e., spring, autumn or cooler months) and their preferred habitat (i.e., shrub-dominated areas) would spur the adoption of protective practices at relevant times of year and areas. Finally, knowledge of how ticks come into contact with humans (i.e., by physical contact, such as by brushing by a blade of grass or shrub—not by jumping or falling from trees) helps predict when tick attachment may happen; this knowledge also informs the types of protective practices that are effective.

The tick-borne disease content area included the following concepts: the process of disease transmission; the proportion of ticks and hosts infected with tick-borne diseases; the severity of tick-borne diseases; and the personal risk of infection to tick-borne diseases. Knowledge of how ticks transmit disease contributes to beliefs in the effectiveness of protective practices, such as self-checks; knowing that ticks take a long time to transmit diseases leads to the belief that ticks found and removed promptly could prevent tick-borne diseases. Knowing that not all ticks or hosts are infected with tick-borne diseases provides an understanding of the prevalence of tick-borne diseases in the environment, and leads to the belief that a tick-bite will not necessarily lead to the transmission of diseases. Knowledge of tick-borne diseases and their health impacts contributes to individuals' concern of tick-borne diseases, affecting their likelihood of adopting protective practices. Risk perception of tick-borne diseases is a product of knowledge of the prevalence and severity of the diseases. However, personal beliefs may also influence risk perception (e.g., the individual may feel confident in avoiding ticks or tick-infested areas). Hence, we also included the perception of personal risk within the tick-borne disease content area.

The protective practices and health care content area included the following concepts: knowledge of personal protective practices; ability to recognize ticks; method of tick-removal; and, diagnosis and treatment of tick-borne diseases. Knowledge of personal protective practices certainly plays an important role in the belief in one's ability to protect oneself, but more importantly, there may be knowledge of inaccurate methods (e.g., looking in trees) that may provide a false sense of protection. In the same vein, the ability to identify ticks will influence

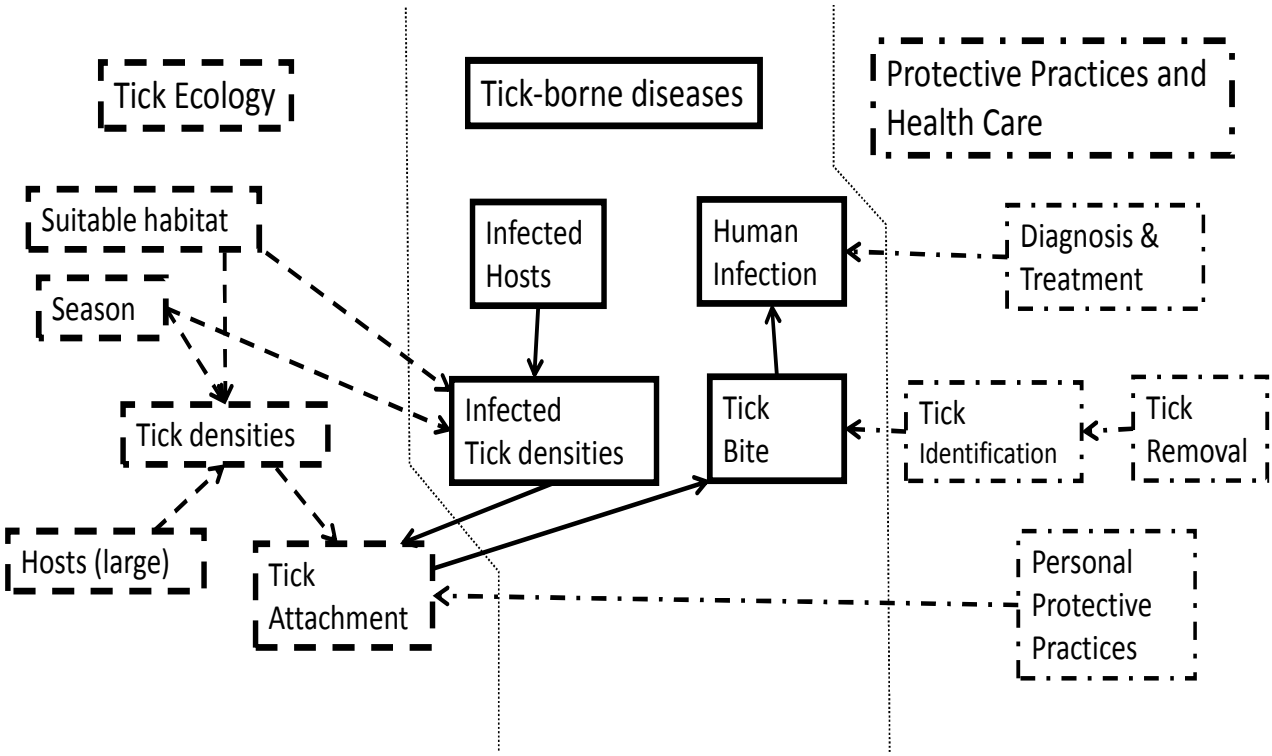
Table 6.1: Description of participants by their attributes

The participants are described by the following attributes: adoption of protective practices; level of concern regarding tick-borne diseases; length of residence in the region; and experience with ticks. These attributes were further described separately for HP, for CLDA members, and for the non-experts, that is residents who were neither health practitioners (HP) nor CLDA members.

	Adoption of protective practices			Level of concern			Length of residence			Experience with ticks		
Participant	Adopt	Adopt infrequently	Not adopt	High	Low, but aware	Not concerned	>5 years	1-5 years	<1 year	Frequent encounters	Rare encounters	Never
All participants	13	8	9	5	10	15	17	4	3	4	15	11
Non-experts	6	5	7	0	9	9	13	3	2	4	5	9
HP	2	2	2	0	0	6	4	1	1	0	4	2
CLDA members	5	1	0	5	1	0	6	0	0	0	6	0

Figure 6.1: The expert knowledge schema of ticks and tick-borne diseases

The knowledge schema is divided into three content areas divided by thin pale dotted lines: the tick ecology content area is indicated by the concepts in thick dashed lines; the tick-borne diseases content area is indicated by concepts in solid lines; and, the protective practices and health care content area is indicated by concepts in dash-dot lines. The relationship of the concepts in the knowledge schema are shown by directional arrows.



whether the adoption of protective practices would be effective, or if they would be adopted at all. As well, if someone is unfamiliar with ticks, finding one on their clothes or attached to their skin may trigger dangerous reactions to get rid of the tick (e.g., burning or cutting). Following this reasoning, knowing how to remove an attached tick (i.e., gentle, firm pulling from where the mouth parts attach to the skin) would reduce the risk of infection, and also increase an individual's confidence in being able to manage their risk to ticks, rather than seek medical attention. Finally, knowing whether tick-borne diseases are difficult or easy to diagnose and treat will influence an individual's level of concern regarding the diseases; if the disease is untreatable, it may increase the desire to avoid them by adopting protective practices.

Based on the expert knowledge schema, we conducted semi-structured interviews with the study participants to elicit their knowledge schemas; the interviews were all conducted by the first author (JT) and were 40-90 minutes in length. The interviews were semi-structured in that they were generally ordered around the three content areas of the knowledge schema, but the order of the interview questions depended on the responses of the interviewee, which resulted from open-ended interview questions. The interviewer avoided leading questions by beginning with broad questions (e.g., what do you know about ticks?), which were then followed by questions that either prompted the participant for concepts they did not cover (e.g., when do you encounter ticks?), or asked them to elaborate a concept previously mentioned (e.g., could you describe how to remove a tick?). The interview questions aimed to obtain responses for each of the concepts in the three content areas of the expert knowledge schema (see section 6.5 Interview Questions).

However, given that expert knowledge schemas are idealized models of scientific understanding, they often do not account for other aspects that may explain non-expert motivations and understanding. These can be obtained by identifying other concepts and themes that emerge from the interviews and that were not expected from the expert knowledge schema. To this end, during the interviews, we asked the participants to elaborate on new concepts and themes related to ticks and tick-borne diseases, but were not contained in the expert knowledge schema. We also asked participants to contextualize ticks and tick-borne diseases by comparing ticks and another potential disease vector in the region, mosquitoes, and by comparing tick-borne diseases with mosquito-borne diseases, particularly West Nile virus.

The interviews were transcribed and analyzed using the software NVivo8. The knowledge schemas of each participant were evaluated by identifying their responses to the

concepts in each content area in comparison to the expert knowledge schema (48). We also recoded themes and concepts that emerged during the interviews and were recurring concerns that may contribute to explaining the patterns we observed. The concepts that were correct and incorrect based on the expert model were scored separately with a value of 1, and summed for each content area; the scoring process was iterative in order to ensure consistency and to observe emergent themes. For instance, if the interviewee responded that ticks were most likely present in the summer months (i.e., June-August) as opposed to the cooler months of spring and fall, then the interviewee would have a score of 1 for the incorrect concept of the season or time of activity of ticks within the tick ecology content area. We then obtained a summed total score for each participants' correct and incorrect concepts within each of the content areas of the knowledge schema. We took this approach as we observed that conflicting concepts can often co-exist in a knowledge schema (e.g., the belief that ticks fall from trees as well as reside in bushes), and thus participants could conceivably have a high level of correct concepts, but also a high level of incorrect concepts. Importantly, the terms "correct" and "incorrect" may be inaccurate and better understood as social constructions; they are based on currently available scientific information, which, as further seen below, can be in contention, particularly aspects regarding the prevalence, diagnosis and treatment of tick-borne diseases.

To determine potential reasons for adoption, we examined the differences among the participants' correct and incorrect content areas of their knowledge schemas. We used Fisher's exact tests and one-way analyses of variance (ANOVA) to identify significant associations between adoption practices and participant attributes, and also identify differences between the correct and incorrect content areas of the participants' knowledge schemas. We used Fisher's exact test, because the contingency matrices we examined had values in the cells that were lower than 5, making Chi-square tests unsuitable (27).

6.3. RESULTS

6.3.1 Differences among participant knowledge schemas

6.3.1.1 Comparing all the participants together

We began by examining whether differences in the adoption of protective practices are related to differences in the participants' knowledge schemas about ticks and tick-borne diseases. When we grouped the participants by their adoption practices, however, there were no significant differences among either the correct or incorrect content areas of the knowledge schemas (Table 6.2). This suggests that adoption is not directly related to differences in the knowledge schemas or to the knowledge of ticks and tick-borne diseases, but rather the result of other attributes of the participants, such as the level of concern regarding tick-borne diseases, the length of residence in the region, and the amount of experience with ticks.

We found that all of the attributes are significantly associated to the adoption of protective practices ($p<0.05$, Table 6.3). We then systematically grouped the participants by their attributes and again examined whether there were differences among their knowledge schemas (Table 6.2). When participants were grouped by length of residence, there were no differences. However, there were two notable differences when participants were grouped by level of experience and concern.

Grouped by level of experience, there were differences in the correct protective practices, where greater experience was related to a more accurate protective practices content area—particularly a higher awareness of how to identify ticks and what to do if a tick is attached ($p<0.01$). The knowledge of protective practices in participants with greater experience of ticks is not surprising, as frequent exposure to ticks should result in better protective measures, especially in the ability to identify ticks. Indeed, participants who rarely or never encounter ticks often had low or incorrect knowledge of protective practices, such that they were not certain they could identify ticks, and often reported improper ways to protect themselves (e.g., looking

Table 6.2: Results of one-way ANOVAs between the correct and incorrect content areas of the knowledge schemas

We used the mean scores of the participants when they were grouped by differences in the four attributes from Table 6.1; we also used the means when they were all grouped by type (i.e., non-experts, HP and CLDA members), and when they were only grouped by HP and CLDA members. The values in the table indicate the values of $F(df_M, df_R)$ followed by p: for all cases, *F(2, 27)*, unless otherwise indicated beside the attribute examined. Shaded cells indicate significant differences in the knowledge schema.

	Attribute	Tick Ecology		Tick-Borne Diseases		Protective Practices and Health Care	
		Correct	Incorrect	Correct	Incorrect	Correct	Incorrect
All participants: *F(2, 27)*	Adoption	0.93, >0.1	2.83, >0.05	0.61, >0.5	0.78, >0.1	1.28, >0.1	0.41, >0.5
	Level of concern	0.20, >0.5	0.20, >0.52	2.78, >0.05	**9.85, <0.01**	2.37, >0.1	0.49, >0.5
	Length of residence	0.45, >0.5	1.28, >0.1	1.28, >0.1	1.29, >0.1	1.97, >0.1	1.29, >0.1
	Experience with ticks	1.15, >0.1	0.19, >0.5	3.11, >0.05	1.05, >0.1	**7.12, <0.01**	2.50, <0.1
	Type (all)	0.06, >0.5	1.25, >0.1	1.94, >0.1	**9.30, <0.01**	1.29, >0.1	1.06, >0.1
	Type (HP and CLDA) *F(1,10)*	0, >0.5	0.09, >0.5	3.91, >0.05	**24, <0.01**	0.62, >0.1	0.77, >0.1

Table 6.3: Relation between differences of adoption and the other three attributes that describe the participants

We used Fisher's exact test with *df*=4 to compare adoption to the following attributes: experience with ticks; level of concern regarding tick-borne diseases; and, length of residence in the region. Attributes and values bolded and with a * indicate significant associations.

	Attribute	*p*	
All participants:	**Level of concern**	**<0.05**	*
	Length of residence	**<0.005**	*
	Experience with ticks	**<0.01**	*
Non-experts:	**Level of concern**	**0.052**	*
	Length of residence	>0.1	
	Experience with ticks	>0.05	
Health practitioner and CLDA members:	Level of concern	>0.05	
	Length of residence	**<0.05**	*
	Experience with ticks	>0.1	

up when walking in the forest, removing ticks by covering the tick in oil or by squeezing them).

Grouped by level of concern, there were differences in the incorrect tick-borne disease content area of the knowledge schema ($p<0.01$). Higher levels of concern are associated with more incorrect tick-borne disease knowledge schemas. Incorrect knowledge included perceptions that the prevalence of tick-borne diseases was higher and that the diseases would have more long-term impacts than that stated by the medical and scientific community.

The differences regarding incorrect knowledge of tick-borne diseases result may be explained by the differences between HP and CLDA members, where the latter are more concerned about tick-borne diseases than the former. Specifically, observations during the interviews suggest that the two groups differ in terms of the concepts regarding the prevalence, diagnosis and treatment of tick-borne diseases (e.g., CLDA members believe the prevalence of tick-borne diseases is higher than stated by the scientific literature) (9, 18). This difference in the incorrect tick-borne disease knowledge schema is better described not as conceptual errors, but as a representation of an unresolved issue.

6.3.1.2 Comparing the HP, CLDA members and non-experts separately

The previous results were obtained by considering all the participants together. However, HP and CLDA members appeared to have different knowledge schemas than the other residents due to their higher experience with tick-borne diseases or familiarity with literature related to tick-borne diseases. Importantly, the differences between the HP and the CLDA members may be masking some of the differences among the other residents (henceforth termed, "non-experts"). To distinguish this, we examined the knowledge schemas of the participants when grouped by type (i.e., HP, CLDA members, and non-experts), and also when the HP and CLDA members were grouped separately (Table 6.2). In both cases, we again found only a difference in the incorrect tick-borne disease content area, following the same trends as before ($p<0.01$). This result was confirmed when we separately compared the HP and CLDA members when grouped by their attributes ($p<0.01$, Table 6.4), suggesting that the strong differences between the HP and CLDA members may be dominating the observed differences in the knowledge schemas when all the participants are grouped together.

We thus examined the non-experts separately from the HP and the CLDA members. Much as before, when the non-experts were grouped by adoption, there were no differences in

the knowledge schemas; this suggests that non-experts' attributes have a stronger role in determining their knowledge schemas. We then tested the relationship of adoption to the non-experts' attributes using Fisher's exact test, finding that only the level of experience with ticks is significantly associated to adoption ($p<0.05$, Table 6.2). This result was confirmed when we analyzed non-experts when they were grouped by their attributes (Table 6.4): grouping the non-experts by level of concern and length of residence reproduced previous results that were related to the correct content area of protective practices; however, we found that grouping the non-experts by level of experience with ticks revealed numerous differences in the content areas of the knowledge schema.

When the non-experts were grouped by experience, we found significant differences in the following content areas ($p<0.05$): correct tick-ecology; correct and incorrect tick-borne diseases; and, correct protective practices and health care. Intriguingly, while non-experts with higher experience have more correct understanding of tick-ecology and protective practices (e.g., knowing when and where to aware of ticks, and how to avoid them), they have the least correct understanding of tick-borne diseases—sometimes not even knowing any tick-borne diseases (Table 6.5).

In other words, our results suggest that communicating information about tick-borne diseases may not have a strong influence on the adoption of protective practices. Instead, having a good understanding of tick ecology may have greater influence. These trends may be explained by the emergent themes we describe in the following section.

6.3.2 Emergent themes

Two themes emerged from the interviews and were not predicted by the expert knowledge schema: fear and disgust of ticks; and, doctor mistrust. The first theme contributes to explaining how adoption of protective practices tends to be associated with non-experts who have more experience with ticks, but less understanding of tick-borne diseases. The second theme contributes to explaining the difference between the HP and the CLDA members in the incorrect tick-borne disease content area of their knowledge schemas.

Table 6.4: Results of one-way ANOVAs in the content areas of the knowledge schema

This table reports the ANOVAs where the participants are isolated into two groups: non-experts; and health practitioners and CLDA members. The values in the table indicate the values of $F(df_M, df_R)$ followed by p: for non-experts *F(2, 15)* and for HP and CLDA members *F(2, 9)*, unless otherwise indicated beside the attribute examined. Shaded cells indicate significant differences in the knowledge schema; the bold box indicates the significant differences among the non-experts as grouped by experience, which are detailed in Table 6.5.

	Attribute	Tick Ecology		Tick-Borne Diseases		Protective Practices and Health Care	
		Correct	Incorrect	Correct	Incorrect	Correct	Incorrect
Non-experts: *F(2, 15)*	Adoption	2.46, >0.1	1.54, >0.1	0.64, >0.5	0.02, >0.5	**7.13, <0.01**	1.09, >0.1
	Level of concern, *F(1,16)*	0.64, >0.1	0.05, >0.5	1.69, >0.1	3.06, >0.05	**4.35, =0.053**	0.13, >0.5
	Length of residence	0.53, >0.5	1.31, >0.1	1.38, >0.1	0.44, >0.5	**4.89, <0.05**	2.01, >0.1
	Experience with ticks	**4.10, <0.05**	1.30, >0.1	**3.81, <0.05**	**3.66, =0.0507**	**6.10, <0.05**	2.04, >0.1
HP and CLDA members: *F(2, 9)*	Adoption	0.73, >0.5	1.33, >0.1	0.90, >0.1	2.67, >0.1	0.26, >0.5	0.48, >0.5
	Level of concern	0.76, >0.1	0.52, >0.5	2.52, >0.1	**11.78, <0.01**	0.40, >0.5	0.71, >0.5
	Length of residence	0.03, >0.5	0.77, >0.1	1.21, >0.1	0.81, >0.1	0.70, >0.5	0.62, >0.5
	Experience with ticks, *F(1,10)*	0.36, >0.5	0.49, >0.1	1.85, >0.1	0, >0.5	2.32, >0.1	2.31, >0.1

Table 6.5: Details of the one-way ANOVAs for the different content areas of the knowledge schema conducted on non-experts

This table reports the mean and confidence intervals for each group of different experience from the non-experts, which was indicated in the bold box in Table 6.4. The stars indicate the content areas that contained significant differences; and, to illustrate the trends in the differences among the participants, the dark shaded cells denote the groups with the highest values for the significantly different content areas, while the lightly hatched cells denote the groups with the lowest values. Note how non-experts with high experience have more accurate knowledge schemas of tick ecology, but the most inaccurate ones of tick-borne diseases.

	Tick Ecology		Tick-Borne Diseases		Protective Practices and Health Care	
	Correct **	Incorrect	**Correct ****	**Incorrect ****	**Correct ****	Incorrect
Frequent encounters	**3.50±0.40**	1.00±0.20	**2.00±0.39**	**2.00±0.32**	**3.75±0.15**	0.63±0.19
Rare encounters	3.33±0.53	1.33±0.86	2.50±0.56	1.75±0.54	3.67±0.21	1.17±0.45
Never	**2.25±0.25**	2.00±2.61	**3.25±0.25**	**0.75±0.25**	**2.75±0.25**	1.25±0.25

6.3.2.1 Fear and disgust of ticks

A theme that emerged from the interviews was that ticks were "creepy" or "disgusting." During the interviews, this theme emerged most clearly when the participants compared their concerns of ticks and mosquitoes from a strictly ecological and physical perspective (i.e., comparing the arthropods themselves, their habitat, and their behaviour). When they described their concerns and the reasons for them, nearly all the participants (i.e., not only CLDA members) expressed some form of fear or disgust regarding ticks, with the notable exception of the participants who had frequent encounters with them.

A recurring concern was how ticks attached themselves to humans: participants were concerned that ticks would "burrow" or "embed" themselves under the skin. Referring to the way ticks attach themselves was usually followed by facial expressions of disgust or shudders. When asked to further develop their comments, participants raised a related concern regarding their ability to remove an attached tick, worrying that even if they did remove it, "its head may be stuck inside" them, and require a health practitioner to properly remove it. Likely as a result of this concern, many were not comfortable with the idea of removing the ticks themselves and would seek medical attention.

Another concern was the unpredictability of ticks, as "you never know when you're going to find one," since they are elusive in their behaviour in comparison to mosquitoes. Mosquitoes announce their presence with buzzing, or are clearly visible, or have a painful bite that participants can respond to. Ticks, meanwhile, are hard to avoid and "something you just can't get away from when you're out there," as they are rarely observable in their natural habitat, and suddenly appear on clothing. As well, the tick bite itself is not noticeable, so ticks can attach to the participant's flesh without causing any sensation. Similarly, participants often compared the mosquitoes' flying in the air to the ticks' crawling on clothes or skin, which often raised reactions of disgust. Besides ticks' behaviour, participants also reported that they had more cause to be afraid of ticks than mosquitoes, as they differ in their survivability: while mosquitoes could be easily killed by swatting or crushing, ticks are "hard to kill," being able to survive crushing, and require isolated force (e.g., a pin or pen) or fire. The following excerpt represents typical comments regarding ticks:

> "(...) because you don't notice them. You may not notice them at first and suddenly you have them crawling on you. With mosquitoes you can see them flying around that you're

> more aware of them flying around. Whereas if you see a tick crawling up your leg you don't know when it got there and I think there's a certain feeling of invasion of privacy."

In contrast, participants who had higher experience with ticks did not express similar feelings of fear or disgust regarding ticks. Most shrugged and considered them to be "just another bug" that was common in the environment, considering mosquitoes to be more of an issue, as they are annoying; indeed, "there are lots of other things to be worried about in the Okanagan" (e.g., black widow spiders, rattlesnakes). These participants also considered ticks to be a regular part of life in the Okanagan, and "the price of admission" and something to be aware of during times ticks are active, when it was common practice to adopt protective practices, as "it was something they just did." One resident with a great deal of experience with ticks made the representative statement,

> "But as long as we have wild animals and—I hope there will be forever—nearby, then we're going to have wild animal parasites, and one of them happens to be ticks and that's just one of the consequences of living here. This is one of the aspects of living here in the Okanagan. That's just part of life here."

This theme of fear and disgust of ticks suggests that the adoption of protective practices is related to attitudes and feelings regarding ticks. Feeling that ticks are a part of the environment may make the adoption of protective practices seem normal and common; whereas feeling that ticks are unpredictable and fearsome may make the adoption of protective practices seem abnormal and uncommon.

6.3.2.2. Doctor mistrust

Another theme was doctor mistrust, regarding both their ability to diagnose tick-borne diseases and their treatment of patients. This theme was present most obviously among the CLDA members; but, it was also present amongst all of the participants, regardless of the level of experience with ticks: over half of non-CLDA participants—including the three health practitioners who were nurses—mentioned doctor mistrust in reference to tick-borne diseases. The theme tended to emerge when we asked the participants to compare their concern of tick-borne diseases and mosquito-borne diseases: most believe that tick-borne diseases are of greater concern and the effects potentially more severe than mosquito-borne diseases. When explaining

their reasons for being more concerned about tick-borne diseases, the concern was related to the severity of tick-borne diseases—which many perceived to be difficult to diagnose and would require long-term treatment.

However, the concern about tick-borne diseases was also related to doctors' ability to diagnose tick-borne diseases. Concerns about the doctors varied along a spectrum of doctor responsibility. On the low end of the responsibility spectrum, doctors' diagnostic ability was a technical issue that had to do with the tests or training available to doctors: doctors may not have access to the proper tests to detect tick-borne diseases; or, the doctors have not been trained properly to identify tick-borne diseases, as they may be coming from foreign locations without such diseases. On the high end of the responsibility spectrum, other participants suggested that doctors may be unwilling to recognize or treat tick-borne diseases due to liability issues or due to other regulatory bodies to which they are beholden (e.g., British Columbia College of Physicians). As a result of this mistrust, participants were concerned that tick-borne diseases are more prevalent, and that many have been misdiagnosed with other diseases. The following is an example of a comment from a participant:

> "I think there are many, many people out there suffering with so-called other things that are actually Lyme disease or its co-infections. The vast majority of people who are suffering from chronic fatigue... I'm not trying to find Lyme disease underneath everything... there are some people who have Parkinson's disease who have Parkinson's. But a portion of those people who have been diagnosed... I would put money on it that for sure they should be tested aggressively for Lyme disease."

An extension of doctor mistrust was a concern about doctors' treatment and respect of patients: there is a concern that doctors are unwilling to recognize or treat tick-borne diseases because they doubt the credibility of possible tick-borne disease sufferers. While this concern was expressed by all 6 of the CLDA members (based on their own experiences with doctors), it was also frequently expressed by non-experts who said that they heard it from someone who had experienced tick-borne diseases, or from another source, such as a media report. The following is an example of this concern about doctor treatment:

> "(My family doctor) happened to be away and she had a locum in for her and he just looked at me and asked me if I was depressed. I said, 'No, I am not depressed I am in a lot of pain.' And he would not let the depression go. He was horrible... my mother was bawling and couldn't believe a doctor could treat another person like that."

Finally, we also observed that comments regarding the doctor mistrust tend to be embedded in a narrative describing the experience of Lyme disease sufferers trying to be diagnosed and treated by doctors. The following is an example of the narrative from a participant who was not a CLDA member:

> "I have a friend who thought she had Lyme disease. They diagnosed her as several things. She finally went and paid for her own blood test to be tested in California. And it came positive with Lyme disease. And when they started treating her she was a cripple and could hardly walk and now she is walking and she is losing weight and it turned her around. So that is the one person that I know personally and see at least once a week. So I know her closely. So I do believe there is such a thing as Lyme disease."

The narrative was present in all of the CLDA members, and mentioned in varying levels of detail by 11 out of 24 of non-CLDA members. Common to the narrative is the inability of a sufferer to get diagnosed and a struggle for credibility with doctors that they have a tick-borne disease. This struggle is resolved when they are diagnosed and receive treatment involving antibiotics over long periods of time and that are expensive.

This theme of mistrust is related to the result that health practitioners and the CLDA members have differences in the incorrect tick-borne disease content area of their knowledge schemas. Given that this mistrust is present not only among CLDA members, but non-experts as well, it is important to consider in risk communication.

6.4 DISCUSSION

We studied the knowledge schemas about ticks and tick-borne diseases of residents in the South Okanagan in order to determine how differences in the beliefs and understanding about ticks may explain the adoption of protective practices against ticks. We found that differences in adoption did not reflect different knowledge schemas, suggesting that knowledge of ticks and tick-borne diseases does not directly lead to increased adoption practices. Instead, adoption was better explained by differences in experience with ticks, where participants with greater experience had increased adoption. However, we found the seemingly contradictory result that, while participants with greater experience tended to have more accurate understanding of tick ecology, they had a less accurate understanding of tick-borne diseases (Table 6.5). This may be explained by the theme of fear and disgust of ticks that emerged during interviews with participants with less experience with ticks: participants with less experience viewed ticks as a frightening hazard against which they felt unable to protect themselves against—a feeling that was heightened by knowledge of tick-borne diseases; in contrast, participants with more experience viewed ticks as a normal, non-fear-inducing part of the environment, and thus something against which it is normal to protect oneself—and where tick-borne diseases have less relevance than the ticks themselves. In other words, the attitudes and feelings regarding ticks, rather than the knowledge of tick-borne diseases, have a strong relationship to adoption practices. Further research may expand on these motivations and develop a better understanding of the public's risk perception using a more systematic mental models analysis, such as by conducting surveys that can verify the trends of our results (48). Indeed, given the limited sample size of the interviewees, these results may not reveal the full extent of the motivations behind the risk perception of ticks and tick-borne diseases. Thus, our results may be used to guide the development of a survey that may applied at a wider-scale and that could confirm the results and reveal other potential reasons for the adoption of protective practices.

The role of attitudes and feelings play a strong role in adoption (8, 43, 69), and, in the case of ticks and tick-borne diseases, is better understood by examining the relationship of fear to the adoption of protective practices. While fear can be a driver of protective practices, high levels of fear can lead to panic or even feelings of powerlessness against an overwhelming hazard (62). Indeed, risk communication strategies regularly face the challenge of balancing messages between raising concern to warrant action, and instilling calm so as not to cause panic (28). However, with ticks and tick-borne diseases, we found that the fear of ticks—even without

considering tick-borne diseases—was already elevated among participants with little experience with them, appearing to be rooted in a visceral reaction common with other arthropods (e.g., spiders) (29, 70). This fear seemed to dominate participants' perception of ticks to the extent that it also affected their belief of the manageability of the risk to ticks: participants often stated that ticks were impossible to avoid, such that protective practices would be useless. Hence, risk communication that emphasizes the dangers of tick-borne diseases with limited or no mention of the ticks may aggravate the fear of ticks and the feeling of powerlessness against them. This is consistent with previous works finding that adoption was low even with high understandings of tick-borne diseases (37), but may be more regularly practiced where tick-borne diseases are endemic and familiarity of ticks more common (36, 55, 64, 72).

Risk communication of tick-borne diseases may then be more effective if it first addresses the fear of ticks themselves before explaining the risks of tick-borne diseases and promoting protective practices. Individuals may view ticks with less fear and disgust if ticks were normalized as an unsurprising part of their environment. Familiarity is, of course, related to the regularity with which ticks are encountered, but this does not necessarily imply that people should be presented with large numbers of ticks as part of a risk communication strategy. Instead, our results suggest that familiarity is based on knowledge of tick ecology, such as when ticks are expected to be active, where they tend to be active, and how they come become attached. This knowledge renders tick encounters more predictable, and consequently makes tick avoidance a manageable possibility. This knowledge may allay some of the fears which make ticks appear unavoidable (e.g., ticks are present everywhere; ticks are active during hot weather; ticks fall from trees or are airborne). As well, knowing how ticks become attached may make individuals adopt correct practices, and more likely to examine their pant legs and keep from brushing them against shrubs and grasses, rather than looking up within trees and potentially missing an easily removable tick.

However, besides the role of fear and disgust of ticks, we also found widespread doctor mistrust, which can influence the effectiveness of risk communication (54, 65, 68). The mistrust was centered around Lyme disease, and had two aspects: doctors' inability to diagnose and treat Lyme disease and other tick-borne diseases—either due to a lack of training or unwillingness to do so; and, doctors' improper treatment and respect of possible Lyme disease sufferers that may involve a lack of respect or disbelief of their suffering. We found that most participants, regardless of their experience with ticks, and even all of the nurses, expressed some form of

doctor mistrust. Notably, though the higher levels of doctor mistrust may be correlated to the presence and activity of CLDA members in the South Okanagan, this concern is not unique to the area: doctor mistrust is widely present at the provincial and national level (15-17, 34), and described in an internationally distributed documentary (80). For these reasons, we feel doctor mistrust regarding tick-borne diseases is widely present in the public and needs to be addressed.

Clearly, doctor mistrust is not constructive for either risk communication or the CLDA members, who do not feel their suffering is being adequately addressed. Distrust of doctors and health care has been recognized as a serious issue that results from social changes, such as the erosion of social cohesion, changes in patterns of illness, and greater access to information (47, 71). This is particularly the case with patients with medically unexplained physical symptoms or with diseases that are still being defined and in contention (e.g., chronic fatigue, Gulf War syndrome), where doctors' inability to treat patients is perceived as a breach of the doctor-patient social contract and leads to feelings of frustration and outrage (30, 58, 81). These feelings are barriers to successful risk communication and management, as they decrease the credibility of the communicator in the view of the public; indeed, works suggest that outrage along with hazard themselves determine the risk to the public and must be considered together (63).

Notably, a concerning aspect of the mistrust of doctors with tick-borne diseases is the relationship between health practitioners and CLDA members, which is often antagonistic (9, 61, 75): on the one hand, some CLDA members may accuse specific health practitioners or officials of malpractice or incompetence; on the other hand, health practitioners may refer to CLDA members as "Lyme nuts" (*pers. observ.*). This mistrust and the resulting antagonism is reinforced by the previously described Lyme-disease-sufferer narrative; the narrative also helps disseminate and popularize doctor mistrust in the public (24, 39).

Decreasing doctor mistrust to facilitate risk communication may be achieved by recognizing the social construction of tick-borne diseases. The theory of the social construction of diseases suggest that some diseases—especially chronic diseases—are not immediately identified by medical practitioners, but may require a significant amount of time to be established through a complex implicit dialogue between patients and health practitioners, and sometimes involving political dimensions, such as patient activism (11). In fact, the conflicts and hurdles identified in a 1991 study of the social construction of Lyme disease are still present (3). These conflicts may be rendered manageable by explicitly recognizing the inherent uncertainty

of medical practice and initiating a dialogue between health practitioners and CLDA members regarding the symptoms they are suffering and other issues that are in contention.

In particular, the following issues have been sources of disagreement between doctors and CLDA members: the prevalence of tick-borne diseases, which CLDA members believe is higher; the diagnosis criteria for Lyme disease and other tick-borne diseases, which CLDA members believe are too restrictive and produce false negatives; the treatment of Lyme disease, which CLDA members believe may require a long course of antibiotics; and, finally, chronic Lyme disease, which some CLDA members believe they are suffering (5, 46). These issues could be considered as unresolved and under further study by the medical and scientific communities; this would allow focus to be placed on the treatment of possible tick-borne disease sufferers—avoiding an antagonistic relationship where doctors and CLDA members believe the other is disingenuous.

To improve the effectiveness of risk communication, tick-borne diseases need to be reframed as two issues: 1. the reduction of exposure to ticks and tick-borne diseases, which can be achieved through the adoption of protective practices—which may not require any mention of the uncertainty surrounding the definition and treatment of tick-borne zoonoses; 2. the definition and treatment of tick-borne diseases, which must be resolved through research and a dialogue between health practitioners and sufferers. Currently, tick-borne diseases and tick protective behaviors are conflated to the detriment of the latter: indeed, recent articles about ticks in South Okanagan publications focus more on the issues surrounding tick-borne disease sufferers and doctor mistrust, and only mention tick protective practices in passing, if at all (44). Similarly, while protective practices are described, provincial safety messages emphasize tick-borne diseases, not tick ecology (7). One approach may be to reframe tick-borne diseases for the public, and make protection from tick-borne diseases a manageable possibility rather than a source of concern and outrage. The framing of a disease strongly influences public perception of the relevant intervention practices (2).

Thus, based on our results of the knowledge schema of the public, we suggest that the risk communication of tick-borne diseases may need to focus less on the disease and more on public perception and fear of ticks themselves. This is relevant in areas where a proportion of the population has little or no experience with ticks—and protective practices against them—but who may recreate or work frequently in wildlife areas, and are therefore at higher risk of being exposed to tick-borne diseases (41). This is certainly the case in the SO, but, as found in Chapter

3, the prevalence of tick-borne pathogens in that area is low; as such, emphasis could thenb be placed mainly on self-protection from ticks. Doctor mistrust needs to addressed as well, as it may decrease the effectiveness of risk communication, both by shifting focus from communicating protective practices, and by decreasing public belief in messages from risk communicators, who may be doctors or associated with them. Importantly, this may alleviate the antagonism between tick-borne disease sufferers and health practitioners.

6.5 INTERVIEW QUESTIONS

1. Background information about themselves and their outdoors activities to determine their attributes

    a. How long have you been a resident in the Okanagan?

    b. What kind of work do you do?

    c. Do you spend time outdoors?

    d. How often do you go outdoors in spring/summer/fall/winter?

    e. If so, where do you go and what are your common activities?

    f. How often do you encounter ticks?

2. Knowledge of tick ecology

    a. What do you know about ticks?

    b. How do ticks attach themselves to you?

    c. Where do you expect to find ticks?

    d. When do expect to find ticks?

    e. What do you know about how ticks reproduce?

    f. What animals do ticks depend on to live?

3. Knowledge of tick-borne diseases

    a. What do you know about tick-borne diseases?

    b. Do you know anyone who has contracted a tick-borne disease?

    c. How do you contract tick-borne diseases?

    d. What do you know about the effects of tick-borne diseases?

    e. How severe are tick-borne diseases?

    f. What do you think the risk is in contracting tick-borne diseases?

4. Knowledge of protective practices and health care

    a. Do you take precautionary measures against ticks?

    b. What kind of precautionary measures do you adopt?

    c. How confident are you at finding a tick with a tick-check?

    d. How do you remove a tick from you?

    e. What do you know about the treatments for tick-borne diseases?

5. Contextual questions to compare ticks and mosquitoes and their diseases
    a. How do you think ticks compare to mosquitoes?
    b. Which one (ticks or mosquitoes) concerns you more and why?
    c. How do you think tick-borne diseases compare to WNv?

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CHAPTER 7: Conclusion

For my thesis, I studied the environmental and social determinants of tick-borne zoonoses in the South Okanagan. I began by reviewing the determinants of tick-borne zoonoses from the most proximate (e.g., the pathogen) to the most distal (e.g., land use practices), and also the management options to prevent diseases; this resulted in the description of an interdisciplinary approach based on integrated assessments that addresses tick-borne zoonoses (Chapter 2). I then took the first steps in this interdisciplinary approach by examining two environmental determinants (the prevalence of tick-borne zoonoses, Chapter 3; and the ecological dynamics of ticks and host species diversity, Chapter 4) and two social determinants (the impact of land use practices on tick densities, Chapter 5; and the reasons for the adoption of personal protective practices against ticks and tick-borne zoonoses, Chapter 6).

The advantage of the breadth of determinants I examined for my thesis was that I was able to develop an integrated understanding of ticks and tick-borne zoonoses. However, there were limitations to this approach, as I was not able to explore the determinants I examined with the same depth as a thesis dedicated to a smaller number of them. For instance, for the prevalence of tick-borne zoonoses (Chapter 3), I was not able to perform active surveys that may have collected *Ixodes spp.*, due to the limitations of the times and habitats chosen and the restriction of being only collecting deer mice; as such, I could not conclusively determine whether pathogens carried by *Ixodes spp.* (e.g., *Borrelia burgdorferi*) was not present in the SO, even though our results suggest they are rare. For the ecological dynamics of ticks and host species diversity (Chapter 4), I was not able to explore more realistic scenarios of competition or predation, due to our need to simplify our mathematical model to render it analytically and numerically tractable; we could then only offer preliminary results regarding the potential influence of competition and predation on tick-host dynamics, which will necessarily be modulated by spatial heterogeneity, ecological factors (e.g., migration behaviour), and stochastic elements (e.g., climate fluctuations). For the impact of land use practices on ticks (Chapter 5), due to the lack of available and suitable study sites, I was not able to examine other covariates that may have influenced large animal host distribution and, consequently, tick density, such as the proximity of sites to large water bodies. For the adoption of protective practices against ticks and tick-borne zoonoses (Chapter 6), I was not able conduct an in-depth mental models analysis, which would have allowed me to gain a better understanding of the public's risk perception and how it may relate to their behaviour; instead, I was only able to develop a preliminary

understanding of the public's knowledge in relation to their adoption of protective behaviours. Yet, despite the lack of depth of my thesis, the integrated and interdisciplinary understanding I gained from this thesis allowed me gain develop a familiarity of empirical and theoretical approaches, as well as qualitative and quantitative methods. Importantly, this familiarity allowed me to also understand their strengths and limitations, and when one approach may have an advantage to addressing a problem over another.

In Chapter 3, "Prevalence of Tick-Borne Zoonoses and Hantavirus in the South Okanagan, British Columbia: Active surveillance of ticks (*Dermacentor andersoni*) and deer mice (*Peromyscus maniculatus*)", I provided the epidemiological information regarding the prevalence of tick-borne zoonoses in the South Okanagan. We found the prevalence of the zoonoses we tested for (*Borrelia burgdorferi s.s.,* the causative pathogen of Lyme disease; *Rickettsia rickettsii*, the causative pathogen of Rocky Mountain Spotted Fever; *Anaplasma phagocytophilum*; *Bartonella henselae*) to be low. This result is consistent with previous results from passive surveys and patient reports in the region (3, 12, 21). This research represents the first active survey of ticks and deer mice in the region, which helps provide a better understanding of the prevalence of tick-borne zoonoses and thus the risk of infection to those diseases. However, as with all active surveys, our research was also limited to specific geographic regions (i.e., in our case, the South Okanagan), and cannot be used to estimate the prevalence of tick-borne zoonoses in other regions of British Columbia (BC). As well, we did not examine the presence of pathogens in other small mammal species besides the main disease reservoir, deer mice; the other species (e.g., Great basin pocket mouse) that were captured were species at risk and we did not have permits to collect them. Other small mammal species have been found to harbour pathogens, but at lower efficiency (7). There was thus a possibility that we did not detect some pathogens that were present; but, as other species are less competent disease reservoirs, the prevalence of the pathogens are likely to lower than or as low as in deer mice. Future avenues of research should then focus on the collection of other species of small mammals that may harbour zoonotic pathogens. As well, given the low prevalence of tick-borne zoonoses in the South Okanagan, a similar active survey may be conducted in other regions where the prevalence of tick-borne zoonoses is unclear to help determine the overall prevalence of tick-borne zoonoses in BC.

In Chapter 4, "The Influence of Host Competition and Predation on Tick Densities and Management Implications," I provided an understanding of how tick populations may respond to

changes in the host species composition of an ecosystem. In contrast to previous works which suggested that increasing species diversity in general can prevent the emergence of zoonoses (19, 27), I found that only specific changes in host diversity will decrease tick densities, as potentially a result of changes in tick and host dynamics. Importantly, our results suggested management approaches to reduce tick densities, as they showed how certain tick life-stages may act as rate-limiting steps that could be targeted to decrease total tick densities. Consequently, with our results, it is possible to better understand in what situations increased species diversity will lower tick densities and why. However, to obtain this understanding, we had to simplify the tick-host model such that the hosts and predators were not dynamic populations, but constants or periodically cycling populations. This simplifying assumption may hold in cases where a parasite has evolved very closely with its host, such that their dynamics have stabilized and their populations could be considered decoupled (17, 20). This, though, will not be the case with hosts being exposed to novel parasites and pathogens, which is the case with emerging diseases and zoonoses. Thus, future work would have to explore coupled tick-host populations and analyze how dynamic and interacting populations of hosts and predators may affect tick densities. This may be followed by examining the spatial dimensions of tick-host dynamics, first in metapopulation models, and then in spatially explicit models.

In Chapter 5, "The Influence of Agricultural Practices on Tick Densities," I provided an understanding of how two agricultural practices could change tick densities in the South Okanagan with respect to the patch size of the suitable habitat available and the landscape context created by the agricultural practices. We examined the influence of grazing agricultural (GA) practices (e.g., grazing pastures) and non-grazing agricultural (NGA) practices in contrast to low human impact (LH) areas (e.g., parks). Tick densities were higher in smaller patches of suitable habitat areas and in agricultural landscape contexts—which is consistent with previous works (29). In contrast to previous works, the effects of patch size and landscape context were studied together, where landscape context was found to have a stronger predictive influence than patch size. These results are particularly relevant in developing regions where land use change is happening at a rapid pace, and new land uses are being introduced and contributing to habitat degradation. Notably though, due to the limited selection of study sites, we were not able to examine tick densities over a full range of habitats of different patch sizes: our study sites were mainly mid-sized (20-50 ha) and large (>100 ha), while other studies had focussed on smaller patches (<7.6 ha) (1). Continuing work should then clarify the relationship of landscape context

at smaller patch sizes, where patch size may have a stronger predictive influence than landscape context at smaller scales. Further, we only examined two agricultural practices, GA and NGA. The effects of other land uses (e.g., forestry, residential) on tick densities should be examined in future works, as well as landscape contexts that are influenced by more than one land use.

In Chapter 6, "Mental Models and the Adoption of Protective Practices Against Ticks and Tick-Borne Diseases in the South Okanagan," I provided an understanding of the general public's adoption (and lack of adoption) of personal protective practices against ticks and tick-borne zoonoses in the South Okanagan. Where previous works focussed on the public's knowledge of tick-borne zoonoses (11, 16), these results added to the understanding of the public's risk perception and attitudes towards ticks and tick-borne zoonoses. In particular, the results of this research suggest that the adoption of personal protective behaviours and the definition and treatment of tick-borne zoonoses are two issues that need to be addressed separately. While the former may be addressed by increasing the public's understanding of tick ecology and reducing misunderstandings regarding ticks, the latter needs to be addressed through dialogue between medical practitioners and patients potentially suffering from tick-borne zoonoses. Conflating the two issues ultimately decreases the effectiveness of promoting the adoption of personal protective practices. However, this study was limited by the number of interviewees it included. Future research should seek a larger sample size of participants, but with a study methodology designed to confirm the validity of the results of this chapter (e.g., mail-out surveys); as well, future research should be conducted in varied regions in BC and Canada where human populations have had differing exposure to ticks and tick-borne zoonoses. Further, the conflict between medical practitioners and potential tick-borne zoonose sufferers should be studied to determine effective methods of decreasing antagonism between the two groups.

In the larger context of human health, the results of my thesis may be used as part of an integrated assessment described in Chapter 2, which could comprehensively prevent tick-borne zoonoses from emerging and spreading. Indeed, the results of my thesis have immediate uses for policies aimed at reducing the infection risk of tick-borne zoonoses. As an example of an integrated assessment for tick-borne zoonoses, the contents of Chapter 2 can be used not only as a basis to develop strategies to reduce the risk of infection to tick-borne zoonoses, but also as a template for other vector-borne zoonoses, such as West Nile virus and Hantavirus. With its assessment of the prevalence of tick-borne zoonoses, the results of Chapter 3 can be used to

determine the infection risk of those diseases for human populations in the South Okanagan, and thus also the relative severity and urgency of those diseases. The better understanding of tick-host ecological dynamics in Chapter 4 can be used to predict how local ecological changes may affect tick densities and the potential exposure of humans to ticks and tick-borne zoonoses. Similarly, the better understanding of landscape changes on tick densities in Chapter 5 can be used to predict how large scale land use practices may affect tick densities and thus also the potential exposure of humans to ticks and tick-borne zoonoses. Hence, the results of Chapter 4 and Chapter 5 are related as they can respectively provide an understanding of changes in tick densities at the small ecological scale and at the large human land use scale; the combined results of Chapter 4 and 5, can then be used to predict how various human activities may potentially increase or decrease tick densities and the infection risk of tick-borne zoonoses. By extension, these results may also be used to guide small and large scale land use management policies to reduce tick densities. Finally, with a better understanding of the reasons for the adoption of protective practices, the results of Chapter 6 can be used to develop risk communication strategies that encourage the adoption of protective practices, as well as reduce social concern regarding tick-borne zoonoses.

Interestingly, with the results of Chapter 3, I found that the prevalence of tick-borne zoonoses was low in the South Okanagan, much like another zoonose of concern, West Nile virus (4, 31). This suggests that specific management practices aimed at reducing tick densities or tick-borne zoonoses—should they be small or large scale (i.e., adaptable from the results of Chapters 4 and 5, and from the review in Chapter 2)—may not be warranted in the South Okanagan at this time. Implementing practices to reduce tick densities (e.g., application of acaricides, controlled burnings) (15, 30, 35) may not be cost effective. Similarly, developing vaccines against tick-borne zoonoses may be expensive and not sufficiently protective (8, 23, 25). Instead, promoting increased public awareness of personal protective practices against ticks (e.g., self-checks, tucking pants into socks) (6, 32, 34, 42) would be cost effective in reducing the risk of infection to tick-borne zoonoses; suggestions for this can be found in Chapter 6. Notably, although tick-borne zoonoses are not prevalent in the South Okanagan, they are prevalent in the north-eastern regions of North America, as well as many other parts of the world (33, 37, 38). In those regions, tick-borne zoonoses pose a major challenge not only in terms of human and livestock health (5, 18, 26, 28), but also in terms of the economic burden of the treatment of the diseases (22, 23, 36, 43). The results of Chapters 4 and 5 may then be applicable

in areas where tick-borne zoonoses are problematic, especially in developing countries with greater dependence on wildlife areas for subsistence and thus higher interaction between human and wildlife populations (10).

In this thesis, I examined the health challenge of tick-borne zoonoses in the South Okanagan. Significantly, adopting an interdisciplinary approach helped determine the scale of the problem of tick-borne zoonoses, and how they may be most effectively addressed. This kind of study can be used as part of an integrated assessment (2, 39, 40), which has been used successfully for complex challenges, such as climate change and infectious disease modeling (9, 13, 14, 24, 41). The benefit of integrated assessments is that they examine a challenge from various perspectives in order to determine not only the main source of it, but also urgency and severity of it. Indeed, the interdisciplinary approach of my thesis may be employed for other similar health challenges (e.g., other zoonoses; heavy metal contaminants) where there are environmental and social determinants that play important roles.

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Appendix I: Behavioural Research Ethics Board Approval

The University of British Columbia
Office of Research Services
Behavioural Research Ethics Board
Suite 102, 6190 Agronomy Road,
Vancouver, B.C. V6T 1Z3

CERTIFICATE OF APPROVAL - MINIMAL RISK

PRINCIPAL INVESTIGATOR:	INSTITUTION / DEPARTMENT:	UBC BREB NUMBER:
Karen H. Bartlett	UBC/College for Interdisciplinary Studies/School of Environmental Health	H08-02206

INSTITUTION(S) WHERE RESEARCH WILL BE CARRIED OUT:

Institution	Site
N/A	N/A

Other locations where the research will be conducted:
This research will conducted in a field station located close to the city of Oliver, British Columbia.

CO-INVESTIGATOR(S):
Jack Teng
Brian Klinkenberg

SPONSORING AGENCIES:
Canadian Parks and Wilderness Society
Mathematics of Information Technology and Complex Systems (MITACS) - Networks of Centres of Excellence (NCE)
Natural Sciences and Engineering Research Council of Canada (NSERC)

PROJECT TITLE:
Mental Models of Tick-Borne Zoonoses in the Okanagan

CERTIFICATE EXPIRY DATE: November 18, 2009

DOCUMENTS INCLUDED IN THIS APPROVAL:	DATE APPROVED: November 18, 2008	
Document Name	**Version**	**Date**
Protocol:		
Research Proposal	N/A	October 10, 2008
Consent Forms:		
Consent Form (revised)	N/A	November 10, 2008
Questionnaire, Questionnaire Cover Letter, Tests:		
Interview Question Examples	N/A	September 18, 2008
Letter of Initial Contact:		
Letter of initial contact	N/A	October 10, 2008
Other Documents:		
Permission from Osoyoos Indian Band	N/A	October 17, 2008

The application for ethical review and the document(s) listed above have been reviewed and the procedures were found to be acceptable on ethical grounds for research involving human subjects.

Approval is issued on behalf of the Behavioural Research Ethics Board and signed electronically by one of the following:

Dr. M. Judith Lynam, Chair
Dr. Ken Craig, Chair
Dr. Jim Rupert, Associate Chair
Dr. Laurie Ford, Associate Chair
Dr. Daniel Salhani, Associate Chair
Dr. Anita Ho, Associate Chair

Appendix II: Animal Care Certificate

THE UNIVERSITY OF BRITISH COLUMBIA

ANIMAL CARE CERTIFICATE

Application Number: A08-0711

Investigator or Course Director: Karen H. Bartlett

Department: School of Environmental Health

Animals:

Mice (deer mice) Peromyscys maniculatus 250

Start Date: **March 1, 2009** **Approval Date:** **February 3, 2009**

Funding Sources:

Funding Agency:	Mathematics of Information Technology and Complex Systems (MITACS) - Networks of Centres of Excellence (NCE)
Funding Title:	The impact of conservation practices on the spread of tick-borne diseases in the southern Okanagan
Funding Agency:	Canadian Parks and Wilderness Society
Funding Title:	The impact of conservation practices on the spread of tick-borne diseases in the southern Okanagan
Funding Agency:	Natural Sciences and Engineering Research Council of Canada (NSERC)
Funding Title:	The impact of conservation practices on the spread of tick-borne diseases in the southern Okanagan

Unfunded title:	N/A

The Animal Care Committee has examined and approved the use of animals for the above experimental project.

This certificate is valid for one year from the above start or approval date (whichever is later) provided there is no change in the experimental procedures. Annual review is required by the CCAC and some granting agencies.

A copy of this certificate must be displayed in your animal facility.

Office of Research Services and Administration
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