Detecting and Monitoring Wildlife Parasites:

Determining the Current Extent and Future Impact of the Winter Tick (*Dermacentor albipictus*) in the Yukon and Beyond.

by

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Department of Physical and Environmental Sciences
University of Toronto

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Abstract

The causes and consequences of species' distributional change has long been of interest in ecology, but it is of ever-pressing importance given increasingly rapid changes to both climate and land. Escalation of established and novel parasite populations in space and time within northern ecosystems has led to growing concern for the health of potential wildlife hosts, but the initial detection, monitoring, and trajectory of wildlife parasites in remote subarctic and Arctic regions is challenging to study and difficult to predict. In this thesis I examine the distribution of the winter tick, *Dermacentor albipictus*, in the northern Canadian territory of the Yukon to 1) assess evidence of historic and current spread of this parasite and determine its apparent northern boundary, 2) identify locations where off-host life stages occur, 3) determine abiotic factors that may increase the likelihood of larval *D. albipictus* occurrence and abundance at local scales, and 4) estimate the current and future transmission potential of *D. albipictus* to keystone hosts (moose, *Alces alces*, and woodland caribou, *Rangifer tarandus caribou*) in the territory. Through the creation of a global, integrated dataset, I show that *D. albipictus* has long had a widespread distribution in North America, but most likely established in the Yukon and the north in the past 50 years. Focusing in on the Yukon, I obtain the first off-host larval detection of this species in the field and show that the occurrence locations and abundances are strongly dependent on mean spring temperatures, but with accumulated degree-days below previously hypothesised thresholds for *D. albipictus* persistence. By designing and implementing a regional community engagement scheme for local hunters, I significantly improve on-host surveillance of *D. albipictus* and show that populations of this parasite may be spatially segregated by host species, changing our perception of the current risk to moose and woodland caribou in the territory. As *D. albipictus* is likely the first of many future species to expand its distributional range into the Yukon and northern North America, this work demonstrates the need to improve methods for detection and ongoing monitoring of species of wildlife health concern in the future.

To John -

for being himself and making life wonderful,

In memory of my grandfather, Dennis Victor Hart -

who so loved the natural world, and would have been proud of this work,

and

For Little Griff -

to show that anything is possible when you keep trying.

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Chapter Acknowledgments

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List of Abbreviations

CrI	Credible Interval
CVPD	Cumulative Vapour Pressure Deficit
GDD	Growing-degree Days
GIS	Geographical Information Systems
GMS	Game Management Subzone
LOO	Leave-One-Out Cross Validation
PC	Principal Component
PCA	Principal Component Analysis
RH	Relative Humidity
SBS	Shifting Baseline Syndrome
TEK	Traditional Ecological Knowledge
VPD	Vapour Pressure Deficit
YWTMP	Yukon Winter Tick Monitoring Project

Chapter 1

Introduction

> *"… we have to accept the proposition that invasions of animals and plants* ***and their parasites…*** *will continue as far as the next Millennium and probably for thousands of years beyond it." – Charles Elton (1958)*

1.1 Defining species distributions in a changing world

The maintenance of biodiversity, given the increasing onslaught of anthropogenic threats in the 21st century, has been recognized globally as a major challenge and ongoing emergency (Urban 2015; Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) 2019). Land-use change and degradation, including the introduction of invasive alien species, continue to be ranked as the greatest threats to biodiversity worldwide (Isbell et al., 2022). Within this framework of threats, climate change stands both as a direct driver that increases and exacerbates the effects of all others (IPBES 2019) and alone, as having many indirect effects that alter both human and wildlife responses to their environment (Chen et al., 2011; Tomiolo & Ward, 2018). Although species' distributions are naturally dynamic, the dispersal of species from their historical range to establish in new areas – or 'range expansion' – presents conservationists and wildlife managers with additional problems under climate change (Carey et al., 2012; McGeoch & Latombe, 2016).

In a changing climate, range shifts are often interpreted as migration farther north, tracking warming temperatures and altered precipitation patterns (Parmesan & Yohe, 2003; Chen et al., 2011), or higher along elevational gradients (Tingley et al., 2012; Grytnes et al., 2014). These 'native invaders' (Simberloff, 2011) blur the boundaries between species traditionally understood to be native (indigenous to a region or ecosystem) and/ or naturally dispersing and the definition of an invasive species as one introduced through human pathways with the potential of future spread and/ or economic or ecological impact (Lockwood et al., 2007), bringing with them ongoing debate and controversy as to the management of species settling in 'new climate' or novel ecosystems (Hobbs et al., 2009). However, this is more than just a question of semantics or academic discourse. The inability to cite policy interventions for range-expanding species that are not classed as ‘invasive’, but with clear negative impacts on recipient systems, can place significant restrictions on beneficial management actions such as the enactment of response timelines or adequate resource allocation (Leung et al., 2014). Understanding if and how range-expanding species may negatively impact recipient communities is, therefore, of increasing importance in an otherwise uncertain future.

1.2 The threat of parasite range-expansion in northern ecosystems

Remote northern ecosystems are considered to be some of the most at risk from the impacts of biodiversity redistribution under climate change, where shifting interactions between species may impact both recipient populations of wildlife and the peoples that rely upon them (Dobson et al., 2015; Ricciardi et al., 2017). Parasitic species, relying on a host for part or all of their life cycle, are some of the most concerning range-expanders given the generally negative effects on their hosts, but whose potential spread and impact is also among the most challenging to forecast. Successful management and mitigation of novel parasites requires the prediction of their range and potential impacts over space and time, but such data are rarely comprehensive and many gaps in knowledge present challenges to ongoing research (Rohr et al., 2011). Some of these barriers are general and apply to many species, such as imperfect detection at extremely low population densities in establishing populations (Gertzen & Leung, 2011; Britton et al., 2011; Rout et al., 2017), while others are more specific, such as the inability to easily observe key components of host-parasite interactions *in situ* (Buhnerkempe et al., 2015; Cable et al., 2017). Wildlife hosts may facilitate parasite dispersal across landscapes through multiple mechanisms, including seasonal movements (migration), foraging, and prospecting (finding new territory / habitat) (Childs, 2007; Boulinier et al., 2016), and through anthropogenic translocation of infected hosts (Kock et al., 2010). The general vastness, difficulties of access, and low densities of fauna in the north add to these challenges of detection. Although the relative simplicity of northern ecosystems has been highlighted as a potential benefit for studying parasite ecology (Kutz et al., 2009), novel interactions due to the shift or redistribution of parasitic species’ ranges may, in fact, be complex, and present additional threats to already vulnerable native fauna in these systems (Carlson et al., 2017).

1.2.1 Northern range-expansion in tick species

Concern over the increasing incidence of tick-borne diseases in a changing climate has played a large role in driving tick research over the past decade (Lafferty, 2009; Ogden et al., 2013; Ogden & Lindsay, 2016; Marselle et al., 2019). As blood-feeding parasites, ticks are key vectors of many bacterial, viral, and protozoan diseases to humans and livestock, and thus garner considerable research interest across fields intersecting epidemiology, ecology and public health (Gabriele-Rivet et al., 2015; Kilpatrick et al., 2017; Mierzejewska et al., 2015). Moreover, ticks, like many arthropod vectors, often show sensitivity in survival, reproduction and efficacy of pathogen transmission under different climatic conditions (Lloyd-Smith et al., 2005), resulting in novel introductions of parasites and pathogenic agents to new hosts and in new ranges (Sonenshine & Mather, 1994). The growing appreciation of the potential interaction between ticks and climate, has raised concerns from both researchers and the public regarding the potential for ticks of all species to expand their native ranges farther north as they track changes in the climate biome (Dantas-Torres, 2015; Khatchikian et al., 2015; Ogden & Lindsay, 2016; Rosen, 2021). These concerns do not appear to be unfounded - recent increases in both the range and size of tick populations in Europe have been linked to higher incidences of tick-borne encephalitis and Lyme borreliosis in the Czech Republic and in Scandinavia (Randolph, 2001; Gray et al., 2009; Zeman & Benes, 2013). In Canada, the northern range-expansion of the Lyme disease vector, the blacklegged tick, *Ixodes scapularis*, has been estimated to spread at a rate of 46 km per year, based on existing data (Leighton et al., 2012; Clow et al., 2017).

1.2.2 The impact of ticks on wildlife

There has been growing recognition over the past two decades that tick infestation may have significant impacts on wildlife host populations, in addition to pathogen transmission (e.g. Jones et al., 2019). Ticks may contribute to population-level declines in their hosts through a number of different mechanisms, from directly reducing breeding success, survival, and growth of young (Brown et al., 1995; Hoodless et al., 2003; Eggert & Jodice, 2008), to negatively impacting mating behaviours (Lanser et al., 2021). Indications that hosts may actively avoid optimal foraging areas where ticks are abundant suggest that many animals recognize the threat that tick parasitism presents (Fritzsche & Allan, 2012; Buck et al., 2018). However, in all but a few cases, our limited understanding of the sublethal or additive effects of tick parasitism on their hosts, and the ecological and evolutionary consequences of recurrent or long-term infestations, means that prioritizing tick species with clear negative impacts on host populations will be beneficial in determining ongoing and future conservation efforts and improve our knowledge of wildlife health in general.

1.3 The winter tick, *Dermacentor albipictus* (Packard, 1869).

> *"The enemies of the Moose are, in order of danger: man, mosquitoes, deer-flies,* ***ticks****, disease, deep snow, wolves, bears, and cougars."*
>
> *– E.T. Seton (1909)*

The winter tick, *Dermacentor albipictus*, is commonly found throughout North America as a dominant ectoparasite of moose (*Alces alces*) (Samuel, 2004; Lindquist et al., 2016). A generalist species, it can feed on a wide range of wildlife hosts including elk (*Cervus canadensis*), caribou (*Rangifer tarandus ssp*.), bison (*Bison bison*), and deer (*Odocoileus hemionus, O. virginianus*) (Samuel, 2004), and has been recorded historically as a pest of cattle (*Bos taurus*) and horses (*Equus caballus*) (Bishopp & Wood, 1913; Gregson, 1956; Lindquist et al., 2016). It is rarely found on humans and, to date, there is limited evidence of it as a vector of disease (Samuel, 2004; c.f. Swei et al., 2019). Despite this, winter tick can pose a significant risk to hosts owing to its ability for rapid population growth that results in tens of thousands of ticks per animal, especially on moose (Seton, 1909; Samuel, 2007; Jones et al., 2019).

1.3.1 Winter tick life cycle and host impacts

The winter tick spends almost its whole life on a single host, beginning with gravid adult females dropping to the ground from their host in spring to lay their eggs before they die (Fig.1.1 (a-b)). Eggs generally hatch around August (Fig.1.1 (c)) (Howell, 1939), whereupon larvae aggregate in clumps at the top of nearby vegetation, awaiting a passing host onto which to transfer, a behaviour known as "questing" (Fig.1.1 (d)) (Drew & Samuel, 1985). Winter ticks take approximately three blood-meals while on the host, accounting for one meal per instar (Fig.1.1 (e-g) (Samuel, 2004), before becoming sexually reproductive adults; mating, and the cycle begins again.

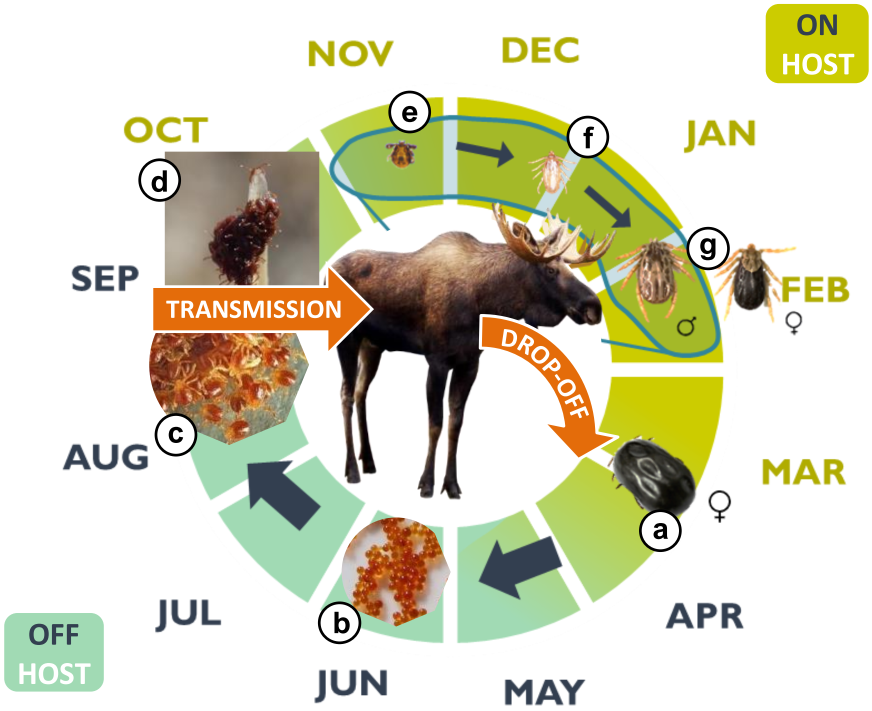

Figure 1.1 Life cycle of the winter tick, *Dermacentor albipictus*. Life stages: (a) Engorged adult females; (b) eggs; (c) hatchling larvae; (d) questing larvae; (e) larvae on host; (f) nymphs; (g) reproductive adult males / females.

There may be several reasons for the severe impact of *D. albipictus* on their host. By the time larvae develop to the nymph stage, feeding can account for considerable blood loss, particularly under high densities of ticks per animal (Samuel, 2004; Jones et al., 2019; Pekins, 2020). Feeding does not occur continuously over this time but in short, discrete periods between life stages, and it has been suggested that synchronized blood-meals during instar development may be responsible for anemia experienced by heavily infested hosts (Samuel, 2004; Musante et al., 2007). *D. albipictus* has been shown to cause mass host mortality in moose in Canada and the U.S.A. over the past century, with parasite densities between 30,000 and 100,000 ticks per animal leading to severe anemia, hair-loss and the eventual death of the host (Bridger & Walsh, 2017; Pybus, 1999; Samuel, 2007). Even at lower tick densities, the weakening and premature loss of winter coat, often described as “ghost moose” due to the white appearance of the host’s broken hair and damaged skin (Samuel, 2004), is known to lead to increased winter mortality in both adult and juvenile moose (Mooring & Samuel, 1998), and has been linked to a 70%

reduction in calf recruitment in Maine, New Hampshire and Vermont, U.S.A. (Jones et al., 2019).

1.3.2 Winter tick in the Yukon

The history of winter tick in the Yukon, along with the purported extent of its range, is not well defined. As such, multiple methods are required to piece together a better understanding of their current dynamics. Anecdotal records suggest that *D. albipictus* was not thought to be present in the Territory, or rarely so, before 1980 (Samuel, 1989). Subsequent reports of *D. albipictus* in the Yukon were on elk that had been translocated from Alberta in the 1950s and again in the 1990s (Environment Yukon, 2010). Ongoing government monitoring of winter tick presence on the hides of hunted and roadkill moose, elk, caribou, and mule deer, has shown evidence of winter tick persistence at low population levels in both elk and mule deer, but the absence of data for moose and caribou – potentially the most vulnerable species to winter tick infestation– has limited the extrapolation of these data to these species, and, therefore, our understanding of the distribution of winter ticks on hosts (Environment Yukon, 2018, *unpubl. data*). Government field studies carried out 2008 to 2010 were also unable to detect any larval winter ticks off-host, continuing to raise questions of how and where *D. albipictus* is completing its lifecycle in the Yukon (Environment Yukon, 2010, *unpubl. data*). Results of genetic comparison of Yukon winter ticks with those from Alberta found that both range-expansion and accidental introduction were possible sources (Leo et al., 2014), but was mostly inconclusive. Although there have been no reports of epizootic events in the Yukon as elsewhere in North America, mounting evidence indicates that, in addition to the introduced tick population in the elk herds, *D. albipictus* may be expanding its natural range from the south, in line with a warming northern climate (Environment Yukon, 2010).

1.4 Challenges in detecting and monitoring parasites

As demonstrated by the Yukon winter tick system, a major barrier in assessing and monitoring parasite species is in its detection. The challenges of tick and other parasite data collection are further exacerbated in the remote ecosystems of the north, where host species often exist at low densities, and in a vast landscape that is difficult for researchers to access (Kutz et al., 2009). Where parasites interact with humans, domestic, or companion animals, representative samples may be collected through medical and veterinary reporting (Duncan et al., 2020; Nelder et al., 2021). For wildlife, however, the options for observing host-parasite interactions *in situ* are limited (Delahay et al., 2009). Active sampling may be restricted for practical reasons, due to logistic infeasibility of site access or the financial cost of capturing wild hosts, subsequent diagnostic tests or need for specialist taxonomic identification (Stallknecht, 2007). As a result, most wildlife health monitoring relies to some degree upon passive surveillance, which is usually unstructured and opportunistic (Ryser-Degiorgis, 2013). This means that, in most cases, information on parasite incidence may need to be compiled from multiple sources of information. For ticks, active sampling might include assessment of the hides of living or dead hosts (Poh et al., 2020), or traditional field sampling methods such as blanket drags to collect host-seeking specimens ("flagging" or "dragging"; Salomon et al., 2020). Depending on the tick species, it may also be relevant to include tick submissions from medical or veterinary sources (e.g. Barrett et al., 2015; Lee et al., 2019), or if available, specimen records may be used to incorporate historical data (e.g. Cuber, 2016). Finally, a contemporary method of data collection that is non-specific to parasites but is becoming increasingly popular is publicly-engaged monitoring schemes, which may be in-person or *via* online, citizen-science platforms (Eisen & Eisen, 2021; Poh et al., 2022). The engagement of non-scientific experts in the collection of parasite data is a departure from traditional sampling methods in the fields of disease ecology and epidemiology and requires considerable effort and commitment on the part of the scientist in terms of both study design and social networking to ensure its success (Martin et al., 2017; Poh et al., 2022).

1.5 Thesis statement and objectives

The winter tick may present a potential threat to moose and other cervid species, but its exact spatial distribution, population densities and dynamics, and host preference in the Yukon remain unclear (Environment Yukon, 2016). Understanding if, and to what extent, *D. albipictus* could impact vulnerable Yukon cervids is essential to inform ongoing wildlife management and conservation planning and may additionally provide insights into optimal methods for detection and monitoring of other parasites, invasive species, or diseases. While the main objective of my thesis is to fill in critical gaps in knowledge surrounding the Yukon -winter tick system, I also aim to develop tools and integrative approaches to data collection that are of wider applicability for the assessment and management of range-expanding and invasive species. To achieve these goals, my research has been structured into three sections, each seeking to examine a different aspect of *D. albipictus* ecology from their wider, global scale, to regional and local scales observed in the Yukon. Within these, I adopt multiple approaches to contribute new and examine existing knowledge, using primary field data collection, statistical modelling, and citizen science, to assess factors affecting winter tick occurrence, abundance, host-specificity, and spread-potential.

Many foundational ecological and biogeographical insights have come directly from mapping the distribution of target species (Elton, 1927). Examining patterns in presence over time and in space has resulted in both new theory (e.g. species richness varies with latitude, (Currie, 1991)) and new practical applications (e.g. protected area planning for conservation, (McGowan et al., 2020); assessing risk of disease transmission, (Lippi et al., 2021)). However, there is growing recognition among many researchers that previous assumptions regarding species ranges, particularly for parasites whose presence may be coupled tightly to that of their hosts, may need to be re-evaluated as rapid changes to climate regimes drive new and altered species interactions (e.g. Johnson et al., 2019). The main aim of **Chapter 2** is to examine the broad-scale past and present winter tick distribution throughout its native range in North America to provide the first baseline and contemporary maps for this species. To achieve this, I assemble a comprehensive spatio-temporal dataset of *D. albipictus* occurrence from 1869 to 2020, comprising multiple data sources (natural history specimens, published and grey literature, unpublished datasets, and citizen science observations). Both the process of dataset collation and subsequent analysis identifies trends and biases in knowledge acquisition over time and in space, providing a new perspective that questions several underlying assumptions regarding when and where this species is found, with particular focus on northern regions.

High-latitude regions are experiencing environmental change at a rapid pace, and, for species at the cool edge of their range, the alteration of abiotic conditions may present an opportunity for spread. However, parasite response to climate warming remains highly uncertain (Kutz et al., 2014), thereby reducing the scope for informed decision-making by managers and conservationists seeking to mitigate negative effects of parasitism on already vulnerable hosts. In **Chapters 3 and 4**, I examine which environmental and climate factors relate most strongly to the distribution of larval winter ticks at their range -edge in Yukon. The local environmental conditions experienced by the off-host, larval life stage of the winter tick from hatching to host-seeking may impact both survival, development, and, ultimately, transmission success to their host (Drew & Samuel, 1985; Yoder et al., 2016). Using field data to model the relationships between off-host life stages and the conditions it experiences *in situ* is an important step in identifying typical requirements that may be expanded to predict its presence or abundance in new, unsampled areas. **Chapter 3** presents the first off-host detection of winter tick larvae for the Yukon, using traditional sampling techniques to collect and quantify larval presence. In **Chapter 4,** I incorporate the data collected in Chapter 3, within a Bayesian hierarchical modelling framework that relates larval tick occurrence and abundance to selected variables predicted to be influential in determining off-host winter tick survival. Overall, Chapters 3 and 4 contribute both a sampling strategy and new data to a growing body of knowledge of tick-climate relationships, which are of practical utility for the ongoing monitoring and potential management of winter tick in the Yukon.

In ectoparasite systems, disease dynamics may be shaped by both the availability of hosts and the composition of that host community over time and space (McCoy et al., 2013; Johnson et al., 2019). Therefore, in my final chapter, I examine the role of host species in the observed winter tick dynamics in the Yukon. Surveillance of winter ticks on moose and caribou (*Rangifer tarandus caribou*) hosts in the territory has relied in part on voluntary submission of hides by hunters since 2011, but few samples were submitted, making assessment of winter tick impact on these species difficult. To address this gap and improve community engagement, I established the Yukon Winter Tick Monitoring Project (YWTMP), a public engagement program, which is the focus of **Chapter 5.** In this chapter, I develop a citizen-science approach to winter tick monitoring by borrowing from diverse fields, such as marketing and social science to increase stakeholder engagement, thereby significantly improving sample collection. The research presented in this chapter reveals geographically separated populations of winter ticks on moose and elk and demonstrates the importance of designing suitable community engagement programs to maximize data collection over a large spatial scale.

My thesis explores factors relating to the past and present distribution of *D. albipictus* in North America and in the Yukon, while employing new methods that are of broad applicability across other parasite systems and within disease ecology as a whole. From data integration to traditional field sampling techniques and widescale community engagement, I demonstrate the value of incorporating both historical and contemporary methods to elucidate patterns in host-parasite distributions and interactions at both local and global scales. Overall, the results of my thesis show the importance of considering potential novel interactions in northern ecosystems at both the interface of wildlife health and biodiversity conservation, increasing its relevance in a rapidly changing climate.

Chapter 2.

Revealing large-scale parasite ranges: An integrated spatio-temporal database and multi-source analysis of the winter tick, *Dermacentor albipictus*.

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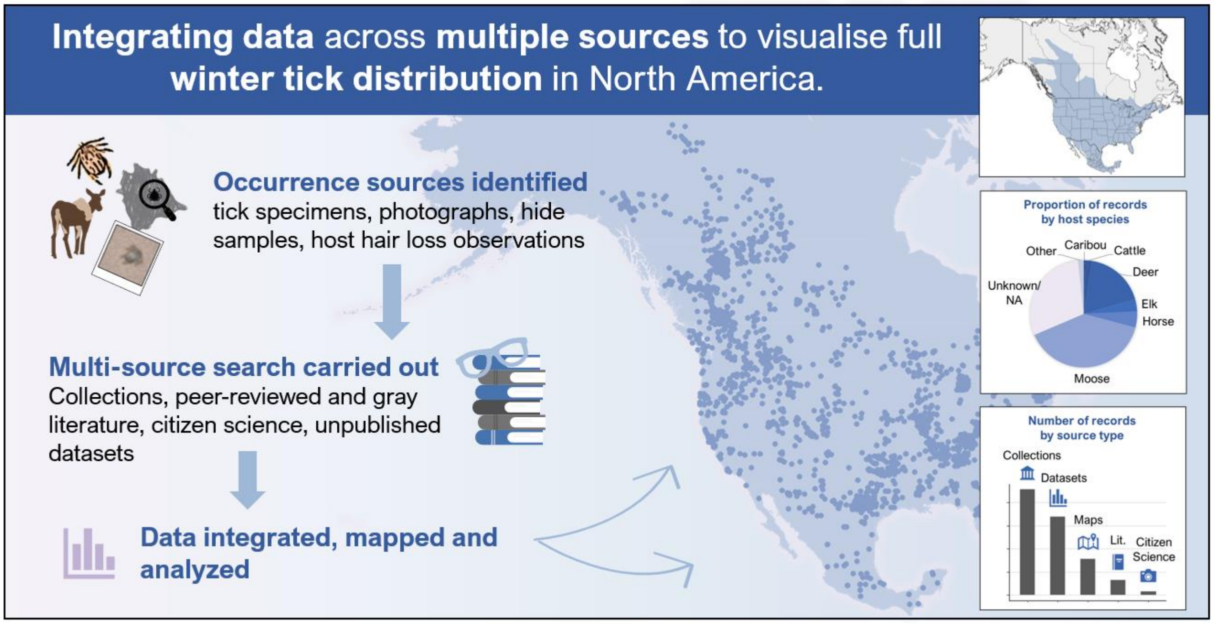
Ecosphere, In press.

https://doi.org./10.1002/ecs2.4376



Integrating data across multiple sources to visualise full winter tick distribution in North America.

Occurrence sources identified
tick specimens, photographs, hide samples, host hair loss observations

Multi-source search carried out
Collections, peer-reviewed and gray literature, citizen science, unpublished datasets

Data integrated, mapped and analyzed

Contributions: Conceptualization, ESC, PKM; methodology, ESC, PKM, NEM; formal analysis, ESC; investigation, ESC; resources, HF, NJH, NEM, PKM; data curation, ESC; writing—original draft preparation, ESC; writing—review and editing, ESC, HF, NJH, NEM, PKM; visualization, ESC; supervision, NEM, PKM; funding NEM, NJH, PKM.

Abstract

Concerns that climate warming may drive the spread of ectoparasites into previously uninhabited areas has increased the need for baseline knowledge of their distributional history. For species of wildlife health concern, presence data are often lacking or outdated, thus limiting our ability to assess range changes and subsequent host impacts. We reconstructed the past and present distribution of the winter tick, *Dermacentor albipictus,* through compilation of a spatio-temporal database to create the first full baseline map of its occurrence throughout its North American range. The ongoing impacts of winter tick epizootics in moose (*Alces alces*), and recent mortality events in elk (*Cervus canadensis*) and white-tailed deer (*Odocoileus virginianus*), have led to a resurgence in interest in the future of this parasite in a warming climate. Over 3,400 unique records of winter tick occurrence were compiled from multiple data sources, dating from 1869 to 2020 and spanning from 16.5 to 66.2 °N latitude. Both conventional, published sources and natural-history records were included along with new records from previously unpublished datasets and citizen-science observations to make this a comprehensive occurrence dataset for this species. Along with standardized location information and year of observation, the dataset includes associated host species and descriptive categorization of the type and source of each record, providing new opportunities to examine host-parasite interactions in the winter tick system over time and space. In presenting these data, we discuss the potential sampling biases and lacunas in our integrated database records, particularly at the winter tick's northernmost range. We also document changes in the types and sources of winter tick information from past to present, highlighting potential issues that should be considered before using these data in further analyses and when collecting ongoing records. Our database demonstrates that collation and synthesis of records beyond conventional sources can shed light on the distributional history of parasite species and serve as a useful baseline for prioritizing future research and management decisions.

Keywords

Dermacentor albipictus; distribution map; georeferenced locations; integrated data; Ixodidae; occurrence; parasite ranges; wildlife

2.1 Introduction

Concerns that climate warming may trigger parasite range shifts has increased the need for baseline knowledge of their distributional history. Creating distribution maps of parasite occurrence may help to identify the limits of species' ranges and provide a vital point of comparison from which to compare geographic and ecological changes over time (Cumming & Vuuren, 2006; Phillips et al., 2008; Botts et al., 2012). As blood-feeding ectoparasites capable of transmitting pathogenic agents to humans, ticks have been a strong focus in parasite-climate research over the past decade, often with the aim of obtaining and improving predictions of their ranges under expected, long-term climate warming regimes (Dantas-Torres, 2015; Gasmi et al., 2018; Sonenshine, 2018). The increasing body of evidence pertaining to climate-mediated range-changes in ticks is reflected in the numerous studies modelling and mapping the distribution of the blacklegged tick, *Ixodes scapularis*, in North America (e.g. Leighton et al., 2012; Lieske & Lloyd, 2018; Glass et al., 2021; Slatculescu et al., 2020) and the castor bean or sheep tick, *I. ricinus*, in Europe (e.g. Boehnke et al., 2015; Fernández-Ruiz & Estrada-Peña, 2020; Zanet et al., 2020; Rochat et al., 2020). Given the role of these species as potential vectors of several disease-causing agents (Sonenshine & Mather, 1994; Dantas-Torres et al., 2012), understanding when and where such species occur and their potential to interact with humans has clear implications for public health (Eisen & Paddock, 2021).

A lack of baseline occurrence data remains a barrier to distribution mapping and associated risk assessments for a large number of tick species (Poulin, 2014; Pappalardo et al., 2020; Eisen & Paddock, 2021), particularly so for those that predominantly affect wildlife (Delahay et al., 2009). From a management perspective, tick incursions in recipient wildlife populations may not be monitored because of a lack of baseline data, and the consequences of altered trophic interactions may be severe and/or irreversible (Cumming & Vuuren, 2006; Léger et al., 2013; Dantas-Torres, 2015). For ticks, occurrence data are generally compiled from one or more sources of information: i) active collection of host-seeking ticks in the field (flagging or dragging: i.e. methods described by Salomon et al., 2020) or via targeted collection from living or dead hosts (hair or hide transects, time-limited counts, necropsies: i.e. methods described in Poh et al., 2020); ii) passive reporting of ticks from medical or veterinary sources, (collected from humans, companion animals or livestock: e.g. Barrett et al., 2015; Lee et al., 2019), and iii) historical records (specimen collections, atlases, other literary sources: e.g. Cuber, 2016). In more recent years, community-based, citizen-science monitoring programs have provided additional sources of tick occurrence data (Eisen & Eisen, 2021). Given the relative increase in data and its availability, online platforms such as the Global Biodiversity Information Facility (GBIF) (GBIF, 2021) that collate presence records from multiple data sources, are becoming increasingly popular for creating integrated occurrence datasets for modelling and mapping (Heberling et al., 2021). The desire to account for biases arising from using integrated data sources has led to new statistical methods for working with these data, opening up new opportunities to examine species distributions across large spatial scales and long timeframes (Isaac et al., 2020). Assessing the quantity and quality of available data for tick species of wildlife health concern underpins both the current, and likely future trajectory, for much tick-distribution research.

The winter tick, *Dermacentor albipictus* (Packard 1869), is one species of interest to wildlife health that is a good candidate for integrated data compilation. Historically, *D. albipictus* has been considered one of the most detrimental parasites to affect moose (*Alces alces*), cattle (*Bos taurus*), and horses (*Equus caballus*) (Seton, 1909; Parish & Rude, 1946; Cowan, 1951), causing a range of symptoms from emaciation and reduced reproductive capacity to higher mortality in young (Teel et al., 1990; Schvartz et al., 2015; Jones et al., 2019; Pekins, 2020). The species remains notorious for high abundance infestations on moose, with severe infestations of 80,000 – 100,000 ticks per individual observed, alongside distinctive patterns of hair loss (McLaughlin & Addison, 1986; Mooring & Samuel, 1998; Samuel, 2004). Since the early 1900s, mass die-offs of moose with winter tick infestations have been reported in Canada (Merrill, 1916; Cameron & Fulton, 1927), and the United States (Dunfey-Ball, 2017; Jones et al., 2019), with recent mortality events in wild elk, (*Cervus elaphus canadensis*), (Calvente et al., 2020) and captive white-tailed deer (*Odocoileus virginianus*) (Machtinger et al., 2021), indicating that species other than moose may also be at risk from the effects of hyperabundance.

Given the clear negative effects of the winter tick on its hosts, comprehensive knowledge of its distribution and host associations is required to inform future management and mitigation. *D. albipictus* is generally considered to have a broad geographic range throughout the United States and Mexico and into parts of Central America, and has commonly been reported throughout Canada (Wilkinson, 1967; Yunker et al., 1986; Samuel, 2004; Lindquist et al., 2016). However, to our knowledge, there are no distribution maps that document the entire known range of the winter tick in North America, and no assessment of changes to this range over time. Given that ecological processes, such as changes to tick range, occur on a spatial scale independent of political boundaries, obtaining a better understanding of the wide-scale distribution of *D. albipictus* is key for conservation and wildlife management across the continent. In the United States, point maps of *D. albipictus* occurrence at the national level were updated several times throughout the early 20th century (Banks, 1908; Bishopp & Wood, 1913; Cooley, 1939; Bishopp & Trembley, 1945), with a shift to state and county level surveillance in more recent decades (Eisen & Paddock, 2021; Poh et al., 2022). Maps of winter tick collection localities in Canada were not produced until the 1950s (Gregson, 1956), and were updated most recently as part of a larger effort to document ticks throughout the country (Lindquist et al., 2016). In Mexico, a recent update to the country's tick checklists has resulted in new records for *D. albipictus*, though generally at a broad spatial scale, i.e., the state level (Chavarría, 1941; Guzmán-Cornejo et al., 2016).

Here, we present combined distributional knowledge of *D. albipictus* throughout its range in North America and examine changes to the composition of data sources over time. We collate known occurrences of *D. albipictus* from the beginning of collection records in 1869 to the present day (2020) based on multiple sources, combining conventional records of presence (natural history specimens, published accounts) and more contemporary sources (e.g. citizen-science observations) that include inferred presence based on distinctive winter tick-induced hair loss on its hosts. Previously unpublished data in grey literature and from unpublished sources, including government and academic research, were acquired to create a comprehensive, although not exhaustive, integrated dataset. We use this spatio-temporal database to 1) produce an up-to-date point map for this species 2) examine the past and present distribution and apparent northern range edge of *D. albipictus*, and its bounds in relation to common host species and 3) explore what the sources and structure of these data can tell us about the history of this parasite species' distribution. Finally, we compare the trends and biases presented in our data to highlight gaps in knowledge in winter tick research and provide perspectives on the challenges of obtaining suitable baseline data for other little-known species.

2.2 Methods

We compiled a database containing information on the known occurrences of *D. albipictus* throughout North America from 1869 to 2020. Search and compilation took place between January 2019 and December 2021. Data were extracted from multiple sources, including the published literature, historical maps and checklists, primary and unpublished occurrences, host hair-loss datasets from state or provincial surveys, natural-history and specimen collection data, and citizen-science observations. We provide an overview of the overall compilation process below; specific methods for each component and data type are detailed in Appendix A.1.

Data compilation was split into two main components: 1) systematic review of the published literature, and 2) targeted searches and data acquisition via relevant databases, collections, and personal contacts (Fig. 2.1). To review published sources, we searched the ISI Web of Science Core Collection and Scopus databases multiple times over three years, with a final search on 13th October 2021. The title, abstract and keywords (‘TS’ in Web of Science; ‘TITLE-ABS-KEY’ in Scopus) of scientific publications were searched using the terms: "winter tick*" OR "*Dermacentor albipictus*" OR "*Ixodes albipictus*" OR *"Dermacentor nigrolineatus*" OR "moose tick*" OR "elk tick*". Online databases of specimen collections were searched for “*Dermacentor albipictus*”, “*Ixodes albipictus*”, or “*Dermacentor nigrolineatus*”, and we contacted curators to request collection records for these species names where online records were not available (Appendix A.1: Table A2). North American wildlife agency personnel known to be engaged in winter tick monitoring activities (i.e. ungulate biologists and/or wildlife health specialists) were contacted by e-mail to request winter tick occurrence records and to suggest other potential contacts for similar data.

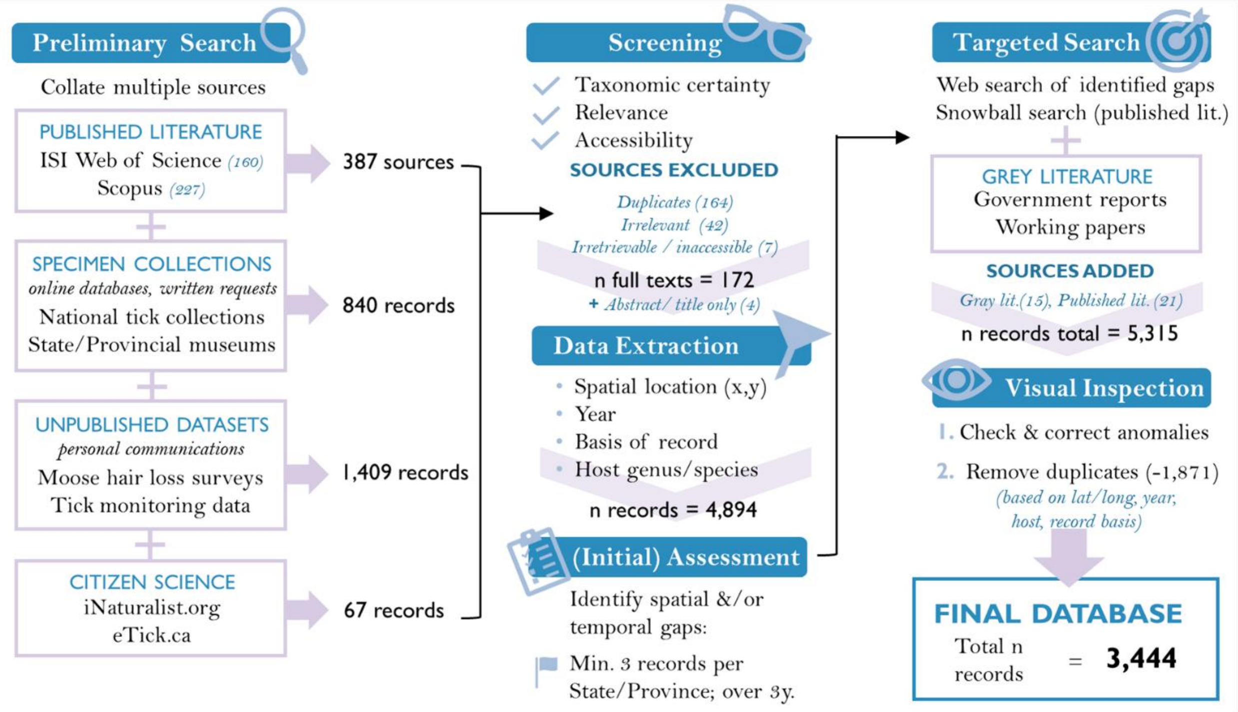


Figure 2.1 Data collection and processing methodology used to construct the *Dermacentor albipictus* spatio-temporal database.

In all cases, the criteria for data to be included were that the species could reasonably be identified taxonomically as *Dermacentor albipictus* (or a common historical synonym, *Ixodes albipictus* (Packard, 1869) or *D. nigrolineatus* (Ernst & Gladney, 1975)) and a point location and year of collection could be determined from the available information. Records purporting to be *D. albipictus* from mountain goat or sheep hosts in the Rocky Mountain region were excluded, given the potential for them to be misidentified specimens of the recently reinstated species *D. kamshadalus* (Apanaskevich & Barker, 2021). Where a year of collection was not given, the date of publication was used, if applicable, while sources lacking any date were excluded (n=2). Information on the host (species or genus) was recorded where available. Records were available at minimum of county (USA) or federal electoral district (Canada) levels in all states or provinces, so we excluded records with precision limited to the level of state or province. However, records for Mexico were far fewer at the equivalent administrative scale (‘municipios’), with many more records only at state level. For this reason, database entries for Mexico include records that are geolocated to state centroid. A few, scattered records exist for *D. albipictus* at the extreme southern edge of its range, from Mexico into Central America

(Lindquist et al., 2016), where *D. albipictus* exhibits a dark morph, previously identified as *Ixodes nigrolineatus* (Packard 1869), or *D. nigrolineatus* (Banks 1907). There has been debate as to whether this morph is a distinct species given similar morphology and hybridization abilities (Cooley, 1939; Bishopp & Trembley, 1945; Ernst & Gladney, 1975). Molecular studies indicated *D. albipictus* to be a single species in Canada (Leo, 2012), but earlier work, that included more southern specimens, was inconclusive (Crosbie et al., 1998). Given a lack of taxonomic clarity in the southern range, particularly among historical records, we do not include observations south of Mexico in our dataset.

Spatial information was recorded in decimal degrees (DD) latitude and longitude with a World Geodetic System Datum of 1984 (WGS84). Coordinates given by sources in alternative formats were converted using the web-based Federal Communications Commission Degrees Minutes Seconds to/from Decimal Degrees online tool (https://www.fcc.gov/media/radio/dms-decimal). Where spatial information was presented in the form of point maps, occurrence points were extracted by georeferencing map images using GIS (QGIS v3.16.10; QGIS Development Team, 2020). In cases where occurrence records lacked specified coordinates, we georeferenced locality data using the Web-based platform GEO-Locate (Rios & Bart, 2021), excluding those where a location could not reliably be determined (i.e. multiple potential locations, or none). All scientific and common names of host species were standardized to current valid taxonomy according to the Integrated Taxonomic Information System database (ITIS, 2021, www.itis.gov, CC0, https://doi.org/10.5066/F7KH0KBK).

Accurate and well-referenced locality data are critical for biogeographical studies, with standard practices laid out to maintain or improve the quality of georeferenced datasets (Chapman & Wieczorek, 2006; Franklin, 2009). We followed common georeferencing guidelines as laid out in Chapman & Wieczorek (2006) to unify data across sources and types during the data collation process, and to provide classifiers that can flexibly represent the various associated uncertainties. We determined categories to classify each entry by type of record and source. The source identity (e.g. table or page number for georeferenced literature, or institutional specimen collection code for museum specimens) was recorded for each entry in the database, along with the full bibliographic reference to ensure traceability to the original source. The basis of each record was coded as one of four classes: 1) *specimen*: a physical voucher of *D. albipictus* that has been taxonomically identified; 2) *hide*: ticks identified in hair-transects of live or dead hosts in the field or on the skins of animals examined at a later date in the laboratory; 3) *hairloss*: presence of distinctive winter tick hair loss on a live host, usually a moose but, in some cases, an elk or another species; and, 4) *other*: for records that are alternative methods for inferring presence, including photographs of ticks via citizen-science applications and anecdotal observations based on literary reports. In the classification of *hairloss* specifically, the loss that can be safely attributed to winter tick, unlike other forms of hair loss in animals, is highly distinctive and has been used for decades as a suitable means of inferring parasite presence (Glines, 1983; McLaughlin & Addison, 1986; Mooring & Samuel, 1998). To avoid potential misattribution, we only included loss meeting standard categories during the months from February to April, which is the period when winter tick damage on-host is most visible (McLaughlin & Addison, 1986; Mooring & Samuel, 1998). Detailed methods for classification of hair loss on moose from citizen science images are described in Appendix A.1, section 3(i). Data type was assigned as one of five classes, based on the source: georeferenced literature, georeferenced map, unpublished dataset, museum, or citizen science. Where relevant, missing information (i.e., record basis or data type) were recorded as NA. We included an estimated accuracy in kilometers for each record as an approximate guideline of spatial uncertainty, which was determined based on a hierarchy of available information following guidelines set out by Wieczorek et al. (2004) (see Appendix A.1, Class II B 3 (i)).

Although our search was not exhaustive, we endeavoured to balance search effort across locations and time periods with dataset completeness, particularly to ensure that potential gaps in occurrence were not due to a lack of search effort during data compilation. Once a preliminary dataset comprising accessible published literature, maps, and specimen collections had been collated, data were inspected for temporal and geographic gaps (Fig.2.1). Locations at the level of state or province with fewer than three winter tick records spanning three or more years were subjected to an additional, targeted search protocol to confirm no further information was available or, otherwise, to incorporate additional sources, such as from grey literature (Appendix A.1, Table A1). Given the one-year life cycle of this species, considering records across multiple years and with more than one record per location endeavours to ensure that these are from established rather than adventitious winter tick populations. Searches were conducted using an incognito browser on Google Search Engine, with the terms “winter tick”, “*Dermacentor albipictus*”, plus the name of the state or province for which data were sparse (e.g. “Idaho”) and examining the first 30 records. Additional materials from this process were screened as per the initial protocol, before being incorporated within the main dataset for coding.

The resulting raw dataset was inspected and cleaned before it was considered final. Duplicate entries were removed based on identical information in all the following fields: latitude/longitude locations, year, host species, record basis and source type (n=1,871 duplicates removed). We plotted and visually inspected all point data using GIS to identify any anomalous records. Points located in waterbodies were checked for transcription errors against the original source, and if otherwise correct, relocated to the nearest landmass. Database metadata, including a full list of sources contained within it and accompanying processing notes detailing exclusion criteria per source, are available in Appendix A.1.

We summarised apparent trends in our dataset by comparing the geographic distribution of all points together and grouped by apparent peaks in research interest over time. To examine potential relationships between the multiple sources of information in our dataset, pairwise Spearman correlations were computed between the number of records within 250 km hexagonal ranges for each data type. This spatial scale was selected to provide a comparable visual unit across all states and provinces, with each cell encompassing multiple winter tick host home ranges. We compared general patterns in spatial occurrence at this scale with large-scale terrestrial ecoregions (Level 1, Commission for Environmental Cooperation (CEC), 1997), and human accessibility in the form of the density of highways and primary roads (Meijer et al., 2018). To examine the informational value of our dataset against an existing alternative, we compared the spatial and temporal range of records in our dataset against those for *D. albipictus* with both locality and date information in GBIF to 31 December 2021 (GBIF, 2021) (n = 1,520 records; Appendix A.2: Figure A3). Records were grouped spatially within 250 km hexagonal ranges to compare percent spatial cover across the North American continent and the number of records per year were compared over time. Spatial overlap between records in our dataset and the estimated ranges of moose, elk, caribou (all sub-species) and mule and white-tailed deer according to the International Union for the Conservation of Nature (IUCN) (IUCN, 2019a-e) were compared using GIS, to calculate the number of dataset records within each purported host range. All data visualization and statistical analyses described above were carried out in R version 4.0.2 (R Core Team, 2020) and mapping in QGIS v.3.16.10 (QGIS Development Team, 2020).

2.3 Results

2.3.1 Dataset composition: Data types and record bases

The dataset is comprised of 107 sources in total, which represent 140 unique references. Approximately half of all records (44.6%) come from a combination of museum and natural history institutions (n = 773) and published maps (n = 764). Unpublished data provided by government and academic institutions makes up an additional 36.4% (n = 1,254), with the remaining records drawn from literature sources (n = 315), citizen-science records (n = 75), or extant datasets (n = 263). Over time, data sources shifted from museum to literature and unpublished datasets (Fig.2.2(a)). More than 50% of all records of *D. albipictus* occurrence have been determined based on direct observation of its hosts (moose hair loss (n = 904), harvested or live inspection of animal hides (n = 929)) and are generally dated from 1970 onwards (Fig.2.2(b)). Collected specimens account for almost all remaining data (n = 1,432, 41.5%), with a small number of unknown (n= 157) or other origin (e.g. photographic citizen-science records of winter tick) (n = 22). Although specimens of *D. albipictus* are present in every decade since 1900, they are the primary basis for most occurrence records in our dataset for the first half of the 20th century (Fig.2.2(b)).

Specimen records derive from almost all other data types, although the majority are drawn from museum and natural history institutions (Fig.2.2(c)). Hair loss and observations from animal hides have been referenced in both literature and mapping sources, but most of these records are drawn from government-collected datasets. Some georeferenced map data are based on unknown records. Citizen-science data are a relatively new basis of *D. albipictus* occurrence records (designated as “other”) (Fig.2(c)).

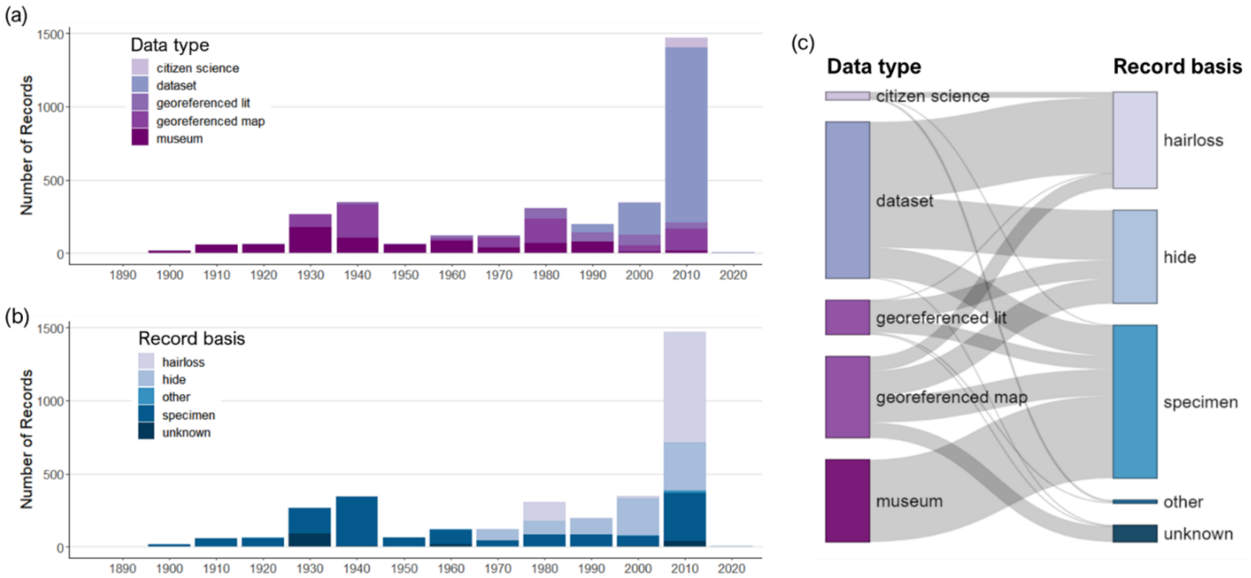


Figure 2.2. Database records over time, grouped by decade, for *D. albipictus* split by **(a)** data type and **(b)** record basis. The relationships between these two types are shown in **(c).**

Comparing the spatial distribution among data sources, there is a strong, significant negative correlation between the number of museum and unpublished dataset records across all geographic locations (r = -0.55, df = 1,156, p<.001) (Appendix A.2: Figures A4-A6). The correlation between the number of records from museums and in the literature was weakly positive (r = 0.13, df = 1,559, p <0.001), as was the correlation between the number of literature and citizen science records (r = 0.16, df = 684, p <0.001). There was a moderately strong positive correlation between the number of records for dataset and literature data types (r = 0.22, df = 1,194, p <0.001). No relationship existed between the number of records provided by unpublished data sources by citizen science (r = 0.02, df = 611, p =0.61), and a weak but significant correlation between number of citizen-science and museum records (r = -0.09, df = 477, p 0.05).

2.3.2 Geographic distribution of the winter tick over time

Our integrated dataset contains 3,444 records of *D. albipictus* occurrence throughout North America from 1869 to 2020, with occurrences spanning latitudes from 16.5°N to 66.2°N, and from Atlantic to Pacific coasts (Fig. 2.3(a)). These records indicate probable *D. albipictus* presence across much of the Nearctic realm, with records in 46 / 50 states (561 / 3,008 counties) in the United States, 10 / 13 Canadian provinces and territories (88 / 338 federal electoral districts), and 26 / 32 Mexican states in the past 150 years. Records include 12 out of 15 continental ecoregions (CEC, 1997) with most records from the northern forests, northwestern forested mountains and eastern temperate forest ecoregions (n=2,539, 75% total dataset). There are currently no records in our dataset for *D. albipictus* in tundra, Hudson plains and Arctic cordillera ecoregions (Appendix A.2: Figure A1). The median density of road networks within 250 km of winter tick occurrence records was 27.7 km of road per km^2 (range = 0-175.7, mean = 34.91, SD ± 29.65), compared with <5 km of road per km^2 in northern regions where winter ticks have not been recorded to date (Appendix A.2: Figure A2).

This geographic distribution extends beyond comparable observations for *D. albipictus* recorded in GBIF, by an estimated 5-10 degrees in the north, and all of Mexico to the south. Approximately 17.6% of spatial locations in our dataset are also identified as occurrence localities based on GBIF records (Appendix A.2: Figure A3). Temporally, over 90% of GBIF records are dated between 1987 and 1990 (n = 1,380 / 1,520), compared with 9.5% in this date range in our dataset (n = 329 / 3451), and are drawn primarily from available online museum records.

In our dataset, the rate of record accumulation has changed over time, showing distinct peaks in the 1950s, late 1980s, and from 2015 onwards (Fig.2.3(b)). Range-edge records have increased in geographic scope over time by approximately 10 degrees in northern latitudes, and by approximately 2.5 degrees in the southern portion of the continent (Fig. 2.3(c)). Prior to 1950, the most northern record for *D. albipictus* was collected in 1948 around 56°N latitude in Saskatchewan, Canada (Agriculture and Agri-Food Canada, 2019): CNC specimen #61400), with anecdotal reports of moose dying with high tick burdens in this region since 1921 (Cameron & Fulton, 1927) (Fig.2.3(c); Fig.2.4). From 1950 to 1980, records reached latitudes of 60.5°N (Wilkinson, 1967), and from 1980 to 2000, the northernmost record is placed at 62.7°N (Environment and Natural Resources NWT, 2019). In the past 20 years, specimens of winter ticks have been removed from moose hides at 66.2°N in the Northwest Territories, Canada, in 2011 (Environment and Natural Resources NWT, 2019; Miller & Poelen, 2017) (Fig.2.3(c); Fig.2.4). In the south, the lowest latitude records prior to 1950 were around 19°N and were from cattle and horses in Puebla, Mexico in 1941 (Guzmán-Cornejo et al., 2016) (Fig.2.3(c)). By 1980, the most southerly records were from 17.9°N (Guzmán-Cornejo et al., 2016), decreasing to around 16.5°N in the Mexican state of Chiapas by the year 2000 (Guzmán-Cornejo et al., 2016)

(Fig.2.3(c)). Detections of winter ticks have been recorded throughout Mexico south to the Guatemalan border in Chiapas.

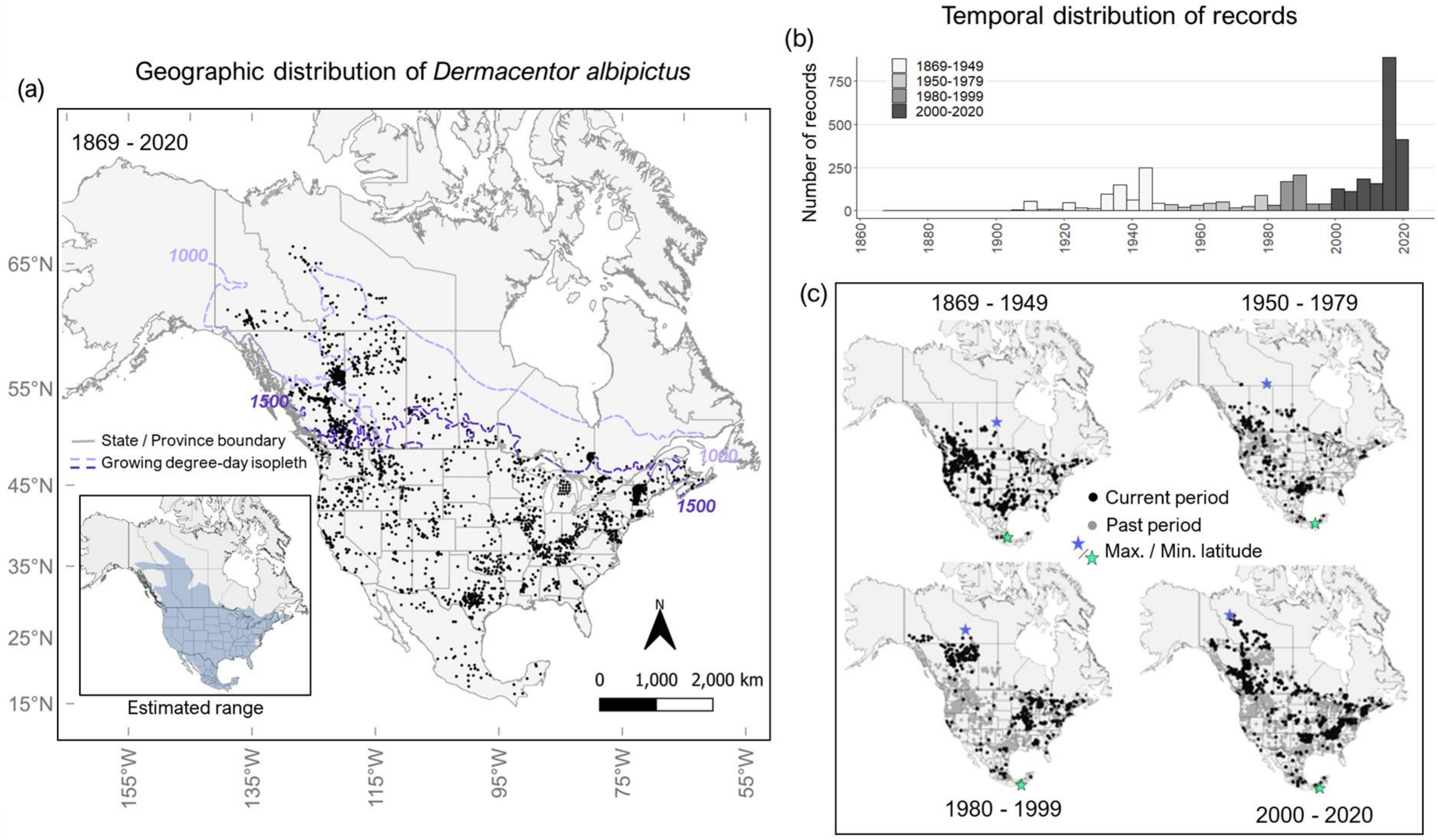


Figure 2.3 Records of *Dermacentor albipictus* occurrence in North America, 1869-2020. (a) point locations for all records (n = 3,444) spanning the years 1869 – 2020 and 1500 and 1000 growing degree-day isopleths to base 5°C (Department of Energy, Mines and Resources, 1981), and the associated observed continental range for *D. albipictus* (inset); **(b)** Number of *D. albipictus* occurrence records present in the database, grouped by year (bars) and separated into four periods of reporting interest (shaded); **(c)** point locations split by years, showing distribution of new records per period (black points) compared with the past (grey points).

The boundary of northern records for *D. albipictus* in the Yukon and Northwest Territories has increased over time (Fig.2.4). In the past two decades, records from the territorial government in both the Yukon and the Northwest Territories have indicated new collection localities in these regions. Specimens of winter tick from hunted and roadkill hides in the Yukon correspond with anecdotal hair loss records made in previous decades, but do not extend above 61.6°N. In the Northwest Territories, specimens collected from hunted hosts provide the most northern record at 66.2°N (Fig.2.4). Over time, the mean latitude of records in the territory increased from 61.1°N before 2000 (n = 6, SD ± 0.94) to 63.1°N after (n = 52, SD ± 1.8), with record numbers increasing almost 9-fold after 2000. We did not find any records of *D. albipictus* in north-west British Columbia or Alaska.

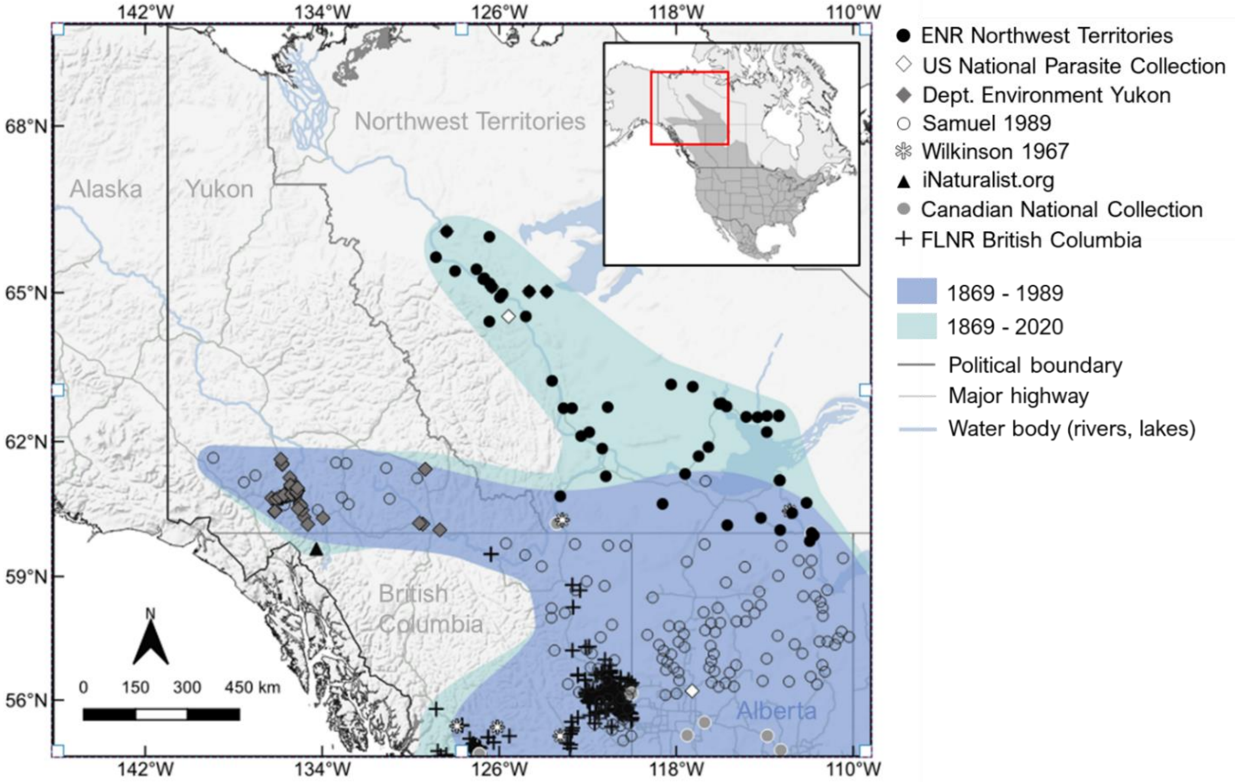


Figure 2.4 Putative northern range for *Dermacentor albipictus* in Yukon and the Northwest Territories based on occurrence dataset records. Multiple sources of data make up this northern edge, given as points (shapes, colours as figure legend). The approximate range for *D. albipictus* is given as the minimum bounding area for points in each of two time periods (shaded

blue, green). Thin grey lines: highways and primary roads; thick grey lines: provincial/territorial and international borders; blue: major rivers and lakes. Legend abbreviations: ENR Department of Environment and Natural Resources; FLNR Ministry of Forests, Lands and Natural Resources.

2.3.3 Winter tick hosts and host ranges

Thirty-five host species are associated with *D. albipictus* records in the database, spread among 26 genera ranging in body mass from a few grams to over 400 kg (Fig.2.5(a)). Not all records have a host association and approximately 30% of the dataset is comprised of records that have unknown or off-host occurrences (“NA”, n = 1,025). A few records indicate winter ticks have occasionally been found on exotic and non-native species, such as feral pig (*Sus scrofa*), chital (*Axis axis*), blackbuck (*Antilope cervicapra*), and more rarely on carnivores such as wolf (*Canis lupus*) and bear (*Ursus* sp.). Most records are associated with cervid hosts (n = 2,126), of which moose are most common (n = 1,362, 39.5%; Fig.2.5(a-b)). Mule and white-tailed deer (n = 616), elk (n = 128) and caribou (n = 16) combined account for 22.1% of the remaining data, and livestock (cattle, horses) account for 7% (n = 243). For these livestock and cervid hosts, the number of records has changed over time (Fig.2.5(b)), with the highest number of records on horses during the earliest period. Where records from horses and cattle have generally declined in number over time, records on elk, caribou, deer, and moose have increased. Given observation bias of hair loss primarily on moose, removing hair loss observations reduces the frequency of records almost 3-fold (n = 460) overall, mostly in the last two decades (Fig.2.5(b)).

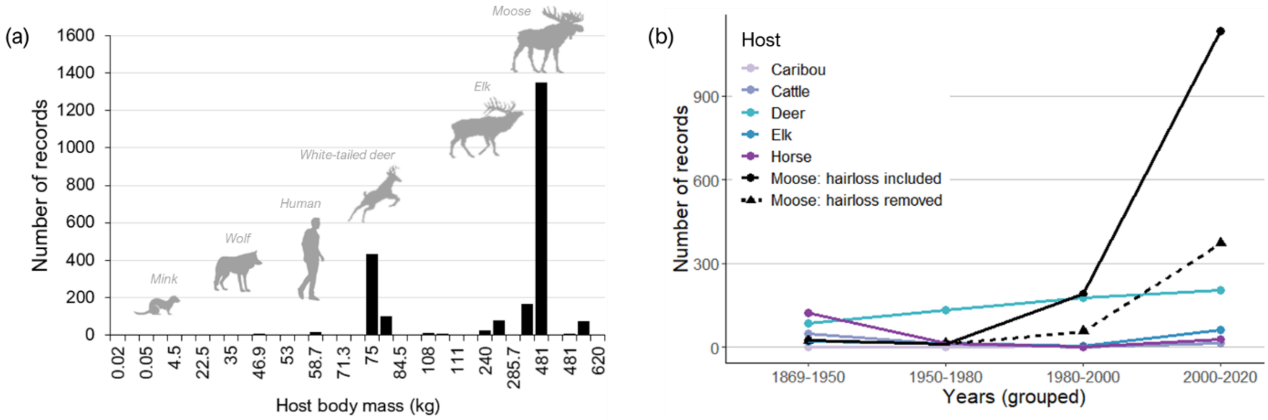


Figure 2.5 Number of database records with associated hosts. (a) Number of records per host species, according to the average adult body mass per host, in kilograms. Common names of host examples are given for a range of masses (grey, pictorial). Host masses were obtained from the PanTHERIA database (Jones et al., 2009). **(b)** Frequency of records on cervids and livestock over time, for all data (solid lines, round points) and with moose hair loss records removed (dashed line, triangular points). Time periods have been grouped by characteristic peaks and troughs in record numbers in the dataset (as shown in Figure 2.2(b)).

Cervid ranges span the entirety of the North American continent and, as such, all *D. albipictus* records coincide with at least one, but often multiple potential host ranges (Table 2.1.; Fig.2.6). Including records where no host association was known, over 61% of *D. albipictus* occurrence points in our dataset overlap with the estimated North American range for moose (Fig.2.6(a)) and almost 15% with that of elk (Fig.2.6(b); Table 2.1). Although the dataset contains relatively few records of winter ticks on boreal caribou, over 18% of all records overlap spatially with the potential range of at least one caribou subspecies (Fig.2.6(c)). The expansive range of both mule and white-tailed deer means that 86% of all dataset records are within the range of one or both species (Fig.2.6(d); Table 2.1).

Die-offs of, or severe impacts on, host species have been reported in jurisdictions spanning the continent, including over 50% of moose range (Fig.2.6(a)), with a few events recorded for elk within their natural range in Wyoming, and translocated location in Pennsylvania (Fig.2.6(b)). Severe impacts on white-tailed deer have also been reported in Pennsylvania (Fig.2.6(d)). To date, no winter tick related die-offs or severe impacts have been reported for any caribou subspecies.

Table 2.1. Spatial overlap between *D. albipictus* dataset records and cervid host range for all subspecies of moose, elk, and caribou, and mule and white-tailed deer (*Odocoileus sp.)* in North America.

Host species (common name)		**Number of records within IUCN host range***	**As percent of total records** (host range overlap)
Moose		2,086	61.2%
Elk		509	14.9%
Caribou		635	18.6%
Deer	- mule	1,784	52.4%
	- white-tailed	2,927	86.0%

* IUCN, 2019a-e

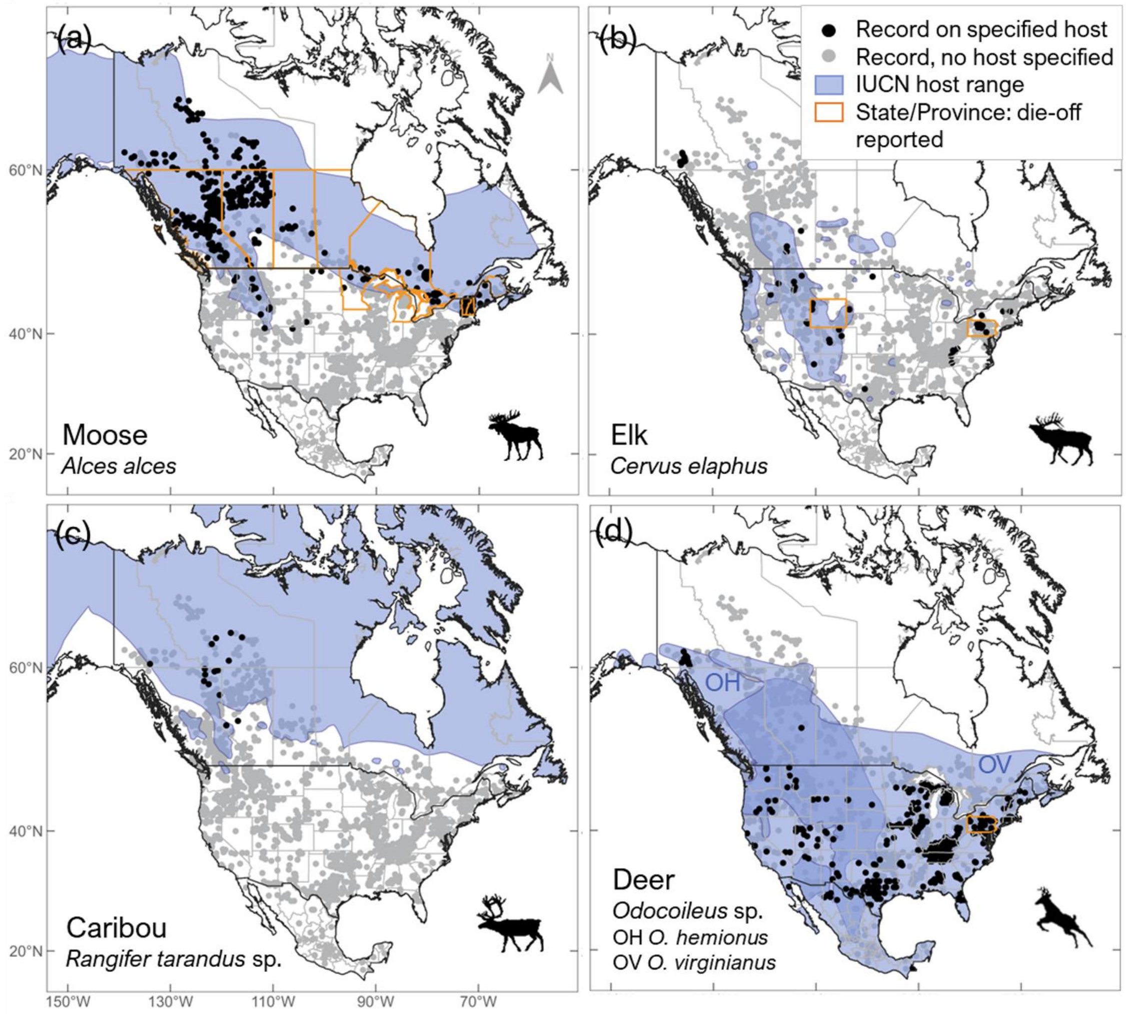


Figure 2.6 Records of *Dermacentor albipictus* in relation to cervid host ranges in North America. Occurrence records within the ranges of (a) moose, (b) elk, (c) caribou (all subspecies), and (d) white-tailed deer (OV) and mule deer (OH). Black points indicate records on each of the specified hosts; grey points represent records for which no host species information is given. Host ranges presented (shaded) are from the IUCN (International Union for the Conservation of Nature) (IUCN, 2019a-e). (References for die-offs: moose (Merrill, 1916; Cameron & Fulton, 1927; Samuel & Barker, 1979; Canadian Wildlife Health Centre (CWHC), 1999, 2002; Pybus et al., 1999; Samuel, 2007; Dunfey-Ball, 2017), elk (Bishopp & Wood, 1913; Calvente et al., 2020), white-tailed deer (United States Department of Agriculture (USDA), 1967; Machtinger et al., 2021).

2.4 Discussion

By mapping the full range of *D. albipictus* in North America we have compiled a large part of the distributional knowledge for this species and its host associations, and methods for assessing and recording its presence over time. Our combined dataset increases both the spatial and temporal resolution of previous mapping studies for this species in the United States (e.g. Bishopp & Trembley, 1945) and Canada (e.g. Lindquist et al., 2016) and indicates potential changes to its geographical range. Notably, presence of *D. albipictus* at this broad geographic scale serves to reinforce that winter ticks can tolerate a broad set of environmental conditions and parasitize a wide range of hosts, corroborating previous laboratory and captive-host studies (Drew & Samuel, 1985; Drew & Samuel, 1986; Addison & McLaughlin, 1988; Welch et al., 1991; Holmes et al., 2018).

Peaks visible in the number of records collected over time may be related most plausibly to punctuated increases in research interest. In many cases, these periods coincide with new methods for detecting and monitoring parasites at a large scale, moving from archived specimens from collectors in the early 20th century, such as Nuttall (Keirans, 1985) and Rothschild (Keirans, 1982), to records stemming from the academic pursuits of Samuel, Addison and colleagues throughout the late 1980s (e.g. Addison & McLaughlin, 1988; Samuel, 2004). Additionally, it is possible that increased interest in the life cycle of *Ixodes* ticks may have driven greater sampling of deer post-1982, after the discovery of the role of white-tailed deer in the transmission of the Lyme disease agent *Borrelia burgdorferi* (Burgdorfer et al., 1982). Ongoing and renewed interest in the detrimental effects of winter ticks on their hosts at the individual and population level has resulted in multiple sources of information drawn from government monitoring and academic research (e.g. Amerasinghe et al., 1992; Environment and Natural Resources NWT, 2019; Jones et al., 2019; Ohio Department of Health, 2020) to community engagement and citizen-science initiatives (eTick.ca, 2021; iNaturalist.org, 2021; Watt, 2021; Chenery et al., 2022). Although the latter currently makes up a small part of the total number of distribution records for *D. albipictus*, citizen-science data are predicted to become an increasingly important source of tick distribution information in the future (Silvertown, 2009; Eisen & Eisen, 2021; Heberling et al., 2021).

2.4.1 Sources and methods for inferring winter tick presence

Understanding the basis of how *D. albipictus* observations are recorded may provide valuable insight into the underlying methods used to detect and monitor this species and inform future practices. In our dataset, there appears to have been a notable shift from the collection of tick specimens to the passive measure of hair-loss detection from which to infer winter tick presence over time. Although many records in our dataset arise from natural history and specimen collections, this form of record has decreased considerably in the past 20 years (Fig.2.2(a)), a trend that has also been noted in the collection of birds (Boakes et al., 2010). There are several possible reasons for this trend. Not all collections have been fully digitized by museums, with many institutions having just a proportion of species records available online (Kharouba et al., 2019; Meineke et al., 2019). Similarly, specimen collections represent a snapshot of records that have been catalogued to date, and it is possible that more recent specimens may still await taxonomic identification (Tingley & Beissinger, 2009). The extent to which natural history institutions have the capacity to continue collecting vouchers that may be considered redundant if already present in a collection is also a factor that could influence the number of recent specimen records and is likely to vary considerably by each museum's collections policy (e.g., National Museum of Natural History, 2017). Distinctive patterns of hair loss caused by host response to winter tick infestation provides an alternative, although potentially host-biased, means of inferring the presence of *D. albipictus.* Although hair loss on moose has been reported since the early 1900s, classification schemes were only used with regularity since the late 1980s, defining loss in four (Glines, 1983) or five categories (Garner & Wilton, 1993), or as percentages of the total coat that appears lost or damaged (McLaughlin & Addison, 1986; Mooring & Samuel, 1998). It is likely that these less invasive and time-intensive methods of *D. albipictus* detection have increased in popularity with the certainty of hair loss as a valuable indicator of winter tick infestation, such as in long-term aerial surveys of moose in Ontario (Wilton & Garner, 1993). Modern technology has further improved efforts to collect hair-loss data, recording images *via* remote wildlife cameras and portable, cellular phones, and reporting observations *via* governmental surveys (Watt, 2021) or through citizen-science applications (e.g. iNaturalist). This relative ease of collection, due in large part to modern technology, may account for the high proportion of hair-loss related observations in our dataset and their recency in the past few decades. We do not have records in our database for non-moose hosts on the basis of hair loss alone, but it should be noted that most cervids do exhibit some degree of winter tick-induced alopecia (Welch et al., 1991; Calvente et al., 2020; Normandeau et al., 2022), even if this is usually less severe than in moose. Extremely high host burdens of winter tick have been found on woodland caribou (*Rangifer tarandus caribou)* and white-tailed deer when hair loss has been absent (Welch et al., 1990; Machtinger et al., 2021), so the reliability of this indicator on non-moose species may be limited, particularly when compared with conventional necropsy techniques.

Although the total number of records per spatial unit are an imperfect proxy for sampling or collection effort (Tingley & Beissinger, 2009), the accumulation of knowledge they present allows us to compare relationships between locations. Variation in the relationships between data types at a regional scale indicated that some sources may provide substitutes for others in the absence of traditional information. For example, the negative correlation between the number of records from museums and the number of records from unpublished datasets suggests that data collected as part of government monitoring schemes and other research endeavors may have filled gaps in *D. albipictus* records at a regional scale at which museum specimens are lacking. The same might be said of the weaker negative relationship between the number of museum versus citizen-science sources. This trend may most plausibly relate to the relative increase in data collection for winter tick in northern Canada based on moose hair loss (e. g. government monitoring in British Columbia; observations on iNaturalist.org), for which there is no good analogue among natural history or museum specimens. Positive relationships between the number of records from museum and the published literature or citizen-science sources, and between literature and unpublished datasets, could indicate areas where winter tick activity is well-established and known among researchers and the general public, such as in New England, USA. The lack of apparent relationship between citizen-science and unpublished data sources may be due to the small number of citizen science records in our dataset at this time, and we might expect a stronger, likely positive relationship between to the two sources as more research and monitoring efforts draw on community based methods of information gathering (Troia & McManamay, 2016; Heberling et al., 2021).

The predominant sources of information on *D. albipictus* that appear in the last two decades are those of unpublished research or monitoring datasets. These records are often collected at regional scales as part of ongoing government surveillance of wildlife health in general, although some have designated winter tick monitoring efforts (e. g. monitoring moose hair loss in British

Columbia; ungulate hide surveillance in the Yukon; Chenery et al., 2022). We sought to include at least some of these unpublished data in our dataset to both fill gaps in the recent record and to assist in making these data accessible to other researchers. However, our inclusion of previously unpublished data was necessarily opportunistic rather than exhaustive and we do not claim to include all records for winter tick that might be available. This raises the importance of specimen banking within national or specialist collections (e. g. U.S. National Parasite Collection; Canadian National Collection of Insects and Arachnids), which has the added benefit of increasingly becoming digitized and drawn upon within other accessible occurrence datasets, such as GBIF.

The proliferation of data arising from community science platforms such as GBIF has been discussed in detail previously (Heberling et al., 2021), particularly with respect to spatial biases (Boakes et al., 2010; Beck et al., 2014; Troia & McManamay, 2016). However, all sources of records in our dataset may be subject to biases of some form, largely stemming from the unstructured methods by which they have been collected. Firstly, it is well known that terrestrial occurrence records may suffer from sampling bias due to accessibility, being most often near to roads or research institutions (Meyer et al., 2015; Monsarrat et al., 2019) and that this can skew mapped and modelled outputs (Kadmon et al., 2004; Hughes et al., 2021). Records in our dataset, even with differing levels of accuracy associated with them, were not found to be heavily road-biased based on the density of roads within a 250 km area of each tick record (median road density 27.7, mean = 34.91, SD ± 29.64), although most records in more remote northern regions are still in more accessible locations by land or via river valleys and may also be reflective of host movement (Wilson & Haas, 2012) (Appendix A.2: Figure A2).

We endeavored to capture a comprehensive picture of *D. albipictus* occurrence across the continent that would include potential geographic gaps in records in addition to areas for which data are plentiful, which naturally results in some spatial clustering at a local scale (Fig.3(a)). These locations, particularly in the eastern USA and to the west, across the Rocky Mountains, are generally ones where human interactions with potentially infested hosts are highest (e.g. through hunting, roadkill, agriculture, or outdoor activities such as hiking), and/or winter ticks are known to have deleterious effects on hosts (e.g. New Hampshire, USA., Jones et al., 2019). This likely leads to biases in favour of detection, whereas relatively remote, northern regions such as NWT or northern Ontario and Quebec, where host densities may be lower and human access limited, likely represent under-estimates of the full extent of *D. albipictus'* range due to a lack of sampling effort. Similarly, some apparent absences of *D. albipictus* records, for example, in the US states of Delaware, Massachusetts, and West Virginia, seem unlikely to be true absences given the number of records in adjacent states and may be more accurately represented as having no suitable geolocated data available (Appendix A.1: Table A1). Despite no current records, it is also feasible that *D. albipictus* is, or soon could be, present in Alaska. Mesocosm experiments in the late 1980s demonstrated that conditions were adequate for adult female winter ticks to survive and oviposit and for eggs to hatch, suggesting that host movement was a primary barrier to *D. albipictus* establishment in this region (Zarnke et al., 1990). The continued detection of winter ticks in neighbouring Yukon over time highlights that Alaska is a key area for monitoring and surveillance efforts to confirm if there is a true absence in this state (Hahn & George, 2019).

2.4.2 Evidence for range expansion

In the current study, we detected potential changes to the northern range edge of *D. albipictus*, and, to a lesser degree, in its southern continental range. *D. albipictus* is reputed to be present in some neotropical regions in Central America (Yunker et al., 1986; Guglielmone et al., 2014), so it is possible that the Mexican records do not represent a true range edge for this species. Additionally, the coarse spatial resolution for many of the Mexican records (to state level only) means that it is not possible to fully determine the extent of latitudinal change that has occurred in this southern portion of *D. albipictus'* range. A report of winter tick on white-tailed deer and red brocket deer (*Mazama americana*) suggested that Mexico was a new locality record for this species in 2005, and that *M. americana* was a new host (Romero-Castañón et al., 2008, p.121). Our findings agree with this latter statement, as we did not find any other records of winter tick on this host species. However, our database contains several records of *D. albipictus* occurrence in Mexico that date back to 1941 (Guzmán-Cornejo et al., 2016), confirming previous assessments that the species has likely been present in the country for some time (Guglielmone et al., 2014).

As with other parasite species, it is possible that *D. albipictus* may expand its existing range farther north as it experiences fewer environmental constraints during the off-host components of its life cycle (Hoberg et al., 2008; Polley et al., 2010). This is of general concern in northern regions given the availability of potential cervid hosts for winter ticks, particularly barren ground caribou (*R. t. groenlandicus*), which are considered to be species at risk and of significant sociocultural importance for northern Indigenous peoples (Kutz et al., 2009; Hahn & George, 2019). Based on comparison of historical and recent records in this dataset, we speculate that the northern range edge of winter tick across North America has been fluctuating for some time between 50^{o}N latitude in the east and around 63^{o}N latitude in the west (Fig.2.3(c); Fig.2.4). Anecdotal reports of hair loss on moose around 62°N present the northernmost detections of this species prior to 1990 (Samuel, 1989), with definitive records from specimens collected from a moose and a wolf at approximately 60.5°N during this time (Wilkinson, 1967). *D. albipictus* records appear to show a clear and stable boundary to their distribution in northern Canada, with potential shifts over the past two decades in the north-west. In the east, the continued absence over time of more than a few records in Quebec, northern Ontario, and Manitoba signals that little geographic change may have occurred, though there is currently a paucity of data in these areas. One possible explanation for fewer records could be that *D. albipictus* is present, but not highly abundant in these regions, with low detectability or little cause for concern to wildlife hosts resulting in reduced reporting. However, no definitive conclusions can be drawn in these regions without additional monitoring and search efforts. Similarly, there are no clear reasons for the absence of records in north-west British Columbia, but we suggest this may be the result of a combination of reduced sampling effort due to limited road access in this location, and/or unique environmental factors. This region is home to both moose and boreal caribou populations that could provide ample hosts for winter ticks (Demarchi, 2011; Kuzyk, 2016), meaning that it is unlikely to be absent due to an unavailability of hosts. The landscape here is characterized by several major mountain ranges, rivers, and valleys that join it to neighbouring Yukon and Alaska, and greatly influence the resulting climate. Winters in this region are described as particularly lengthy and severe (Demarchi, 2011), which could impact off-host survival and oviposition success of *D. albipictus* females in early spring (Drew & Samuel, 1989) and transmission of larvae to hosts in autumn (Musante et al., 2010). However, detections of winter ticks in environmentally similar conditions to the north and the east (Fig.2.4) suggest that this absence should be treated with caution.

In the Yukon and Northwest Territories, data collected over the past 10-20 years by government and academic researchers can be compared with historical records in the form of museum specimens and anecdotal reports (Fig.2.4). No substantive records of *D. albipictus* were found prior to Wilkinson's treatise in 1967, which places the northernmost records of winter tick in Fort Liard and Fort Smith (60.2-60.5°N) on the Northwest Territories – Alberta border (Wilkinson, 1967). It is possible that winter ticks were present, at least in the Yukon, as early as the 1930s based on moose hair loss reported within Samuel's survey of trap line owners, which potentially increases this northern edge to just below 62°N in its historical range (Samuel, 1989). However, it was the introduction of infested hosts - elk, translocated from Alberta to the Yukon on several occasions between the 1950s and 1990s - that has most likely influenced the subsequent distribution of *D. albipictus* in the territory (Yukon Elk Management Planning Team, 2008; Kutz et al., 2009; Strong et al., 2013; Leo et al., 2014). In recent years, increased sampling effort in the Yukon has resulted in both off-host, larval detections of winter ticks (Chenery et al., 2020) and observations stemming from on-host, hide sampling (Department of Environment, Yukon, 2019; Chenery et al., 2022). However, all records remain below 62°N, consistent with the findings of Samuel's earlier survey (1989). Although most of these records remain concentrated around the Ibex Valley and Braeburn regions that form the core management area for elk, detections farther east and south of this location indicate that this is unlikely to be the sole source of the winter tick population (Fig.2.4) (Environment Yukon, 2010; Chenery et al., 2022). There are several records across the Southern Lakes region prior to government records on elk and deer (2007), including from a moose in Watson Lake in 1994 (Environment Yukon, 2010). Additional sampling of moose and caribou hides up to 67.5°N has returned no winter tick occurrences and, similarly, samples assessed as far as 139.6°W, less than 100km from the Alaskan border, have returned no ticks (Chenery et al., 2022). The combination of multiple record bases for detection over time, from hair loss to specimens and field data, suggests that *D. albipictus* has most likely been in present in the Yukon for several decades. Within the confines of currently available information, a 62°N limit seems a reasonable approximation of the winter tick's current range in the territory.

As in the Yukon, comparisons between historical and current records in the Northwest Territories are challenging to make because we cannot know if an absence of records equates to a lack of survey effort prior to 2000. Kutz et al. (2009) have previously discussed the possibility that more recent occurrence reports may be a sign of winter tick range expansion in the Northwest Territories due to increasing moose densities and the indirect effects of climate change. They note that community interviews conducted within the Sahtu Settlement Area in 2005 indicated that physical specimens of *D. albipictus* had rarely been encountered by local people historically, and that winter tick induced hair loss on moose was also uncommon (Kutz et al., 2009). This evidence is in accordance with the additional records presented in our dataset from government surveillance, which have increased both the number and geographic scope of occurrence localities in the Northwest Territories since 2000 (Environment and Natural Resources NWT, 2019). All records to date appear east of the Mackenzie Mountain range, which separates the territory from the Yukon, and many of the most northern detections fall in the tundra plains alongside the Mackenzie River (Fig.2.4). These areas are of high importance for potential ungulate host species such as moose and mountain caribou (*R. t. caribou*) (Wilson & Haas, 2012), and detections may also be the result of relative ease of access to hunted hosts in this location for sampling. Reduced snow depth over winter has also been linked to an increasing encroachment of smaller-bodied deer species in northern areas, including neighbouring Yukon and Alaska, which may present additional opportunities for tick range expansion in the north (Gilbert et al., 2017; Kennedy-Slaney et al., 2018).

2.4.3 Factors affecting winter tick distribution

Ecological theory predicts that the distribution of resources, individual dispersal abilities, and fundamental abiotic tolerances of organisms ultimately determine their distribution in space and time (Grinnell, 1917; Elton, 1927). We cannot infer much from winter tick occurrence data alone beyond the fact that their apparent broad distribution suggests a remarkable tolerance of varied environmental conditions throughout their range. However, there are a few interesting examples that warrant further discussion. Climate and environmental factors have previously been considered as critical in limiting winter ticks in northern climates, with one of the earliest hypotheses presented by Wilkinson (1967) being that the northern range edge of *D. albipictus* (around 60^{o}N latitude) is limited by a requirement of at least 1500 growing degree days above a 42^{o}F (~5°C) base. Zarnke et al. (1990) discussed this with respect to a potential Alaskan establishment by winter ticks, indicating that accumulated temperature conditions were already being met in some parts of the state. Comparison with our dataset shows that there are many records north of the 1500 growing degree-day isopleth at base 5°C (Fig.2.3(a)), in contrast with Wilkinson's original hypothesis (1967). This finding could be for several reasons, including already significant changes in climate since the 1960s which has shifted the average isopleth north (Zhang et al., 2019), or possible differences in the calculation methods of the degree-days themselves (e.g. length of growing season used) (Sridhar & Reddy, 2013). However, it is also likely that factors influencing winter tick survival at the population level act at a much smaller spatial scale than is fully captured by thermal isopleths, as with other tick species (Dobson et al., 2011; Hacker et al., 2021; Dumas et al., 2022). Winter ticks have a short, but critical, window of opportunity for important life-cycle processes to occur during their off-host life stages. For example, heavy snow may impact the reproductive success and survival of adult females when they drop from the host in early spring, and physically encumber larval transmission in autumn (Drew & Samuel, 1985). Locations where snow depth may be impeded due to topography or vegetation cover at these times of year are likely to benefit winter tick populations. Such microhabitat factors may explain, in part, the current range edge for *D. albipictus* in northern latitudes, given the assumed availability of potential hosts in this region (Fig. 2.6), but further research into the effects of environmental conditions on winter tick distribution is needed. Additionally, projected climate-driven changes to the ecological biomes will likely impact the community composition of the winter tick's potential hosts in these northern areas. In the Yukon, projections indicate that up to 90% of the Southern Lakes region that is currently dry boreal wooded grasslands and forests will shift in composition to prairie and grassland habitat under current climate warming in the next 50-70 years (Rowland et al., 2016), providing ideal forage for smaller-bodied deer species to naturally colonize this region (Veitch, 2001; Kennedy-Slaney et al., 2018). Such natural colonisations present an opportunity for *D. albipictus* to be continually re-introduced *via* deer, and to provide additional hosts for existing winter tick populations.

Our database records indicate that winter ticks have been found on numerous host species over the past 150 years, though most commonly on moose and other large-bodied cervids. This lack of host-specificity is likely one of the traits that has allowed winter ticks to become distributed at such a wide spatial scale (Shenbrot et al., 2007; Leo, 2012). Although moose are associated with many winter tick records in our dataset, it is important to note that this may be due to factors that are independent of the true distribution of *D. albipictus* among wild hosts. For example, our dataset includes biases in records, such as moose-specific hair-loss observations, and datasets resulting from active monitoring in areas where epizootics have occurred previously (e.g. New England; Vermont Fish and Wildlife, 2019). The relatively high number of regions where winter tick -related die-off events have been reported for moose (Fig.2.6(a)), compared with other species (e.g. elk, Fig.2.6(b); white-tailed deer, Fig.2.6(c)), may explain the greater degree of research attention, given known impact. When we examined the number of records for each host species, removing those records based on hair-loss observations, most winter tick records were associated with deer until approximately 20 years ago, with continued detections in recent times (Fig.2.5(b)). As previously noted, the increasing trend for records associated with mule and white-tailed deer in recent decades may be due to the cooccurrence of *D. albipictus* with other tick species that are more commonly sampled for diseases of public health concern, such as Lyme disease. Additionally, given that the combined range of *Odocoileus* species covers a large part of North America, it is not surprising that they have the highest level of range overlap with locations where winter ticks are found (Table 2.1). The relatively low number of records on caribou and elk in our dataset may be more reflective of a bias in research interest towards moose-winter tick interactions rather than their competency as hosts. Given the proximity of detections of winter ticks on mountain caribou in the Northwest Territories, the potential for barren ground caribou to become infested in future is also of concern (Kutz et al., 2009).

Spatially, the high degree of range overlap between competent cervid hosts suggests that it is unlikely that host factors are the primary limitation driving winter tick distribution at this continental scale. The importance of host range in determining the distribution of parasitic species has been widely discussed (Cumming, 1999; Phillips et al., 2010; Estrada-Peña & de la Fuente, 2017), with most evidence indicating that only ticks with a high degree of host-specialism are likely to be restricted in their resultant range (McCoy et al., 2013). Winter ticks are only transmissible to hosts during the larval stage in their life cycle, exhibiting host-seeking (“questing”) behaviour from mid- to late-August (Drew & Samuel, 1985; Samuel, 2004). The locations for questing larvae are determined by the locations of infested hosts the previous spring, as adult females drop from the host to oviposit, around March (Drew & Samuel, 1989). This means that differences in foraging preference between species, and at different times of year, could either reduce or increase the extent of spatial overlap between winter ticks and hosts in certain areas.

One of the more immediate movement mechanisms that may be influencing current or future winter tick distribution is the translocation of hosts. In addition to the movement of elk from Alberta to the Yukon, the interstate relocation of livestock and big game species over the past century has presented opportunities for winter ticks to colonise new localities through this anthropogenic movement pathway (Slabach et al., 2018). During the process of dataset assembly, we found evidence of multiple translocation events of *D. albipictus* on horse, deer, cattle, and moose over the past 150 years (Fig.2.7). These records do not imply establishment of winter ticks in these areas, but nevertheless, they present a risk to recipient host populations (Corn & Nettles, 2001; Gerhold & Hickling, 2016). Similarly, the movement of disease-free hosts into areas where winter ticks are already present, thereby increasing the number of potential hosts, may exacerbate the epizootic frequency of tick outbreaks (Samuel, 2007). It is also concerning that *D. albipictus* has been moved across the globe on at least two separate occasions, on a racehorse to Germany (Liebisch et al., 2006) and on white-tailed deer hides imported to China (Zhao et al., 2020). Current federal regulations for the interstate transport of wild cervids in the United States focus largely on the risks posed by Chronic Wasting Disease (CWD) and Bovine Tuberculosis (TB), with no apparent mention of ectoparasites such as *D. albipictus* (e.g. 9 CFR §81.1-81.6, 2012; United States Department of Agriculture (USDA), 2020). This suggests that the degree of veterinary assessment of animals will likely vary across states, and that within-state movement is likely to be even less regulated. A simple solution to reduce the risks of accidental introduction would be to move animals during the winter tick off-host period whenever possible, from mid-May to July, which is credited with the absence of *D. albipictus* on moose in Newfoundland (Samuel, 2004).

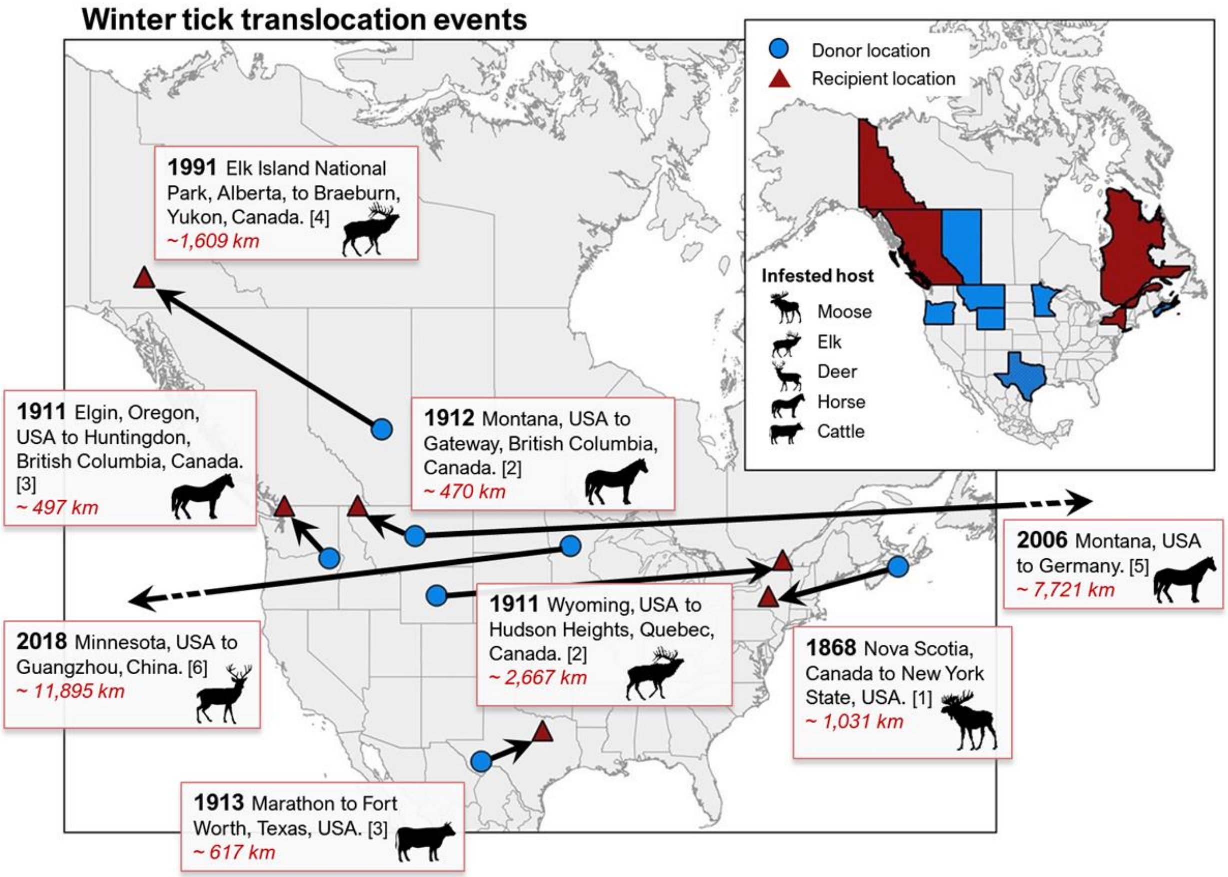


Figure 2.7. Reported introductions of winter ticks via host translocation of infested hosts. These records indicate known events whereby *D. albipictus* has been moved along with host animals, both within and outside of North America. Note that these translocations alone do not imply winter tick establishment in recipient areas but indicate how easily such anthropogenic introductions could occur. References: [1] Hays, 1869; [2] Hewitt, 1915; [3] Bishopp & Wood, 1913; [4] Yukon Elk Management Planning Team, 2008; [5] Liebisch et al., 2006; [6] Zhao et al., 2020.

2.5 Conclusions

Setting a baseline for the winter tick distribution is a prerequisite to understanding ecological preferences at a global scale, and for establishing the likelihood of future range expansions in local and regional areas. Through the comprehensive collation of records for *D. albipictus* into a single, spatio-temporal database, we have produced the first, full historical and current distribution maps for this species throughout its North American range and discussed its potential range expansion. Inadequate data have been a barrier to this in the past, and we hope that assembling much of the combined knowledge on *D. albipictus* over time and space will provide context for future research, including the potential identification of priority areas for monitoring or mitigation from natural expansion or anthropogenic introductions. In particular, the inclusion of winter tick – host relationships in these data present a further opportunity to examine potential interactions across their ranges and may offer the possibility of additional risk analysis for cervid and livestock hosts. We caution, however, that, although these occurrence data may be a valuable resource for researchers wishing to predict winter tick distributions, there are challenges to working with multi-source datasets such as ours (Isaac et al., 2020). Unstructured data contain multiple methods and motivations in their collection, such as samples from structured transect surveys that have been combined alongside opportunistic observations (e.g. Pagel et al., 2014) or data arising from presence-only records that have been combined with abundance data collected through systematic surveys (e.g. Dorazio, 2014). As a result, the differing underlying statistical assumptions of the observation process(es) by which the data were collected require careful consideration prior to analysis (Franklin, 2009; Merow et al., 2017). By examining the sources and structure of multi-source data in advance, researchers can make more informed decisions when selecting suitable modelling methods and inferring results, as shown by the increasing guidance aimed at ecologists in using integrated distribution modelling (Fletcher Jr. et al., 2019; Miller et al., 2019; Zipkin et al., 2019). Being cognizant of the limitations and biases inherent to multi-source data can also present new opportunities to model distributions for little-known or under-studied species, where single, standardized sources of information may be sparse or absent (Heberling et al., 2021).

We have discussed the apparent changes in common sources and record bases over time and how the move towards passive measures and away from specimen data could bias the *D. albipictus* occurrence record by focusing on moose at the expense of other potential hosts. Often, such patterns are ignored without considering how and why such collection biases might occur in space and time but understanding these accumulations and shortages in knowledge may provide insights of direct relevance to the way in which species occurrence information is acquired, analyzed, and stored in future. Measuring and predicting the future impact of winter ticks, and other wildlife parasites and diseases, depends on the continued collection of consistent and comparable data (Tingley & Beissinger, 2009; Boakes et al., 2010). Endeavours to archive georeferenced specimens in accessible collections, and the digitization of those collections, will continue to form a necessary backbone of occurrence data, but integration of new sources of information from citizen science and community engagement may make important contributions to the accumulation of data in future.

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Author contributions

Conceptualization, ESC, PKM; methodology, ESC, PKM, NEM; formal analysis, ESC; investigation, ESC; resources, HF, NJH, NEM, PKM; data curation, ESC; writing—original draft preparation, ESC; writing—review and editing, ESC, HF, NJH, NEM, PKM; visualization, ESC; supervision, NEM, PKM; funding NEM, NJH, PKM. All authors read and approved the final manuscript.

Conflict of interest statement

The authors declare that they have no conflict of interest.

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Data availability

The winter tick occurrence database, citation file and source processing notes are openly available in Figshare at DOI 10.6084/m9.figshare.20170952. Code to reproduce all data figures (Figures 2(b), 4, and 6) is available in Github at https://github.com/EmilyChenery/winter-tick-range/

Chapter 3

First records of *Dermacentor albipictus* larvae collected by flagging in Yukon, Canada.

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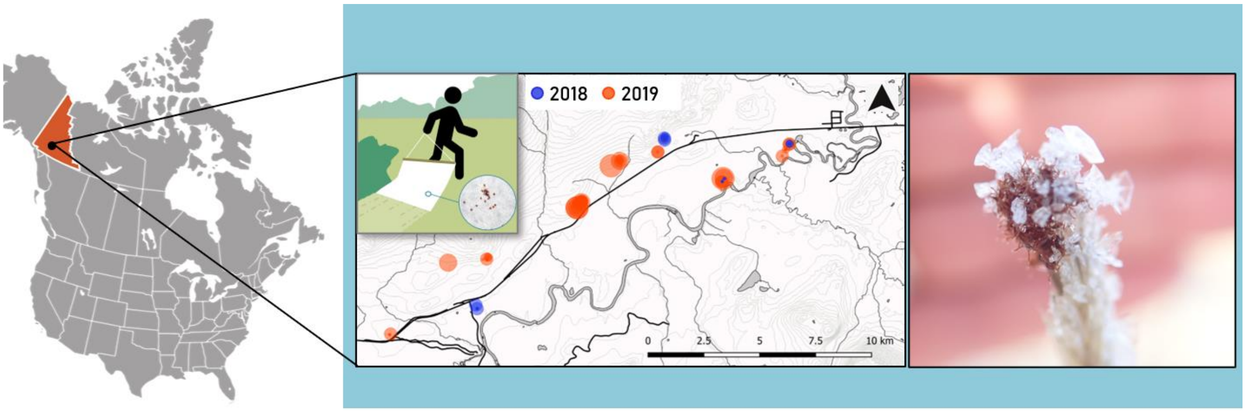

Contributions:

ESC, NJH and PKM conceived the study and obtained funding to support the research. ESC, PKM, and NEM designed the flagging study methodology. EC conducted the investigation in the field, collected and analyzed all larval and environmental data, visualized the data and wrote the original manuscript. PKM and NEM provided supervisory support to ESC, and NJH provided access to resources and laboratory space for tick sample processing.

Abstract

The winter tick (*Dermacentor albipictus*) has garnered significant attention throughout North America for its impact on wildlife health, and especially for moose (*Alces alces*), where high tick burdens may result in host hair loss, anemia, and can prove fatal. The environmental transmission of *D. albipictus* larvae to a host is a critical event that has direct impact on infestation success, yet in-field observations of this life stage are lacking. In the Yukon, Canada, *D. albipictus* had previously been found on hosts, but its larval life stage had not been detected in the field, despite previous sampling attempts. We sampled for *D. albipictus* larvae using traditional flagging methods in Ibex Valley and Braeburn, Yukon. Sites were sampled repeatedly for *D. albipictus* larvae by flagging from late August to end of October in 2018 and late August to end of November 2019. Larvae of *D. albipictus* were collected throughout the valley, at approximate densities ranging from 0.04 to 4,236 larvae /100 m^2. Larvae were present primarily on grassy vegetation on south-facing slopes in the Ibex Valley region and in Braeburn. Highest average larval numbers suggest peak questing activity was towards the end of September and beginning of October, as elsewhere in North America. To the best of our knowledge, we report the first successful collection of the off-host, larval life stage of *D. albipictus* by flagging, north of 60° latitude in the Yukon, Canada. These new observations provide critical information on the spatial distribution of the host-seeking life stage of *D. albipictus* and confirm that this species is completing its whole life cycle in southern Yukon. Understanding the environmental conditions where larvae spend their vulnerable period off-host in this northern location can inform both management strategies and projections of future range expansion which may occur with a changing climate.

Keywords

Dermacentor albipictus, Flagging method, Larval tick, Winter tick, Yukon, Canada

3.1 Introduction

Understanding the off-host dynamics of tick life cycles has profound implications for designing successful surveillance programmes (Clow et al., 2018), predicting future risk to humans and wildlife (Zeman and Benes, 2013; Arsnoe et al., 2019), and determining appropriate management options Stafford and Kitron, 2002). Prior to our study, collection of the off-host, larval life stage of the winter tick, *Dermacentor albipictus* (Packard, 1869) had not been documented at what is believed to be one of the northernmost limits of their range, in the Yukon Territory, Canada (Wilkinson, 1967; Samuel, 2004; Environment Yukon, 2010).

Dermacentor albipictus is a one-host ixodid tick with a one-year life cycle, which primarily feeds on cervids such as moose (*Alces alces*), elk (*Cervus canadensis*), caribou (*Rangifer tarandus*), and deer (*Odocoileus* sp.). Although it shows no host specificity, infestation in moose is well-known for causing significant hair and blood loss, the effects of which can be fatal (Samuel, 2004; Seton, 1953; Jones et al., 2018). Winter ticks have also been implicated in the death of elk, showing similar pathological features (Calvente et al., 2020). It is not known to be a vector of any significant diseases of public or wildlife health concern, although ongoing research suggests *D. albipictus* may be a reservoir for some pathogens, such as pseudorabies (Musante et al., 2014) and *Babesia duncani* (Swei et al., 2019).

The initial introduction of *D. albipictus* to southern Yukon was likely through the translocation of elk from Elk Island National Park, Alberta, Canada, in the 1950s and 1990s (Samuel, 1989; Leo et al., 2014; Environment Yukon, 2019). Prior to this, the ticks were not believed to be present north of 60°N latitude (Wilkinson, 1967; Samuel, 2004) though likely present up to 66°N latitude in the adjacent Northwest Territories (Wilkinson, 1967; Samuel, 1989; Kashivakura, 2013). Samuel's comprehensive survey of trappers in northwestern Canada in 1987 indicated that, anecdotally, some Yukon moose may have had hair loss indicative of *D. albipictus* infestation as far back as the 1930s (Samuel, 1989), but no field studies had been otherwise conducted. Monitoring by the Yukon government has recorded nymphal and adult *D. albipictus* by examining cervid hides since 2012, but no larval ticks had been detected in the environment, despite multiple flagging attempts 2010–2012 (Environment Yukon, 2010, 2016).

Here, we report for the first time the collection of larval *D. albipictus* by flagging in 2018 and 2019, in important cervid habitat in Yukon, Canada, thus confirming that winter ticks are successfully completing their life cycles despite the high latitude.

3.2 Methods

The Ibex Valley is located in the Boreal Cordillera ecoregion of southern Yukon, Canada (60°50'42"N, 135°38'18"W, elevation *c.*721 m), approximately 16 km west of the city of Whitehorse (Fig. 3.1). It is primarily settlement land of the Champagne and Aishihik and Kwanlin Dün First Nations and is presently undeveloped, with a few agricultural holdings of livestock and private residences. The approximately 152 km^2 area also forms the core range for a managed population of elk (*Cervus canadensis*) that moved into this region following their introduction in 1959 (Strong et al., 2013; Environment Yukon, 2016). Other potential host species found here include moose, mule deer (*Odocoileus hemionus*), and semi-feral horses (*Equus caballus*). Vegetation composition is mixed, with characteristic boreal forests of conifers mixed with wetlands and aspen stands, interspersed with dry, grassy south-facing slopes and glacial lacustrine valley bottoms (Smith et al., 2004). Several areas have shown slow regeneration since forest fires in 1958 (Smith et al., 2004) and are sparsely vegetated.

The Ibex Valley formed part of a pilot study in 2018 aimed at obtaining an initial detection of *D. albipictus* larval presence, and it was the only location where any larvae were found (Fig. 3.1). In 2019, all sampling efforts focused on this region with the aim of confirming larval detections made the previous year. Twelve sites, each a minimum of 500 m^2 were selected across the valley based on habitat type (sub-polar grassland, barren-ground) and host activity (game trails, pellets, tracks). One additional site was also chosen in the Braeburn elk range (61°25'20.2"N, 135°43'52.1"W, elevation *c.*835 m), 40 km to the north of Ibex Valley. Flagging was conducted at each site, focusing on areas with visible cervid game trails. Sampling events were repeated, at minimum, every two weeks from 26 August to 30 November 2019 during daylight hours and did not take place on days of heavy rain or high winds but continued after snowfall (8 October 2019

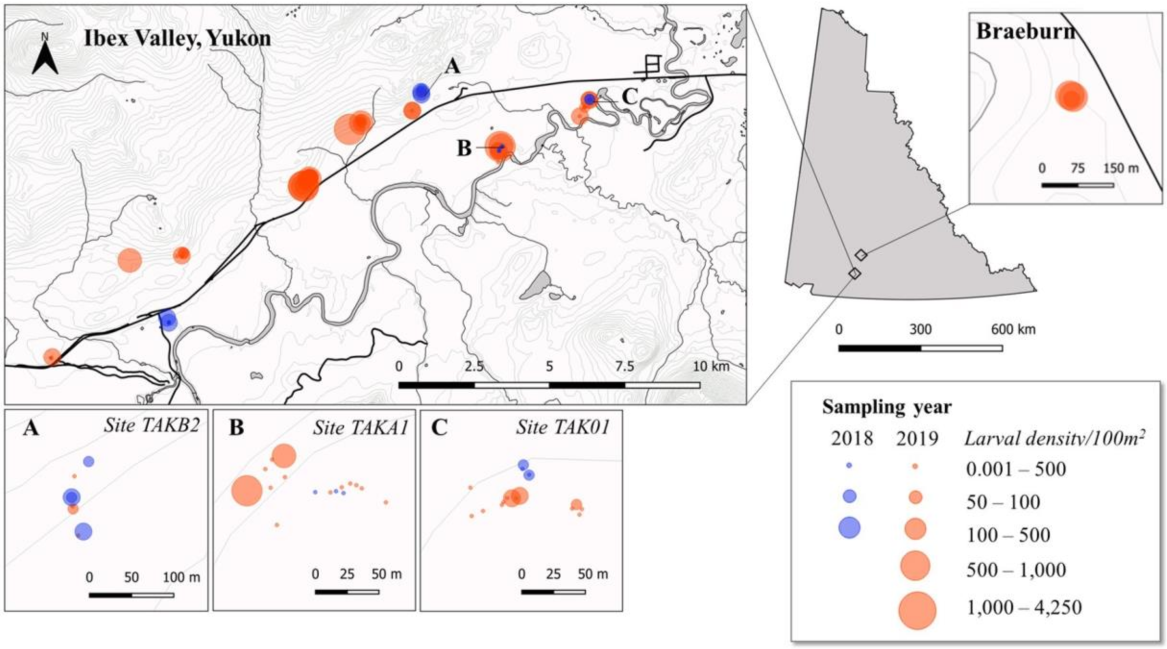

Figure 3.1. Locations of larval tick sampling sites in 2018 (blue) and 2019 (orange) in Ibex Valley and Braeburn, Yukon, Canada, either side of the Alaska Highway (black line). Bubble size indicates the average densities of D. albipictus larvae collected per 100 m2. Highest larval densities sampled were in the central region of Ibex Valley, and up at Braeburn. Larvae were often detected at almost identical locations in 2019 as the previous year (inset: A, B) or at very close proximity to these locations (inset: C).

onwards). Low densities of larval ticks were immediately removed from flag samplers in the field using lint rollers, and lint sheets were placed in sealed plastic bags. Flags with high larval abundances were removed and placed directly in sealed bags. All lint and flag samples were labelled in the field and returned to the lab for identification and counting. Where possible, questing vegetation was identified to family or species level in the field, consistent with Cody (1996). Vouchers and photographs were collected of any species not positively identified in the field and were later identified with the assistance of a Yukon Government expert (B. Bennett, *pers. comm.,* 26/09/19). Local temperature and relative humidity data were collected for each sampling location using a Kestrel environmental meter (Kestrel 5000 handheld Environmental Meter, Nielsen-Kellerman PA, USA). In both sampling years, tick identification was carried out *via* microscopy on a subset of each sample, based on morphological characteristics provided in Lindquist et al. (2016) and as reported in Clifford et al. (1961). Additionally, in 2018, several specimens were preserved in 70% ethanol and submitted for confirmatory identification (Canadian Science Centre for Human and Animal Health, Winnipeg, Manitoba, Canada). All larvae were confirmed to be *D. albipictus* and no other tick species were detected.

3.3 Results and discussion

A cumulative total of 6,924 *D. albipictus* larvae were collected across Ibex Valley in 2018 (21 September – 18 October), and 135,582 in 2019 (30 August – 30 November). Approximate densities ranged from 0.22 – 146.2 larvae per 100 m^2 in 2018, and from 0.04 – 4,236 larvae per 100 m^2 in 2019 (Figs. 3.1, 3.2). The difference, in both detection periods and approximate numbers and densities of ticks per season, is likely due to our increased knowledge of suitable sampling locations and associated efforts in 2019, rather than a reflection of actual tick activity each year. A total of 7,238 *D. albipictus* larvae, ranging 184.8–3,293.7 larvae per 100 m^2, were also collected in Braeburn in 2019 during two sampling events (19 September and 4 October). Only sites in Ibex Valley were sampled until 30 November 2019, but it seems plausible that larvae continue actively questing at all previous tick detection locations until at least this date. In all but one of the locations where larvae were found in 2018, larvae were also present in 2019, often at almost identical points (Fig. 3.1: insets A, B), or in extremely close proximity to the previous sampling points (Fig. 3.1: inset C). This finding suggests a high degree of site fidelity among cervid and equine hosts may result in spatial ‘hotspots’ of larvae that are consistent year-to-year.

We observed larvae actively questing from 30 August to 29 November 2019. On average, the number of larvae collected per day across all tick-positive sampling sites was highest during the very last week of September and first week of October (Fig. 3.2). Due to the limited data available for 2018, conclusions regarding questing peak for that year cannot be drawn. This apparent peak in questing activity observed in 2019 is similar to the reported behaviour for *D. albipictus* elsewhere in North America (Drew and Samuel, 1985; Samuel and Welch, 1991; Aalangdong, 1994; McPherson et al., 2000; Addison et al., 2016), and a lack of difference in the north may indicate that questing is not solely driven by temperature, as has been previously suggested (Wilkinson, 1967; Drew and Samuel, 1985; Samuel and Welch, 1991; Aalangdong, 1994).

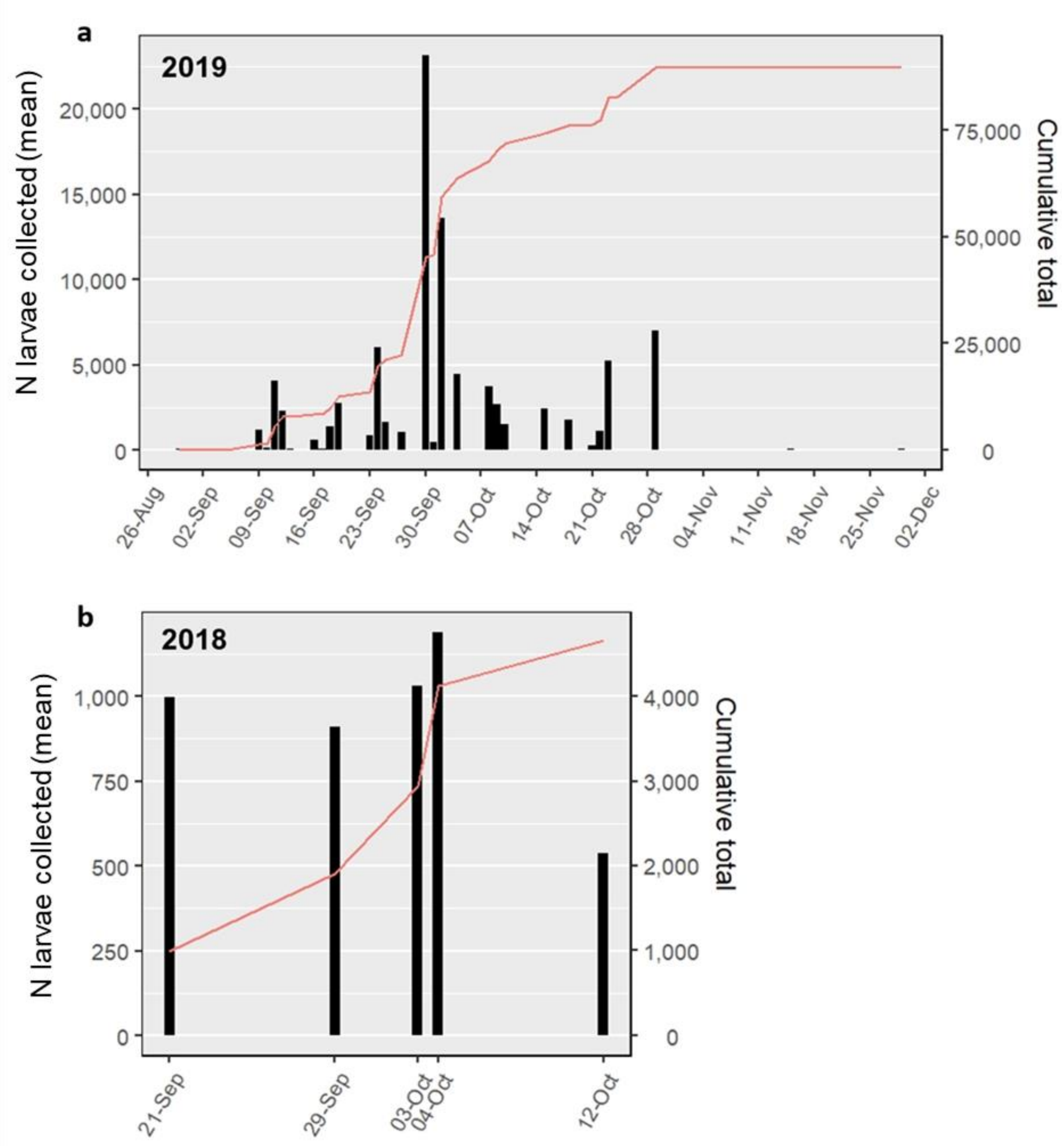

Figure 3.2. Average number of *D. albipictus* larvae collected per sampling day (black bars) and cumulative total (red line) across all sites sampled in Ibex Valley, 2019 (a) and 2018 field seasons (b). Although two weeks of sampling were missed end of October-beginning of November 2019, both average daily collection numbers and cumulative total suggest that peak questing most likely occurred during the last week of September and first week of October.

Table 3.1. Averaged weekly measurements of temperature and relative humidity, collected in the field across sampling locations in 2019, Ibex Valley, Yukon, Canada.

		Temperature (°C)				**Relative humidity (%)**		
Sampling week, 2019		**Min**	**Mean**	**Max**	**5-day mean**	**Min**	**Mean**	**Max**
1	19-24 August	–	–	–	7.9	–	–	–
2	26-31 August	25.0	27.8	33.5	8.8	23.9	25.1	25.7
3	2-07 September	23.0	23.4	25.0	18.2	29.5	35.7	44.8
4	9-14 September	16.7	21.2	29.7	8.8	15.6	34.8	59.6
5	16-21 September	13.7	17.3	20.1	10.2	39.9	51.1	69.2
6	23-27 September	12.0	16.1	22.6	5.4	25.5	33.2	59.0
7	30 September - 5 October	8.0	15.0	19.5	–	34.6	54.6	91.5
8	7-12 October	-2.3	5.8	9.7	–	46.4	56.1	67.7
9	14-19 October	0.9	1.8	3.6	–	33.0	50.4	85.3
10	21-26 October	3.6	4.8	5.6	-2.6	–	52.0	–
11	28 October - 2 November	6.1	6.2	6.3	-0.5	–	56.2	–
12	4-9 November	–	–	–	-7.7	–	–	–
13	11-16 November	-0.6	2.5	6.0	-7.7	69.6	70.5	71.3
14	18-23 November	4.6	5.2	5.8	-0.4	50.1	55.6	61.1
15	25-30 November	–	-0.5	–	-10.7	–	58.3	–

Temperature and relative humidity measured on site over this sampling period varied considerably, from -2.3 to 33.5 °C, and 15.1–91.5%, respectively (Table 3.1). Field temperatures were generally warmer than the daily reported averages by 5–19 °C, reinforcing the value of field measures in capturing microhabitat conditions influential for tick survival and development at this high latitude (Table 3.1). Critically, previous laboratory experiments of the cold tolerance of *D. albipictus* from New Hampshire, USA, have suggested unlikely survival of larvae after contact with ice (Holmes et al., 2018), yet we frequently observed active larvae under these conditions in the field in Yukon (Fig. 3.3). Previous genetic analysis of a sample of Yukon *D.*

albipictus adults suggested that this population is most likely a combination of translocated ticks from Elk Island National Park in Alberta, Canada, and *D. albipictus* that have expanded their range from nearby northern British Columbia (Leo et al., 2014). Early experiments have also shown that adult females are capable of egg-laying in adjacent Alaska (Zarnke et al., 1990), suggesting that environment and habitat may not be as critical a limiting factor in this species distribution, as once thought (Wilkinson, 1967; Samuel, 2004; Environment Yukon, 2016). In absence of any clear genetic differences, however, we might hypothesise that phenotypic changes may have arisen in this Yukon population in the decades since their first arrival. Given this, and the apparent contradiction between our observations and those of *D. albipictus* survival in more southerly regions (e.g. Holmes et al., 2018), further comparisons between northern and southern populations of *D. albipictus* larvae may be warranted to determine if there are significant differences in their ability to tolerate environmental extremes across latitudes.

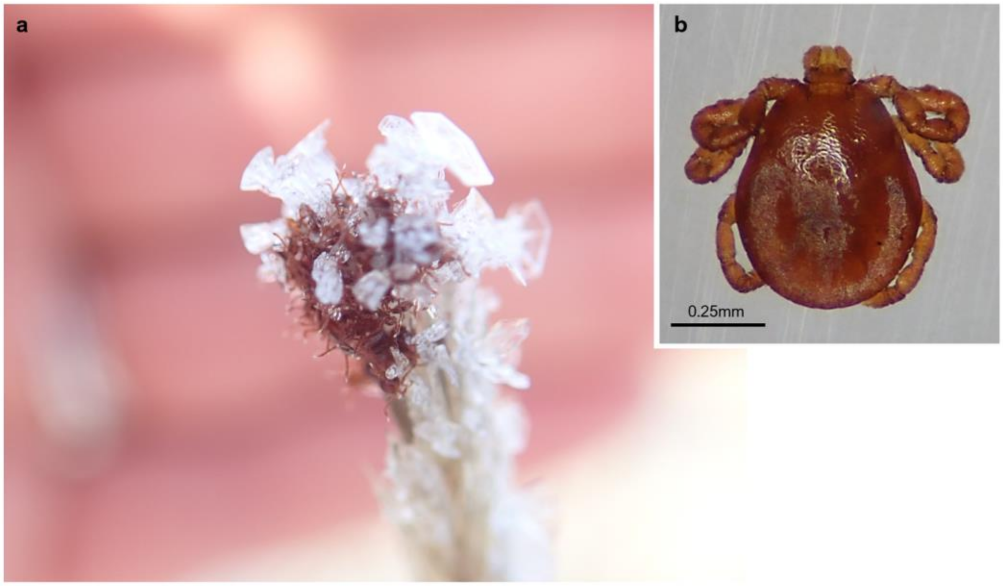

Figure 3.3. a) Larvae of *D. albipictus* actively questing beneath ice crystals, Ibex Valley, Yukon, Canada, on 21 October 2019. Once contact was made, these larvae were still capable of attaching to a flag sheet, suggesting that relatively extreme conditions in early winter may not significantly reduce transmission to a host during this period. **b)** Magnified dorsal view of *D. albipictus* larva. (Image credits: E.S. Chenery)

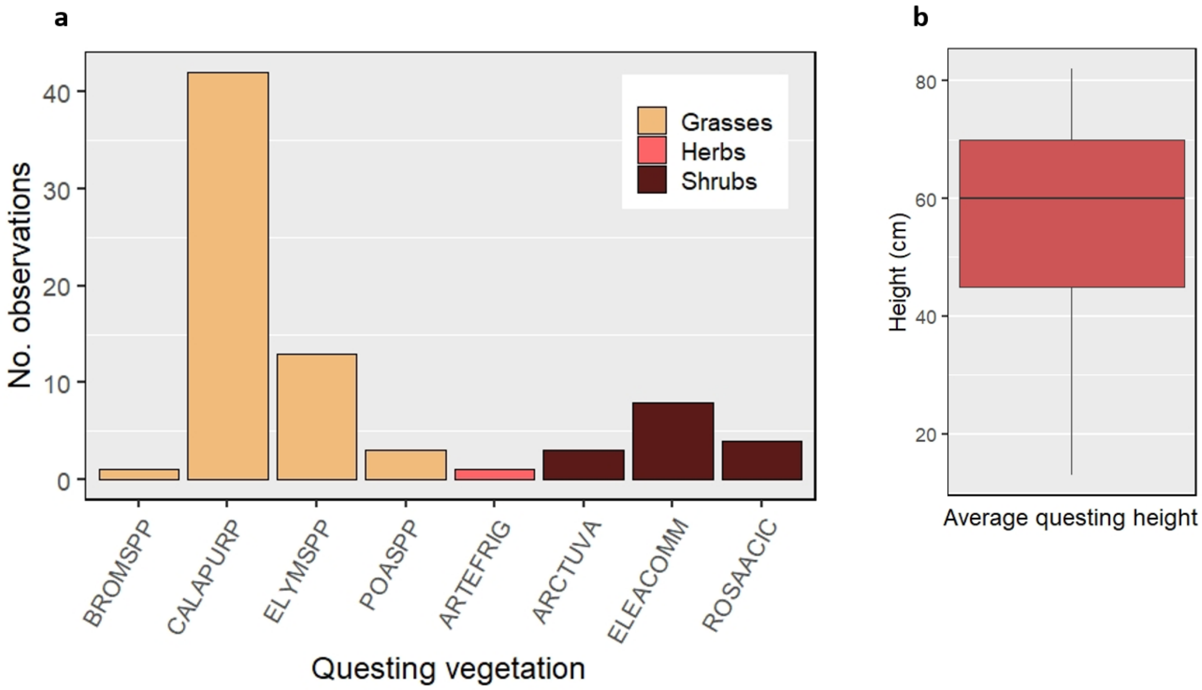

Figure 3.4. a) Vegetation species and groups upon which larval *D. albipictus* were found questing in 2018 and 2019. Species codes are as follows: (Grasses) BROMSPP = *Bromus* sp., CALAPURP = *Calamagrostis purpurea*, ELYMSPP = *Elymus* sp; POASPP = *Poa* sp., (Herbs) ARTEFRIG = *Artemisia frigida*, (Shrubs) ARCTUVA = *Arctostaphylos uva-ursi*, ELEACOMM = *Eleagnus commutata*, ROSAACIC = *Rosa acicularis*. **b)** Average height of questing aggregations, 2018 and 2019. In almost all cases, questing height was identical to the observed maximum height of the vegetation available.

Most questing aggregations were observed on grasses, particularly *Calamagrostis purpurea*, however, larvae were also found on other vegetation where it was available (Fig. 3.4(a)). No detections were made in coniferous forest or closed canopy areas, consistent with previous studies of egg development and hatching success (Drew and Samuel, 1986; Addison et al., 2016). Questing aggregations ranged vertically from 13–82 cm above ground level, with an average questing height of 56.8 cm (Fig. 3.4(b)), or generally the observed maximum height of available vegetation. Experimental studies have shown *D. albipictus* will preferentially aggregate at twice the maximum we observed, around 120 cm, or cervid host torso height (McPherson et al., 2000). Given ongoing infestation of Yukon cervids, vegetation height alone does not appear to be significantly limiting larval transmission to hosts in this system.

Understanding the location of the larval stage of *D. albipictus* may have important implications for future management of this species. Strategic burning of known larval hotspots has been proposed as a short-term control measure (Drew et al., 1985), or the development of known predators of larvae, such as entomopathogenic fungi, as a topically applied biological control agent (Yoder et al., 2017). Although there is little evidence that Yukon wildlife are currently adversely affected by tick infestation, the negative impact of *D. albipictus* hyperabundance elsewhere in North America suggests monitoring locations where larvae are found may provide options for proactive management or mitigation in future.

Our confirmed detection of *D. albipictus* larvae in Yukon using the flagging method represents a significant step in accumulating knowledge of this species *in-situ* in northern regions. All previous reported detections in Yukon and neighbouring Northwest Territories have been of adult and nymphal *D. albipictus*, either on-host (Environment Yukon, 2016; Kashivakura, 2013), or through anecdotal reports of potentially related hair loss on moose (Samuel, 1989). Detection of the off-host life stages of this tick provides evidence that suitable conditions exist for *D. albipictus* to complete its whole life cycle in Yukon, corroborating previous assertions of establishment potential (Samuel, 1989; Zarnke et al., 1990; Kutz et al., 2009), and provides critical information to inform ongoing monitoring and potential management or mitigation. Our detection may also forewarn of other tick species able to expand their range in the north, in line with a warming climate.

Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on request.

Competing interests

The authors declare that they have no competing interests.

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Chapter 4.

Parasites at the edge: Abiotic factors associated with larval *Dermacentor albipictus* occurrence and abundance at a northern range boundary.

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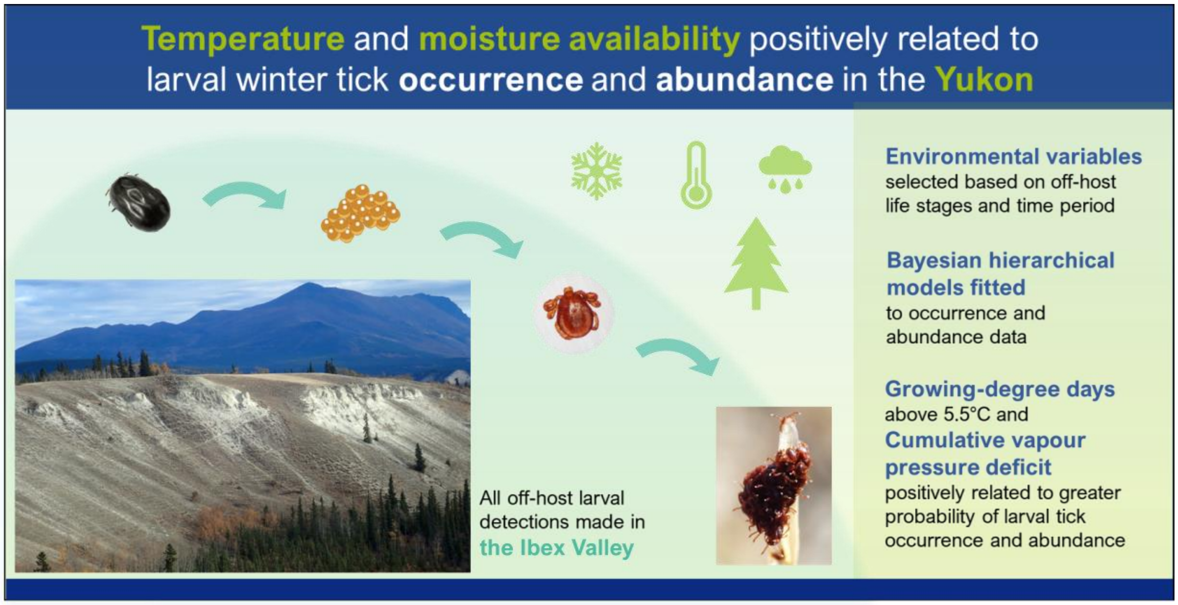


Temperature and **moisture availability** positively related to larval winter tick **occurrence** and **abundance** in the **Yukon**

Environmental variables selected based on off-host life stages and time period

Bayesian hierarchical models fitted to occurrence and abundance data

Growing-degree days above 5.5°C and **Cumulative vapour pressure deficit** positively related to greater probability of larval tick occurrence and abundance

All off-host larval detections made in **the Ibex Valley**

Contributions: Conceptualization, ESC, NJH, NEM, PKM; methodology, ESC, LA; formal analysis, ESC, LA.; resources, NJH; data curation, ESC, writing—original draft preparation, ESC; writing—review and editing, ESC, LA, NJH, NEM, PKM; visualization, ESC; supervision, NJH, NEM, PKM; project administration, NJH, ESC; funding acquisition, NJH, PKM.

Abstract

An organism’s range may shift over time in response to changes in species interactions and abiotic stressors, including anthropogenic disturbances such as climate change or translocation.

With high-latitude regions predicted to experience significant environmental and ecological challenges in the future, studying these pioneer or transplanted populations at their range boundaries presents a critical opportunity to determine the factors that may be limiting a species' distribution. For the blood-feeding winter tick, *Dermacentor albipictus*, whose high numbers can result in death of its hosts, concern over winter tick infection of local moose (*Alces alces)* and woodland caribou (*Rangifer tarandus caribou*) in the Yukon, Canada, has driven a need to better understand factors affecting the northern range limits of winter tick. We used Bayesian hierarchical models to examine the relationship between *D. albipictus* presence and abundance and select abiotic factors, chosen based on key components of the winter tick life cycle. *D. albipictus* occurrence in the Yukon was most strongly related to changes in ambient moisture availability (cumulative vapour pressure deficit), with drier areas over the egg to larval life stages having a greater probability of larval tick presence. The accumulation of heat (number of growing-degree days) across the entire off-host period also showed an apparent threshold for presence, with no detections in localities with fewer than 734 degree-days above 5.5°C. Contrary to many suggestions in the literature, there were no strong effects for the proportion of snow cover in determining presence or abundance in our data. Our models also returned no strong effects for any predictors included in abundance models, most likely signaling the importance of small, microhabitat, spatial scales in influencing the number of ticks per location. Although current conditions in the far north of the Yukon do not appear suitable for winter tick establishment based on these variables and an absence of detections to date, future climate projections suggest that increasing temperature and precipitation regimes and decreased snow cover will likely provide new regions for *D. albipictus* to persist in the next 50 years, potentially presenting new opportunities for interaction with a greater number of hosts. Our findings reiterate that subarctic regions may be at high risk of parasite and disease incursions in future, given rapid environmental changes at these cool-edge limits, though the magnitude of effects requires analysis at a finer scale.

Keywords

Range margin, species distribution, tick, ixodid, winter tick, *Dermacentor albipictus,* moose, caribou, cool edge

4.1 Introduction

Studying the distribution and behaviour of species at the edges of their range is crucial for predicting their future response to changing environmental conditions. An enduring explanation for the manifestation of species' range boundaries is that their physiological tolerances and capacity to endure short-term changes in abiotic conditions plays a principle role in determining their ecological niche (Grinnell, 1917; Odum, 1971; Gaston, 2003; Holt & Keitt, 2005). This appears particularly true of individuals at the "cold-edge" extremes of their species' range, generally defined as geographic locations towards the Earth's poles. Darwin was one of the first to observe that the "injurious action of climate" plays a principal role in determining species' richness and abundance in high latitude or high altitude populations (Darwin, 1860) and the apparent causes and consequences of these patterns has been of continued interest in ecology (Elton, 1958; MacArthur, 1982; Brown, 1995; Gaston, 2000; Oldfather et al., 2020).

Empirical studies have largely corroborated the hypothesis that abiotic factors are most limiting at cool-edge range margins (Hargreaves & Eckert, 2019; Paquette & Hargreaves, 2021), yet the dynamics of many populations in high-latitude regions are becoming more challenging to predict due to a rapidly changing climate (Intergovernmental Panel on Climate Change, 2001). In terrestrial systems, increasing temperatures and changes to precipitation patterns may significantly alter habitat, species movement and behaviour (Tingley et al., 2012; Pecl et al., 2017), but this could vary considerably depending on species' individual tolerances and life history (Van der Putten et al., 2010; Hurford et al., 2019). Where some range-edge communities may creep farther north, tracking their existing niche (Chen et al., 2011; Lenoir & Svenning, 2015), others may lag behind depending on a combination of factors such as dispersal ability, original range size, and net reproductive capacity (Phillips et al., 2010; Le Galliard et al., 2012; Alexander et al., 2018). The resultant uncertainty surrounding a species' response to changing environmental conditions at their range edge therefore presents challenges for future management, given that colonization by range-expanding species may have unforeseen consequences for recipient communities (Parmesan & Yohe, 2003; Chen et al., 2011; Tomiolo & Ward, 2018).

One growing concern is the potential introduction of new, or amplification of existing, parasites and pathogens, with potentially negative consequences for wildlife health (Kutz et al., 2009;

Polley et al., 2010; Altizer et al., 2013; Dobson et al., 2015). In the Canadian north, the relatively recent arrival of the winter tick, *Dermacentor albipictus*, has raised questions as to the potential suitability of northern regions to parasite species, which were previously considered as unsuitable due to their extreme climates (Zarnke et al., 1990; Kutz et al., 2014; Hahn & George, 2019). Primarily an ectoparasite of large-bodied cervids, *D. albipictus* is best known for an aggressive hyperabundance on moose (*Alces alces*) that leads to severe hair and blood loss (Samuel, 2004) and has long been implicated in mass die-offs of hosts in both the eastern United States (Samuel, 2007; Jones et al., 2019) and in several locations across Canada (Cameron & Fulton, 1927; Pybus et al., 1999; Samuel, 2007). In the Yukon, its presence is suspected to be linked to the translocation of infected elk (*Cervus canadensis*) in the 1950s and 1990s (Environment Yukon, 2010; Leo et al., 2014), although observations of potential winter tick-induced hair loss on moose could indicate a longer history of presence in this region (Samuel, 1989). The consequences of a *D. albipictus* range expansion could be severe, with heavy infestations likely to threaten already vulnerable populations of barren ground caribou (*R. t. groenlandicus*), and moose (Kutz et al., 2009). Yet, despite the apparent availability of suitable hosts, and detections as far as 66°N (Environment and Natural Resources NWT, 2019; Chenery et al., 2023) in neighbouring Northwest Territories, *D. albipictus* has not been found farther north than 62°N in Yukon to date (Chenery et al., 2022). This suggests that other factors, including environmental conditions, may still be limiting *D. albipictus*' survival and/or reproduction at this apparent edge of its range.

To better understand *D. albipictus* persistence at a cool range edge, we examine the relationship between key abiotic factors and winter tick presence and abundance based on recent field data collected of off-host, larval winter ticks in Yukon (Chenery et al., 2020). We first identify several biologically relevant environmental variables from the literature, based on their reputed effects at critical periods during the off-host tick life cycle. Selecting those variables with the broadest applicability across all stages, we incorporate them within hierarchical models that account for the sampling methods used to examine how well these variables explain our data. Because of the wide range of potential variables, we compare our models with those containing additional relevant abiotic and biotic factors. Finally, we discuss our findings with a view to assessing apparent similarities and differences between the range-edge population in Yukon and what is known regarding *D. albipictus* populations elsewhere in North America, to highlight factors that may require greater research attention in future for forecasting winter tick dynamics.

4.2 Materials and methods

4.2.1 Larval tick collection

Field sampling for the *D. albipictus* detection data reported here is described in detail in Chenery et al (2020). Briefly, in 2018, 16 1 km^2 sites were selected within southern Yukon based on locations of known *D. albipictus* activity on cervid hosts and representing samples from all major landcover classes (Fig.4.1). Sites in Braeburn (61° 32' 24.3" N, 135° 49' 13.6" W, n=3), the Ibex Valley (60°50′42″N, 135°38′18″W, n=6), Marsh Lake (60° 31' 6.3" N, 134° 19' 44.1" W, n=3), and Watson Lake (60° 2' 6.6" N, 128° 43' 46.7" W, n=4) were repeatedly sampled for larval ticks along three to four defined transects approximately 250 m long.

Sampling events took place every two weeks from 21 August to 12 October 2018, using standard flag and drag sampling procedures (Chenery et al 2020). Detections of *D. albipictus* larvae were only made in the Ibex Valley, which then formed the focus of almost all sampling efforts in 2019. Four sites remained the same in 2019 as the previous sampling year, with an additional seven sites selected across the Valley based on known elk movement patterns the previous spring (Government of Yukon 2018, unpublished data). One additional site was sampled in Braeburn, 40 km to the north of Ibex Valley, based on apparent similarity of habitat characteristics to those in Ibex Valley: grassy, south-facing slopes and outcrops with known elk presence. As in 2018, all sites were sampled repeatedly between 26 August to 30 November along three to four ~250 m transects per site. Due to increased snowfall in November limiting field access, only three sites were sampled from 29 October onwards.

Tick collection in the field followed the same process in both years. All tick samples were returned to the lab for confirmatory identification, whereby a subset of each sample was identified via microscopy based on morphological characteristics (Clifford et al., 1961; Lindquist et al., 2016). In 2018, several specimens were submitted for confirmatory identification (Canadian Science Centre for Human and Animal Health, Winnipeg, Manitoba, Canada).

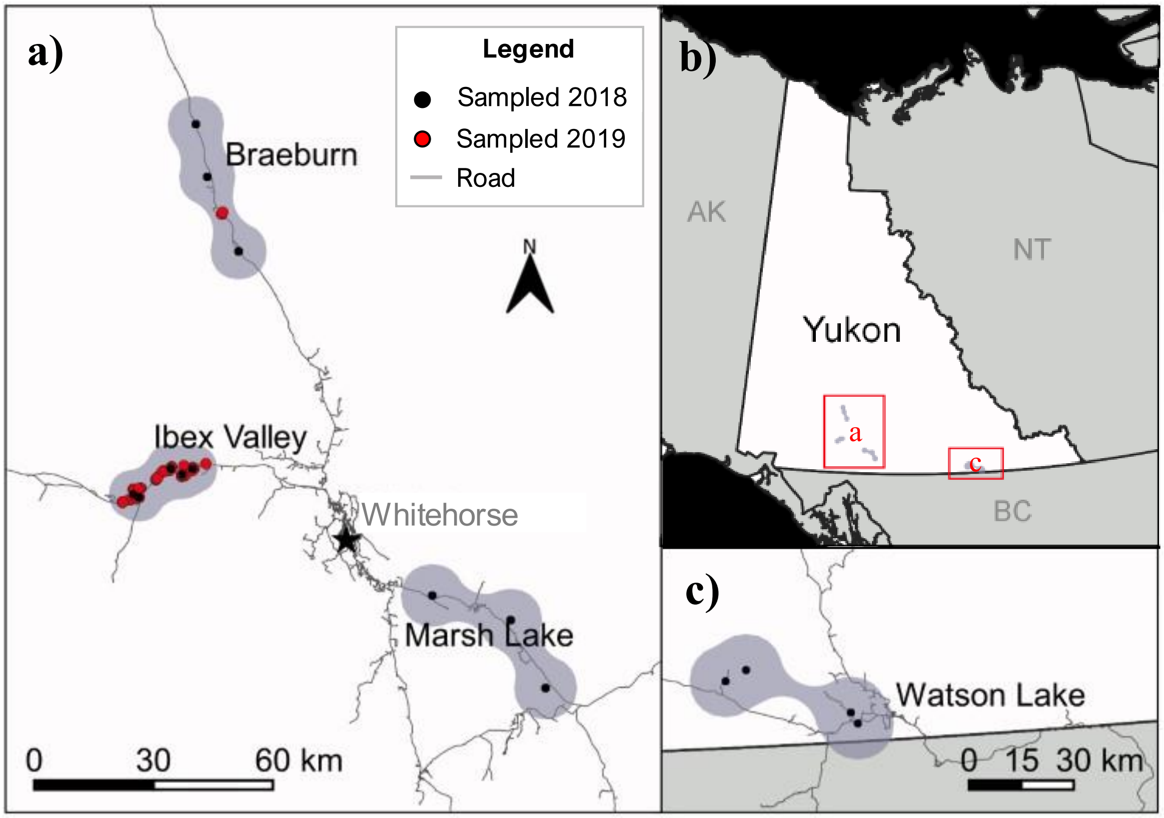


Figure 4.1. Study area and site locations of *D. albipictus* larval collection, 2018 and 2019, Yukon. Sampling sites (black dots) were located across four localities (shaded polygons) in southern Yukon. **a)** South-central site locations in the Southern Lakes region of the Yukon. The city of Whitehorse (star) is marked for reference only and was not sampled; **b)** Situation of two main study areas in the Yukon (red boxes); **c)** south-eastern site locations in the Liard region of the Yukon.

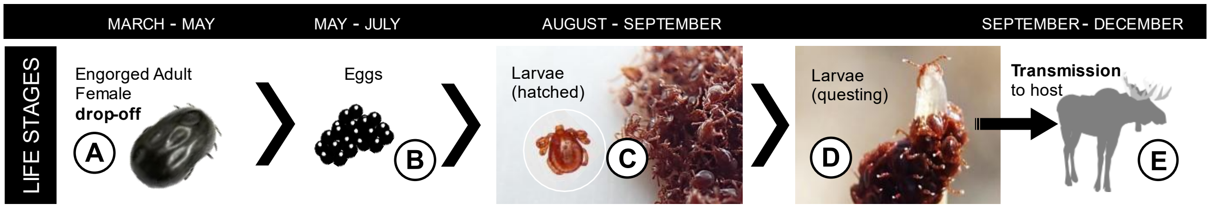
In both 2018 and 2019, all larvae were confirmed to be *D. albipictus* and no other tick species were detected.

Larval ticks were counted in the lab to give total counts per transect and per site. For occurrence models, per site values >0 were set to present, or otherwise recorded as absent. For abundance models, because not all sites had the same number of transects and transect lengths occasionally differed across sites due to natural variation in the terrain during sampling, we used the tick count per transect divided by the total transect length in metres to give the mean number of ticks per metre. We calculated the average number of ticks per metre across all transects per site, which was rounded to the nearest whole number prior to analysis (Appendix C.1, Fig.C1).

4.2.2 Selection of relevant environmental factors

We selected eight potential predictors of larval presence and abundance based on knowledge of the off-host stages of the *D. albipictus* life cycle, when ticks are most affected by environmental conditions (Table 4.1). Female *D. albipictus* survival and subsequent oviposition success between March and May is posited to be driven by three main factors: temperature (Drew & Samuel, 1987; Samuel, 2007), snow cover at drop-off (Drew & Samuel, 1986), and moisture availability during egg laying (Drew & Samuel, 1986) (Table 4.1: life stage A). After mating on-host at the end of the winter, engorged adult females drop to the ground to lay their eggs, disengaging from their host at a seasonally varying rate that peaks in the months of March and April (Drew & Samuel, 1989). Egg laying is usually completed by the end of May at a site on the ground not far from their initial drop-off location, after which, the females die (Glines, 1983; Drew & Samuel, 1986, 1987; Addison et al., 2016). Both the eggs, and subsequently, hatchling *D. albipictus* larvae are particularly vulnerable to desiccation, requiring moisture from the surrounding habitat to maintain an adequate water balance (Addison et al., 2016; Yoder et al., 2016) (Table 4.1: life stages B, C). Drier conditions can result from temperature and/or precipitation and may be influenced by the degree of exposure afforded given available vegetation and ground cover (Burtis et al., 2016; Ginsberg et al., 2020). In general, the eggs of *D. albipictus* remain in the leaf-litter or below the duff layer for an incubation period of up to four months before hatching (Wilkinson, 1967; Drew & Samuel, 1986).

Table 4.1. Selected environmental variables and potential associations with *Dermacentor albipictus* occurrence and abundance. Variables were chosen based on their potential impact on off-host stages of the *D. albipictus* life cycle (top row) and grouped temporally to account for discrete life history events. Snow cover, growing-degree days and cumulative vapour pressure deficit were included in occurrence and abundance models; all variables were included in a Principal Component Analysis for the purpose of reducing the number of dimensions for additional occurrence/abundance models.



Factor *Variable name(s)*	**Description**	**Predicted effect** *Life stage*	**Hypothesised mechanism**	*PC Model component (% contribution)*
Snow cover *snow_0305*	Mean proportion of snow cover (%) from March -May for each sampling year.	- A	Adult female mortality can increase if there is a high proportion of snow cover when detaching from their host (Drew & Samuel, 1986). Sustained exposure to below -zero temperatures can result in reduced oviposition rates, and mortality below -20°C (Drew & Samuel, 1987; Samuel 2007). Female ticks on snow are also more visible and therefore, vulnerable, to predation (Addison et al., 1989).	PC1 (0.12%) PC2 (32.2%) PC3 (1.04%)
Growing-degree days *gdd5.5*	Accumulated number of growing-degree days (GDD) above 5.5 °C since March 1st of each sampling year.	+ A,B,C	Both eggs and larvae develop most successfully in warmer temperatures (Drew & Samuel, 1986) but this rate can be variable, with larvae enduring short periods of colder conditions (Holmes et al., 2018) and with optional quiescence (Wright, 1969). Wilkinson (1967) hypothesised the winter tick distribution is limited below the 1500 GDD at 42°F (5.5°C) isopleth line.	PC1 (22.9%) PC2 (0.9%) PC3 (1.3%)
Vapour pressure deficit *cvpd*	Accumulated vapour pressure deficit (CVPD) since May 1st of each sampling year	- B,C,D	Linked to both temperature and moisture availability, VPD may indicate desiccation risk and development speed of eggs and larvae (Addison et al., 2016). CVPD is also considered an important factor explaining survival, development and questing behaviour of other Ixodid species (e.g. Hacker et al., 2021).	PC1 (4.3%) PC2 (3.9%) PC3 (52.6%)
OTHER SELECTED VARIABLES				
Temperature *tDay_0305* *tDay_0608*	Mean land surface temperature (°C) from March-May and June- August for each sampling year.	+ A, B, C	Adult female survival off-host is highest at warmer temperatures with mortality increasing at sustained negative temperatures (Drew & Samuel, 1987). Females also produce more eggs, faster, at higher temperatures (Drew & Samuel 1986, 1987). As temperatures increase above 15°C, eggs develop and hatch at faster rates, with little development below this threshold (Howell, 1939). Eggs and larvae risk desiccation in warmer, drier conditions (Yoder, 2016).	*tDay_0305* PC1 (19.3%) PC2 (5.7%) PC3 (8.9%) *tDay_0608* PC1 (7.6%) PC2 (16.5%) PC3 (10.8%)
Precipitation *precip_since0105*	Accumulated precipitation (mm) since May 1st each year	+ B,C,D	Eggs and larvae risk desiccation in drier conditions (Yoder, 2016). Larvae do not descend vegetation to rehydrate, and may also use moisture availability as a cue for questing by avoiding very dry conditions (Addison et al., 2016).	PC1 (15.8%) PC2 (9.0%) PC3 (4.0%)
Grass & shrub cover *shrub*	Proportion of each site that is covered with grass and shrub (%).	+ A-E	Open, grassy areas provide greater insolation and warmer temperatures, but also provide some ground cover for all life-stages to avoid desiccation over summer (Drew & Samuel, 1985, Addison et al., 2016). Vegetation may also provide suitable questing locations to aid transmission (McPherson et al., 2000).	PC1 (13.1%) PC2 (7.4%) PC3 (3.8%)
Coniferous tree cover *conifer*	Proportion of each site that is by coniferous tree canopy (%).	- A-E	Reduced insolation in closed canopy forest may reduce egg and larval development (Drew & Samuel, 1986; Addison et al., 2016), and may also limit questing materials available.	PC1 (13.5%) PC2 (8.0%) PC3 (12.9%)
Hillslope *slope*	Degree of terrain slope at the sampling location (site average).	+ A-E	May influence other variables, such as snow cover, temperature and vegetation. May also relate to host movement in drop-off and transmission periods (resource selection, predator avoidance, ease of movement).	PC1 (7.6%) PC2 (16.5%) PC3 (10.8%)

Survival and hatch rate are also dependent on temperature and moisture availability, with consistently warmer, wetter conditions resulting in higher, faster hatch rates (Addison et al., 2016) and increased larval survival (Yoder et al., 2016). As with egg survival, larval survival over this time is linked closely with moisture availability and temperature with the greatest risk of mortality being desiccation (Samuel, 2004; Yoder et al., 2016). Host-seeking larvae actively aggregate together in clumps of tens to hundreds of individuals beginning in late August and finishing by December in Yukon (Chenery et al., 2020), a behaviour thought to be driven by a need to mitigate individual water loss during this time of increased exposure (Yoder et al., 2016) (Table 4.1: life stage D). Saturation vapour deficit and vapour pressure deficit have been found to impact other ixodid tick species across life stages (Berger et al., 2014; Ginsberg et al., 2020; Hacker et al., 2021), and we might expect a similar response from larval *D. albipictus* in the field as in the lab (Yoder et al., 2016). Finally, a minimum threshold of 1500 growing-degree days above 5.5°C required for off-host development to take place has been suggested to determine the cool edge of the winter tick range (Wilkinson, 1967).

Based on this winter tick life history, we identified two temperature variables of direct influence (mean daily land surface temperature and number of growing-degree days above 5.5°C) and three moisture influencing variables (proportion of snow cover, amount of precipitation accumulated, the cumulative vapour pressure deficit). Because the structure of the landscape will affect the environmental conditions experienced, we also selected two descriptions of vegetation cover (proportion of coniferous forest cover and proportion of shrub and grassland) and one topographic variable (degree of hillslope). Coniferous (needleleaf) forest was chosen for its potentially negative effect on recruitment due to reduced insolation through the evergreen overstorey and relative lack of understorey for shelter (Aalangdong, 1994; Addison et al., 2016). The combined proportion of shrub and grassland was selected due to its importance as forage for potential winter tick hosts, and the high proportion of groundcover that may reduce exposure for eggs and larvae (Addison et al., 2016). Hillslope was selected as it may have a direct influence on temperature and moisture availability through exposure to insolation, wind, and other elements (Jouda et al., 2004; Gilbert, 2010) and in defining vegetation patterns.

We obtained the nearest available meteorological data for each site from Environment and Climate Change Canada historical data (https://climate.weather.gc.ca/historical_data) using the ‘weathercan’ package in R (LaZerte & Albers, 2018). Air temperature, relative humidity and precipitation data were acquired for the approximate winter tick off-host period (May 1 – November 30) for each sampling year (2018 and 2019). The average distance between sampling sites and the nearest weather station was 41 km (range: 10.5-68.1 km; SD +- 23.7). Hourly air temperature and relative humidity values were converted to daily averages, and used to calculate daily vapour pressure deficit (VPD_t; following Murray, 1967) and cumulative daily vapour pressure deficit (CVPD). Where the formula for VPD_t, measured in kilopascals (kPa), is given as:

$$VPD_t = \left(\frac{100-RH_t}{100}\right) \times SVP_t \ ,$$

where RH is the average daily relative humidity on day *t*, and where SVP_t is the daily saturation vapour pressure in pascals, calculated as:

$$SVP_t = \ 610.7 \ \times \ 10^{\left(\frac{7.5\mathrm{T}}{237.3+\ \mathrm{T}}\right)}$$

where T is the average daily air temperature in degrees Celsius. Daily VPD values were summed from May 1st until the sampling date to create the CVPD variable. We calculated the number of growing-degrees per day (*t*) according to the 'average method' described by Baskerville & Emin (1969), using mean daily land surface temperature values as follows:

$$Growing - degrees \ / \ day_{\ t} = \frac{T_{max\ t} - \ T_{min\ t}}{2} - \ T_{base}$$

Where $T_{max(t)}$ and $T_{min(t)}$ are the maximum and minimum daily surface temperatures on day *t*, and T_{base} is the threshold temperature in Celsius above which the number of growing-degrees are calculated. We used this equation to calculate the number of growing-degree days (GDD) above base 5.5°C, summing the daily growing-degree values from March 1 of each sampling year, when all winter tick females could be considered off-host, until each sampling date. We extracted percentage of snow cover (MODIS/Terra Snow Cover Daily L3 Global 500m Grid, v6: Hall and Riggs, 2016) and land surface temperature (MOD11A1 MODIS/Terra Land Surface Temperature/Emissivity Daily L3 Global 1km SIN Grid V006: Wan et al., 2015) for each sampled location using the Application for Extracting and Exploring Analysis Ready Samples (AppEEARS) online interface (AppEEARS v.2.43, 2020). The topographical variable of slope was extracted for each site and sampling location from the Canadian Digital Elevation Model

(CDEM) at 20 m spatial resolution (Natural Resources Canada, 2016). Forest-cover classes for each site were obtained from Earth Observation for Sustainable Development of Forests (EOSD) satellite imagery (provided by Yukon Department of Environment) and vegetation classes from NRCan Landsat 7 raster data (Natural Resources Canada (NRCan), 2017). Proportions of both coniferous forest and shrub and grassland cover were calculated for each 1 km^2 site based on 25 x 25m cells in GIS (QGIS v.3.16.10, QGIS Core Development Team, 2020).

To account for differences in the relative importance of some of these factors during the discrete periods of *D. albipictus* development off-host, we considered the temporal variability in the resulting set of eight variables by selecting time periods of greatest relevance to specific life stages, bringing the total number of variables to nine (Appendix C.1, Figure C2). Snow cover and mean daily land surface temperature were averaged for each site and sampling year from March to May (adult female drop-off and egg-laying stages) and mean daily land surface temperature from June to August (eggs and larvae). Some variables were calculated cumulatively up to the date of sampling, with the number of growing-degree days above a 5.5°C threshold from March 1 (all off-host life stages), and amount of precipitation and vapour pressure deficit calculated from May 1 (eggs and larvae) of each sampling year. Vegetation cover was a mean value computed across all seasons, and hillslope was not expected to change temporally.

Due to a high degree of correlation among some predictors (Pearson's r >0.5) (Appendix C.2, Table C1), we selected three key abiotic variables (snow cover, growing-degree days, cumulative vapour pressure deficit) for inclusion as predictors in our main models. Each of these have been highlighted by previous studies as potential drivers of winter tick presence/occurrence (Table 4.1), while also having a low degree of correlation with one another (Appendix C.2, Table C1). However, because all nine variables could play a role in *D. albipictus* presence or abundance, we conducted a Principal Component Analysis (PCA) using singular value decomposition (SVD) and used the resultant components as predictors in additional models of occurrence and abundance (see *Statistical analyses* section, below, and Appendix C.2).

4.2.3 Statistical analyses

To examine whether larval *D. albipictus* occurrence or abundance in the Yukon was associated with our selected key predictors (Table 4.1), we fit two sets of Bayesian hierarchical models. Using a Bayesian framework allowed us to account for the hierarchical structure of our data that was defined during sampling, despite its relatively small sample size (Cressie et al., 2009; Hobbs & Hooten, 2015). The two sets of models were: i) occurrence models, examining tick presence/absence per site; and, ii) abundance models, based on a measure of abundance of larval ticks collected at each location (mean number of ticks per metre, measured across all transects per site). We defined a random effects structure that allowed the intercepts to vary across sampling sites for both sets of models. Because tick abundance (but not occurrence) indicated temporal variation that was unrelated to our predictor variables, we also allowed intercepts to vary by sampling week in the abundance models. The structure of fixed effects predictors was the same for both sets of models (as outlined in Table 4.1): snow cover + growing-degree days + cumulative vapour pressure deficit. All predictors were scaled to have a mean of 0 and standard deviation of 1 prior to inclusion in analysis.

To model larval tick occurrence – codified as 0 (absent) and 1 (present) – we used a binomial probability distribution with logit link. We used weakly informative prior distributions of *Normal*(0, 1.5) for the intercept and *Normal*(0, 0.5) for the slopes of all predictors, ensuring relationships of varying strengths were sampled (Appendix C.4). Larval tick abundance, measured as the mean number of ticks per metre of transect sampled, was modelled using a negative binomial distribution with log link. We used weakly informative prior distributions of *Normal*(1, 0.5) for the intercept, *Normal*(0, 0.25) for the slopes of all predictors and carried out prior predictive checks for confirmation of their suitability (Appendix C.4). Due to the high number of zeros in our dataset we also fit the model with and without a zero-inflation term (logit link) to account for an excess of zeros by site. We compared the predictive accuracy of both models using Leave-One-Out cross validation (LOO) (Vehtari et al., 2017). This procedure is particularly useful for small datasets as it systematically drops a single observation and compares posterior predictions to that observation *n* times, where *n* is the number of total observations in the dataset (Gelfand et al., 1992). The zero-inflated model had higher predicted accuracy according to LOOIC and was used in all subsequent analyses (LOOIC was 776 and 796 for models with and without zero-inflation respectively, ellipsoid difference = -7.98, SE = 3.7). The full hierarchical structure describing both occurrence and abundance models can be found in Appendix C.3.

To examine the effect of all identified predictor variables, we conducted additional analyses using dimensionality reduction. Because it was not possible to include all predictors given our limited dataset and autocorrelation between some of them, we used PCA to reduce the overall number of variables (Gregorich et al., 2021), implemented in R version 4.11 (R Core Team, 2021) using the package *FactoMineR* (Le et al., 2008). The top three principal components (PCs), accounting for more than two-thirds (76%) of the variation in our predictors, formed distinct variable groups: PC1 (39.0%) temperature, vegetation and precipitation; PC2 (24.7%) snow cover and summer temperature; and PC3, (13.5%) moisture availability (see Appendix C.2, Fig.C4(a)-(b); Table C1). To explore the combined effects of each of the variable groups, we built a second model (hereafter termed “PC models”) for each response variable that contained the additive effects of the three PCs as predictor variables (i.e., two additional models, one PC model for tick occurrence and one PC model for tick abundance). Although using PCs as variables in regression models limits our biological interpretation of model coefficients (Graham, 2003), this allowed us to qualitatively examine how the grouped covariates might play a role in explaining our data. We used the same distributions and same prior specification as described for the occurrence and abundance models.

All models were specified, and posterior distributions estimated for each parameter using No-U-Turn Hamiltonian Monte Carlo sampling via the R package *brms* (Bürkner, 2018), implemented in R version 4.11 (R Core Team, 2021). We used weakly informative priors for all slope and intercept parameters and confirmed our prior choices through prior predictive simulation (Appendix C.4). This was justified by our lack of prior knowledge in the likely magnitude of change in response variables given our predictors and allowed us to ensure that distributions reflected a reasonable range of values for each parameter. Because models fit to small datasets can be strongly influenced by the priors chosen (Hobbs & Hooten, 2015; Banner et al., 2020), we also conducted a sensitivity analysis of the priors by varying the slope priors to allow more sampling of stronger or weaker associations (Appendix C.5). As expected, parameter coefficient estimates in both models were sensitive to prior choices, although the magnitude of overall change across models was generally small (within 1 scaled unit of our chosen model).

Model runs used four MCMC chains, each with 2000 iterations for occurrence models and 6000 iterations for abundance models, with the first 50% draws discarded as warmup, resulting in 4000 and 12000 posterior draws per model for occurrence and abundance, respectively. We confirmed good chain mixing and model convergence based on the visual assessment of trace plots, high numbers of effective samples sizes, and a scale-reduction statistic, $\hat{r}$, between 0.9 and

1.01 (Gelman & Rubin, 1992). Posterior predictive checks to assess model fit were made based on the visual comparison of the original data with 10 simulated datasets drawn from the posterior distribution, ensuring similarity in both observed and predicted distributions. All models showed the same qualitative pattern suggesting an adequate fit to the data (Appendix C.6).

4.3 Results

4.3.1 Occurrence

The estimated probability of larval tick presence showed variable responses to our predictors of interest (Fig.4.2(a-c)). The median of the posterior distribution for the slope of snow cover was -0.23 (95% CrI [-1.08, 0.65]; Table 4.2). The proportion of the posterior that was less than zero indicated a 69% probability that tick presence declined with increasing snow cover and that the odds of tick presence decreased by 20% for every scaled unit increase in this predictor (Fig.4.2(a)). For growing-degree days (GDD), the median of the posterior distribution for the slope of this variable was 0.71 (95% CrI [-0.21, 1.57]; Table 4.2). The proportion of the posterior that was greater than zero indicated a 93% probability that this relationship was positive, and the odds of tick presence doubled with each unit increase in (scaled) GDD (Fig.4.2(b)). We also noted that no larval ticks were present at sites with fewer than 734 growing-degree days (Fig.4.2(b), dashed line). Finally, the median of the posterior distribution for the slope of cumulative vapour pressure deficit (CVPD) was 0.74 (95% CrI [0.07, 1.44]; Table 4.2). Similar to GDD, the proportion of the posterior greater than zero indicated a high probability (98%) that tick presence increased with increasing CVPD (Fig.4.2(c)). For every scaled unit increase in CVPD, the odds of tick presence more than doubled (110%).

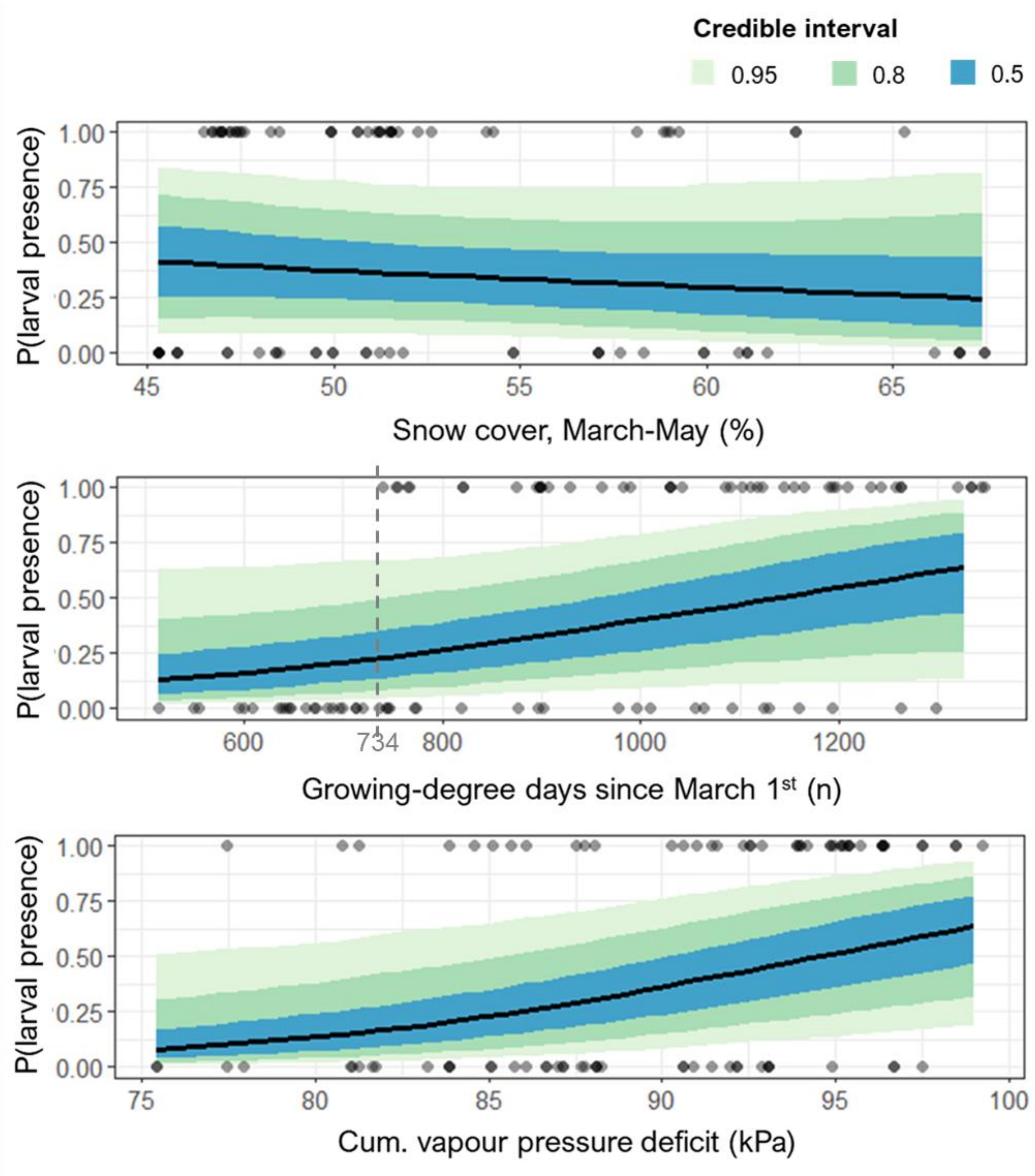


Figure 4.2. Relationship between the probability of larval *D. albipictus* presence and predictor variables: a) proportion of snow covering a site between March and May, **b)** number of growing-degree days accumulated above 5.5°C since March 1st, and **c)** the cumulative vapour pressure deficit. Black lines and shading indicate the median and 95%, 80% and 50% credible intervals from the model estimate. Dots indicate original observations (transparency for clarity of overlapping observations). Grey dashed line (b) indicates an apparent threshold of 734 growing-degree days, below which there are no observations of *D. albipictus* presence. Variables are shown on their original scale.

Table 4.2. Posterior estimates for coefficients and 95% credible intervals from the models explaining variation in *D. albipictus* occurrence and abundance across all sites (occurrence) and sites and weeks (abundance) sampled in Yukon. R-hat = potential scale reduction factor indicating MCMC convergence when close or equal to 1. GDD = growing-degree days; VPD = vapour pressure deficit.

Model *Response variable*	**Coefficient**	**Median**	**Q2.5**	**Q97.5**	**R-hat**
Occurrence *Presence / absence*	Intercept	-0.62	-2.44	1.15	1.00
	Snow cover (Mar-May)	-0.23	-1.08	0.65	1.00
	GDD >= 5.5°C (May 1st →)	0.71	-0.21	1.57	1.00
	VPD (May 1st →)	0.75	0.07	1.44	1.00
Abundance *Larval ticks / metre transect*	Intercept	0.43	0.34	1.25	1.00
	Intercept (zero-inflated)	-0.41	-2.92	1.96	1.00
	Snow cover (Mar-May)	-0.19	-0.63	0.25	1.00
	GDD >= 5.5°C (May 1st →)	0.13	-0.30	0.55	1.00
	VPD (May 1st →)	0.15	-0.36	0.68	1.00

4.3.2 Abundance

There were no strong responses in larval tick abundance (ticks/m) observed in any of our selected predictors (Fig.4.3(a-c)). The posterior estimate for the slope of snow cover was similar to that in occurrence models, with a median of -0.19 (95% CrI [-0.63, 0.25]; Table 4.2). The proportion of the posterior that was less than zero indicated an 80% probability that tick abundance declined with increasing snow cover. For every scaled unit increase in snow cover, the number of ticks/m declined by 17% (Fig.4.3(a)). The median of the posterior estimate for the slope of GDD was 0.13 (95% CrI [-0.30, 0.55]; Table 4.2), with the proportion of the distribution

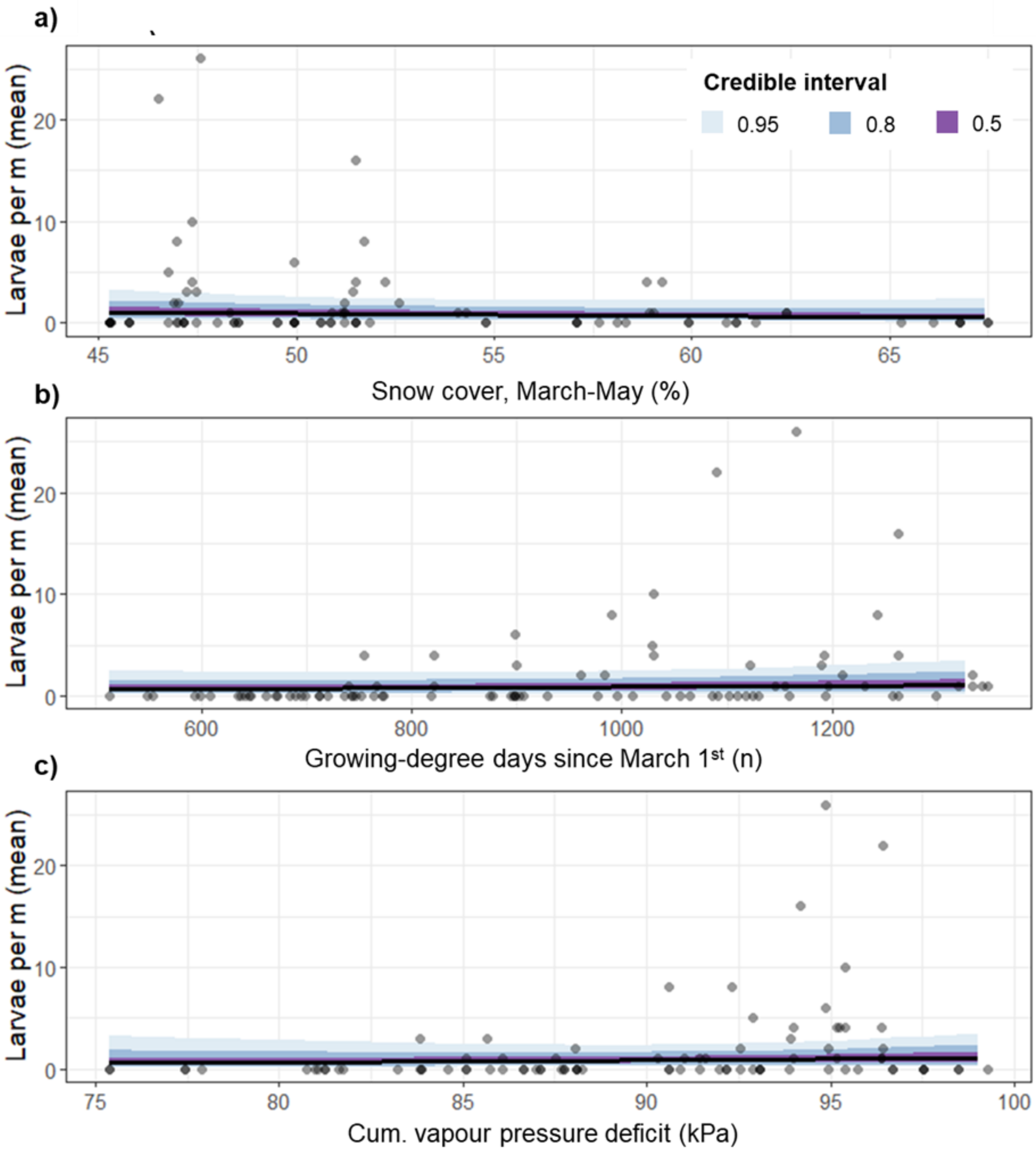
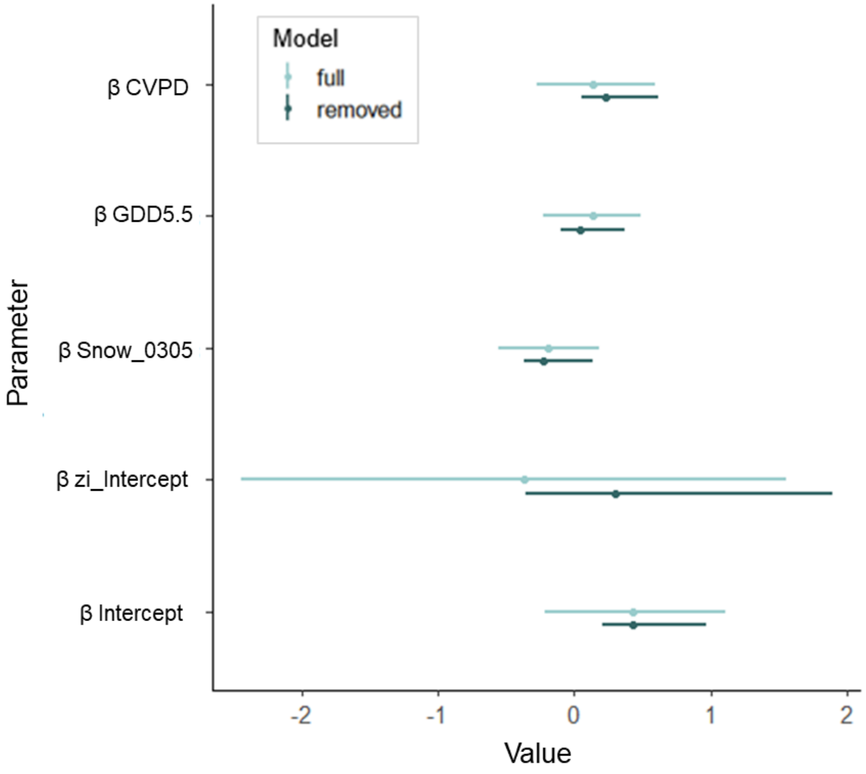


Figure 4.3 Relationship between the mean number of larval *D. albipictus* per metre sampled and predictor variables: a) proportion of snow covering a site between March and May, **b)** number of growing-degree days accumulated above 5.5°C since March 1st, and **c**) the cumulative vapour pressure deficit. Black lines and shading indicate the median and 95%, 80% and 50% credible intervals from the model estimate. Dots indicate original observations (transparency for clarity of overlapping observations). Variables are shown on their original scale.

greater than zero indicating a 73% probability that tick abundance increased with increasing numbers of GDD. The number of ticks/m showed a weak increase of 14%, for every scaled unit increase in this variable. The median of the posterior estimate for the slope of CVPD was 0.15 (95% CrI [-0.36, 0.68]; Table 4.2). The proportion of the posterior greater than zero indicated a 70% probability that tick abundance increased with CVPD, with a 16% increase in ticks/m for every scaled unit increase in this predictor.

There were three data points that could be considered extreme values, with greater than 15 larval ticks/m compared with an average across all sites of 2 ticks/m. To examine the effect of these potential outliers, we refit the abundance model excluding these datapoints, but found this had minimal impact on posterior estimates (Fig.4.4). Changes to the median of the posterior estimate for the slope of all predictors were less than 10% compared with the model using all data.

Figure 4.4 Posterior estimates for the slope of predictor variables for full abundance model ("full") and the same model with extreme data values excluded ("removed").



4.3.3 Inclusion of additional variables (Principal Component models)

The estimated probability of larval tick presence generally showed much stronger responses to principal components (PC) predictors than was observed in our first occurrence model (Fig.4.5(a-c)). The median of the posterior estimate for the slope of PC1 (primarily temperature variables, precipitation, and shrub and conifer cover) was 1.04 95% CrI [0.12, 1.93]; Table 4.3). The proportion of the posterior greater than zero indicated a high probability (98%) that larval presence increased with increasing values of PC1, with almost three-times greater odds of larval tick presence for every scaled unit increase in PC1 (Fig.4.5(a)). For PC2 (primarily snow cover, mean land surface temperature from June to August), the median of the posterior estimate for the slope was 0.49 (95% CrI [-0.36, 1.28]; Table 4.3). The proportion of the posterior greater than zero indicated an 87% probability that larval presence increased with PC2 variables, with a 63% increase in the odds of larval tick presence for every scaled unit increase in PC2 (Fig.4.5(b)).

Table 4.3. Posterior estimates for coefficients and 95% credible intervals from principal component models explaining variation in *D. albipictus* occurrence and abundance across all sites (occurrence) and sites and weeks (abundance) sampled in Yukon.

PC model *Response variable*	**Coefficient**	**Median**	**Q2.5**	**Q97.5**	**R-hat**
Occurrence *Presence / absence*	Intercept	-0.43	-2.23	1.14	1.00
	PC1: Temp., precip., veg. cover	1.04	0.12	1.93	1.00
	PC2: Snow cover, summer temp.	0.49	-0.36	1.28	1.00
	PC3: VPD, conifer cover	0.33	-0.35	1.09	1.00
Abundance *Larval ticks / m*	Intercept	0.40	-0.41	1.24	1.00
	Intercept (zero-inflated)	-0.81	-3.30	1.61	1.00
	PC1: Temp., precip., veg. cover	0.27	-0.19	0.71	1.00
	PC2: Snow cover, summer temp.	0.17	-0.24	0.59	1.00
	PC3: VPD, conifer cover	-0.19	-0.63	0.29	1.00

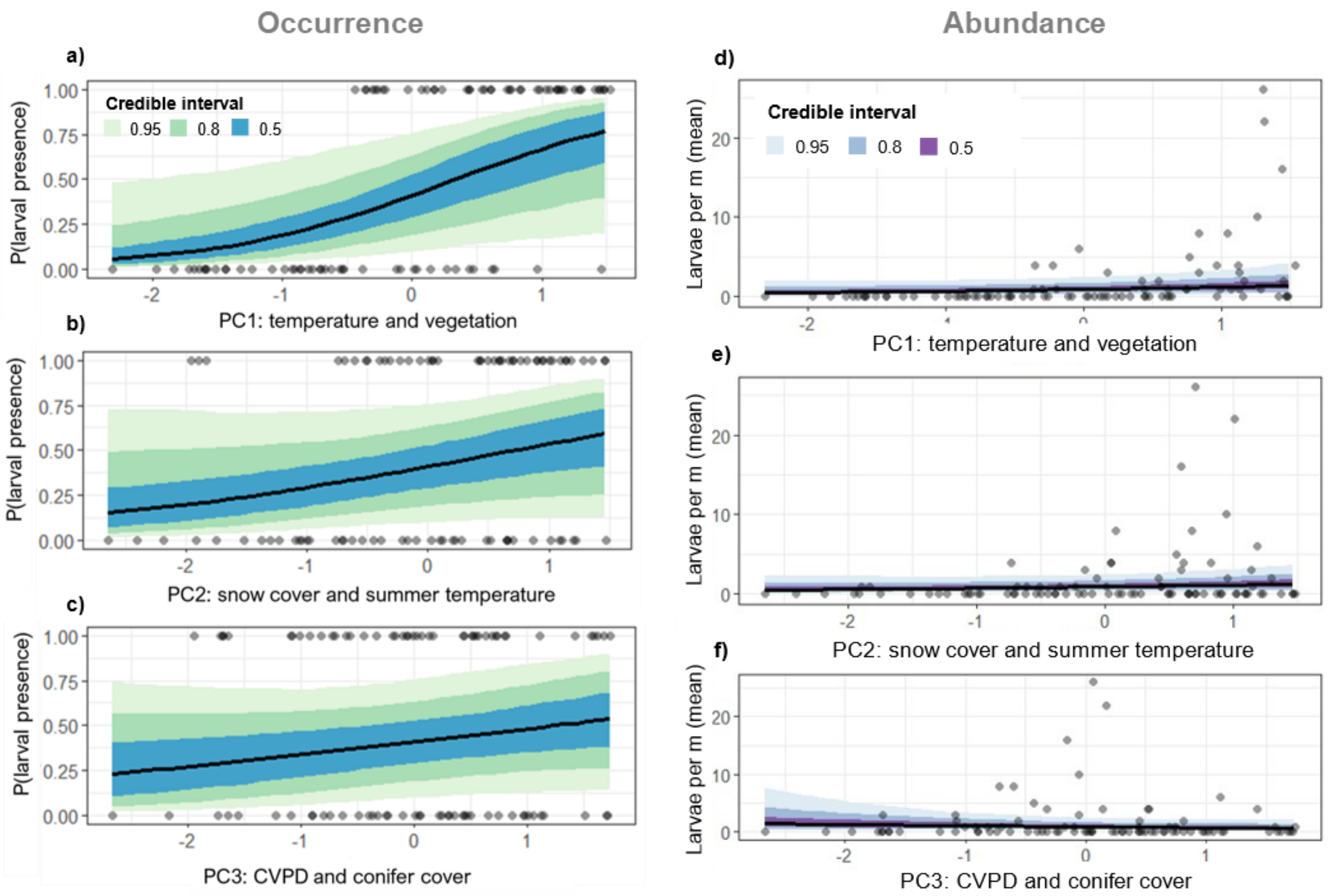


Figure 4.5 Relationship between the probability of larval *D. albipictus* presence (a-c) and abundance (d-f) and the first three dimensions of our Principal Component Analysis (PCA). PCs are described based on the highest contributing variables (Table 4.1; Appendix C.2). **a), d)** temperature and vegetation cover **b), e)** snow cover and summer temperature, and **c), f)** cumulative vapour pressure deficit and coniferous forest cover. Black lines and shading indicate the median and 95%, 80% and 50% credible intervals from the model estimate. Dots indicate original PC scaled coefficients (transparency for clarity of overlapping observations).

The median of the posterior estimate for the slope of PC3 (primarily CVPD and conifer cover) was 0.33 (95% CrI [-0.35, 1.09]; Table 4.3), with the proportion of the distribution greater than zero indicating an 81% probability that larval presence increased with increasing values of PC3. The odds of larval tick presence increased by 39% for every scaled unit increase in PC3 (Fig.4.5(c)).

As with the abundance model with the restricted number of variables, the PC abundance model showed much weaker relationships between the number of larval ticks per metre and the PC predictors; however, the width of the credible intervals was much narrower across all predictors (Fig.4.5(d-f)). The median of the posterior estimate for the slope of PC1 was 0.27 (95% CrI [-0.19, 0.71], Table 4.3), and the proportion of the posterior distribution greater than zero indicated an 87% probability that tick abundance increased with PC1. Tick abundance was estimated to increase by approximately one-third for every scaled unit increase in the PC1 predictor (Fig.4.5(d)). PC2 also showed a weakly positive relationship with our response variable, with a posterior estimate of the median of the slope of 0.17 (95% CrI[-0.24, 0.59]; Table 4.3), of which the proportion of the distribution greater than zero indicated an 78% probability that the number of larval ticks/m increased with increasing PC2. Larval abundance increased by 19% for every scaled unit increase in PC2 (Fig.4.5(e)). Finally, PC3 showed a weakly negative relationship with abundance, with an estimate of -0.19 (95% CrI[-0.63, 0.29]; Table 4.3). There was an 80% probability that larval tick abundance decreased with increasing PC3, given the proportion of the distribution less than zero. This relationship showed a relatively small (17%) decrease in the number of ticks/m for every unit increase in PC3 (Fig.4.5(f)).

4.4 Discussion

Our analysis of larval winter tick field data in the southern Yukon revealed positive relationships between presence and, to some extent, abundance, and measures of temperature and moisture availability. The width of the posterior distribution varied across predictors but showed the strongest evidence of a positive relationship with cumulative vapour pressure deficit from May 1 to sampling date, and with temperature-related variables. In general, we found that warmer, drier areas, particularly in the Ibex Valley, were not only more likely to have larval *D. albipictus* present (Table 4.2; Fig.4.3; Fig.4.5) but, potentially, also in greater numbers (Table 4.2; Fig.4.4). Conversely, locations that were cooler or had a high proportion of snow cover were less likely to contain winter ticks (Fig.4.4(a); Fig.4.5(b)), which may explain their absence at least in more densely forested sites, as noted for *D. albipictus* elsewhere in North America (Addison et al., 2016; Powers, 2019). However, not all the observed relationships between occurrence or abundance aligned with our expectations based on knowledge of winter tick physiology and findings of previous studies (Table 4.1), raising some interesting questions that challenge both our assumptions regarding this species' tolerances, as well as the limitations of our data.

4.4.1 Factors likely influencing larval winter tick occurrence

The ability of our models to detect relationships between larval *D. albipictus* occurrence and our selected predictors suggests that, at the 1 km scale measured, several of our selected environmental variables capture aspects of the winter tick niche that are important to their survival. Of these, temperature-related variables (GDD, land surface temperature from March to May; June to August) appear to play the most significant role. In addition to the positive estimate for GDD in the occurrence model, the predominance of temperature-related variables in the PC model of occurrence (PC1, almost 50% total variation; Table 4.1) and the positive posterior estimates of the associated lower and upper credible interval suggests that localities with warmer temperatures increase the probability of larval tick presence (Fig.4.5(d)). This finding is in accordance with the known role of temperature and development success in both laboratory studies of winter tick (Glines, 1983; Drew & Samuel, 1987; Holmes et al., 2018) and in other ixodid tick species at lower latitudes than Yukon, particularly on oviposition rate, and egg and larval life stages (Ogden et al., 2004; Lysyk, 2014; Burtis et al., 2016). Most sites where larval *D. albipictus* were detected in Yukon were in the Ibex Valley, where sparsely vegetated, south-facing slopes feature prominently and are among the first snow-free and vegetated areas providing spring forage for elk and other cervids due to their topography (Smith et al., 2004; Strong et al., 2013). The relatively higher land surface temperatures and associated longer period of heat summation in the Ibex Valley could explain larval presence in this location compared with the more densely forested locations of other sites.

Our observation of a possible threshold number of >734 growing-degree days above 5.5°C required for larval *D. albipictus* presence (Fig.4.2(b)) is interesting for its contrast to Wilkinson's (1967) previous suggestion of a minimum of 1500 growing-degrees needed at this northern range edge. We chose this base temperature of 5.5°C firstly, for direct comparison with previous studies (e.g. Wilkinson, 1967; Zarnke et al., 1990) and secondly, as a conservative estimate of the minimum threshold required for adult female survival, egg hatching, and larval development. Given that most experiments in the lab and field, along with field observations, have been made at temperatures that are on average much higher than 5.5°C (e.g. Drew & Samuel, 1986, 1987; Holmes et al., 2018), and that imprecise threshold assumptions may bias climate change impact predictions (Molnár et al., 2017), further investigation of the realized thermal tolerance thresholds may be warranted. The maximum number of GDD that we observed across all sites was 1,348 with a mean of 988 GDD (SD ± 215.7), with tick-present sites generally exhibiting a higher number on average (mean: 1,087; SD ± 165.6). In an assessment of the potential for *D. albipictus* to establish in neighbouring Alaska, researchers observed that only locations of experimental mesocosms that met the 1500 degree day threshold above base 5.5°C (42°F in their study) resulted in successful adult female oviposition (Zarnke et al., 1990). To our knowledge, there have been no other conclusive experiments or other observations of degree-day thresholds yet made for this species, which makes consideration of the potential uniqueness of the Yukon population of *D. albipictus* difficult. However, this disparity could be due, firstly, to the few northern records for winter ticks at the time of Wilkinson's assessment of the species' range edge, with the most northern being Fort Liard and Fort Smith, Northwest Territories, both of which are around 60° latitude (Wilkinson, 1967). It is likely that winter ticks have been present in northern regions and in the Yukon at least since the 1950s (Samuel, 1989; Chenery et al., 2023), so it seems likely that a 1500 GDD limit was simply a misinterpretation of the correlation with available records at the time of Wilkinson's writing (1967). Similarly, Zarnke et al. (1993) do not report the spatial scale or timeframe over which they calculated GDD, and we assume they used the same standard growing period from March 1. Although the apparent absence of larval ticks below 734 GDD at our field sites in the Yukon is not proof such a threshold exists, it does warrant further research, particularly at a finer spatial scale that is more reflective of the tick's experience on the ground, given microclimate conditions. From a biological perspective, it is also plausible that *D. albipictus* can tolerate suboptimal thermal conditions over a longer period by utilizing an optional period of quiescence after larval hatching (Drew & Samuel, 1989; Belozerov, 2009; Holmes et al., 2018; Addison et al., 2021). Similarly, one of the key limitations of using growing-degree models as a proxy is that these models assume a linear relationship between temperature and growth, which is at best an approximation of the true, underlying association between this species and temperature. (Molnár et al., 2017). The approach does not account for effects of temperature-fluctuations beyond changing daily averages (e.g., day-to-night temperature differences), nor does it account for potential negative effects of increasing temperatures (e.g. increased mortality), or extreme weather events (e.g., heat waves causing an inability to develop and/or high fatality rates. Alternative statistical (Van der Vijver et al., 2018) and mechanistic approaches (Molnár et al., 2013, 2017) may allow disentangling of these driving forces to provide more accurate estimates of the winter tick's thermal niche, but would require collection of additional data using dedicated thermal performance experiments both in the lab and in the field. Understanding the behaviour and thermal developmental responses of this species may prove particularly useful for choosing appropriate control or mitigation measures, and in making broad-scale predictions regarding suitable and unsuitable locations for winter tick establishment in future.

Similarly, snow cover has been proposed as an important factor affecting the survival of adult female *D. albipictus* when they drop from their host in the spring (Drew & Samuel, 1986, 1987; Addison et al., 1989), but we did not observe a particularly strong relationship between the proportion of a sampling site covered with snow from March to May, and the probability of larval tick presence in our dataset (Fig.4.2(a); Table 4.2). Although the negative direction of the relationship was as expected based on knowledge from previous studies (Table 4.1), there is uncertainty in the median estimate, expressed as a wide credible interval of the posterior distribution (Table 4.2). Snow cover averaged across the period of interest ranged from approximately 40-70%, indicating that within the 1 km scale of our sites, there could have been one or more suitable areas for adult female ticks to have dropped from the host. It is likely that, with data at finer spatial scales, the strength of this relationship could be better ascertained.

We observed an unexpected relationship between larval tick presence and cumulative vapour pressure deficit. Our models suggest that sites with higher CVPD (amounting to drier conditions over time) appear positively related to larval tick presence (Fig.4.2(c); Table 4.2), which runs counter to our original expectations regarding increased desiccation risk (Table 4.1; Addison et al., 2016; Hacker et al., 2021). There could be several possible reasons for this finding. Firstly, the spatial scale on which we were able to calculate CVPD (10.5-68.1km; SD +- 23.7) is unlikely to truly reflect on-the-ground experience of larval winter ticks, whose movement is within a range of a few metres at most (Yoder et al., 2017). Small-scale, microhabitat and associated microclimate factors are known to result in variability in other ixodid tick abundances across various environmental gradients (Needham & Teel, 1991; Li et al., 2012; Ginsberg et al., 2020). Locations of high CVPD in the Ibex Valley, where most larval detections were made, may present warmer, drier locations at a large scale, but could contain small mosaics of refugia for off-host winter ticks that explain their presence in seemingly inhospitable conditions. However, there may also be biologically plausible explanations for this disparity. We only measured CVPD from May onwards each sampling year, which does not account for the survival and reproductive success of adult female ticks dropping several months earlier. Although we did not observe any strong correlations between CVPD and any of our other predictors (Appendix C.1, Fig.C3), areas with high CVPD are likely to be more exposed, receive greater insolation, and may be warmer than low CVPD areas, which could result in conditions earlier in the year that are more conducive to female tick survival and oviposition (Drew & Samuel, 1986; Addison et al., 2016). Even if this is not the case, it is still possible that the effect of CVPD on larval occurrence results from the experience of the adult female life stage. Experimental studies conducted by Yoder et al. (2016) have shown that the conditions experienced by adult females during the pre-oviposition period can have a direct effect on larval fitness, with mothers exposed to lower humidity conditions (85% RH) producing offspring that are more drought tolerant than those exposed to excess humidity (95% RH) (Yoder et al., 2016). Given the generally dry conditions in the Ibex Valley (Appendix C.1; Figure C2), it seems plausible that, particularly late-dropping adult females, could experience a higher level of CVPD (drier conditions) that would lead to offspring that are more drought tolerant, and, therefore, better able to reap the benefits of increased temperatures for egg-hatching and development (Drew & Samuel, 1986, 1987). Such findings could corroborate observations that warmer, but not necessarily wetter, spring seasons give rise to a larger number of locations where winter ticks survive and thrive the following year (Addison et al., 2016; Samuel, 2004) and raise important questions regarding *D. albipictus'* survival potential in seemingly sub-optimal or range-edge environments.

4.4.2 Spatial scale and factors affecting abundance

Factors affecting measures of larval tick abundance in our dataset could occur at one or more of three stages in their natural history: oviposition success of adult females; egg development and hatching; and, larval survival and subsequent questing success (Table 4.1). As mentioned above, small-scale, microhabitat conditions, driven largely by topography, land use, water and snow cover, can strongly affect ixodid tick survival and development (e.g. Dobson et al., 2011; Ledger et al., 2019; Dumas et al., 2022). Although the occasional mismatch between our 1 km site scale and the resolution of our environmental predictors does not appear to have influenced the ability of our models to detect relationships with occurrence, we were not able to find strong relationships between our predictors and tick abundance (Fig.4.3; Fig.4.5(d-f)). It is likely that a fine spatial scale also plays an important role in determining the abundances of *D. albipictus* larvae found in the Yukon, and the relative coarseness of our variables, in comparison, could explain why stronger relationships were not detectable in our small dataset. Although our study was not initially designed to examine fine-scale relationships, we did detect a high degree of variability in abundances across sites that suggests some important response to heterogeneity in environment or climate (Appendix C.1: Fig.C1). Both adult female and larval *D. albipictus* have limited mobility on the ground, moving less than two metres from the site of drop-off or egg hatching (Addison et al., 2016; Yoder et al., 2017), suggesting that the ticks themselves have a limited scope for selecting suitable habitats within more than a few centimetres of their initial location once off-host. Given that site selection at the scale of host animals across our field sites is also likely to be within tens to a few hundred metres, as evidenced by detected larval locations year-to-year (Chenery et al., 2020), host and parasite associations with the environment need to be understood at the local scale, which is similar to findings for moose hosts elsewhere in North America (Healy et al., 2018; Blouin et al., 2021).

Our study design could also be considered spatially biased towards access roads, which other studies have found to affect model outcomes, though mainly with respect to mapping species distributions (Kadmon et al., 2004; Hughes et al., 2021). In this study we did not examine the distribution of ticks themselves, rather, the relationship between their locations and environmental predictors. Because we have no reason to believe that the distribution of predictor variables is systematically biased by road proximity across either year of sampling or site location, which was included within the hierarchical modelling framework as a random effect, it is unlikely that these spatial biases have strongly affected model outcomes (Kadmon et al., 2004). However, comparison with locations from more distant and remote areas, as in all ecological studies, would provide a valuable perspective in future sampling (Hughes et al, 2021).

As with occurrence models, we observed a weak, negative relationship between snow cover and our response variable (number of larval ticks/m) (Fig.4.3(a); Table 4.2). This is consistent with previous studies that suggested female winter tick oviposition rate may be negatively affected due to either the effect of sustained cold temperatures (Drew & Samuel, 1986; Addison et al., 2021), or submergence in snowmelt (Sullivan et al., 2022). The knock-on effects of reduced reproductive capacity of adult females in some locations could explain relatively lower larval abundances the following fall, although a larger sample size and finer-scale measure of snow cover may be required to adequately detect the strength of this relationship. The proportion of snow cover was the only metric at the spatial scale relevant to our sampling sites available to us at the time of this study. Future studies might consider alternative or analogous measures of snow presence that could potentially impact tick survival and could be measured at a fine spatial scale, such as snow depth (e.g. Addison et al., 2021), snow water equivalence (e.g. Boelman et al., 2019) or physical classification (e.g. El Oufir et al., 2021).

The very weak positive effects that we observed of GDD and CVPD on tick abundance followed the same pattern of association as with occurrence models. Wilton and Garner (1993) observed that higher mean April temperatures appear positively related to subsequent winter tick infestation severity on moose the following year, suggesting that although we found only a weak association between temperature-related variables and larval tick abundance in our dataset (Fig.4.3(b); Fig.4.5(d,e)), the effect may be more easily detectable at the scale of the host. Warmer summer temperatures were found to be positively correlated with higher degrees of moose hair loss in Isle Royale, Michigan (Hoy et al., 2021), which may also indicate higher abundances of larval ticks in warmer years.

The greater need for inclusion of microclimate or microhabitat conditions in assessment of species' distributions is a well-recognised challenge across changing ecological systems (Potter et al., 2013). Recent research in similar boreal and tundra ecosystems of northern Europe has shown considerable thermal heterogeneity at very fine scales (Aalto et al., 2022), demonstrating the benefit of obtaining similar measurements in the analogous northern systems of North America. We suggest that the weak associations detected in our data warrant further attention, given their potential influence on winter tick abundance and hyperabundance that is of importance in assessing potential host impact.

4.4.3 Winter ticks in the Yukon versus elsewhere in North America

By examining the potential relationships between larval *D. albipictus* presence and abundance in the Yukon, we also sought to determine how this population at a northern limit might compare with other North American populations. The expected response of species persisting at range boundaries remains mixed (Gaston, 2009; Oldfather et al., 2020); local adaptation may allow for future dispersal, tracking environmental gradients with some benefit for future spread (Levin, 2000; Hargreaves & Eckert, 2019), or it may lead to reduced fitness among individuals, and remain fixed due to limitations of climate and environment (Brown et al., 1996; Harsch & Hille Ris Lambers, 2016). Given the broad distribution of *D. albipictus* throughout North America (Chenery et al., 2023), the apparent northern limit for this species suggests that it is the latter –

climate and environmental limitation – that most likely explains their range edge in the Yukon, as has been posited historically (Wilkinson, 1967; Zarnke et al., 1990; Samuel, 2004). Our findings suggest that temperature and, to a lesser extent, snow cover, could explain the presence and, therefore, persistence, of winter ticks in the Ibex Valley, both of which are commonly described factors for *D. albipictus* survival across the continent (Aalangdong, 1994; Addison et al., 2016; Dunfey-Ball, 2017). The potentially lower-than-expected growing-degree day requirements and lack of response to drier conditions (as shown through cumulative vapour pressure deficit) in our dataset could suggest some degree of cold- and drought- adaptation, which requires further research.

The absence of *D. albipictus* detections north of 62°N latitude in the Yukon (Chenery et al., 2022) combined with the findings presented here, suggest that environmental conditions may not currently be suitable for winter tick establishment throughout the territory. However, the ongoing effects of climate change are predicted to significantly alter vegetation patterns across the Yukon in the near future, increasing the proportion of warm, dry, grassland and shrubland areas, which, as we have shown, seem particularly suitable for *D. albipictus* to complete its life cycle (Rowland et al., 2016; Reid et al., 2022). These environmental changes are also likely to alter patterns of host habitat use, with elk and mule deer predicted to colonize new, grassy areas of forage and potentially taking winter ticks and other parasites and diseases with them (Sibernagel, 2010; Nobert, 2012). Such changes bring about new opportunities for potential host interactions and increased infection risk, and add to the many challenges cervid species are already experiencing in the north (Kutz et al., 2009; Dobson et al., 2015). Understanding the limits to establishment for parasites like the winter tick, therefore allow for more informed prioritization among wildlife managers and conservationists in an otherwise, uncertain, future.

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Conflict of interest

The authors declare no conflicts of interest.

Author contributions

Conceptualization, ESC, PKM, NJH; methodology, ESC, PKM, NEM; formal analysis, ESC, LAA; investigation, ESC; resources NJH, NEM, PKM; data curation, ESC; writing—original draft preparation, ESC; writing—review and editing, ESC, LAA, NJH, NEM, PKM; visualization, ESC, LAA; supervision, NEM, PKM; funding NEM, NJH, PKM, ESC. All authors read and approved the final manuscript.

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Chapter 5.

Improving widescale monitoring of ectoparasite presence in northern Canadian wildlife with the aid of citizen science

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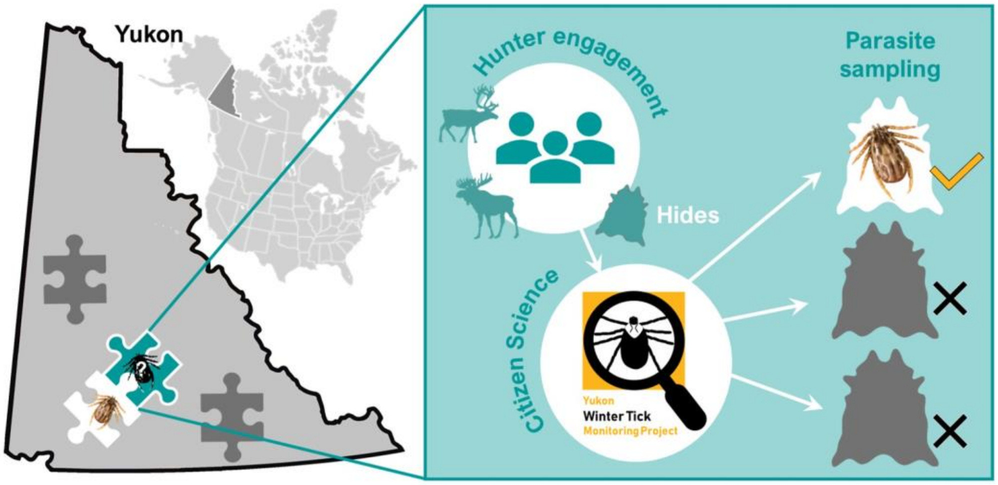


Contributions: Conceptualization, ESC, NJH, PKM; methodology, ESC, MH; formal analysis, ESC.; investigation, ESC, NJH, MH, KM.; resources, NJH; data curation, ESC, MH; writing—original draft preparation, ESC; writing—review and editing, ESC, KM, MH, NJH, NEM, PKM; visualization, ESC; supervision, NJH, NEM, PKM; project administration, NJH, KM, ESC; funding acquisition, NJH, PKM.

Abstract

Sampling hides from harvested animals is commonly used for passive monitoring of ectoparasites on wildlife hosts, but often relies heavily on community engagement to obtain spatially and temporally consistent samples. Surveillance of winter ticks (*Dermacentor albipictus*) on moose *(Alces alces*) and caribou (*Rangifer tarandus caribou*) hosts in Yukon, Canada, has relied in part on voluntary submission of hides by hunters since 2011, but few samples were submitted. To enhance sampling efforts on underrepresented moose and caribou hosts, we implemented a three-year citizen science program, the Yukon Winter Tick Monitoring Project (YWTMP), to better engage with hunters in hide sample collection. A combination of in-person and social media outreach, incentivized engagement, and standardized hide sampling kits increased voluntary submissions of moose and caribou hides almost 100-fold since surveillance began. Citizen science samples expanded the northernmost geographic extent of existing sampling efforts for moose by 480 km and for caribou by 650 km to reach 67.5 °N latitude. Samples also resulted in new detections of winter ticks on moose hides that are spatially separate to those submitted for other cervids in Yukon. Findings from the YWTMP have provided an essential baseline to monitor future winter tick host-parasite dynamics in the region and highlighted priority areas for ongoing tick surveillance.

5.1 Introduction

Engaging non-scientists in tick surveillance has demonstrated benefits to public health in obtaining new records of tick detection (Lee et al., 2019; Lyons et al., 2021), assessing the risks of tick-borne illness (Eisen & Paddock, 2021; Nieto et al., 2018; Ripoche et al., 2018), and educating communities on tick-bite prevention (Lewis et al., 2018). Targeted engagement of key community demographics at higher risk of contact with ticks, such as school children (Prunuske et al., 2021; Seifert et al., 2016), hikers, hunters, and outdoor enthusiasts (Sgroi et al., 2021), and those with a general interest in tick monitoring in their community (Lewis et al., 2018; Nieto et al., 2018; Porter et al., 2019) not only provides high-quality data for modelling and mapping tick distributions and that of their associated pathogens, but may also build long-term relationships of benefit to researchers and citizen participants alike (Brook et al., 2009; Theobald et al., 2015; Tulloch et al., 2013). Many examples of citizen science-led tick monitoring to date have focused on passive collection of samples encountered by participants, such as mail-in tick schemes aimed at describing tick-borne disease risk to humans in the USA (Lieske & Lloyd, 2018; Nieto et al., 2018; Porter et al., 2019), Canada (Lewis et al., 2018; Ripoche et al., 2018), and Spain (Sgroi et al., 2021) and reporting tick presence on domestic horses in Canada (Schvartz et al., 2015). In most cases, ticks collected in these programs are a direct result of the tick's natural host-seeking process, with submissions primarily from humans or domestic animals or from peri-urban environments. Monitoring ticks that primarily infect wildlife species, as opposed to humans, presents additional challenges to both sampling methodology and community engagement, owing to inherent logistical barriers for collection.

The nature of on-host sampling means that tick detection is necessarily limited by access to physical host specimens, which may be particularly challenging to obtain when assessing presence in vast and remote areas. Surveillance of ticks on large game species, such as cervids, has a reasonably standardized methodology, commonly using set time- or length-based searches across transects in the hair of living or dead host animals (Poh et al., 2020). These methods are increasing in popularity for ectoparasite monitoring, being less time consuming and labor intensive than hide digestion techniques, which destroy the hide and require laboratory processing using chemical agents (Sine et al., 2009; Welch & Samuel, 1989). Additionally, conducting visual searches of hides for ticks can be carried out *in situ* at hunter check-stations or on live-captured hosts, or from samples of hides taken from hunted or roadkill animal carcasses (Addison & Smith, 1981; Apperson et al., 1990; Cortinas & Kitron, 2006).

In northern Canada, where communities continue to engage in hunting for both food and traditional cultural purposes, community-based integration of hunters in wildlife health surveillance has demonstrated its value for both researchers and community members alike (Brook et al., 2009; Curry, 2009). Submission of the hides of harvested moose (*Alces alces*) and caribou (*Rangifer tarandus*) from the Sahtu Settlement Area in the Northwest Territories confirmed the presence of the winter tick, *Dermacentor albipictus* (Kashivakura, 2013; Kutz et al., 2009b), a wildlife parasite of particular concern for cervid health, in this northern region. Winter ticks are blood-feeding ectoparasites that have been implicated in mass die-offs of moose in North America (Cameron & Fulton, 1927; Pybus et al., 1999; Samuel, 2007; Seton, 1909), including ongoing declines in local moose populations in the US (Jones et al., 2017). Burdens upwards of 50,000 – 60,000 ticks per moose may result in host death due to several combined factors, including hair loss, blood loss, and reduced foraging behaviors (Jones et al., 2017;

Mooring & Samuel, 1998b; Pekins, 2020b; Samuel, 2007). Winter tick impact on other cervid species has historically been considered less severe (Samuel, 2004; Samuel & Welch, 1991), although is also less studied. Recent reports raise concerns over the potential impact of winter ticks on caribou (Bondo et al., 2019; Welch et al., 1990), elk (*Cervus elaphus canadensis*) (Calvente, Chinnici, et al., 2020; Calvente, Pelletier, et al., 2020), and white-tailed deer (*Odocoileus virginianus*) (Machtinger et al., 2021). Surveillance of winter ticks on all cervid species is important for understanding their distribution among host populations and in monitoring their effects. Although widely used in southern Canada and the U.S., the use of hunter check stations in remote northern Canada is not a practical or reliable method for collecting samples. Further, due to the life cycle of the tick, checking hides in the field in the early part of the hunting season (ie. September and October) may also have low tick detection success as the ticks are still in their larval form and nearly undetectable (<1mm). This means that submission of hide samples by hunters for thorough visual checks using laboratory tools likely improves detection, and therefore provides a consistent and long-term means of monitoring winter ticks in the north.

The Yukon Winter Tick Monitoring Project was a collaboration between the Yukon Government's Animal Health Unit (AHU) and researchers at the University of Toronto. Established in 2018, the project sought to enhance existing territorial monitoring of winter ticks on cervids by expanding AHU's hide submission scheme and to complement field-based sampling efforts for larval winter ticks off-host (Chenery et al., 2020). Government monitoring of winter ticks on hides in the territory began in 2011, following detection of the parasite on a managed population of elk in the Ibex Valley (Government of Yukon, 2016). Hides from roadkill, illegal kills, conflict kills, and animals found dead are also submitted voluntarily as part of this scheme but, unlike the annual harvest, are necessarily opportunistic in nature. All hides are sampled for winter ticks according to a standardized 'hair transect' protocol commonly used for checking ectoparasites on cervids (Environment Yukon, 2012; Sine et al., 2009) (and see *Materials and Methods*, *2.4 Sample processing*). To explore if winter ticks in Yukon are solely maintained by elk and to examine the potential spread of the ticks to other host species, the hide sampling program also includes harvested moose, caribou, and deer, to be submitted on a voluntary basis.

Voluntary participation in scientific research has generally been split into two main categories of motivation: intrinsic (interest or enjoyment driven), and extrinsic (outcome or reward driven) (Lakomý et al., 2020; Lotfian et al., 2020). A call for voluntary submissions of moose and caribou hides was included in the Yukon Hunting Regulations Summary starting in 2014, but few samples were received each season (April 1st – March 31st), despite the majority of hunters commonly holding a seal for one or both of these species (Milligan, 2018). The low number of voluntary moose and caribou hide submissions to the AHU scheme from 2011-2017 indicated that engagement from the hunting community was low if only intrinsic factors were considered. This was likely due to the considerable effort of bringing the large, heavy hide from the field, particularly in cases where the hunter would not normally keep this part of the animal.

We sought to determine whether changes to the existing hide-submission program could increase voluntary moose and caribou hunter participation across Yukon, as a means of improving detections of winter ticks in the territory. For this study, we do not include data on voluntarily submitted animals that were killed by non-hunted means (e.g. roadkill, found dead), but focus solely on engagement with the hunting community. The YWTMP study took place over three hunting seasons (2018 – 2020) and was designed to appeal to volunteer motivations, offering incentives and simplified hide sample submission kits that reduced participant burden. Success of the scheme was evaluated based on the number of hides or samples returned by hunters across each hunting season in the study (2018-2020) relative to previous engagement in prior seasons (2011-2017). We also considered the level of conformity with hide sample kit submissions as an indicator of data quality. To determine the efficacy of this approach for widescale monitoring across the territory, we compared the total number and geographic location (Game Management Subzone, GMS) of samples received before and after YWTMP scheme implementation and their winter tick infection status. In presenting these findings, we show how increased engagement with the hunting community to boost sample numbers can supplement existing monitoring efforts and, critically, improve knowledge of tick distribution on hosts at a regional level.

5.2 Methods

5.2.1 Voluntary and mandated hunted hide submission schemes

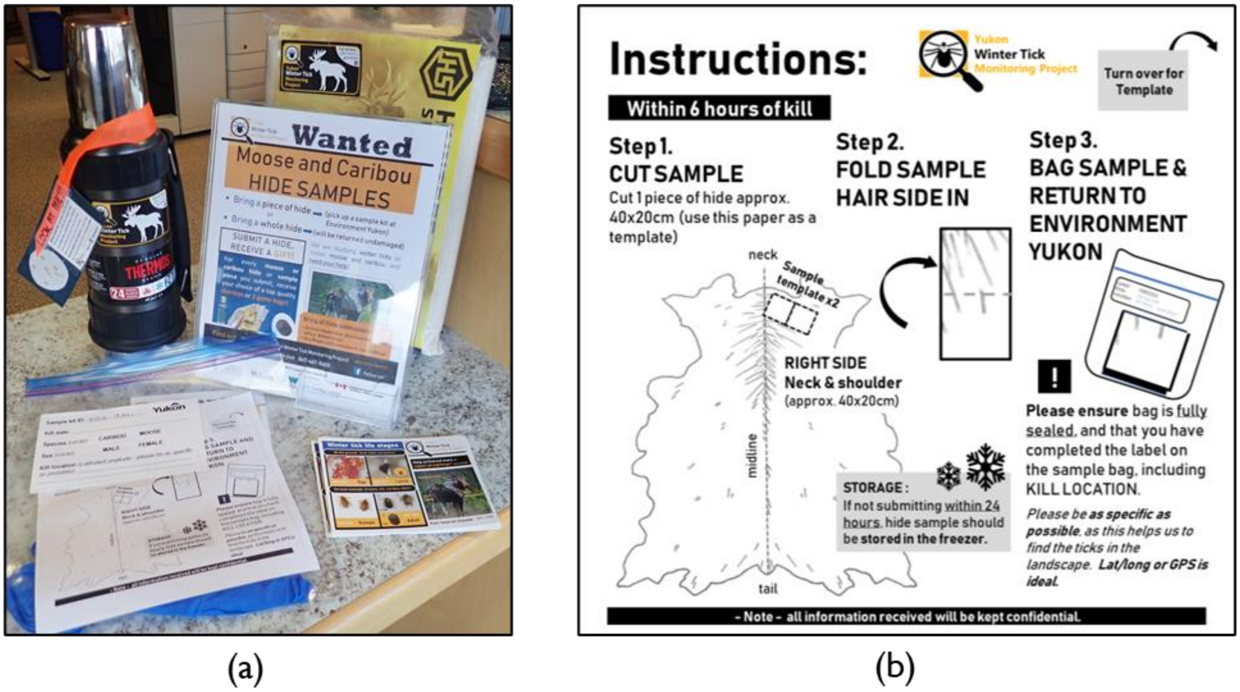
The Yukon government's hide submission program began in 2011 and continued throughout the duration of the YWTMP study, processing mandatory harvested hide submissions for elk and from 2018 onwards, mule deer (*O. hemionus*). Moose and caribou samples on the other hand, continue to be submitted only on a voluntary basis. Hides of mandatory submissions are required to be taken to a Department of Environment office within 15 days of the harvest (Wildlife Act: Wildlife Regulation, 2012). All hides can be returned to the owner post-sampling if requested.

5.2.2 Hide incentives program

Beginning in August 2018, hunters were offered their choice of an incentive (a stainless-steel thermal flask or two high-quality game meat bags) for every hide sample submitted to the YWTMP scheme during that season. The scheme was advertised through the Yukon Hunting Regulations, during the government's Hunter Education and Ethics Development (HEED) course, via YWTMP social media posts (Facebook, Twitter), and through printed material in Department of Environment and First Nations offices and local businesses throughout the territory (Fig.5.1(a)). Incentives were received by participants at the time of sample submission to a Department of Environment office. The incentives scheme also applied to the 2019 and 2020 seasons for participants returning full moose and caribou hides or samples for these species, as part of YWTMP hide sample kits.

5.2.3 Hide sample collection kits

To increase ease of collection for participants and encourage consistency in sample collection, we designed a relatively small, lightweight sampling kit that could be taken into the field with the hunter (Appendix D.1). Winter ticks are found at the highest densities in the neck and shoulder region of their hosts (Addison & McLaughlin, 1988; Samuel, 2004), and this body region has been shown to provide a suitable location for tick detection on moose (Samuel, 2004; Sine et al., 2009). We therefore followed methods of collection and visual inspection adapted from Sine and colleagues' (Sine et al., 2009) standardized collection methods, requesting one 20 x 40 cm hide sample from the right shoulder of the animal. The size of the hide sample was chosen because it balanced ease and therefore portability of collection with detection probability. The sample was collected from a standardized location where winter tick abundance is generally highest (Samuel, 2004). Sample kits consisted of a large ZipLoc™ plastic bag (26.8 x 27.3 cm) that contained a single piece of paper printed with written and visual instructions that also doubled as a hide sample template (20 x 20 cm) (Fig.5.1(b)), and a pair of single-use nitrile gloves (primed Prima Touch® Nitrile Extra Strong). Each kit was labelled with a unique identifier and had fillable form fields designating hunted species (moose or caribou), sex, and kill date and locality. Participants were asked to cut one sample of hide, approximately twice the size



Instructions:

Within 6 hours of kill

Step 1. **CUT SAMPLE**
Cut 1 piece of hide approx. 40x20cm (use this paper as a template)

Step 2. **FOLD SAMPLE HAIR SIDE IN**

Step 3. **BAG SAMPLE & RETURN TO ENVIRONMENT YUKON**

STORAGE: If not submitting within 24 hours, hide sample should **be stored in the freezer.**

Please ensure bag is fully sealed, and that you have completed the label on the sample bag, including KILL LOCATION.

*Please be **as specific as possible**, as this helps us to find the ticks in the landscape. **Lat/long or GPS is ideal.***

- Note - all information received will be kept confidential.

Figure 5.1 Yukon Winter Tick Monitoring Project (YWTMP) hide submission scheme materials. (a) Display at Department of Environment license and permit desk, Whitehorse. Incentives were displayed along with sample kits for collection and informational materials on winter ticks. **(b)** Front side of hide sample template with instructions for collection and storage, as included in each sample kit (see also Appendix D.1).

of the template, from their kill and to return it inside the Ziplock™ bag to any Department of Environment office. No personal or identifying information relating to the participant was collected. Hunters were requested to collect the hide sample within six hours of a kill to reduce the likelihood of ticks leaving the dead host (Sine et al., 2009) and advised that samples that could not be submitted within 24 hours should be frozen. Care was taken to remind participants that larval winter ticks may not be easily visible to the naked eye and to submit samples even if they appear to be tick-free. Although winter ticks are infrequently known to bite humans (Samuel, 2004; Lindquist et al., 2016), hunters were verbally reminded during kit pick up to conduct a tick-check on themselves and to wear the gloves provided when handling the hide.

Physical kits were distributed via Department of Environment offices in Whitehorse, Haines Junction, Watson Lake, Teslin, Mayo and Dawson, the Yukon Fish and Game Association office in Whitehorse, and several First Nations harvest offices throughout the southern region. Double-sided informational postcards accompanied the kits showing all winter tick life stages and additional information on the species. Additionally, hide-sample templates and winter tick information cards were available to download in e-copy via the YWTMP Facebook page (https://www.facebook.com/tickymoose). Kits were available throughout the moose and caribou hunting seasons of 2019 and 2020 (September to December) and samples were encouraged to be returned within this same timeframe. Although accepted throughout the year, no kits were returned past December each year.

5.2.4 Sample processing

Comparable protocols were used to sample both full hides and YWTMP hide samples for winter ticks (Appendix D.2). Full hides (both mandatory and voluntary submissions) were assessed using a standard line transect method for surveying ectoparasites on hides, following a protocol based on Sine and colleagues (Environment Yukon, 2012; Sine et al., 2009). Hides were laid on a flat surface and five equal transects 70 cm long and spaced approximately 2.5 cm apart were taken either side of the midline, running from the neck, down the shoulders and back. Transects were measured using a flat meter rule and the hair parted to the skin using a knitting needle, along which ticks were removed and counted. The total number of ticks were recorded by life stage along each transect and summed to record the total number of ticks per hide. In cases where a full hide could not be processed immediately, it was stored frozen at -20 °C and left to thaw for up to 24 hours before sampling. Hide samples from YWTMP kits were immediately frozen on receipt and left to thaw at room temperature for approximately eight hours prior to processing. The length and width of each hide sample was recorded, before being separated into transects approximately one cm apart and running the full length of the sample. Hide samples were first placed under a magnification lamp (Intertek GS-T00589) and, as with the full hide transect method, a knitting needle was inserted under the hair along each transect to record and remove ticks. All sample bags were also checked for loose ticks before disposal, but none were found. In all cases, a subset of ticks was identified *via* microscopy (Olympus SZ61) to species based on morphological characteristics as given in Lindquist et al. (2016), and specimens archived within the Animal Health Unit’s collection.

5.2.5 Evaluating YWTMP success

Defining what constitutes success in citizen science projects is challenging, but commonly used indices are participant numbers and ongoing commitment to the project over time (Cox et al., 2015; Freitag & Pfeffer, 2013). In addition to the number of hunters engaging (taking hide kits) and actively participating (returning samples), we also considered the level of conformity with hide sample kit instructions as an indicator of successful participant engagement. Submissions were scored based on two components of the kit: 1) size of hide sample submitted; and 2) completeness of information as requested on the sample label. For each kit returned, hide samples were measured (length and width, cm) and sizes were converted to area measurements (cm^2). These measurements were scored according to their closeness to the requested sample size as per the template provided (800 cm^2), with samples between 700 and 900 cm^2 receiving a score of 1, and all others scored as 0. Label information included kill date, species, and sex (each scoring 1 if complete, 0 if blank), and kill location. Localities recorded as point locations as requested were scored as 2; those with descriptive locations that allowed us to later estimate their coordinates were scored as 1; all others received 0. We used the final sum of scores across all categories to assess compliance level for all participants, with a maximum achievable score of 6 indicating a near perfect hide sample size and all information exactly as requested. All statistical analyses were carried out using R statistical software (version 4.1.1, R Core Team, 2021), and locations mapped according to GMS using GIS (QGIS v.3.16.10, QGIS Core Development Team, 2020).

5.3 Results

No species of tick other than *D. albipictus* were found among hide samples from any of the submission methods.

5.3.1 YWTMP engagement and participation

One full moose and one full caribou hide were received for sampling during the 2018 season (Fig.5.2), accounting for approximately 0.1% moose and 0.4% caribou harvested by licensed hunters over this time (Table 5.1, Fig.5.3). Approximately 8.5% of all licensed hunters took a hide sample submission kit for the 2019 season (n=435/5,135), of which approximately 10% were returned with samples (n=44 kits) (Table 5.2). A total of 31 full hides and 48 hide samples (4 partial, no kit) were received over the 2019 season, comprising 53 moose and 25 caribou

(Fig.5.2). Submissions accounted for approximately 7.5% of the total moose and 5.5% of total caribou harvested during the 2019 season, up from an average from 2011-2017 of 0.1% for both moose and caribou respectively (Table 1, Fig.5.3). The 2020 season saw eighteen full hides and 58 hide samples submitted, of which there were 51 moose and 25 caribou. These submissions accounted for approximately 9% of moose and 8.5% of caribou reported to have been killed by licensed hunters during this season (Table 5.1, Fig.5.3).

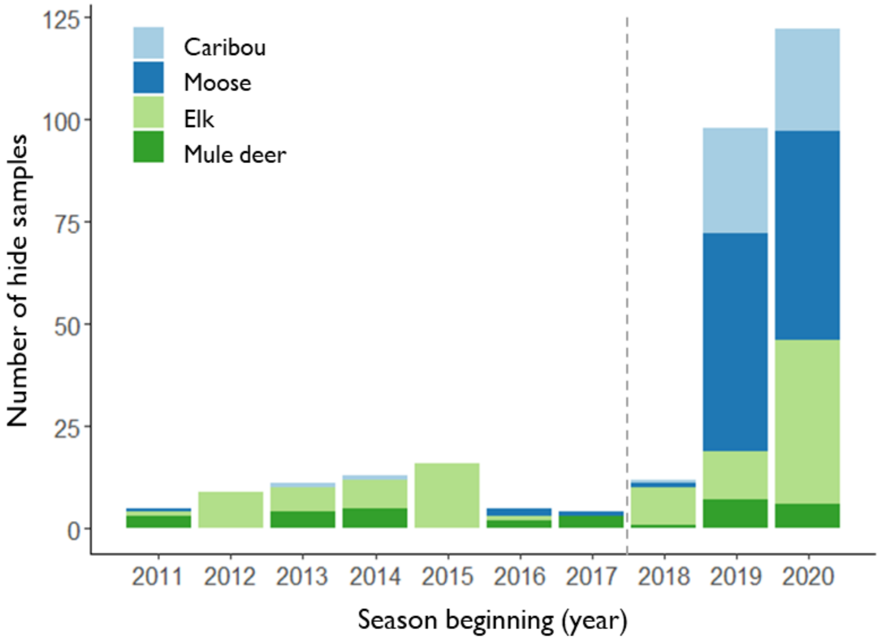


Figure 5.2 Total number of hunted hide and hide sample submissions per annual hunting season (April 1st – March 31st), grouped by species (shaded, stacked bars). The Yukon Winter Tick Monitoring Project scheme first came into effect within the 2018 season, indicated by the grey dotted line. Hide sample submission kits were available from 2019 onwards.

Table 5.1 Number of moose and caribou hides received (2011 – 2020), as a percentage (%) of the total number of animals of each species that were reported as part of the licensed game hunt each season. Values for seasons during which the Yukon Winter Tick Monitoring project was active (2018-2020, shaded) are given in bold.

Harvested species:	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**
Moose	0.2	0	0	0	0	0.3	0.1	**0.3**	**7.5**	**9.0**
Caribou	0	0	0.3	0.4	0	0	0	**0.8**	**5.5**	**8.5**

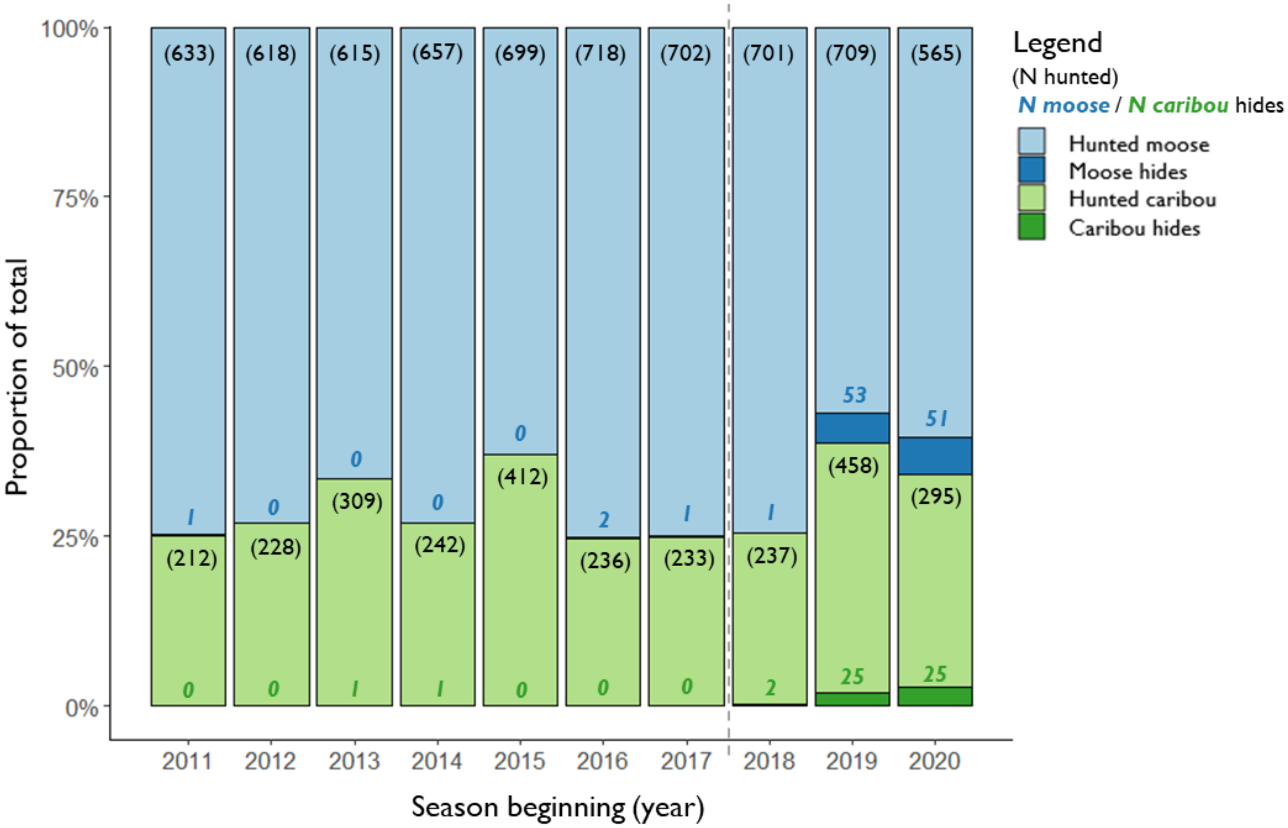


Figure 5.3 Proportion of the number of moose and caribou reported harvested relative to the number of hide samples voluntarily submitted for each species each season, 2011 – 2020. Numbers in parentheses refer to the number of animals reported in the licensed big game harvest each year; bold numbers are the total number of moose *(blue)*, and caribou *(green)* hides received that season. Years that the YWTMP was active are indicated to the right of the grey dotted line.

Table 5.2 Number of hide sample kits distributed and returned relative to licensed hunting statistics for Yukon each season. Note: hide sample kits were not available in 2018. Engagement: *All hunters* = kits distributed / hunting licenses, *With seals* = kits distributed / mean (moose + caribou seals), *Successful harvest* = kits distributed / harvested animals; Participation = kits returned / kits distributed. Licensed hunters must have a seal for the species they intend to harvest that season; not every hunter with a seal will make a kill. Harvested animal numbers as reported in the annual Yukon Hunting Regulations Summary for 2020-2021 [50] and 2021-2022 [51]; number of hunting licenses and seals issued each year provided by Yukon Department of Environment (*unpublished data*).

Number of:	**2019**	**2020**
Hunting licenses	5,135	5,125
Hunting seals issued — Moose	3,957	3,950
Caribou	3,467	3,668
Harvested animals (Moose + Caribou)	1,167	860
Kits distributed	435	617
Kits returned	44	56
Engagement —		
All hunters	*8.5%*	*12.0%*
With seals (average)	*11.7%*	*16.2%*
Successful harvest	*37.3%*	*71.7%*
Participation	*10.1%*	*9.1%*

5.3.2 YWTMP hide sample kit conformity

Variability in completeness scores was similar within hunted species and between years, though generally higher among moose hunters than caribou hunters (caribou: coefficient of variation [CV] 2019 15%, 2020 14.9%; moose: CV 2019 22.2%, 2020 24.9%). In both 2019 and 2020 sampling years, all sample submissions contained complete information on kill date, host species, and sex.

In 2019, the average area of returned hide samples in the sample kits was 805.2 cm^2 (SD +- 250.7 cm), with a mean width of 25 cm (SD +- 4.6 cm) and length of 32.4 cm (SD +- 8.4 cm) compared with the 800 cm^2 20 cm x 40 cm size requested. Twenty-two participants submitted kill locality coordinates, 20 gave detailed locality information that allowed for estimation of a point location, and two participants returned inadequate locality information or none. Five out of 44 (13.6%) submissions fully met exact submission specifications (hide size, location coordinates) receiving a perfect score of six, compared with a mean completeness score over all submissions of 4.5 (range 3:6, SD+- 0.7) (Fig.5.4 (a)).

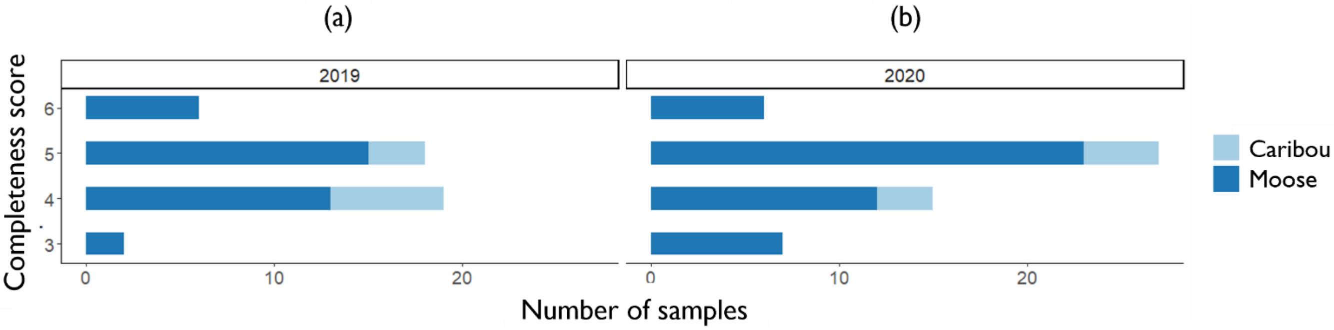


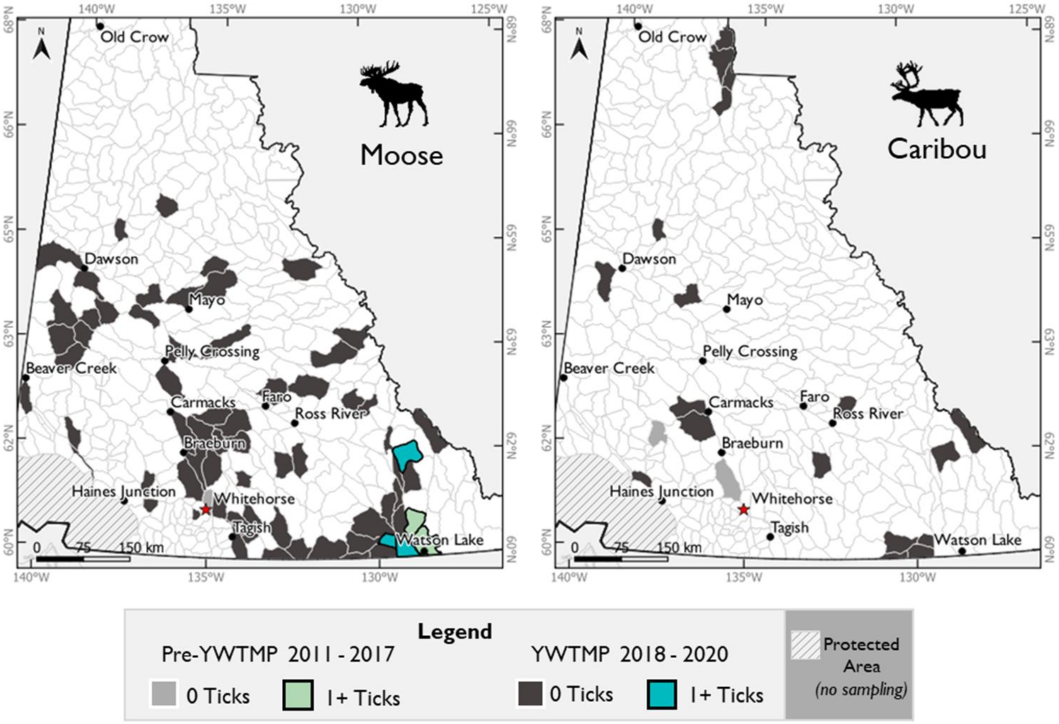
Figure 5.4. Level of hide sample kit conformity for moose and caribou in a) 2019 and **b)** 2020, as measured by completeness scores (see *Section 2.5* for description of scoring method).

In 2020, the average area of hide samples was 669.2 cm (SD+- 204.1 cm), with a mean width of 23.7 (SD +- 4.7 cm) and length of 28.6 cm (SD +- 8.4 cm). One sample was excluded as it was clearly not from the body region (shoulder) requested. Of the remaining 55 samples, locality information in the form of coordinates was submitted by 23 participants, with 19 providing detailed information that allowed for estimation of a point location. Thirteen participants gave locality information that was too vague or missing. On average, samples in 2020 received a score of 4.5 out of six (range: 3:6, SD +- 0.9) with seven of the 56 (12.5%) submissions fully meeting the requested specifications (Fig.5.4(b)).

5.3.3 Distribution of winter ticks on hunted cervids in Yukon

Winter ticks have been recovered from hunted moose, elk, and mule deer hides in Yukon since sampling began in 2011 (Fig.5.5). Prior to the YWTMP scheme, winter ticks had been found on one or more hides submitted from five of ten sampled GMSs, ranging from latitudes 60.1-61.7 °N and longitudes 128.6-137.8 °W. Tick detections on hunted animals were mostly on mandatory submissions of elk and mule deer (n=28 elk, n=12 deer), with few detections on moose (n=2). No ticks were found on hunted caribou prior to the YWTMP scheme. During the first season of the YWTMP in 2018, winter ticks on hunted animals were only found on elk (n=4) and in only three GMSs. During the 2019 hunting season, YWTMP samples were received from 50 GMSs, including 49 subzones that had not previously been sampled, and ranging from latitudes 60.0-67.5 °N and longitudes 128.5-139.9 °W, an increase in the northern limit sampled since 2011 of 480 km for moose and 650 km for caribou. In 2020, the overall geographic range of YWTMP samples was similar to the previous year with latitudes ranging from 60.0- 67.1 °N and longitudes 128.5-139.7 °W within 54 GMSs. Of these, 31 subzones were included that had not previously been sampled. This now brings the cumulative number of GMSs in the territory that have received hide submissions to 87, representing an almost nine-fold increase in sampling locations achieved in two years. Winter ticks were found on hunted moose (n=3) in three of these newly sampled subzones (Fig.5.5(a)), in addition to continued detections from mandatory submissions of hunted elk (n=8) and mule deer (n=5) (Fig.5.5(b)). These new detections indicate winter tick presence on moose that is spatially separated by over 450 km from the managed elk core range.

(a) Voluntary submissions (including YWTMP), 2011–2020



(b) Mandatory submissions, 2011–2020

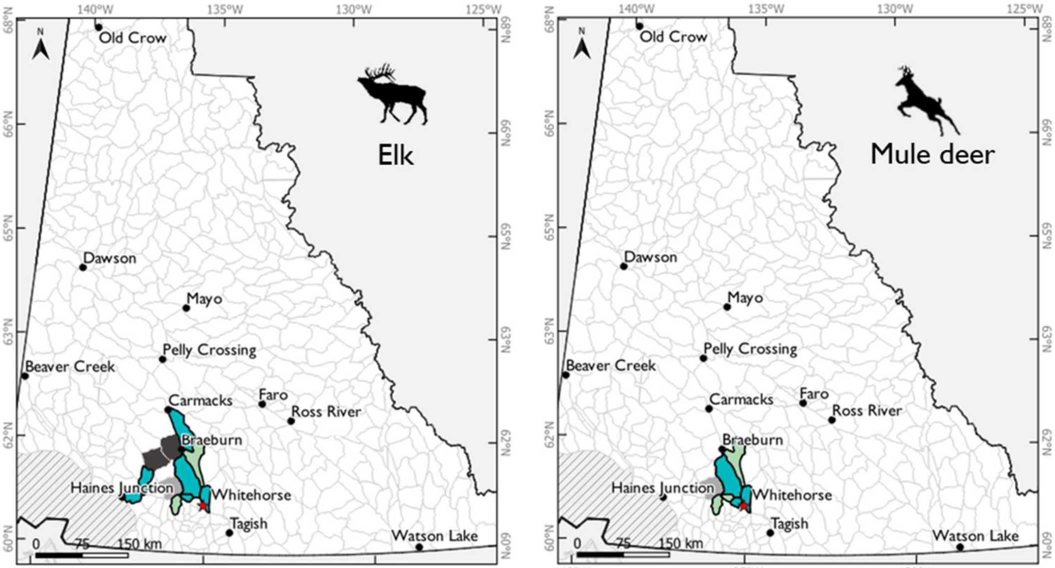


Figure 5.5 Game Management Subzones (GMS) in Yukon where hunted cervid hides have been received through either (a) voluntary, or **(b**) mandatory sources, as dictated by hunted species: moose, caribou, elk, and mule deer. Shading indicates where one or more hide samples have been received per subzone, and their status: winter ticks present, or absent. In cases of multiple samples per subzone per year, shading relates to the most recent time period or positive tick detection. White subzone areas have not been sampled. Note: hides from roadkill, illegally killed, conflict kill, and animals found dead are not included here. For full map of all species see Appendix D.3.

5.4 Discussion

We found that widescale monitoring of winter ticks at the territorial level in Yukon was significantly improved through voluntary citizen science participation by hunters. The highest level of engagement in sample submission occurred when hunters were provided with simplified sampling kits and incentivized returns, compared with voluntary submissions alone. These findings are broadly in agreement with other studies examining participant motivation, where ease of contribution and recognition of its value to ongoing research are considered important factors driving engagement numbers and volunteer retention (Lakomý et al., 2020; Lotfian et al., 2020).

Due to differing aims and objectives across citizen science projects, there are no standardized measures used to define success (Cox et al., 2015; Freitag & Pfeffer, 2013). Our project first and foremost aimed to increase the number and geographic range of sample submissions for monitoring and surveillance of winter ticks on potential hosts, and so in this regard, the program may be considered successful given the sharp increase in hide submissions over its duration. However, the overall spatial range covered by these samples is still inconsistent across large parts of Yukon, and hide numbers represent only a small proportion of the total moose and caribou hunted in the territory each season. Although we saw a significant increase in engagement compared with the previous eight years of the voluntary scheme, the total number of submissions suggests that most licensed hunters (~90%, Table 5.2) did not participate. We did not collect data on hunter demographics during this study that might indicate whether, for example, non-resident hunters may be less likely to engage with sample collection than residents. Similarly, due to anonymity of submissions, we cannot evaluate whether the same hunters are more likely to return hides or samples on an annual basis. It seems likely that, as in other citizen science and volunteer engagement schemes, the majority of participation will be by a passionate few (Lotfian et al., 2020), represented here by the approximately 10% of hunters intending to hunt moose or caribou (with seals) that participated in the program (Table 5.2).

The economic cost of running incentivized public engagement programs may be a potential limitation in the short-term, though they frequently generate data or knowledge that would otherwise take years to accumulate (Tulloch et al., 2013). Although commonly used in marketing surveys, providing incentives to participate in science-based research may still be considered controversial, though concerns are generally levelled at studies for which human participants are themselves the source of data collection, such as in medicine or social sciences (Zutlevics, 2016). Studies on participatory engagement have noted that receipt of some form of recognition for their effort is not an uncommon expectation among volunteers (Lakomý et al., 2020; Martin, 2017) and may serve to improve rates of response (Khadjesari et al., 2011). Based on the limited participation in the first year of the YWTMP in 2018 we observed that incentives alone did not appear to be the sole motivating factor in hunter engagement. Reduced burden, in the form of simplified sample collection, may have played an important role in determining participation. Although the convenience of submitting a smaller hide sample appeared popular, accounting for over half of all submissions in 2019 (n=44/79), more hunters chose to submit full hides for winter tick analysis during that season than in any previous year. Full hides submitted by moose hunters accounted for 20% of all moose submissions (n=11/53), three times the number received voluntarily from 2011-2017 inclusive (Fig.5.3). From caribou hunters, this number was even higher, with 19 full hides submitted for winter tick checks in 2019 (76% of all samples, n=19/25; Fig.5.3), and 15 full hides in 2020 (60% of all samples, n=15/25). It seems likely that both the 2019 and 2020 seasons benefitted from an increased awareness of the YWTMP incentive scheme among hunters since it was first advertised in September 2018 and that time-to-engagement may have been delayed. Recognizing the value of community contributions, particularly in cases where participation requires considerable effort in the collection, transportation, and submission of physical samples, not only serves to partly compensate volunteers for their time and efforts but emphasizes the importance of the data collected as part of a larger research program. These findings suggest that appealing to the extrinsic motivations of voluntary participants may be particularly worthwhile to boost sample receipt over time. In our case, alternative options to immediate physical rewards, such as prize draw entries, could potentially optimize financial costs in future while maintaining engagement (Khadjesari et al., 2011; Martin, 2017).

The impact on data quality is one concern that has been raised with regards to engagement of non-scientists in research projects (Eisen & Eisen, 2021; Kullenberg & Kasperowski, 2016). We found that the overall level of conformity with sampling method and data collection requests, although not perfect, was still high. Size of hide samples had the greatest variability and was likely due to challenges in accurately cutting hides in the field, and only three out of 44 samples were too small to trust transect findings. Obtaining kill locality data is often difficult among hunters who wish to protect the knowledge of prime hunting locations, even for the purposes of scientific research. By way of comparison, a similar incentivized, hunter-based sample scheme run in the neighboring Northwest Territories by Kashivakura and colleagues from 2010 – 2012 also found relatively high levels of missing locality data in their submissions (Kashivakura, 2013). Repeated assertions of data confidentiality and personal anonymity throughout the YWTMP, and association with a known, long-term partner (territorial government) may have assisted in building participant trust in this regard and resulted in the relatively high number of point locations (latitude and longitude, and GPS coordinates) provided. Despite uncertainties in precision, these data are still valuable for ongoing research, as they can be used to assist in determining more focused field sampling locations for off-host studies of larval ticks, for which small spatial scales can be important (Ginsberg et al., 2020; Ogden et al., 2013).

Data from hunted sources may include biases with respect to sample demographics (age, sex), collection time (hunting season) and geographic locations selected (permit hunt areas; hunting exclusion zones) (Bunnefeld et al., 2009; Martínez et al., 2005). Hunting season for moose and caribou in Yukon coincides with the breeding season for both moose and elk and is also the same period that winter tick larvae are actively seeking a host (Machtinger et al., 2021). The large majority of hunted cervids are adult males, with very few female animals hunted and only by First Nations communities as part of traditional practice (Government of Yukon, 2021). In Maine, USA, a survey of winter ticks on moose hunted in October found that male moose may contain both greater abundances and ticks at a higher stage of development than female moose or calves (Yoder et al., 2019). This suggests that although our detections of winter tick presence are unlikely to be negatively affected by biases in selection by sex, there may be limits in the inferences regarding winter tick prevalence at the population level.

Informal discussions throughout the YWTMP scheme with local hunting groups, associations and First Nations residents indicated that to date, hunters have rarely interacted with ticks in Yukon. One of the benefits of the YWTMP program has therefore resulted from outreach with community members, highlighting tick presence in Yukon that was not previously common knowledge for some hunters. Although winter ticks do not frequently bite people, they are generalists and will attach to a wide range of hosts (Lindquist et al., 2016). A growing body of evidence suggests that, in some cases, winter ticks may also be able to vector diseases communicable to humans (Baldridge et al., 2009; Swei et al., 2019). Increasing public awareness of ticks in northern communities, particularly among groups at high risk of contact, including hunters, may serve to improve both tick reporting and commitment to tick bite prevention practices in future (Lewis et al., 2018; Schotthoefer et al., 2020; Seifert et al., 2016).

Overall, the absence of winter ticks detected on samples from above 62°N in Yukon remains consistent with past records, with all anecdotal reports of moose with distinctive, likely winter tick-induced hair loss from below this latitude (Samuel, 1989). However, the inclusion of voluntarily submitted hides of hunted moose and caribou changes our perception of the current spatial distribution of winter ticks on Yukon hosts when compared with mandatory submissions alone. The increased number of hide submissions, while providing a relatively low sample size overall, has revealed three new localities of winter ticks on moose in the Liard region of Yukon, around Watson Lake, thus, beginning to build a clearer picture of winter tick activity in this southeastern region of the territory. Without these additional samples, the only other confirmed detections of winter ticks on hunted hosts and from field studies are in and around the Ibex Valley, approximately 40 km northwest of Whitehorse, in managed elk core habitat (Fig.5.5(b)). The large distance between these areas of detection (~450 km) indicates that it is unlikely that moose have become infected with winter ticks from elk and may represent range expansion of ticks from British Columbia where they are found on moose (Watt, 2021) and caribou (Bondo et al., 2019). Understanding the origin and likely host interactions with ticks in these regions is critical for pinpointing locations of interest for future monitoring of cervid health and provides baseline information from which to assess changes to winter tick distribution in future (Carlson et al., 2017; Kutz et al., 2009).

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Data Availability Statement: Data available in a publicly accessible repository. The data presented in this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.19249064.

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Conflicts of Interest: The authors declare no conflict of interest.

Chapter 6.

Synthesis and conclusions

Understanding the potential for parasitic species to impact novel host communities is, and will continue to be, a critical part of ecology and wildlife epidemiology under global environmental change (Cumming & Vuuren, 2006; Rohr et al., 2011; Dobson et al., 2015). To be successful, researchers need novel methods for overcoming challenges inherent to the collection of host-parasite data (Ryser-Degiorgis, 2013; Cable et al., 2017) and to embrace new means of utilizing existing data where possible (Hoberg et al., 2008; Buhnerkempe et al., 2015; Heberling et al., 2021). The main objectives of this thesis were to provide an epistemological foundation for the distribution, current impacts, and future potential spread of *D. albipictus* in the Yukon, while developing frameworks of practical utility for ongoing data collection, wildlife management, and conservation. Through this work, I have contributed to winter tick-specific knowledge, and provided new insights and frameworks that are widely applicable to the fields of global change biology, invasion ecology, and wildlife health.

6.1 Summary of findings

Across this thesis, I have demonstrated the utility of using multiple methods to build a more comprehensive picture of the winter tick distribution at the global (Chapter 2), regional (Chapter 5) and local (Chapter 3) scales. This research also sheds light on potential factors limiting or enabling winter tick establishment at its northern limit in Yukon (Chapter 4), which is a key component of future research at this range edge.

A baseline distribution of a species' range is a necessary starting point from which to consider changes over time (Fortin et al., 2005; Tingley & Beissinger, 2009). However, for many parasites, including *D. albipictus*, obtaining this information can be challenging and multiple-sources may need to be collated to build a more complete picture of both historical and current boundaries to a species' distribution (Jore et al., 2011; Fletcher Jr. et al., 2019). In Chapter 2, I directly address this gap in knowledge for the winter tick, by bringing together multiple sources of spatially explicit occurrence data to recreate the species' range over the last century. The extensive integrated dataset created as part of this process provides researchers with opportunities to further model the winter tick range, while gaining a better understanding of how the sources of information could impact our view of model outputs. Finally, this work provides a baseline map for managers to understand the historical relationship between winter tick and its geographic range and to better identify and monitor potential spread in new regions.

Understanding host-parasite dynamics ideally requires knowledge of all components of the parasite life cycle, but off-host life stages can be particularly challenging to detect in the field due to practical and logistical difficulties in sampling large and /or remote areas (Stallknecht, 2007; Delahay et al., 2009). In Chapter 3, I used traditional field sampling techniques, stratified across habitat types, to obtain the first larval detections of *D. albipictus* in the Yukon. This work contributes critical information previously missing in the Yukon, by providing a fine-scale dataset of larval winter tick occurrence and abundance, including absences during repeated sampling efforts. I also showed evidence of larval questing behaviour in seemingly sub-optimal environmental conditions that questions existing assumptions regarding physiological tolerances of this species' *in situ*.

The persistence of species at range boundaries has long been of ecological interest in understanding factors that limit distributions at large spatial scales (Odum, 1971; Holt & Keitt, 2005; Oldfather et al., 2020). In Chapter 4, I examined the relationship between potential abiotic variables and the occurrence and abundance of larval *D. albipictus* at its Yukon range edge and determined that some factors may not be as critical as previously assumed. For winter tick occurrence, I found that warmer, drier areas are more likely to contain larvae and, similarly, that these areas may also be related to higher abundances. Contrary to several previous descriptions in the literature (e.g. Drew & Samuel, 1986), I did not find strong support that larval winter tick presence is strongly affected by snow cover at adult female drop-off, observing only weak effects. Not only do these findings indicate that the Yukon has suitable climate and habitat conditions for *D. albipictus* to complete its life cycle this far north, but they highlight key areas for future research into this species physiological tolerances in the field.

Wildlife managers and conservationists face challenges in the detection and ongoing monitoring of host species for parasites of concern and can rarely rely on live capture to obtain adequate samples at a wide spatial scale (Kutz et al., 2009; Cable et al., 2017). Through the Yukon Winter Tick Monitoring Project presented in Chapter 5, I show that well-designed community engagement schemes can successfully increase hunter engagement in the Yukon to obtain a more representative sample of on-host winter tick detections for moose and caribou. In addition to raising awareness of *D. albipictus*, an otherwise novel species to many Yukoners, the research presented in this chapter highlights that there may be at least two, currently geographically isolated, winter tick populations in the territory; on elk and deer in the Ibex Valley, and on moose in the Liard region around Watson Lake (Chapter 5; Chenery et al., 2022).

6.2 Current and future winter tick dynamics in the Yukon

6.2.1 Identifying range expansion

Monitoring changes in the distribution of range expanding species warrants research attention as it not only brings insights into species' dynamics, but the potential causes and consequences of changing ranges (Lindström et al., 2013; McGeoch & Latombe, 2016). The question of whether the winter tick population in the Yukon represents a true range expansion is a complex one. Ultimately, my research has shown that *D. albipictus* has likely been present in the territory for at least 30 years, but most probably longer, based on historical observations (Chapter 2; Chenery et al., 2023). The current distribution off-host appears highly restricted to the Ibex Valley based on recent field sampling efforts (Chapters 3 and 4; Chenery et al., 2020) and detections on hunted hosts, which have similarly been observed below 62°N latitude only (Chapter 5; Chenery et al., 2022). The evidence presented in this thesis suggests that, in the case of the Ibex Valley population of winter tick, this is most likely a translocated population that has arrived *via* jump dispersal on the translocated elk (in broad agreement with the tentative findings of Leo, 2014) and is not currently expanding its range, at least at detectable levels, beyond this locality. However, the detection of *D. albipictus* on several moose hides around Watson Lake could indicate different host-parasite dynamics at the Yukon-British Columbia border (Chapter 5; Chenery et al., 2022) that deserves further attention. Challenges in detecting species at their range edges are common, particularly during early stages of the invasion / spread process, and our inability to detect larval ticks off-host in this region could be due to imperfect detection during sampling at this time, potentially due to low population sizes or highly clustered spatial aggregations (Berec et al., 2014; Guillera-Arroita, 2017). There is the additional possibility that *D. albipictus* may not yet be completing its life cycle with great success in this region, which has very different topographical and environmental conditions compared with what we see in the Ibex Valley population. The Liard region of Yukon is low elevation, with moderate precipitation and long, warm summers that result in thick forest growth (Smith et al., 2004). Although this boreal forest is prime habitat for moose, highly forested areas were absent of *D. albipictus* larvae during field sampling in the territory (Chapters 3 and 4; Chenery et al., 2020), which is consistent with findings in both Alberta (Aalangdong, 1994) and Ontario (Addison et al., 2016). Continued monitoring of winter tick on hunted moose hosts is likely the easiest means of determining the frequency and potentially the on-host abundance of ticks, but identification of local habitat suitable for transmission may present a challenge without more detailed sampling efforts in this region.

6.2.2 Implications for management of winter ticks

Given the widespread distribution of *D. albipictus* throughout North America and its continued detections in the Yukon over several years, it is likely that this species will remain a part of the Yukon ecosystem for the foreseeable future. Other northern regions might also expect that the rapidly changing climate will herald the eventual arrival of winter ticks, as habitats become both more accessible and amenable to them and their hosts. This thesis provides comparable information to that of similar work in the adjacent Northwest Territories (e.g. Kutz et al., 2009; Kashivakura, 2013) and highlights key factors of relevance to the neighbouring state of Alaska, U.S.A., where *D. albipictus* is yet to be detected (Hahn & George, 2019), but could almost certainly establish (Zarnke et al., 1990). Understanding the management strategies for winter tick will, therefore, be of great interest to wildlife managers in all of these northern regions.

It is clear that, given the widespread distribution of potential winter tick hosts in the Yukon and our relatively limited ability to monitor them (Chapter 5; Chenery et al., 2022), topical applications of acaricidal treatments to hosts would be logistically infeasible. Such direct interventions would be potentially suitable for captive or domestic populations (e.g. elk farms, cattle, horses), although the efficacy of compounds used in the past has been variable and few contemporary studies currently exist (e.g. Parish & Rude, 1946; Drummond et al., 1959, 1971; Heath, 1986). The application of fungal pathogens known to increase larval mortality in *D. albipictus* to locations of known tick activity prior to questing (e.g. Sullivan et al., 2020a, 2020b, 2021) could, in theory, be suitable for reducing the winter tick population in the Ibex Valley. However, introducing biological control agents of this nature within a naïve ecosystem could have unforeseen consequences for native plant, fungi, and insect life and requires further research. Similarly, controlled burns of pasture and grassland where *D. albipictus* is known to be active has generally been shown to have inconsistent effects on overall host burdens (Gibson, 2000; Polito et al., 2013). The time of year when burns are most effective is during larval questing (Gibson, 2000), which would not only be disruptive to the cervid rutting period but also presents a considerable wildfire risk at the end of the summer and would need careful management to avoid unintended negative effects on wildlife and habitat. As noted by other authors, if employed, this method may also be considered short-term at best and could result in higher host burdens in the long-term as hosts are attracted to regrowing vegetation, thus increasing tick transmission success over time (Drew et al., 1985). It is worth noting here that the greater frequency of wildfires in sub- and pan-Arctic regions under climate change (McCarty et al., 2021) may therefore help rather than hinder *D. albipictus* populations, with unknown additive effects to hosts and ecosystems.

However, the off-host period of *D. albipictus* may still present the weakest-link in its life cycle in terms of management. The findings presented in Chapters 3 and 4 indicate a high degree of site fidelity among winter tick hosts in the Ibex Valley, which is undoubtedly reinforcing the transmission – drop-off cycle (Figure 1.1) among hosts in this region. Restricting host access over successive years to areas of known high densities of larvae in the fall may assist in reducing individual host burdens over time, as larvae are not transmitted and die. This method would not require penning of host animals as has been attempted by the Government of Yukon in the past (Environment Yukon, 2010) and, given ongoing infestations, likely left active tick populations in the penning zones that were picked up by host animals the following fall. Overall, no single method of management will result in the complete eradication of *D. albipictus* in the Yukon nor neighbouring states and provinces, but ongoing monitoring of both host animals and larval activity in the field, as presented in this thesis, will help inform decision-making in the future.

6.2.3 Implications for management and conservation of cervid hosts

The growing number of threats to northern wildlife under a changing climate are likely to have combined effects on the future of many species (Boonstra et al., 2018; Krebs et al., 2019). The winter tick is just one of the many challenges that moose and caribou in the north now face, with increased thermal stress due to milder and shorter winters (McCann et al., 2013), nutritional stress due to changing patterns of vegetation, phenological mismatches in growth, or competition from newly colonizing deer (Murray et al., 2006; Festa-Bianchet et al., 2011), and increased predation (Barber et al., 2018) all likely contributing to declining populations. The importance of moose and caribou for traditional and cultural hunting practices to northern peoples means that managers must ensure sustainable harvests despite the unpredictable impacts these combined challenges present (Guyot et al., 2006). Understanding the additive or multiplicative effects of *D. albipictus* parasitism in addition to the other climate and anthropogenic disturbances may, therefore, help to disentangle the contribution of this species to deterioration in the health of moose and caribou, and forecast population impacts in the future.

The culling or selective reduction of moose hosts has been posited as a potential management strategy in areas where winter tick epizootics occur (DeBow et al., 2021). Given that host density is often related to parasite transmission potential (Anderson & May, 1978; Van Buskirk et al., 1995), reducing the number of individuals per unit area should in theory reduce tick burden across the host population. However, these strategies do not currently account for the total number of potential hosts in a given area, which, for a generalist parasite like *D. albipictus* will likely play a critical role in parasite transmission in a multi-host system. As previously mentioned, understanding the role and of host community composition, including other cervid hosts such as white-tailed deer and elk, will be of great importance in obtaining accurate estimates of the impact of culling on winter tick-host dynamics on local and regional systems; information that is currently missing for most geographic locations where winter ticks are considered problematic.

6.3 Connotations for parasite research in a changing climate

The detection, monitoring, and mitigation of range-expanding parasites will become increasingly challenging with the progression of global environmental change anticipated over the next few decades (IPBES, 2019). As hosts alter patterns of movement in response to habitat changes, parasite range boundaries are likely to become increasingly blurred, with novel interactions presenting new opportunities for some, and losses for others (Carlson et al., 2017). Overcoming barriers to the collection of parasite data in an uncertain future therefore requires a combination of approaches, including the efficient utilization of existing data (e.g. data integration: Chapter 2; Chenery et al., 2023) and traditional field techniques (e.g. flag sampling: Chapter 3; Chenery et al., 2020), and additionally embracing alternative forms of data acquisition (e.g. citizen science:

Chapter 5; Chenery et al., 2022). Although winter ticks are unlikely to be vectors of disease to humans their impact on the health of wildlife populations, particularly in Northern communities for whom hunting is an important traditional and cultural practice, places this work firmly in a One Health framework. For widescale monitoring and detection of wildlife parasites in particular, strengthening lines of communication between hunters, state/provincial government agencies, and other groups working directly with wild animals or frequenting remote regions (e.g. game processors, taxidermists, wildlife rehabilitators, backcountry guides) presents a promising means of enabling continued data acquisition, as well as community engagement (Poh et al., 2022). The identification of priority areas for long-term sampling efforts in the field will not only enable comparison of presence and abundance data in the future and reduce potential biases that arise from *ad hoc* sampling (Dobson, 2013), but may also provide valuable, local-scale information to inform future site selection. By overcoming these barriers to decision-making, researchers, managers and conservationists stand a better chance of mitigating, if not preventing, the impacts of problematic parasites to both wildlife and human health in the future.

6.4 Future research directions

6.4.1 Incorporating alternative forms of knowledge

Not all parasites will expand their ranges under climate change (Carlson et al., 2017) and, of those that do, not all are likely to have significant, population-level effects on recipient host communities (Delahay et al., 2009). The combined findings presented in this thesis provide a partial baseline from which to continue monitoring (Chapter 3, Chenery et al., 2020; Chapter 5, Chenery et al., 2022) and to assess future changes to the currently observed winter tick range, but gaps remain in the history of this species in the territory. Shifting Baseline Syndrome (SBS), or the acceptance of the current ecological or environmental conditions as the *status quo* in absence of historical reference conditions (Pauly, 1995), has commonly been referenced with respect to once common, but increasingly, rare species (Soga & Gaston, 2018; Jones et al., 2020) or previously invasive species now considered native (Clavero, 2014). However, the absence of descriptions of *D. albipictus* in the Yukon prior to the 1950s (Samuel, 1989) may be due not to the lack of knowledge at a local scale (Local Ecological Knowledge, LEK), but rather the absence of indigenous, Traditional Ecological Knowledge (TEK), that may be captured within the SBS paradigm (Rahman et al., 2019; Peacock et al., 2020). Although First Nations and local hunting communities were consulted throughout the period of fieldwork in the Yukon presented here, it was beyond the scope of this thesis to build the long-term relationships and carefully design the studies needed to meaningfully integrate either TEK or LEK within its framework. A formal program of interviews with First Nations and other local hunters, as has been carried out in the Northwest Territories (Brook et al., 2009; Kutz et al., 2009), would ensure these other forms of knowledge are fully represented within the current records for this species, help to consolidate gaps in our current understanding of the historical winter tick distribution across northern regions, and would also allow expanding and adjusting current programs to account for community priorities and knowledge regarding additional wildlife health concerns.

6.4.2 Addressing biases in winter tick research

One of the greatest challenges in winter tick research is addressing the current imbalance in sampling across host species. Despite being a generalist parasite, *D. albipictus* is frequently studied as if it is a specialist of moose, as I have shown in Chapter 2. Although an understandable research priority in terms of determining the causes and consequences of severe impacts on moose hosts, the absence of data for other cervids leaves a significant gap in knowledge with regards to host-parasite community dynamics. In other host-parasite systems, we know that some species may act as 'decoys' for parasites, deflecting some proportion of possible infections from other hosts that might otherwise be severely affected (Johnson & Thieltges, 2010). Some evidence suggests that deer and elk are better able to reduce winter tick burdens than moose due to effective grooming strategies (Mooring & Samuel, 1998; Normandeau et al., 2022), which raises interesting questions regarding potential winter tick dynamics in multi-host systems that are also of critical importance for host management. The role of host community composition in determining potential dilution or amplification of host infections (Van Buskirk & Ostfeld, 1995; Schmidt & Ostfeld, 2001; Keesing et al., 2006), particularly to moose, therefore, requires greater research emphasis to be placed on obtaining potential contact rates between winter ticks and all available host species. In Chapter 5, I also address imbalances in sampling effort among hosts in the Yukon by engaging local hunters to increase sample size, a targeted strategy that could also be applied in other geographic areas where information regarding winter tick infestation on deer and elk is currently absent. Given the significant crossover in host ranges where *D. albipictus* has been found (Chapter 2; Chenery et al., 2023), and the desire to determine effective management strategies in systems where moose are severely affected (Jones et al., 2019), increasing effective sampling among host species should be considered a priority in future winter tick research. For example, non-invasive monitoring using camera traps has shown promise in surveillance of other wildlife diseases such as mange in wolves (*Canis lupus*) (Oleaga et al., 2011), and foxes (*Vulpes vulpes*) (Carricondo-Sanchez et al., 2017). Images from remote cameras would allow monitoring of host habitat use in areas where *D. albipictus* is known to be active (Chenery et al., *In prep.*) and for some hosts, such as moose and elk, in classifying proportion of hair loss as a proxy for impacts on hosts (Hoy et al., 2021).

Although monitoring host impact is important, research into the off-host life stages of winter tick using traditional techniques as demonstrated in Chapter 3 (Chenery et al., 2020) is currently uncommon within this field. The majority of flagging studies were carried out in the 1980s and 1990s (e. g. Drew & Samuel, 1985; Aalangdong, 1994; Addison et al., 2016), leaving a significant gap in records that makes estimation of the impact of subsequent environmental and climate change on off-host life stages difficult. Detecting and monitoring patterns in larval activity in space and time provides essential information on establishment and survival success of winter ticks that is of direct relevance in estimating current and future host burdens, and should be considered alongside other, on-host monitoring techniques to ensure a full picture of the winter tick life cycle is obtained.

6.5 Conclusions

The way in which we detect, monitor, and record parasite distributions over time and space informs our understanding of their dynamics and can provide insight into fluctuations in population abundances, host burdens, and associated impacts. I have shown that using multiple methods to collect distributional and abundance data for *D. albipictus* at different spatial scales can fill gaps in knowledge for this species that are essential to define both global and regional baselines for monitoring future spread. Engaging non-scientists in the ongoing assessment of winter ticks on hosts is an effective means of increasing sample size across a large geographic area from which to monitor on-host abundances and impacts, but also plays an important role in raising awareness of potential range-expanding or novel parasite species in northern regions among critical stakeholders. Although I conclude that there is a low likelihood that *D. albipictus* is currently spreading in the Yukon from its apparent point of introduction, it is expected that this may change over the coming decades with ongoing warming. The legacy of this research in the form of community engagement will hopefully continue to drive ongoing monitoring that is essential for determining future changes in this problematic species. Overall, the combined findings and new data contributed by this thesis highlight the value of integrative approaches to the study of range-expanding species and illustrates their applicability for biodiversity conservation and wildlife management in a changing climate.

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Appendix A

Supporting information for - Revealing Large-Scale Parasite Ranges: An Integrated Spatio-Temporal Database and Multi-Source Analysis of the Winter Tick, *Dermacentor albipictus.*

Emily S. Chenery, N. Jane Harms, Heather Fenton, Nicholas E. Mandrak, and Péter K. Molnár.

Ecosphere, In press.

Contents:

A.1 Detailed metadata for Winter Tick Occurrence dataset v1.0

Class I - Data set descriptors

A. Data set identity

Title: Revealing large-scale parasite ranges: An integrated spatio-temporal database and multi-source analysis of winter tick.

B. Data set identification code

1. Data are openly accessible on the Figshare repository at the following DOI: 10.6084/m9.figshare.20170952.

2. Two additional supporting files are associated with this dataset, available on the Figshare repository at DOI 10.6084/m9.figshare.20170952:
  a) Full citations list (WTOcc_citations.csv)
  b) Source processing notes (WTOcc_source_notes.xlsx)

C. Data set description

1. Originator(s)

Emily S. Chenery (Department of Physical and Environmental Sciences, University of Toronto Scarborough, 1265 Military Trail, Toronto, Ontario, M1C 1A4), N. Jane Harms (Government of Yukon Department of Environment, Animal Health Unit, 10 Burns Road, Whitehorse, Yukon, Y1A 4Y9), Heather Fenton (Department of Environment and Natural Resources, Government of Northwest Territories, 50102 50 Ave, Yellowknife, NT X1A 2L9, Canada), Nicholas E. Mandrak, Péter K. Molnár (Department of Biological Sciences, University of Toronto Scarborough, 1265 Military Trail, Toronto, Ontario, M1C 1A4, Canada). (emily.chenery@mail.utoronto.ca).

2. Abstract

Concerns that climate warming may drive the spread of parasites into previously unoccupied areas has increased the need for baseline knowledge of their distributional history. For species of wildlife health concern, presence data are often lacking or outdated, thus limiting our ability to assess range change and subsequent host impact. We reconstructed the past and present distribution of the winter tick, *Dermacentor albipictus,* through compilation of a spatio-temporal database to create the first full baseline map of its occurrence throughout its native North American range. The ongoing impacts of winter tick epizootics in moose (*Alces alces*), and

recent mortality events in elk (*Cervus canadensis)* and white-tailed deer (*Odocoileus virginianus*), has led to a resurgence in interest in the future of this problematic parasite in a warming climate. Over 3,400 unique records of winter tick occurrence were compiled from multiple data sources, dating from 1869 to 2020 and spanning from 16.5 to 66.2°N latitude. Both traditional, published sources and natural-history records have been included along with new records from previously unpublished datasets and citizen-science observations to make this a comprehensive occurrence dataset for this species. Along with standardized location information and year of observation, the database includes associated host species and descriptive categorisation of the type and source of each record, providing new opportunities to examine host-parasite interactions in the winter tick system over time and space. In presenting these data, we discuss the potential sampling biases and lacunas in our database records, particularly at the winter tick's northern range edge. We also document changes in the types and sources of winter tick information from past to present, highlighting potential issues that should be considered before using these data in further analyses and when collecting ongoing records. Our database demonstrates that collation and synthesis of records beyond traditional sources can shed light on species distributional history and serve as a useful baseline for prioritizing future research and management decisions.

D. Key words

North America; Distribution map; Ixodid ticks; occurrence data; parasite ranges; georeferenced locations

Class II - Research origin descriptors

A. Overall project description

1. Identity

A multi-source dataset containing the spatio-temporal distribution of the winter tick, *Dermacentor albipictus,* throughout its North American range.

2. Originators

Emily S. Chenery, N. Jane Harms, Heather Fenton, Nicholas E. Mandrak, Péter K. Molnár.

3. Period of study

2019 - 2022

4. Objectives

To provide comprehensive data on *D. albipictus* spatial locations and its hosts over time, and a baseline map of the perceived winter tick range to 2020. Data were collated from the primary literature, grey literature, natural history specimen collections, previously unpublished data sources and citizen science observations. These data are a necessary prerequisite for investigating winter tick relationships with environment, climate and host factors.

5. Abstract

As Class I.C.2.

6. Sources of funding

a. Harms, N.J., Molnár, P. K., Crown Indigenous Relations and Northern Affairs Canada (CIRNAC) Climate Change Preparedness in the North Program (CCPN) grant: Predicting the effects of climate change on winter ticks (*Dermacentor albipictus*) and their hosts in Yukon, Canada. April 2018 to March 2022 (CIRNAC CCPN Agreement #1718-HQ-000103).

B. “Specific subproject” description

1. Site description

Records for the winter tick, *Dermacentor albipictus* (Packard 1869) or one of its synonyms (moose tick, elk tick, *D. nigrolineatus, Ixodes albipictus*) were collected from systematic review of the published literature, and targeted searches and data acquisition via relevant databases, collections, and personal contacts.

2. Experimental design

Data collection attempted to identify and collect the majority of winter tick records across North America from its initial description (1869) to the present day (2020).

3. Research methods

i) Data collection

Primary literature

We searched for published records on winter ticks on ISI Web of Science Core Collection and Scopus, beginning January 2019, and screened them for spatial occurrence information. Because our aim was to capture as broad a set of records that included winter ticks as possible, searches included synonyms and common names in both databases and covered all years available. We searched the title, abstract and keywords (‘TS’ in Web of Science; ‘TITLE-ABS-KEY’ in Scopus) of scientific publications using the terms: "winter tick*" OR "Dermacentor albipictus" OR "Ixodes albipictus" OR "Dermacentor nigrolineatus" OR "moose tick*" OR "elk tick*". Records were compiled to include Scopus’ ‘secondary documents’, which include non-indexed materials such as theses and journals not covered by Scopus’ citation index. All articles were first screened for relevance based on the title and abstract, excluding duplicates and irrelevant materials that were clearly not related to *D. albipictus*.

In all cases, the criteria for data to be included were that the species could reasonably be identified taxonomically as *Dermacentor albipictus* (or a common historical synonym, *Ixodes albipictus* (Packard, 1869) or *D. nigrolineatus* (Ernst & Gladney, 1975)) and a point location and year of collection could be determined from the available information. Records purporting to be *D. albipictus* from mountain goat or sheep hosts in the Rocky Mountain region were excluded, given the potential for them to be misidentified specimens of the recently reinstated species *D. kamshadalus* (Apanaskevich & Barker, 2021). Where a year of collection was not given, the date of publication was used if known, and temporally unidentifiable sources were excluded. Information on the host (species or genus) was recorded where available. Records were available at minimum of county (USA) or federal electoral district (Canada) levels in all states or provinces, so we excluded records whose precision was limited to the level of state or province. However, records for Mexico were far fewer at the equivalent administrative scale (‘municipios’), with many more records only at state level. For this reason, database entries for Mexico include records that are geolocated to state centroid. Given a lack of taxonomic clarity in the southern range, we have extended our mapping of *D. albipictus* beyond individual countries to include its full North American range, but do not include observations south of Mexico.

- **Online searches by State / Province**

Locations at the level of state or province with fewer than three winter tick records spanning three or more years were subjected to an additional, targeted search protocol to incorporate additional sources, such as from grey literature, and otherwise confirm search completion (Table S1).

Searches were conducted using an incognito browser on Google Search Engine, with the terms “winter tick”, “Dermacentor albipictus”, plus the name of the state or province for which data were sparse (e.g., “Idaho”) and examining the first 30 records. Additional materials from this process were screened as per the initial protocol, before being incorporated within the main dataset for coding.

Table A1. Localities subjected to additional search protocol due to low number of records / years recorded.

State / Province	N obs.	N years	Search date	New sources (n)	Sources / notes
Canada					
Quebec	3	3	03-Jul-21	0	No new sources found.
United States of America					
Alabama	3	3	01-Jul-21	2	Durden et al., 1991; Heine et al., 2016
Alaska	0	0	04-Jul-21	0	No new sources found. Note: results of passive tick surveillance in Alaska in 2019 had no observations of *D. albipictus* https://dec.alaska.gov/eh/vet/ticks/tick-results.
Arkansas	1	1	01-Jul-21	2	The Arkansas Tickborne Disease Project, 2017 (https://www.uaex.uada.edu/farm-ranch/special-programs/arkansas-tick-project.aspx); McAllister et al., 2016.
Connecticut	1	1	01-Jul-21	3	Anderson and Magnarelli, 1980; Magnarelli et al., 1986; Main et al., 1981
Delaware	0	0	04-Jul-21	0	No new sources found. Only informal state level reports are available in the form of public health notices, no official detections recorded.
Florida	3	1	01-Jul-21	1	Forrester, 1992
Georgia	1	1	02-Jul-21	1	Wedincamp and Durden, 2016
Hawaii	2	2	04-Jul-21	1	Fullaway, 1959.
Indiana	0	0	04-Jul-21	1	USDA, 1961.
Kansas	3	1	02-Jul-21	1	Peterson, 1995.
Kentucky	7	2	01-Jul-21	2	Lockwood et al., 2018; Slabach et al., 2018
Louisiana	4	1	02-Jul-21	0	No new sources found. Note: emailed Louisiana State Arthropod Museum (curator) 02 Jul 21, who confirmed they do not have any *D. albipictus* in their collection.
Maryland	1	1	02-Jul-21	2	Amerasinghe et al., 1992; Oliver et al., 1999

State / Province	N obs.	N years	Search date	New sources (n)	Sources / notes

Massachusetts	0	0	04-Jul-21	0	No new sources found. Only state level reports were available in the form of checklists - these lacked both the spatial and temporal information required for inclusion.
Nebraska	3	2	03-Jul-21	1	Cortinas & Spomer, 2014
New Hampshire	3	3	03-Jul-21	2	Jones et al., 2019; Powers, 2019
New Jersey	0	0	04-Jul-21	1	Occi et al., 2019
North Dakota	8	2	04-Jul-21	0	No new sources found.
Pennsylvania	20	2	04-Jul-21	3	Baer-Lehman et al., 2012; Farone et al. 2017; Calvente et al., 2020
Rhode Island	0	0	04-Jul-21	2	Hyland and Mathewson 1961; Anderson & Magnarelli, 1983
Virginia	0	0	04-Jul-21	1	Oliver et al., 1999
West Virginia	0	0	04-Jul-21	0	No new sources found. Only anecdotal reports (e.g. West Virginia EPI-LOG newsletter v32(4)p2-3). WV Fish and Wildlife do not list winter ticks on their state wildlife disease page.

Natural history collections and other online sources

Online databases of national museums, and biodiversity records repositories were searched for species names “Dermacentor albipictus”, “Dermacentor nigrolineatus”, “Ixodes albipictus”, and common name “winter tick” (Table S2, below). All data were either downloaded or transcribed into a common spreadsheet format, and point locations checked, converted or obtained as described in *ii) Data extraction and accuracy estimation*, below.

Table A2. Online and natural history collections searched for records of winter tick, *Dermacentor albipictus*, and their status within the Winter Tick Occurrence database v1.0.

Collection name	Access method (URL)	*D. albipictus* records Y/N
Arctos	Online database search (https://arctos.database.museum/)	Y*
Integrated Digitized Biocollections (iDigBio.org)	Online data portal (https://www.idigbio.org/portal/search)	Y*
Global Biodiversity Information Facility (GBIF)	Online data portal (https://www.gbif.org)	Y
Global Mammal Parasite Database (GMPD)	Search of published dataset associated with Stephens et al., (2017). (https://doi.org/10.1002/ecy.1799)	Y
VectorMap	Online data portal (http://vectormap.si.edu)	Y†
Canada		
Canadian National Collection of Insects, Arachnids and Nematodes	Email contact with collection curators	Y
United States of America		
United States National Tick Collection, Georgia Southern University	Email contact with collection curators	Y
National Ecological Observatory Network (NEON)	Search of open data source: Data Product DP1.10093.001 "Ticks sampled using drag cloths" (http://data.neonscience.org)	N
United States National Parasite Collection, Smithsonian Museum of Zoology	Open data downloaded via Zenodo (https://doi.org/10.5281/zenodo.846275)	Y
Illinois Natural History Survey (INHS): Insect Collection Database	Online database (http://inhsinsectcollection.speciesfile.org/InsectCollection.aspx)	Y*

Collection name	Access method (URL)	*D. albipictus* records Y/N
University of Michigan Museum of Zoology, Insect Division Collection	Online database (https://quod.lib.umich.edu/i/insect2ic)	N
Louisiana State Arthropod Museum	Email contact with collection curators	N
Harold W. Manter Laboratory Parasite Collection	Online database (http://hwml.unl.edu/resources/database-68)	Y
	Mexico	
Universidad Nacional Autonoma de Mexico Colección Nacional de Arácnidos	Open data downloaded from government website (https://datos.gob.mx/busca/dataset/coleccion-nacional-de-aracnidos)	N
Universidad Nacional Autonoma de Mexico Colección Nacional de Ácaros	Open data downloaded from government website (https://datos.gob.mx/busca/dataset/coleccion-nacional-de-acaros)	Y

*entries duplicated in entirety by GBIF; removed from dataset during de-duplication process
† all entries removed from dataset during de-duplication process

Citizen Science observations

We included searches of “Dermacentor albipictus” from two online citizen science sources: a Canadian portal specifically for tick submissions - eTick (eTick.ca) – and the global online application iNaturalist (inaturalist.org).

- **eTick**

After creating an online eTick account, photographic records are submitted to the eTick platform by members of the public where they are identified by eTick’s team of experts (eTick.ca, 2021). We used publicly available records from eTick Public Data list to search for “Dermacentor albipictus” on 04 July 2021 (https://www.etick.ca/etickapp/en/ticks/public/list). Locations were extracted based on the locality string provided and comparison with mapped data (see Extraction of spatial data).

Note, at the time of searching, eTick contributions were only able to be submitted for the provinces of Ontario, Québec, Saskatchewan, New Brunswick, and Newfoundland, but at the time of writing (2022), the range has been expanded to include British Columbia, Alberta, Nova Scotia, Prince Edward Island, and Manitoba.

- **iNaturalist**

Members of the public who sign up to iNaturalist can submit photographs to the platform of any form of biodiversity. A first pass identification is computed algorithmically based on the image(s) provided, and a textual reference by the submitter can be included for each observation (iNaturalist, 2021). The geographic location of the observation can be set by the user or will otherwise be determined from the image's metadata. Other members of the iNaturalist community then confirm or suggest alternative identification, with two or more confirmations resulting in a status of 'Research Grade' (iNaturalist.org, 2021). Research Grade observations are also indexed by the Global Biodiversity Information Facility (GBIF) and included in their occurrence datasets (*GBIF*, 2021; iNaturalist.org, 2021).

  - *Winter Tick Observation Network project*

There are few records of ticks that can be confidently identified from photographs. However, the distinctive pattern of winter tick-induced hair loss on hosts has been used for decades as a suitable means of inferring the parasite's presence (Glines, 1983; McLaughlin & Addison, 1986; Mooring & Samuel, 1998). Therefore, we established the 'Winter Tick Observation Network' project on iNaturalist (https://bit.ly/wton2021) specifically to collect images of moose, elk, or other hosts with notable winter tick hair loss, in addition to confirmed identifications of winter tick. We searched observations of wild moose with photographs for signs of winter tick hair loss in months from February to April (the period of maximum observable loss: (McLaughlin & Addison, 1986; Mooring & Samuel, 1998) for all years available until April 2020.

Images for each of the resulting 1,015 recorded observations were assessed by the primary author (EC) for presence of winter tick hair loss that matched patterns shown in the standard Hair Loss Index (HLI) for moose (McLaughlin & Addison, 1986; Mooring & Samuel, 1998). Owing to the qualitative nature of this assessment, only records with distinctive hair loss were included to minimize chances of misclassification. Images were excluded that were not of moose (e.g. scat, tracks), were of poor photographic quality (e.g. where the whole animal could not be viewed clearly), or if locality information for the record was obscured. Because images with historical dates can be uploaded at any time to iNaturalist, thus changing the data available, the search and screening process was completed multiple times between February 2019 and December 2020.

Assessment of 1,060 observations resulted in 82 images of winter tick hair loss on moose. Finally, records for which Creative Commons licencing was not provided by the submitter were excluded; therefore, 64 observations freely available to the public were added to our dataset.

ii) Data extraction and accuracy estimation

Georeferenced data were extracted and accuracy classified in one of three ways, depending on the format provided:

Coordinates provided (in-text, table)

Coordinates given in degrees, minutes, seconds (DMS) were converted to decimal degrees using the Federal Communications Commission Degrees Minutes Seconds to/from Decimal Degrees online tool (https://www.fcc.gov/media/radio/dms-decimal). If necessary, geodetic datum was converted to WGS84 using the National Geodetic Survey's NADCON online conversion tool (https://www.ngs.noaa.gov/cgi-bin/nadcon.prl). For more than 10 individual points, locations were batch converted using GIS (QGIS v3.16.10, QGIS Development Team, 2020).

Unless otherwise stated, if a record came from unpublished scientific research data collected in the field (all dated 2010 or later), the precision was assumed accurate to 0.1 km, which is the approximate precision of most handheld Global Positioning System devices.

Map of point or area-based presence

Maps were saved as .jpeg image files at the highest resolution possible before being read into a GIS program (QGIS v3.16.10, QGIS Development Team, 2020) using the geolocator tool. This tool allows the image to be warped so that distinctive points (locations of administrative boundaries, cities etc) match up with a standard North American projection. Point locations can then be obtained by creating a new layer and manually extracting each point, or by extracting the centroid of the polygon, depending on the data provided in the map. All points were obtained as geodetic datum WGS84 and using the relevant North American projection, dependent on location.

We followed the "point-radius" method for estimating spatial accuracy of all records (Wieczorek et al., 2004). We used the centroid of circular points from an original point map as the location for each coordinate. Locations that were given as polygons (counties, townships, wildlife management areas) were obtained by extracting the centroid of the polygon.

The estimated accuracy was calculated as the radius of a circle, measured from the original point in kilometers, or, if the point had become highly skewed during the reprojection process, half the length of the maximum axis of the polygon. For localities described as areas, we first took the centroids of sites, collection areas, and counties / districts as the point location, and estimated accuracy as half the maximum axis length of the polygon, which provides a radius from the point that fully encompasses the area.

Locality text strings (descriptive locations)

Sources where locality information was given in the form of a text string were geolocated using the Web-based platform GEO-Locate (Rios & Bart, 2021). If there were fewer than 10 location records, the search was conducted using the standard web based client (https://www.geo-locate.org/web/WebGeoref.aspx); grouped record numbers >10 were submitted as batch files (https://www.geo-locate.org/web/WebFileGeoref.aspx). In each case, each locality estimate made by GEO-Locate was checked on Google Earth via the online interface. Records that could not be reliably determined – either given as multiple potential locations or none – were excluded from the winter tick database. Accuracy estimates were given as per GEO-Locate's calculation, or otherwise set based on the number of decimal places estimated to.

Missing or inestimable accuracy

In cases where accuracy could not be determined, an uncertainty estimate of 111 km was used, which is the estimated precision of latitude in decimal degrees to one decimal place, following best practice guidelines for georeferencing (Chapman & Wieczorek, 2006).

iii) Data verification

Each source and associated entries were checked three times during the collation process: first, during the transcription or extraction phase; second when adding into the main database; and for a third time when cross-checking each final database entry and ensuring processing notes were complete.

The resulting raw dataset was inspected and cleaned before it was considered final. Duplicate entries were removed based on identical information in all the following fields: latitude/longitude locations, year, host species, record basis and source type (n=1,871 duplicates removed). We plotted and visually inspected all point data using GIS to identify any anomalous records. Points located in waterbodies were checked for transcription errors against the original source, and if otherwise correct, relocated to the nearest landmass within 10 km.

4. Project personnel

Emily S. Chenery, Nicholas E. Mandrak, Péter K. Molnár.

Class III – Data set status and availability

A. Status

1. Latest update

June 30th, 2022

2. Latest archive date

N/A

3. Data verification

All data were checked twice against the original source; once immediately after initial entry, against original source, and again once the final dataset was complete.

B. Accessibility

1. Storage location and medium

Raw data are stored on servers in the Quantitative Global Change Ecology Lab at the University of Toronto Scarborough, Ontario, Canada.

2. Contact person(s)

Emily Chenery (emily.chenery@mail.utoronto.ca), Department of Physical and Environmental Sciences, University of Toronto Scarborough, Toronto ON M1C 1A4

3. Copyright restrictions

These data are published under a Creative Commons Attribution 4.0 International Public License (https://creativecommons.org/licenses/by/4.0/legalcode).

4. Proprietary restrictions

None

5. Costs

None. We ask that authors using these data cite this paper:

Chenery E.S., N.J. Harms, H. Fenton, N.E. Mandrak, and P.K. Molnár. 2022. Revealing Large-scale Parasite Ranges: An Integrated Spatio-temporal Database and Multi-source Analysis of Winter Tick. Ecosphere.

Class IV – Data structural descriptors

A. Data set file

1. Identity

DataS1 (WTOcc_NAmerica_1869_2020.csv)
CitationsS1 (WTOcc_citations.csv)
SourceNotesS1 (WTOcc_source_notes.xlsx)

2. Size

WTOcc_NAmerica_1869_2020.csv : 3445 lines / 18 columns, 1.29Mb
WTOcc_citations.csv: 134 lines / 2 columns, 32.5 Kb
WTOcc_source_notes.xlsx: 110 lines / 11 columns, 37.6 Kb

3. Format and storage mode

All data files are available as comma-separated values (.csv), with UTF-8 encoding. Supplementary notes on how each source was processed is available as a Microsoft Excel file (.xlsx).

4. Header information

Variable details have been listed under Section S1 “Variable information”.

5. Alphanumeric attributes

Mixed

6. Special characters / fields

N/A

7. Authentication procedures

N/A

B. Variable definitions

Variables for Winter_tick_occurrence_North_America_1869-2020_Data.csv were collected and verified as described under Class II.B.3. Definitions for each are given in Section S1.

C. Further acknowledgments

We would especially like to thank the following people for their assistance in acquiring winter tick occurrence data: C. Jones, K. Watt (British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development), L. Garrett (Ohio Department of Health), R. Pesapane (Ohio State University), L. Trute, P. Gelok, L. Maringh, E. Kessler (Ontario Ministry of Natural Resources and Forestry), C. Alexander, N. Fortin (Vermont Fish and Wildlife), F. Beaulieu, W. Knee (Canadian National Collection of Insects, Arachnids and Nematodes), L. Beati (US National Tick Collection), S. Gardner and G. Racz (Harold W. Manter Laboratory Parasite Collection). We also wish to thank E. Lindquist and T. Galloway for making providing the original data used to create Map 3 in Lindquist et al., 2018.

D. Additional information

Section S2 Geographic locations represented in the Winter Tick Occurrence database v1.0

Section S3 Genus, common name and species name for host animals included in the Winter Tick Occurrence database v1.0

E. Sources cited

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Section S1: Variable descriptions in the Winter Tick Occurrence database v1.0

			DATA TYPE						DATA FORMAT		
Col. num	**Variable name**	**Definition**	**Unit**	**Storage type**	**Categories / Codes**	**Range min.**	**Range max.**	**Missing values**	**Length**	**Decimal places**	**Remarks**
1	recID	Unique identifier in database	hexadecimal string	character	-	-	-	(none)	up to 9 characters	-	
2	spec	Scientific name of species	qualitative	character	-	-	-	(none)	22 characters	-	All records are for *Dermacentor albipictus.*
3	year	Year of observation	whole number	integer	-	1869	2020	(none)	4 numbers	-	Exact year of observation is if given by original source, otherwise publication date (literature source) or identification date (museum / collections specimen).
4	long	Longitude (Datum WGS84)	decimal degrees W	integer	-	-157.8	-61.9	(none)	up to 8 characters	1-3	
5	lat	Latitude (Datum WGS84)	decimal degrees N	integer	-	16.5	66.2	(none)	up to 8 characters	1-3	
6	accKm	Estimated spatial accuracy of lat/long coordinates	kilometers	integer	-	0.008	500	NA	up to 6 characters	0 - 3	Point accuracy estimate, if not provided with original source, is given based on datum type (*see also* **datType**): *"Georeferenced map"* : Point provided is centroid of location marker. [Circular area] - accuracy is approximately +/- the radius of the point location marked [Irregular shaped area (e.g. county/ township)] - accuracy is approximately +/- half the maximum length of shape's longest axis. *"Literature", "Museum", "Citizen Science", "Private"* : Point location is assumed accurate to the number of decimal places provided. .001 = 0.1km, .01 = 1.1km, .1 = 11.1km, 0 = 111km
7	country	Country of observation	qualitative	character	Canada, United States of America, Mexico	-	-	(none)	up to 24 characters	-	
8	stateProv	U.S. or Mexican *state* , or Canadian *province* of observation	qualitative	character	(see List A)	-	-	(none)	up to 21 characters	-	
9	countyDistr	U.S. *county* or Canadian *Federal electoral district* of	qualitative	character	(see List A)	-	-	NA	up to 50 characters	-	
10	hostCommon	English common name for host species	qualitative	character	(see List B)	-	-	NA	up to 26 characters	-	Names given as valid taxonomy November 2021 on the Integrated Taxonomic Information System (www.itis.gov).

			DATA TYPE						DATA FORMAT		
Col. num	**Variable name**	**Definition**	**Unit**	**Storage type**	**Categories / Codes**	**Range min.**	**Range max.**	**Missing values**	**Length**	**Decimal places**	**Remarks**
11	hostGen	Scientific name of host genus	qualitative	character	(see List B)	-	-	NA	up to 10 characters	-	Names given as valid taxonomy November 2021 on the Integrated Taxonomic Information System (www.itis.gov).
12	hostSpec	Scientific name of host species	qualitative	character	(see List B)	-	-	NA	up to 27 characters	-	Names given as valid taxonomy November 2021 on the Integrated Taxonomic Information System (www.itis.gov).
13	recBasis	Basis of record	qualitative	character	hairloss hide specimen other	-	-	NA	up to 8 characters	-	Category definitions: *"Hairloss"* visual assessment of the pelage of a host animal, indicating loss or damage, usually on live host. Either observer report, camera trap or other photographic evidence. *"Hide"* visual assessment of the hide/pelt of a live or dead animal resulting in winter tick observation. May be full animal or just the skin. *"Specimen"* preserved or recorded physical specimens of winter tick (all life stages). May be natural history museum (ID number given in **sourceID**) or field data record. *"Other"* Photographic, anecdotal or other recorded observation of winter tick occurrence.
14	datType	Datum type	qualitative	character	citizen science, dataset, georeferenced lit, georeferenced map, museum	-	-	(none)	up to 17 characters	-	Describes the methods used to collect each record for this dataset compilation (see also Processing Notes for individual source details). *"citizen science"* photographic observations provided by members of the public (e.g. via *"dataset"* Data provided from a previously compiled published or unpublished source (e.g. GBIF, field data from a researcher or government, published dataset) *"georeferenced lit / map"* geolocated text string obtained from literary source referecne (lit) using web application GEOLocate (www.geo-locate.org); scanned or photograph images of maps (map) containing winter tick point locations processed using GIS to extract location data from each point. *"museum"* catalogue records. May be from digitized collections from museum / specimen collection databases, or transcribed from digitized collection records.

			DATA TYPE						DATA FORMAT		
Col. num	**Variable name**	**Definition**	**Unit**	**Storage type**	**Categories / Codes**	**Range min.**	**Range max.**	**Missing values**	**Length**	**Decimal places**	**Remarks**
15	source	Citation or reference code of record	qualitative	character		-	-	(none)	up to 27 characters	-	Describes where record was obtained for this data compilation. E.g. shortened name of database, in-line citation of paper. (see also Processing Notes for details of individual sources):
16	sourceID	Original source unique identification number or code	qualitative	character		-	-	(none)	up to 22 characters	-	Original source unique identification number, or location of in-text citation. Described as follows: *"georeferenced map/lit"* Figure, table or page number where the record location was obtained *"museum", "citizen science", "other" C* atalogue or specimen number, GBIF / iNaturalist identification number for the individual record
17	sourceType	Type of informational source	qualitative	character	book, citizen science, grey literature, journal, published data, specimen collection, thesis, unpublished data, webpage	-	-	(none)	up to 19 characters	-	Describes the type of informational source each record was obtained from, classified as follows: *"book"* published book. *"citizen science"* iNaturalist.ca or eTick.ca record submitted by a member of the public and released as part of each citizen science initiative. *"grey literature"* government document, technical report or similar, not otherwise published at the time of Winter Tick Occurrence database compilation. *"journal"* peer-reviewed publication *"published data"* data from a peer-reviewed publication or published dataset *"specimen collection"* from collection data accompanying natural history specimen or special collection materials. *"thesis"* academic thesis (Undergraduate, Master's, Doctoral) *"unpublished data"* field data from an academic or government institution, not published at the time at which Winter Tick Occurrence dataset was compiled. *"webpage"* online only record of institutional data, not published elsewhere.
18	recRef	Bibliographic reference	qualitative	character		-	-	(none)	up to 500 characters	-	Full bibliographic reference for the record, or contact name and details if datType *dataset*

Section S2: Geographic locations represented in the Winter Tick Occurrence database v1.0

- **Country**
  - **State** (*U.S., Mexico*) / **Province** (*Canada*)
    - County (U.S.) / Federal electoral district (Canada)

Canada

- **Alberta**
  - Banff--Airdrie
  - Battle River--Crowfoot
  - Foothills
  - Fort McMurray--Cold Lake
  - Grande Prairie--Mackenzie
  - Lakeland
  - Livingstone--Macleod
  - Medicine Hat--Cardston--Warner
  - Peace River--Westlock
  - Red Deer -- Mountain View
  - Red Deer--Lacombe
  - Yellowhead
- **British Columbia**
  - Cariboo--Prince George
  - Central Okanagan--Similkameen--Nicola
  - Chilliwack--Hope
  - Courtenay--Alberni
  - Cowichan--Malahat--Langford
  - Esquimalt--Saanich--Sooke
  - Kamloops--Thompson--Cariboo
  - Kootenay--Columbia
  - Mission--Matsqui--Fraser Canyon
  - Nanaimo--Ladysmith
  - Nickel Belt
  - North Island--Powell River
  - North Okanagan--Shuswap
  - Prince George--Peace River--Northern Rockies
  - Skagit
  - Skeena--Bulkley Valley
  - South Okanagan--West Kootenay
  - Vancouver Granville
  - Victoria
  - West Vancouver--Sunshine Coast--Sea to Sky Country
- **Manitoba**
  - Brandon--Souris
  - Churchill--Keewatinook Aski
  - Dauphin--Swan River--Neepawa
  - Portage--Lisgar
  - Provencher
  - Selkirk--Interlake--Eastman
  - Winnipeg Centre
- **New Brunswick**
  - Acadie--Bathurst
  - Beauséjour
  - Fredericton
  - Miramichi--Grand Lake
  - Moncton--Riverview--Dieppe
  - New Brunswick Southwest
  - Tobique--Mactaquac
- **Northwest Territories**
  - Northwest Territories
- **Nova Scotia**
  - Central Nova
  - Halifax
  - Halifax West
  - Kings—Hants
  - NA
  - Sackville--Preston—Chezzetcook
  - West Nova
- **Ontario**
  - Algoma--Manitoulin—Kapuskasing

- Carleton
- Don Valley West
- Durham
- Glengarry--Prescott—Russell
- Haliburton--Kawartha Lakes—Brock
- Halton
- Kenora
- Lanark--Frontenac—Kingston
- Nipissing--Timiskaming
- Ottawa Centre
- Parry Sound--Muskoka
- Peterborough--Kawartha
- Renfrew--Nipissing--Pembroke
- Sault Ste. Marie
- Thunder Bay--Rainy River
- Timmins--James Bay

Quebec

- Argenteuil--La Petite-Nation
- Capitale-Nationale
- Estrie
- Joliette
- Pontneuf--Jacques-Cartier
- Rimouski-Neigette--Témiscouata--Les Basques

Saskatchewan

- Battlefords--Lloydminster
- Carlton Trail--Eagle Creek
- Cypress Hills--Grasslands
- Desnethé--Missinippi--Churchill River
- Moose Jaw--Lake Centre--Lanigan
- Prince Albert
- Regina--Qu'Appelle
- Regina--Wascana
- Souris--Moose Mountain
- Yorkton--Melville

Yukon

- Yukon

Mexico

Note: Most records found for Mexico did not have *municipios* associated with each state and therefore have missing data (“NA”).

Aguascalientes

- NA

Baja California

- NA

Campeche

- NA

Chiapas

- NA

Chihuahua

- Aldama
- Buenaventura
- Ignacio Zaragoza
- Madera
- NA
- Namiquipa

Coahuila

- NA

Distrito Federal

- NA

Durango

- NA

Estado de Mexico

- NA

Guanajuato

- NA

Guerrero

- NA

Hidalgo

- NA

Jalisco

- NA

Michoacan

- NA

Nayarit

- NA

Nuevo Leon

- Doctor Arroyo

Puebla

- NA

Queretaro

- NA

Quintana Roo

- NA

San Luis Potosi

- NA

Sonora
NA
Tabasco
NA
Tamaulipas
NA
Veracruz
NA
Yucatan
NA
Zacatecas
NA

United States of America

- **Alabama**
  - Barbour
  - Bullock
  - Butler
  - Chambers
  - Clarke
  - Dallas
  - Elmore
  - Lee
  - Macon
  - Talladega
  - Tallapoosa
  - Wilcox
- **Arizona**
  - Apache
  - Cochise
  - Coconino
  - Maricopa
  - Navajo
  - Pima
  - Santa Cruz
- **Arkansas**
  - Arkansas
  - Crawford
  - Garland
  - Izard
  - Polk
  - Washington
  - Yell
- **California**
  - Alameda
  - Contra Costa
  - El Dorado
  - Fresno
  - Humboldt
  - Inyo
  - Lassen
  - Los Angeles
  - Madera
  - Marin
  - Mendocino
  - Modoc
  - Monterey
  - Napa
  - Nevada
  - Placer
  - San Benito
  - San Bernadino
  - San Diego
  - San Mateo
  - Santa Barbara
  - Siskiyou
  - Solano
  - Sonoma
  - Yuba
- **Colorado**
  - Boulder
  - Denver
  - Douglas
  - El Paso
  - Garfield
  - Gilpin
  - Gunnison
  - Jackson
  - Larimer
  - Mesa
  - Moffat
  - Park
  - Rio Blanco
- **Connecticut**
  - Fairfield
  - Hartford
  - Middlesex
  - New Haven
  - New London
  - Tolland
  - Windham
- **Florida**
  - Alachua
  - Calhoun
  - Citrus
  - Clay
  - Jackson
  - Lake
  - Marion
  - Volusia
- **Georgia**
  - Bryan
  - Bulloch
  - Emanuel
  - Jefferson
  - Johnson
  - Washington
- **Hawaii**
  - Honolulu
- **Idaho**
  - Ada
  - Adams
  - Bannock
  - Boise
  - Bonneville
  - Camas
  - Clearwater
  - Custer
  - Idaho
  - Latah
  - Lemhi
  - Lewis
  - Nez Perce
  - Oneida
  - Twin Falls
  - Valley
- **Illinois**
  - Adams
  - Alexander
  - Brown
  - Bureau
  - Calhoun
  - Carroll
  - Cass
  - Champaign
  - Clark
  - Clay
  - Coles
  - Franklin
  - Fulton
  - Gallatin
  - Grundy
  - Hancock
  - Hardin
  - Henderson
  - Henry
  - Jackson
  - Jefferson
  - Jersey
  - Johnson
  - Kane
  - Knox
  - LaSalle
  - Macoupin
  - Madison
  - Marshall
  - Mason
  - Massac
  - McDonough
  - Menard
  - Mercer
  - Morgan
  - Ogle
  - Peoria
  - Perry
  - Pike
  - Pope
  - Pulaski
  - Putnam
  - Randolph
  - Saline
  - Sangamon

- Schuyler
- Scott
- Tazewell
- Union
- Warren
- Washington
- Williamson
- Winnebago
- Woodford

Indiana
- Miami
- Perry

Iowa
- Allamakee
- Black Hawk
- Decatur
- Delaware
- Des Moines
- Dubuque
- Fremont
- Henry
- Jefferson
- Johnson
- Keokuk
- Page
- Polk
- Ringgold
- Van Buren
- Wapello
- Washington

Kansas
- Allen
- Anderson
- Atchison
- Barber
- Barton
- Butler
- Chautauqua
- Clark
- Coffey
- Comanche
- Cowley
- Crawford
- Elk
- Ellsworth
- Ford
- Greenwood
- Jefferson
- Johnson
- Leavenworth
- Linn
- Lyon
- Marshall
- Miami
- Morris
- Nemaha
- Neosho
- Pottawatomie
- Pratt
- Rawlins
- Reno
- Riley
- Sedgwick
- Stafford
- Woodson

Kentucky
- Bath
- Bell
- Boone
- Bourbon
- Breathitt
- Butler
- Calloway
- Carlisle
- Carter
- Casey
- Fayette
- Fleming
- Franklin
- Green
- Greenup
- Harrison
- Hart
- Henderson
- Henry
- Hopkins
- Jackson
- Jefferson
- Jessamine
- Knott
- Lawrence
- Lewis
- Livingston
- Logan
- Madison
- Marion
- Martin
- Menifee
- Montgomery
- Morgan
- Muhlenberg
- Nicholas
- Ohio
- Owen
- Perry
- Robertson
- Rowan
- Russell
- Scott
- Shelby
- Taylor
- Todd
- Trigg
- Webster
- Whitley
- Woodford

Louisiana
- Concordia
- Madison
- Tensas

Maine
- Androscoggin
- Aroostook
- Cumberland
- Hancock
- Kennebec
- Penobscot
- Piscataquis
- Somerset

Maryland
- Allegany
- Anne Arundel
- Baltimore
- Calvert
- Caroline
- Carroll
- Cecil
- Charles
- Dorchester
- Frederick
- Garrett
- Harford
- Howard
- Kent
- Montgomery
- Prince George's
- Queen Anne's
- Somerset
- St. Mary's
- Talbot
- Washington
- Wicomico
- Worcester

Michigan
- Alcona
- Alpena
- Arenac
- Baraga
- Charlevoix
- Cheboygan

- Clare
- Clinton
- Crawford
- Delta
- Dickinson
- Eaton
- Emmet
- Gladwin
- Houghton
- Iosco
- Iron
- Kalkaska
- Keeweenaw
- Keweenaw
- Mackinac
- Marquette
- Menominee
- Missaukee
- Montmorency
- Ogemaw
- Ontonagon
- Osceola
- Oscoda
- Otsego
- Presque Isle
- Roscommon
- Schoolcraft

Minnesota
- Aitkin
- Beltrami
- Cass
- Clearwater
- Cook
- Lake
- Morrison
- Pine
- St. Louis
- Wilkin

Mississippi
- Attala
- Calhoun
- Carroll
- Claiborne
- Franklin
- Hinds
- Issaquena
- Jefferson
- Leake
- Lee
- Perry
- Warren
- Washington
- Webster

Missouri
- Putnam
- Ripley
- Stoddard
- Taney

Montana
- Beaverhead
- Broadwater
- Cascade
- Flathead
- Golden Valley
- Granite
- Lake
- Lewis and Clark
- Lincoln
- Madison
- Meagher
- Mineral
- Missoula
- Park
- Pondera
- Powder River
- Ravalli
- Rosebud
- Sanders
- Teton
- Wibaux

Nebraska
- Banner
- Cass
- Cherry
- Custer
- Dawes
- Dawson
- Douglas
- Lancaster
- Lincoln
- Morrill
- Nemaha
- Perkins
- Red Willow
- Richardson
- Sarpy
- Scotts Bluff
- Sheridan
- Sioux
- Washington

Nevada
- Clark
- Lander
- Nye

New Hampshire
- Carroll
- Coos
- Grafton
- Hillsborough
- Merrimack
- Sullivan

New Jersey
- Burlington
- Monmouth

New Mexico
- Colfax
- Doña Ana
- Grant
- Hidalgo
- Lincoln
- Otero
- San Miguel
- Sandoval
- Socorro
- Valencia

New York
- Essex
- Hamilton
- Livingston
- Southern Tier
- St. Lawrence
- Warren
- Washington

North Carolina
- Craven
- Cumberland
- Guilford
- Haywood
- Madison

North Dakota
- Benson
- Billings
- Burke
- McHenry
- McKenzie
- Richland
- Stark

Ohio
- Adams
- Athens
- Belmont
- Carroll
- Clermont
- Columbiana
- Coshocton
- Gallia
- Geauga
- Guernsey
- Hocking
- Jackson

Jefferson
Knox
Licking
Lorain
Meigs
Monroe
Morrow
Muskingum
Perry
Scioto
Summit
Vinton
Washington

Oklahoma

Adair
Atoka
Blaine
Bryan
Canadian
Carter
Cherokee
Choctaw
Comanche
Creek
Delaware
Dewey
Garfield
Garvin
Harper
Haskell
Johnston
Latimer
Le Flore
Major
Marshall
Mayes
McCurtain
Murray
Muskogee
Noble
Oklahoma
Okmulgee
Osage
Pawnee
Payne
Pittsburg
Pontotoc
Pushmataha
Sequoyah
Stephens

Oregon

Baker
Benton
Clatsop
Coos
Crook
Curry
Douglas
Grant
Harney
Jackson
Jefferson
Josephine
Klamath
Lake
Malheur
Morrow
Tillamook
Umatilla
Union
Wallowa
Wasco
Wheeler

Pennsylvania

Berks
Bradford
Cameron
Centre
Clearfield
Clinton
Dauphin
Elk
Erie
Franklin
Huntingdon
Indiana
Luzerne
Lycoming
Montour
Northumberland
Pike
Potter
Snyder
Union
Venango

Rhode Island

Newport

South Carolina

Chester
Horry
Sumter

South Dakota

Brule
Custer
Fall River
Lawrence
Pennington

Tennessee

Anderson
Bledsoe
Campbell
Cheatham
Claiborne
Cumberland
Davidson
DeKalb
Dickson
Dyer
Fentress
Hamilton
Henry
Houston
Humphreys
Jackson
Knox
Lawrence
Loudon
Marion
Marshall
Maury
McMinn
Monroe
Montgomery
Overton
Rhea
Roane
Scott
Sequatchie
Stewart
Sumner
Van Buren
Wayne
Weakley
White

Texas

Anderson
Angelina
Armstrong
Bandera
Bexar
Blanco
Bosque
Brazos
Brewster
Brown
Burleson
Burnet
Caldwell
Cameron
Chambers

- Comal
- Concho
- Coryell
- Dallas
- Dimmit
- Eastland
- Edwards
- El Paso
- Erath
- Freestone
- Gillespie
- Goliad
- Grimes
- Guadalupe
- Harris
- Hays
- Henderson
- Hidalgo
- Hudspeth
- Jack
- Jeff Davis
- Johnson
- Kendall
- Kerr
- Kimble
- Kinney
- La Salle
- Lampasas
- Llano
- Mason
- McCulloch
- Menard
- Nacogdoches
- Palo Pinto
- Panola
- Pecos
- Polk
- Presidio
- Real
- Robertson
- San Saba
- Schleicher
- Sutton
- Tarrant
- Taylor
- Terrell
- Tom Green
- Travis
- Tyler
- Uvalde
- Val Verde
- Webb
- Williamson
- Wilson

Utah

- Box Elder
- Cache
- Daggett
- Grand
- Iron
- Juab
- Millard
- Salt Lake
- San Juan
- Sanpete
- Tooele
- Uintah
- Utah
- Wasatch

Vermont

- Addison
- Bennington
- Caledonia
- Chittenden
- Essex
- Franklin
- Lamoille
- Orange
- Orleans
- Rutland
- Washington
- Windham
- Windsor

Virginia

- Caroline
- Fairfax

Washington

- Adams
- Asotin
- Chelan
- Clallam
- Douglas
- Ferry
- Garfield
- Grant
- Grays Harbor
- Jefferson
- Kittitas
- Lewis
- Lincoln
- Okanogan
- Pend Oreille
- San Juan
- Spokane
- Stevens
- Thurston
- Whitman

Wisconsin

- Ashland
- Barron
- Bayfield
- Columbia
- Fond du Lac
- Grant
- Iowa
- Juneau
- La Crosse
- Marathon
- Marinette
- Oneida
- Price
- Rusk
- Sawyer
- Shawano
- Washburn

Wyoming

- Albany
- Big Horn
- Carbon
- Converse
- Fremont
- Laramie
- Park
- Platte
- Sublette
- Teton

Section S3: Genus, common name and species name for host animals included in the Winter Tick Occurrence database v1.0

- **Genus**
  - **English common name**
    - *Scientific name (species if known)*

- **Alces**
  - **Moose**
    - *Alces alces*
    - *Alces americanus*
    - *Alces americanus americanus*
- **Ammotragus**
  - **Barbary sheep**
    - *Ammotragus lervia*
- **Antilocapra**
  - **Pronghorn**
    - *Antilocapra americana*
- **Antilope**
  - **Blackbuck**
    - *Antilope cervicapra*
- **Axis**
  - **Chital**
    - *Axis axis*
- **Bison**
  - **Bison**
    - *Bison bison*
- **Bos**
  - **Cattle**
    - *Bos taurus*
- **Canis**
  - **Domestic dog**
    - *Canis familiaris*
  - **Wolf**
    - *Canis lupus*
- **Cervus**
  - **Elk**
    - *Cervus elaphus*
    - *Cervus elaphus canadensis*
  - **Sika deer**
    - *Cervus nippon*
- **Dama**
  - **Fallow deer**
    - *Dama dama*
- **Equus**
  - **Donkey**
    - *Equus asinus*
  - **Horse**
    - *Equus caballus*
  - **Mule**
    - *Equus mulus*
- **Felis**
  - **Wild cat**
    - *Felis silvestris*
- **Homo**
  - **Human**
    - *Homo sapiens*
- **Liomys**
  - **Mexican spiny pocket mouse**
    - *Liomys irroratus*
- **Marmota**
  - **Marmot**
    - *Marmota*
- **Mazama**
  - **Red brocket deer**
    - *Mazama americana*
- **Neovision**
  - **American mink**
    - *Mustela vison*
- **Odocoileus**

Mule deer
Odocoileus hemionus
White-tailed deer
Odocoileus virginianus

Oreamnos

Rocky Mountain goat
Oreamnos americanus

Ovis

Bighorn sheep
Ovis canadensis

Peromyscus

Brush mouse
Peromyscus boylii
Deer mouse
Peromyscus maniculatus

Rangifer

Caribou
Rangifer tarandus
Woodland caribou
Rangifer tarandus caribou

Sus

Feral pig
Sus scrofa

Ursus

Bear
Ursus
Black bear
Ursus americanus

Vulpes

Red fox
Vulpes fulva

A.2 Supplementary figures accompanying Chenery et al., 2023

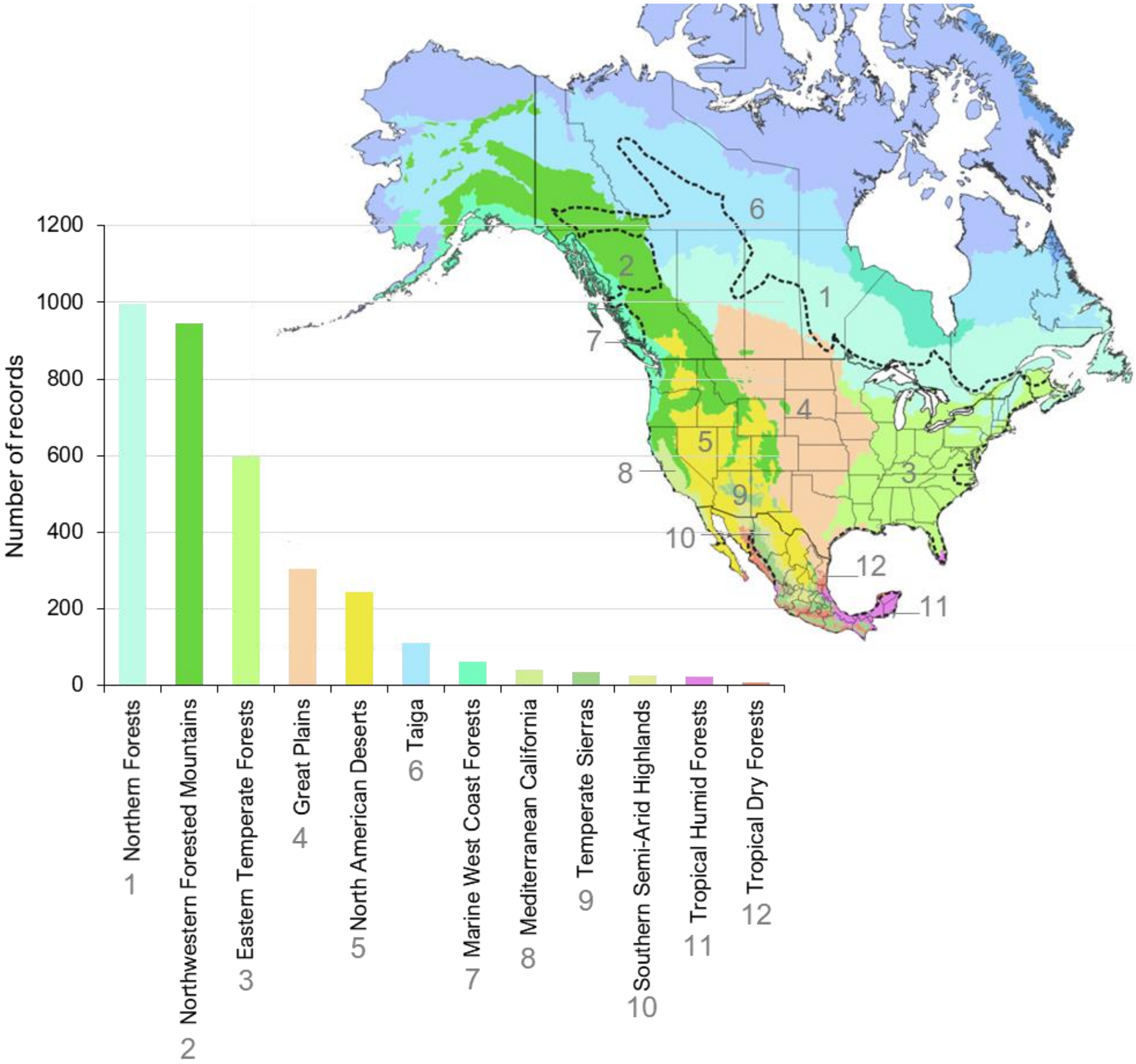

Figure A1. Number of records for *D. albipictus* in the winter tick occurrence dataset per ecoregion (bars). Terrestrial level 1 ecoregions (*inset, shaded; numbered*) coarsely represent all major habitat groups and associated climatic regions, except Arctic tundra, across North America (Commission for Environmental Cooperation (CEC), 2021), and are shown with respect to the current (2020) observed range edges for *D. albipictus* (black dotted lines).

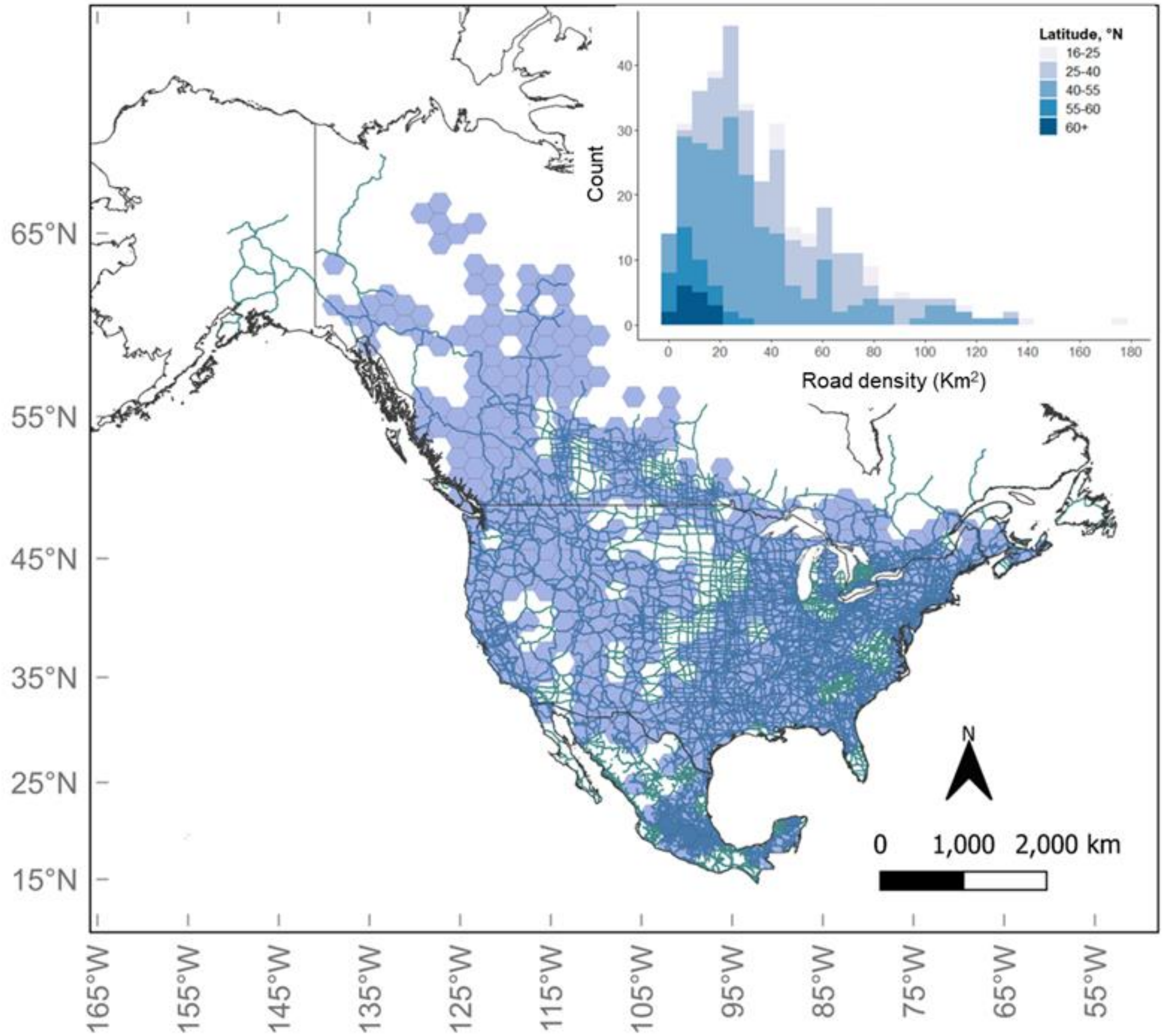

Figure A2. Winter tick occurrence records, grouped within 250km hexagons *(shaded)*, **and associated major road densities per location** *(inset)*. Road data are from the Global Road Infrastructure Project dataset (Meijer et al., 2018), showing major road types (green lines: highway and primary road types) in the United States, Canada, and Mexico. The distribution of the density of roads in square kilometers within each winter tick occurrence grouped by 250 km hexagons (*shaded*) are shown in the histogram (*inset*). The median road density in locations where winter ticks have been found is approximately 27.7/km^2 (mean = 34.91, SD ± 29.64).

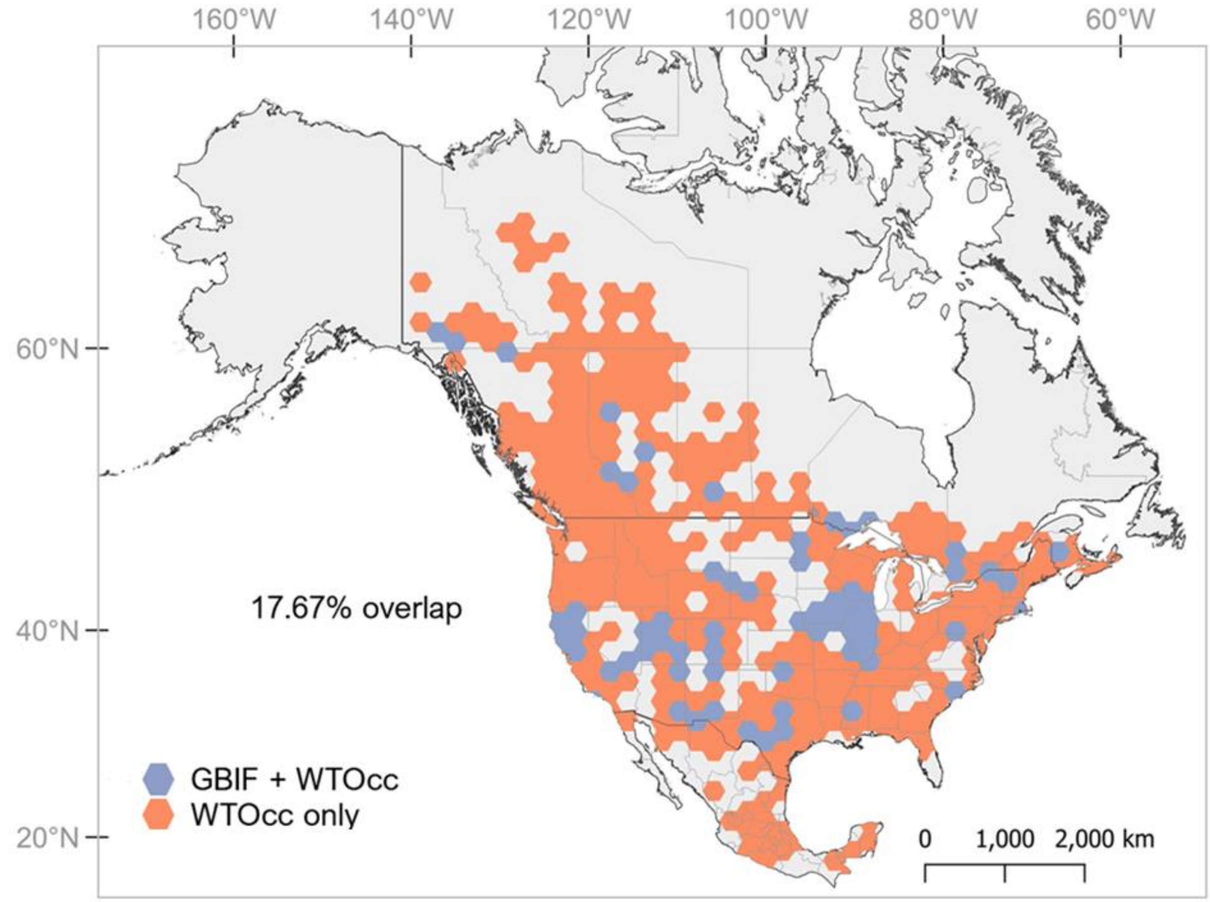

Figure A3. Overlap analysis between GBIF and winter tick occurrence dataset (present study) at a 250km hexagon spatial resolution. All GBIF records to 31 December 2021 that are identified as *D. albipictus* and have spatial data (latitude and longitude coordinates) and an associated year of collection are included (n=1,519 records). At this spatial resolution, all GBIF record localities also appear in the winter tick occurrence dataset. After dataset de-duplication, GBIF records account for 3.2% of the winter tick occurrence dataset (n=112 records). There is a 17.67% spatial overlap between GBIF records and the extent of occurrence indicated by our dataset.

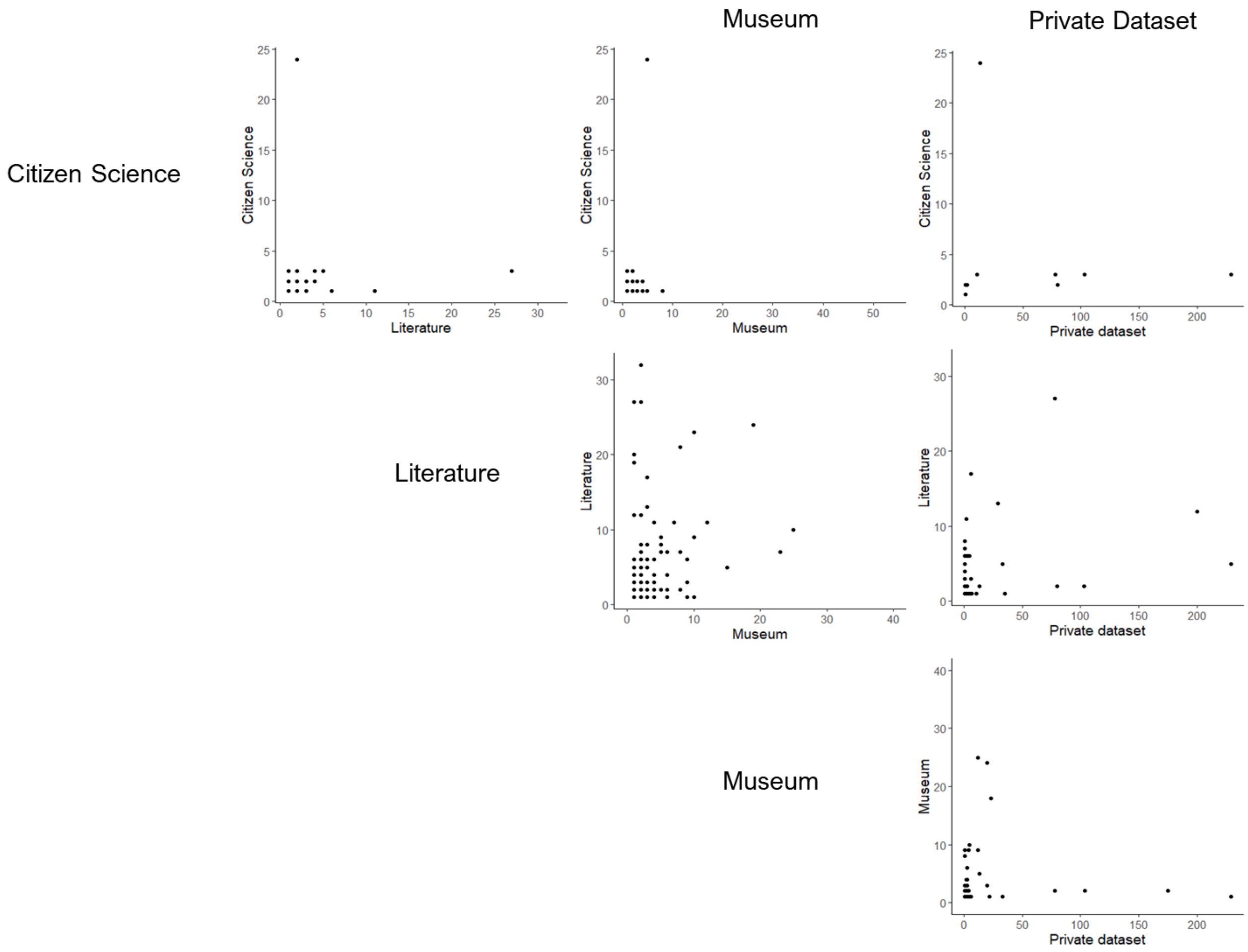

Figure A4. Pairwise comparison of the number of records in the winter tick occurrence dataset, grouped per 250km hexagon, according to data type.

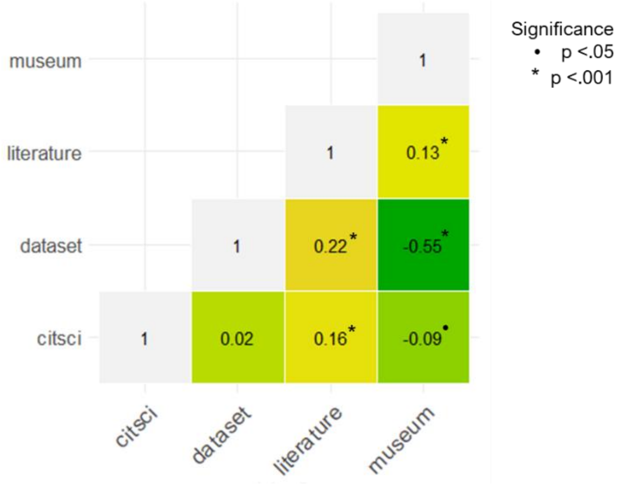

Figure A5. Spearman’s rank correlation coefficients between the number of records for pairs of data types in the winter tick occurrence dataset, grouped at a 250km spatial resolution.

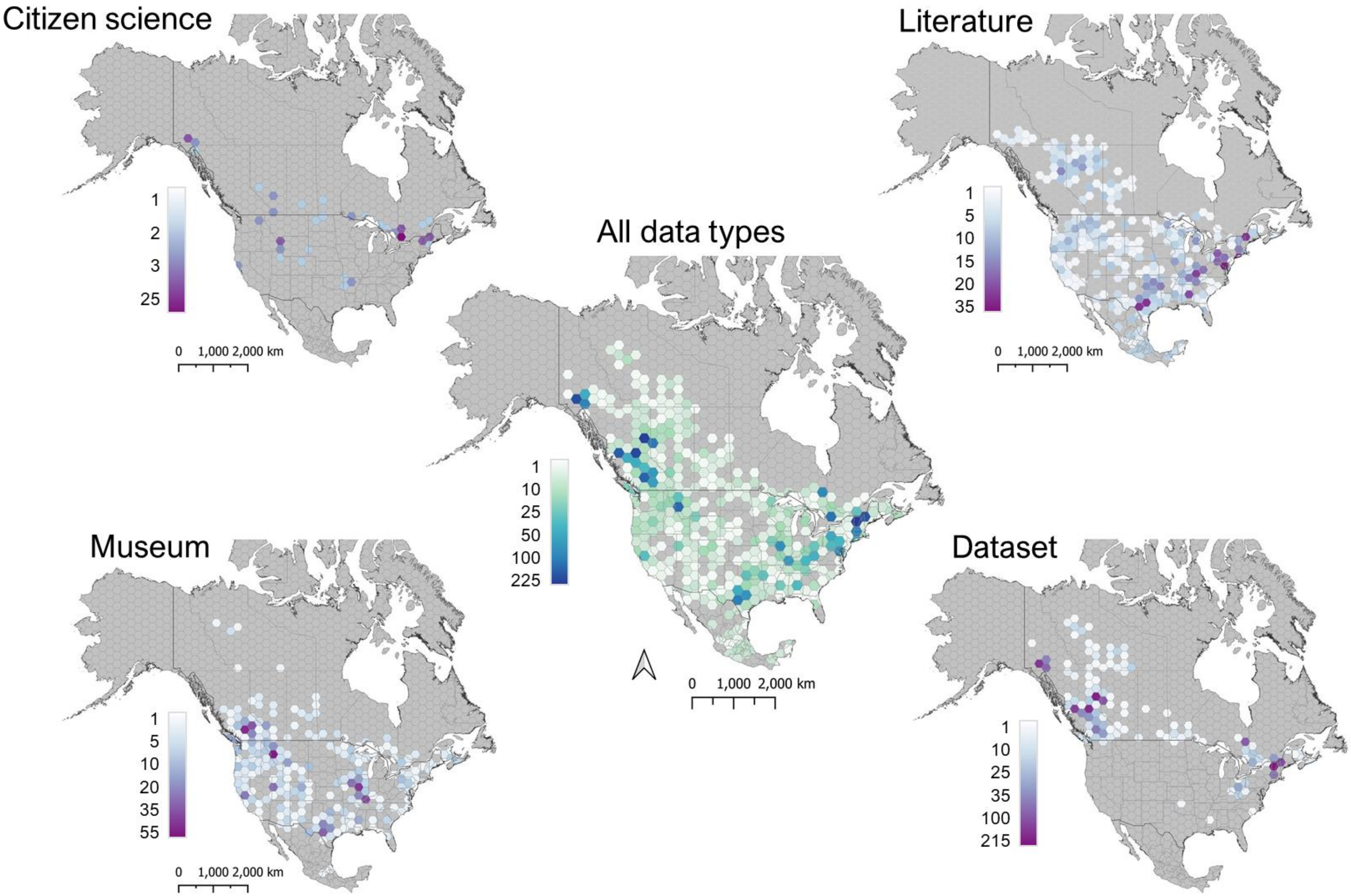

Figure A6. **Spatial distribution of the number of records in the winter tick occurrence dataset.** Records have been grouped within 250km hexagons for all data sources (centre) and split by each of the four data sources categorised within the dataset

References

Commission for Environmental Cooperation (CEC). 2021. North American Environmental Atlas - Level I Terrestrial Ecoregions, 2021. Spatial data accessed 1 March 2022 *via* http://www.cec.org/north-american-environmental-atlas/

GBIF.org 2022. GBIF Occurrence Download (11 March 2022), https://doi.org/10.15468/dl.m5pdgr

Meijer, J. R., M. A. J. Huijbregts, K. C. G. J. Schotten, and A. M. Schipper. 2018. Global patterns of current and future road infrastructure. Environmental Research Letters 13(6), 064006. https://doi.org/10.1088/1748-9326/aabd42.

Appendix B

Field sampling protocol and procedure associated with –First records of *Dermacentor albipictus* larvae collected by flagging in Yukon, Canada.

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Parasites & Vectors 13(1),565

DOI: 10.1186/s13071-020-04425-3

This protocol provides further detail on the field sampling design and implementation in Yukon associated with the above paper but has not been published. In addition to recording the methods used in data collection, the intention of the detailed protocol is to allow other researchers or community groups to conduct their own sampling for winter ticks in Yukon.

Contents:

B.1 Sampling protocol and methods

Background

The winter tick, *Dermacentor albipictus*, is a common blood-feeding parasite in North America that feeds mainly on large deer species (Figure S1). It primarily parasitizes moose but is also known to feed on a range of hosts including caribou, elk, and deer. It is rarely found on humans and carries no known diseases, but for wildlife, infestations with winter tick can be severe when the ticks are present in extremely high numbers (Samuel, 2004). Moose are particularly at risk, where individual animals have been found with more than 30,000 ticks, which often proves fatal. Lower tick densities per host are still of great concern, resulting in reduced body condition, anaemia and general weakness from blood loss, secondary infection, and extensive loss of hair due to increased grooming intensity. This weakening and loss of winter-coat, sometimes known as "Ghost Moose", may also lead to increased winter mortality in both adults and juveniles (Samuel, 2004).

Although documented in the territory since the 1990s, little is known about the current distribution and potential impact of winter ticks on host species in Yukon. Winter ticks are present throughout North America, where severe infestations are implicated in the ongoing decline of moose populations in Vermont, Maine and New England (Jones et al., 2018). In Canada, winter tick related hair loss was reported in 61% of moose observed across British Columbia in 2016. Understanding the potential changes to the winter tick distribution with climate is therefore critical in assessing the risk it poses to Yukon species.

Climate is an important factor in the abundance and development of parasites, and influences the distribution, behaviour, and potentially the vulnerability of hosts to tick infestation. As such, climate change is likely to alter the distribution of ticks and parasitism levels on hosts, with important consequences for the health of key harvested species in Yukon, including moose.

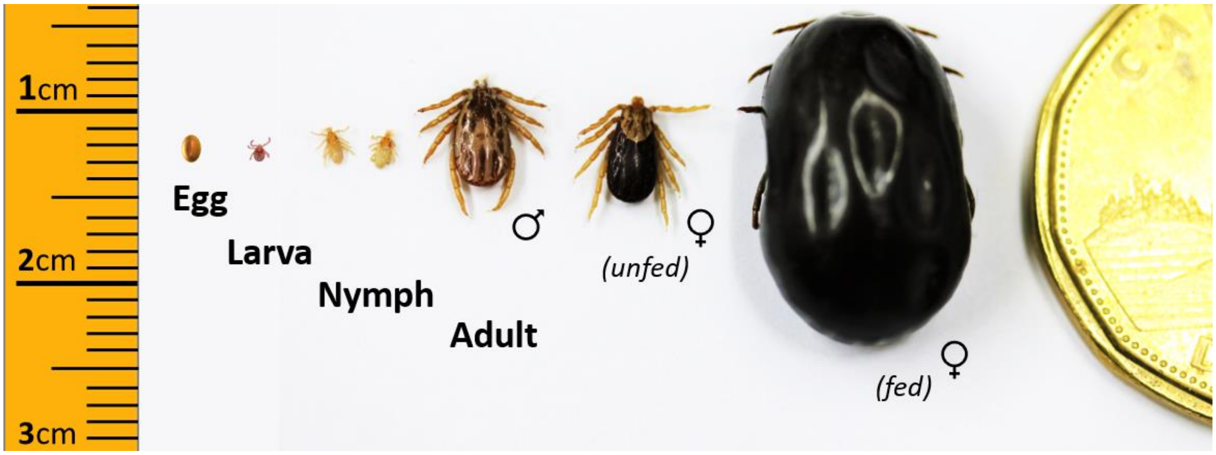

Figure B1. Life stages of *D. albipictus.* The tick grows considerably in size during development from larvae (left) to nymph, to adult male / female and engorged female (right).

Scope

To better understand the current distribution and predict the future range of winter ticks in Yukon, comprehensive data collection in the field is required. This protocol outlines methods that will be used to actively sample for the off-host (larval) life stage of winter ticks in the field.

Standard Operating Procedures (SOPs) for collection of hard-bodied (Ixodidae) ticks are fairly well established (E.g. Ontario Agency for Health Protection and Promotion (Public Health Ontario), 2015; National Ecological Observation Network (NEON), 2015), but are necessarily species-specific due to differences in life-history across different ixodid species and climates. Similarly, the level of documentation on sampling methods is strongly linked to research interests and priorities. For example, owing to their potential agricultural impact in spreading diseases among cattle in South Africa, ixodid ticks of the genus Amblyomma and Rhipicephalus have been more thoroughly sampled, and these sampling processes well-documented (E.g. Spickett, et al., 1991; Cumming, 1999; Rulison et al., 2013; Miguel et al., 2014).

In North America, host-seeking life stages of ixodid ticks are usually collected from the environment in one of two ways: i) via active ‘flagging’ or ‘dragging’, or ii) by using passive carbon dioxide traps. The latter is only suitable for ticks with mobile host-seeking life stages. As *D. albipictus* is only present in the environment as ‘seed ticks’ or larvae, which are largely immobile, flagging has been shown the most effective means of assessing their presence and abundance (Bergeron & Pekins, 2014).

Here, I adapt the established technical operating protocols and procedures for ixodid tick collection as designed by the National Ecological Observatory Network (NEON; Tsao, 2017) and used by the Jardine Lab at the University of Guelph (Claire Jardine, *pers. comm,* 2018). Published material from previous field and lab studies to date (Wilkinson et al., 1982; Drew & Samuel, 1985; McPherson et al., 2000) have been used to incorporate the necessary species-specific collection information for *Dermacentor albipictus*.

This document provides a standard framework that can be iteratively improved to guide ongoing sampling and winter tick monitoring efforts. If successful, this protocol can be used in other areas of Yukon to increase sampling extent and effort in future.

Study design: determining when and where to sample

Determining a general sampling window

Detection success for winter tick larvae has a strong temporal component; understanding when larvae are likely to be seeking a host ('questing') is vital for successful sampling. Elsewhere in Canada, *D. albipictus* larvae exhibit host-seeking behaviour in a short period from mid-September and throughout November (Wilkinson, 1967; Drew & Samuel, 1985; Lindquist et al., 2016). Triggers for questing are unknown but hypothesised to be due to one or a combination of factors, probably primarily driven by changes in temperature and/or photoperiod.

Onset and cessation of sampling

Given the relative paucity of larval tick observations in Yukon to date, this first field season (2018) will extend the sampling period prior to and beyond the expected questing window, to identify a temporal peak in host-seeking behaviour, as well as spatial locations of tick larvae.

- Sampling onset (all sites): before first frost of Summer (mid – August);
- Cessation of sampling (all sites): when snow depth accumulated >3" (est. late October, early November).

In future, site-specific estimates of onset and cessation dates may be determined using locally available meteorological data to determine when temperature thresholds will be met

Location: deciding where to sample

Choosing sampling areas and plots

Large scale study areas should initially be determined based on tick detection history (hide samples, in-field observations) and associated host species' ranges and activity (e.g. antler rubs, pellets and tracks, gametrails). On a smaller scale, a range of habitats should be sampled within these areas, to determine tick habitat preferences in a Yukon context. Selection and transect siting methods are described further in Figure B2.(a) and B2.(b), below. In total, each 4km^2 should have a total length of 1km of transect samples (250 m per transect, per sub-site) taken per sampling event. Repeated sampling visits at a different time are an important means of decreasing uncertainty in detection due to the larval questing window.

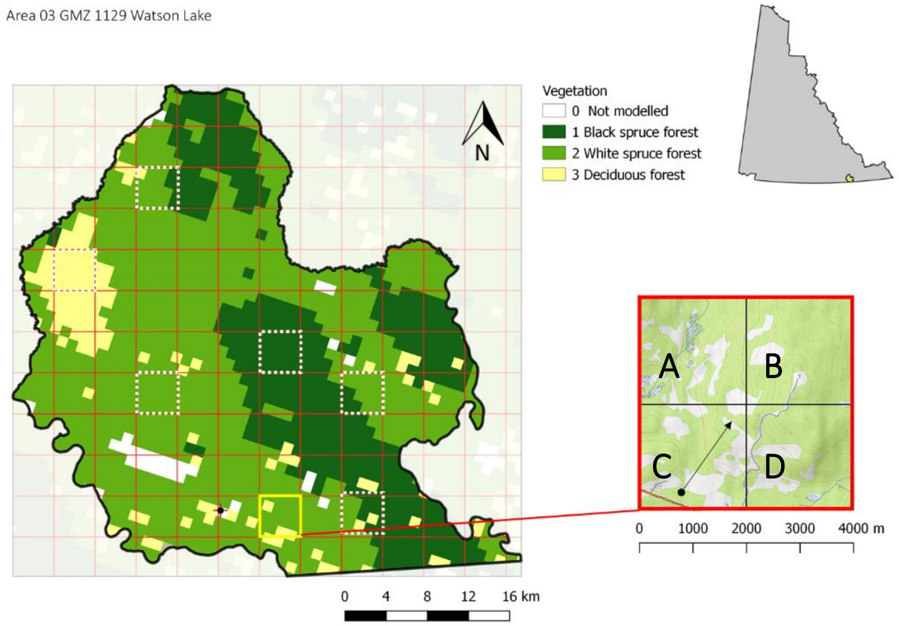

Figure B2. a) Sampling location schematic: 4km^2 plots across the whole study area are chosen by random stratified sampling, which is based on dominant vegetation cover so that all habitats are represented throughout each study area, including ecotone habitat where possible. *Inset:* Each plot is subdivided into four, and labelled A-D from left-right. Transects should be located within each of these squares (A-D), following the same transect method.

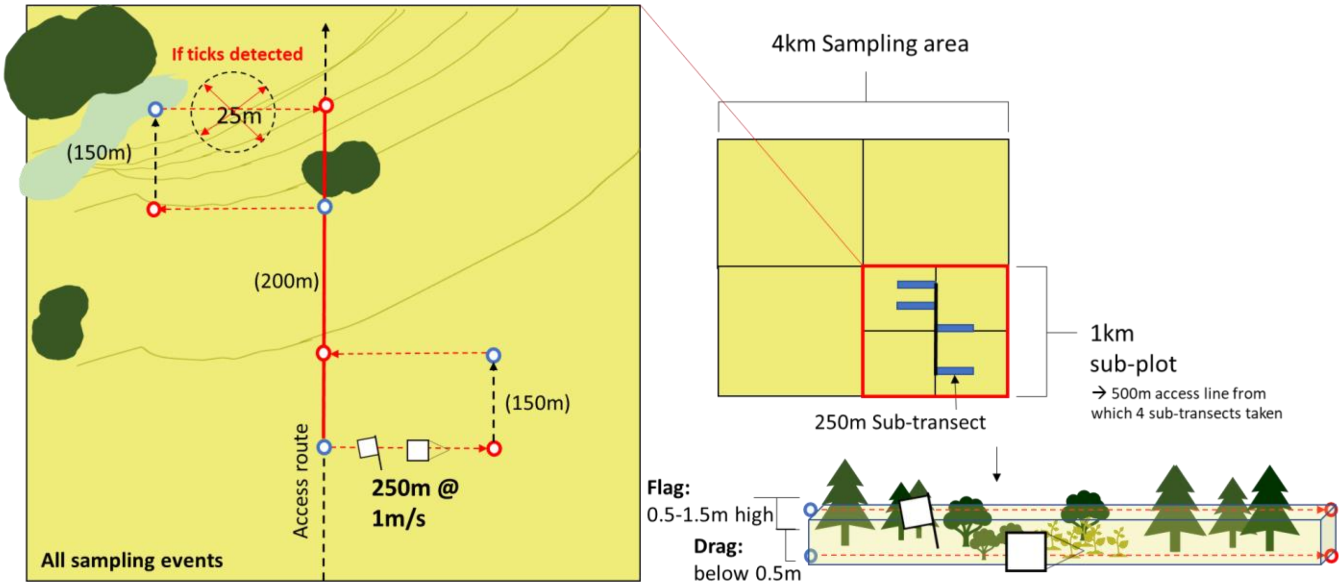

Figure B2. b) Transect method diagram: each sampling plot has two starting locations chosen along the perimeter from north-south (first sampling) or east-west (repeated site visit), totaling 1km length (250m per transect). Where possible, a complete elevational gradient is represented across all transects. Flagging and/or dragging is used according to the vegetation cover, at a slow and steady pace (approximately 1m/second). Any area where ticks are found should be marked with flagging tape, and sampled within a 25 m circle, in all directions, until no more are found within a 5-minute period. A second site visit should ensure this area falls within a repeated sample when siting the east-west transects, or, for areas with multiple tick detections, all areas where ticks were found should be resampled within a 25 m radius of the initial detection area.

When to relocate a transect within a site

As described above, most sampling locations will be decided in advance of any sampling event, to ensure representation of all habitat types and consistency across the sampling season. Sampling teams should attempt to complete transects as close to the original GPS location for that site, however, situations may arise that would make sampling inappropriate or unsafe (e.g. site becomes flooded, trees become uprooted / damaged, unforeseen obstruction such as logs, rocks).

Criteria for relocation:

- If the delay is only temporary, the site should be rescheduled as close to its original sampling date as possible (*see: 4. Dealing with delays).*
- Small obstructions such as thick vegetation, rocks or creeks can be deviated around (within a 50 m deviation limit) or flagging / dragging stopped and the cloth carried over before sampling continues.
- Long-term delays or unsuitable on-the-ground conditions necessitate a transect in the same site that fulfils similar habitat / elevation criteria as the original transect (*see: 4. Dealing with delays)*
- Conditions that would result in considerably more time required (effort) per unit area for sampling than on other sites (E.g. obstacles covering >50% planned transect, or very thick vegetation), are reason to relocate a transect completely to a new area.

Timing: deciding when to sample

An overall sampling window based on expected larval questing behaviour has already been determined in advance (Yukon: mid August – late November). Throughout this period, tick sampling will be heavily weather-dependent. Drag/flag sampling should only be carried out in suitable and safe conditions:

- *Environment is safe.* Sampling should be rescheduled if there is any sign of immediate threat: E.g. presence of wild animals on the site or nearby, any sign of hunting activity in the vicinity (gunshots, visible hunters), or other cause that temporarily makes the environment unsafe. If there are signs that the structural integrity of the site is unstable (broken/overhanging trees, cliffs or subsiding ground) then the site should be marked permanently unsamplable, and the cause noted.

- *Ground is dry.* The flagging/dragging sampling method is most effective during dry conditions, keeping the cloth open and less prone to becoming tangled or snagged on vegetation. Avoid sampling in the early morning (heavy dew), or following / during rain, wet snow. If the flag sampler does become wet / dirty during a sampling session, a clean, dry one should be used as a replacement.

- *Conditions are calm.* To increase the likelihood of sampling success, sampling should not take place in very windy conditions. High winds (>20 mph) may reduce efficiency of sampling by interfering with the sampling cloth and preventing its contact with the surrounding vegetation and therefore tick larvae. It is unknown whether tick larvae actively respond windy conditions, or if they may be dislodged in high winds, which again, may impede tick collection.

Note: *D. albipictus* does not show the same response to temperature fluctuations as other questing ticks, remaining in questing position indefinitely once established. Unlike other tick sampling methods, there is therefore no need to alter sampling schedules with respect to changes in temperature and efforts should be made to continue sampling throughout the season until it is no longer feasible.

Dealing with delays

As all sites are planned to be sampled multiple times, delays may result in data gaps for a given site or location.

If a site has not yet been sampled and is delayed <7days:

- reschedule sampling as close to original date as possible

  If a delay persists >21 days or by 15 September whereby no samples have been taken, the site should be relocated to an area that meets similar habitat/elevation criteria as the original (see*: 3. When to relocate a site*), and the cause of the delay and subsequent relocation noted for the original site record.

If a site has previously been sampled and is delayed <7 days

- reschedule sampling as close to original date as possible

  If a delay persists >30 days or by first snow, repeated samples at other, previously sampled sites should be prioritized, particularly if ticks have been found at or adjacent to that site. The delayed site should then be noted as only having one sampling event, and the cause of the delay noted for that site record.

Materials and methods

FIELD

Preparation for sampling event (*at least 1 day before)*

Recording data

Ensure enough field datasheets (see Appendix B.3) have been printed on waterproof (rite-in-the-rain) paper. Field teams should carry a minimum of 1 sheet per site, plus an additional 3-4 spare sheets.

Some data will be logged using mobile electronic devices, which must be fully-charged at the beginning of each field day and spare batteries packed: environmental meter, GPS and field camera. Should these devices fail in the field, all data must be recorded on the paper field datasheets.

It is recommended that field teams also carry a field notebook that can be used for additional field observations or excessive detail that do not fit on individual datasheets, and as contingency should all technology fail. Any additional notes in a notebook should be clearly highlighted on the corresponding field datasheet, and the datasheet ID similarly noted alongside any comments in the notebook to ensure easy cross-referencing, if necessary.

Field equipment and resources

Detailed topographic maps of each sampling site (4 km^2) should be printed in advance of each sampling event, and key access routes, waypoints and hazards should be annotated.

Consumable supplies, such as ethanol, should be mixed and decanted into a spray bottle ready for use, and stock levels checked and reordered ahead of time as necessary. Site labels can be pre-printed ready for use. (see *Sample labelling*).

Field safety

Safety in the field is a combination of good planning and preparation, careful use of suitable equipment, and assessment of site-specific hazards prior to and during sampling. A full safety assessment should be carried out before the beginning of the field season in accordance with institutional guidelines.

Field teams should also consider specific safety requirements for each site in advance of sampling (E.g. proximity to roads, rivers, elevation, cellular coverage) and build this into preparations ahead of time.

Just before sampling event (*day of / 1 day before*)

- Gather all necessary equipment and supplies – (*see Section B5: Field Equipment Checklist*).
- Ensure all electronic equipment is fully charged and that spare batteries have been packed.
- Use of insect repellent (including in clothes) has been shown to significantly reduce sampling success for ticks. Physical barriers such as head nets / bug jackets, long-sleeved tops, trousers tucked into socks and gloves should be used instead, where possible. If insect repellent is a necessity, this should be applied at least 30mins before arriving in the field. Do not apply near to the sampling equipment. After application, wash hands thoroughly with soap and water before handling any sampling equipment.

Sampling day

On arrival at site

- Check in with First Nations Department office, if available, to inform of where and for how long the team will be sampling, and to ask of any potential safety concerns (e.g. presence of bears or ongoing hunting activity). Also ask if any tick sightings have been reported and where.
- Using GPS, locate desired 4 km plot. Park as near to sampling area as feasible. Carry out all field safety checks prior to exiting vehicle (check for bears, large ungulates, hunters – *see Field safety*).

Prepare for dragging / flagging; collect environmental and habitat data

- Prepare the site field data sheet (see Appendix B.3), using GPS to record lat/long coordinates for transect start. Carry out initial transect survey, and determine which sampling method would be most appropriate, given vegetation cover (*see Section B1. Sampling equipment & methods)*. Ensure that all environmental and habitat variables listed on the data sheet are collected using a handheld environmental meter (temp, windspeed, relative humidity), and that dominant vegetation types are classified.
- Assemble flag/ drag (or both, as necessary), determined during initial transect survey. Ensure that the full 1m^2 of cloth remains available for sampling.
- Divide the transect into sections and allocate between field team. The total continuous distance to be sampled is 1km per site (min. 100 sampling minutes), at a slow and steady walking speed, equivalent to approximately 1m/s. (E.g. team of 2 people = 250 km transect each, 25 sampling minutes per transect.)
- Ensure each team member has a stopwatch / timer, safety whistle, data sheet and pencil, lint roller in a Ziplock™ bag, wire pegs marked with flagging tape, and bear spray. These can be carried in a small backpack or fanny pack, to be accessible at all times.

Drag / Flag for ticks (active sampling)

- Each team member should navigate to the start of their allocated sub-transect, taking care not to disturb other sampling areas, where possible. Mark the start of each transect on the ground or nearby tree using a rod marked at the top with flagging tape. Enter this location as a waypoint on the GPS. Carry out a quick (10-20sec max) tick check of self before starting to sample.
- Begin sampling: flag/drag continuously for 2 mins or 100 m (walking at a slow and steady pace, approximate speed of 1 m/sec), then check both sides of the flag carefully and systematically, using a magnifier if necessary. Pause the timer during all tick checks. Ensure the cloth lies flat throughout the sampling process, keeping in contact with ground / surface vegetation.
- Remove any larvae using the lint roller, replace the roller with larvae or labelled sheet in a Ziploc bag, and record location on datasheet. Mark approximate location of collection using wire peg and flag before continuing. If large numbers of larvae are present, the

sampling sheet may need to be removed from pole and replaced, following the larval collection method (*see Section B3: Larval sample preservation in the field*).

- Repeat until allocated sampling time complete (not including cloth inspection and tick removal/recording) has elapsed or transects totaling 250m have been covered. Teams may decide to sample beyond this time if only a small area of transect remains (<100m). If sampling has been slow due to thick vegetation or difficult terrain, sampling should cease at this time and the total distance sampled recorded, along with a reason for the lengthy sampling time.

Process site samples

- At the end of active sampling, team members should ensure larval ticks are carefully collected and recorded in the field data sheet, according to the larval collection methods outlined in this protocol.
- All samples must be clearly labelled with the Site ID code and stored in a labelled Ziploc bag.
- Disassemble all sampling cloths from handles, do a final tick check, and place in the site labelled Ziploc bag for transporting back to the lab.
- Once back in the lab, samples should be placed in a freezer at -20°C for at least 24 hours, and until ready to be processed.

Tick check

- Personnel should do a thorough tick check before moving sites, and also each evening to ensure no ticks are on their person. Check especially behind the knees, underarms and groin.
- If any ticks are found, remove immediately and keep in a plastic bag. Disinfect skin. Report bite to Team Leader immediately, along with the tick sample.

LAB

Taxonomic identification of samples

In the field, a magnifier will be used to check for ticks on the flagging material. Given the minute size of *D. albipictus* larvae, all formal tick identification will take place in the laboratory with the aid of microscopy equipment. Potential tick larvae can be keyed out using a published dichotomous key for the ticks of Canada from Lindquist et al. (2016).

Any arthropods that are unable to be identified via this method should be preserved in ethanol and sent to an external lab for identification as soon as possible.

Prepare lab space

- A clear space on a lab bench is required for tick sorting and identification. To ensure any ticks accidentally dropped from the sample packet can easily be found, cover the work area with white copier paper.
- Collect all lab processing equipment and materials (*see Section B3: Table S2.)* and the tick sample packets and associated field data sheets.

Process tick samples

- Remove all lint sheets from the sample packet and transfer to a dish. Randomly select a few individuals for a taxonomic identity check under the microscope, using a dichotomous key to aid identification. Ticks can carefully be removed from lint sheets to aid identification by soaking the sheets in water and dilute washing liquid.
- Once species has been confirmed as *Dermacentor albipictus*, count the number of individuals. If there is more than one sample for that site, keep a note of the number of ticks per location, but remember to total the number of ticks per transect too. Discard any organisms that are not tick larvae.
- Complete the bottom portion of the Field Datasheet (back) with lab data.

If the larvae are unable to be identified as *D. albipictus*, collate a subsample in a labelled vial and send to an external lab for identification as soon as possible.

Data entry

- Complete the WinterTick_FieldData.xls spreadsheet using the Field datasheet that now contains final lab data.
- File and archive the paper datasheet for future reference.

If no ticks were found, or if the larvae are cryptic and require external validation, data from the field datasheet should still be digitally transcribed into the spreadsheet as soon as possible, no later than 1 week from the date of collection.

Storage and maintenance of field equipment

Sampling cloth should be placed in a freezer at -20oC for at least 24 hours at the end of any sampling day, to kill any larvae that may still be attached to the material. A thorough check of the cloth should be carried out using a hand magnifier, and any seeds stuck to the cloth should be removed and discarded.

Wash any used cloths with scent-free detergent and dry. Ensure the cloth is free of holes, rips and is in good condition before replacing in its site-labelled Ziploc bag.

Clean any other equipment as necessary, using diluted fragrance-free detergent, and repair ahead of its next use.

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B.2 Sampling equipment and sample preservation

Sampling method: “Flagging” and “Dragging”

In general, there are two main methods for tick collection, both of which use a piece of white cloth to collect questing larvae from the surrounding vegetation:

<u>For vegetation >=1m high</u> (rigid stemmed shrubs, densely forested areas)

→ use **Flag** sampling (A);

<u>For ground cover <1m high</u> (grasses, low scrub, leaf litter and forest understorey)

→ use **Drag** sampling (B).

Whether flagging (A) or dragging (B), the main aim is to keep as much of the sheet in contact with vegetation / ground cover as possible, at all times. Care should be taken to avoid “surfing” where too much air below the sheet makes the material raise off the ground and only superficial contact is achieved.

Dragging is most effective for leaf-litter and lower vegetative ground cover, whereas **flagging** is most effective means of getting the sampling cloth underneath shrubs and taller or more dense vegetation. If necessary, weights can be clipped to the bottom edge of the material to help keep it in contact with the surfaces being sampled.

The process of sampling should be:

- Drag continuously for 2 mins or approx. 50-90m; Flag continuously for 1min or approx. 60m walking at a slow and steady pace (approximate speed of 1m/sec – think about saying *"1,mississippi"* with every step);
- Check both sides of the flag carefully and systematically, using a magnifier if necessary to distinguish larval ticks from other arthropods or debris. Ensure that any creases where the cloth is attached is also checked. Note that flagging requires more frequent cloth checks, as sampling in dense vegetation is more likely to dislodge any larvae that are attached to the cloth.
- Remove any larvae using the larval collection method (see *Larval sample preservation in the field*), and record on datasheet.
- Repeat until 50mins active sampling time has elapsed or transects totaling 1km have been covered.

IMPORTANT: To ensure that any tick detections can be clearly linked back to an exact sampling location, separate flag / drag cloths must be used for each site and sampling event.

All flag/drag cloths should be thoroughly checked in the lab when the sampling session is complete and washed once a week in unscented laundry detergent prior to reuse.

A. Flag sampling

Materials

- 1 x 1.1m white cotton flannel sheet *
- 1.5m wooden dowel (approx. 3/4" diameter), marked at 1m
- Duct tape
- 1 gallon Ziploc plastic bag (labelled per site)

* additional flagging material kept separately, use clean flag(s) per site.

Assembly

Lay the flannel sheet out flat, with the 1m marks clearly visible. Place the dowel vertically across the flag, so that the pole aligns with the 1m marks on the left-hand side, and the bottom edge of the flag is in line with the line on the dowel handle. This should leave approximately 50cm of dowel as a handle.

Turn flag over, fold the small excess of the flag back, over the dowel so that there is no gap where it adjoins the front of the dowel. Duct tape securely along the width. This should result in 1m^2 of flagging material with a stiff stick attached along one edge. Secure the ends of the tape at either end of the flag with more duct tape.

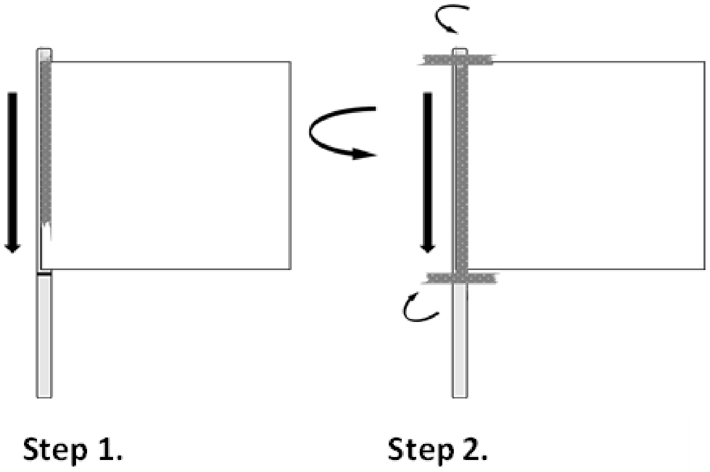


Figure B3. Flag sampler assembly.

B. Drag sampling

Materials

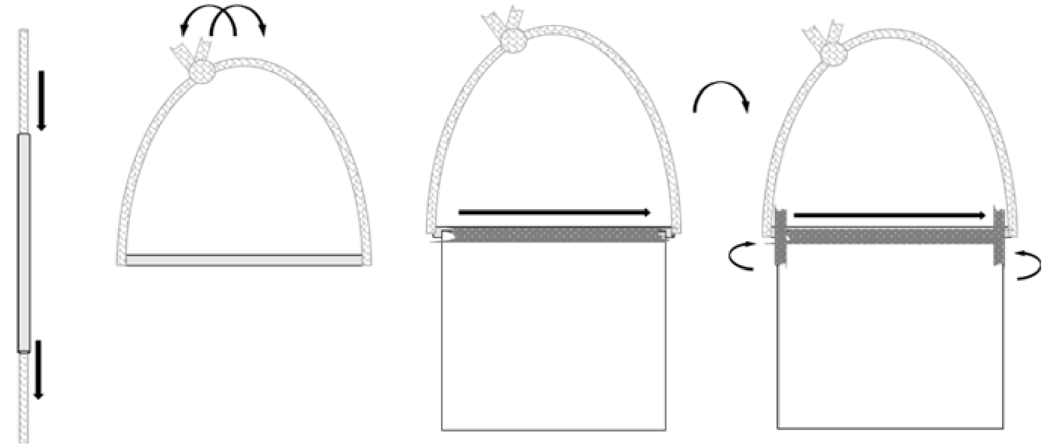
- 1 x 1.1m white cotton flannel sheet *
- 1.1m PVC piping (approx. 3/4" diameter)
- 3m length nylon rope
- Duct tape
- 1 gallon Ziplock plastic bag (labelled per site)

* additional flagging material kept separately, use clean flag(s) per site.

Assembly

Lay the flannel sheet out flat, with the 1m marks clearly visible. Place the dowel vertically across the flag, so that the pole aligns with the 1m marks on the left-hand side, and the bottom edge of the flag is in line with the line on the dowel handle. This should leave approximately 50cm of dowel as a handle.

Turn flag over, fold the small excess of the flag back, over the dowel so that there is no gap where it adjoins the front of the dowel. Duct tape securely along the width. This should result in 1m^2 of flagging material with a stiff stick attached along one edge. Secure the ends of the tape at either end of the flag with more duct tape.



Step 1. Step 2. Step 3. Step 4.

Figure B4. Drag sampler assembly

C. Larval sample preservation in the field

Materials

- Lint (sticky) roller
- Forceps
- Ziplock plastic bag

Methods

Using the lint roller, carefully roll over larvae attached to the flag/drag material. All individuals should become stuck to the roller. Any individuals that are more firmly attached can be removed separately, using forceps.

Label each sheet carefully with location, date, and sampling equipment (see *D. Sample labelling*) using a permanent marker or pen.

It may be necessary to use multiple lint sheets, or in the event of high density of larvae on the sampling sheet during sampling, the sheet can be removed from its pole and carefully placed within a labelled, Ziploc plastic bag. Whole bags should be placed in a freezer for a minimum of 24 hours to ensure larval death prior to processing in the lab, following the same tick-removal methods (lint roller) as described above (Figure S3), and subsequent sample labelled as previously frozen.

Figure B5 Sample labelling on lint sheet containing winter tick larvae, that were previously frozen in the lab before processing.

D. Sample labelling

It is critical that any larval samples collected can be traced back to an exact geographic location and specific date, and thus carefully labelled. The following format incorporates all key information and maintains consistency across study areas.

<u>Example</u>

A sample taken in the Takhini Valley study area, transect 1, on the 12th September 2018, collected by flag (as opposed to drag) sampling, would result in the following information being recorded:

Site_code	Date	Transect_No	Method
TAK	12 Sep 18	01	Flag

Resulting ID code for that sample: TAK01_TR1_12Sept2018_flag

Labels can be pre-printed per site, with space left for date and transect specific information, to use for labelling ziplock bags and associated field data sheets, or a waterproof permanent marker (e.g. Sharpie) used to label lint sheets and bags in the field.

E. Site Codes

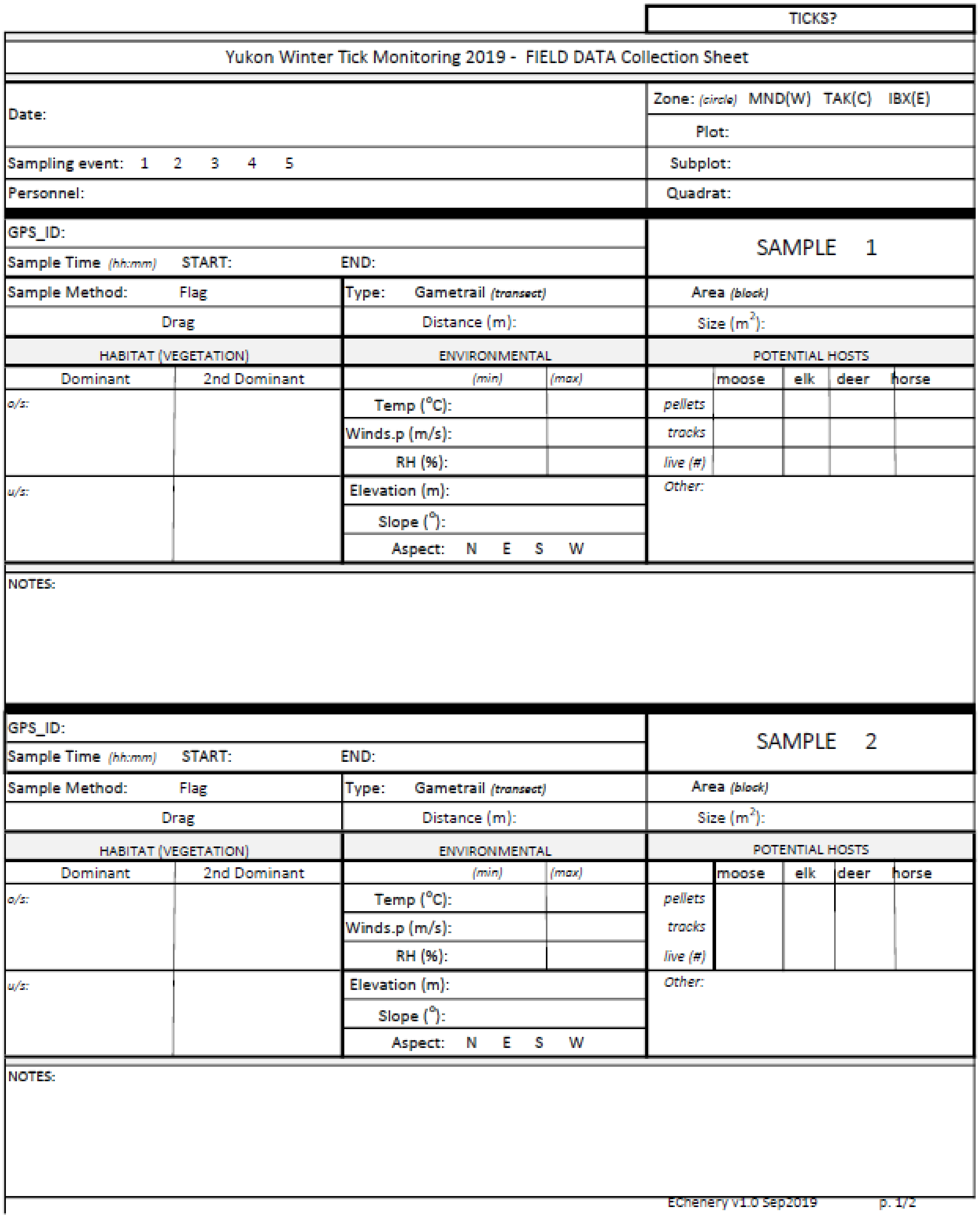
Codes are used to describe sites for sampling during 2018-19 field season. These shortened codes form a fast, easy descriptor for locations (as described in *D. Sample labelling*, above) and should be used in all data recording where possible, for consistency.

New codes should be made for any new sampling locations used during the field season that fall outside of the designated GMZ per region.

Table B1. Site codes used in 2018 and 2019 sampling seasons.

Study Area	GMZ	Site Name	Site Code
01	550	Takhini (Ibex Valley)	**TAK**
01	804	Braeburn	**BRB**
02	816	Marsh Lake	**MLK**
03	1129	Watson Lake	**WTL**

B.3 Field collection datasheets



TICKS?

Yukon Winter Tick Monitoring 2019 - FIELD DATA Collection Sheet

Date:	Zone: *(circle)* MND(W) TAK(C) IBX(E)
	Plot:
Sampling event: 1 2 3 4 5	Subplot:
Personnel:	Quadrat:

GPS_ID:		SAMPLE 1
Sample Time *(hh:mm)* START:	END:	
Sample Method: Flag	Type: Gametrail *(transect)*	Area *(block)*
Drag	Distance (m):	Size (m^2):

HABITAT (VEGETATION)		ENVIRONMENTAL			POTENTIAL HOSTS				
Dominant	2nd Dominant		*(min)*	*(max)*		moose	elk	deer	horse
o/s:		Temp (°C):			*pellets*				
		Winds.p (m/s):			*tracks*				
		RH (%):			*live (#)*				
u/s:		Elevation (m):			*Other:*				
		Slope (°):							
		Aspect: N E S W							

NOTES:

GPS_ID:		SAMPLE 2
Sample Time *(hh:mm)* START:	END:	
Sample Method: Flag	Type: Gametrail *(transect)*	Area *(block)*
Drag	Distance (m):	Size (m^2):

HABITAT (VEGETATION)		ENVIRONMENTAL			POTENTIAL HOSTS				
Dominant	2nd Dominant		*(min)*	*(max)*		moose	elk	deer	horse
o/s:		Temp (°C):			*pellets*				
		Winds.p (m/s):			*tracks*				
		RH (%):			*live (#)*				
u/s:		Elevation (m):			*Other:*				
		Slope (°):							
		Aspect: N E S W							

NOTES:

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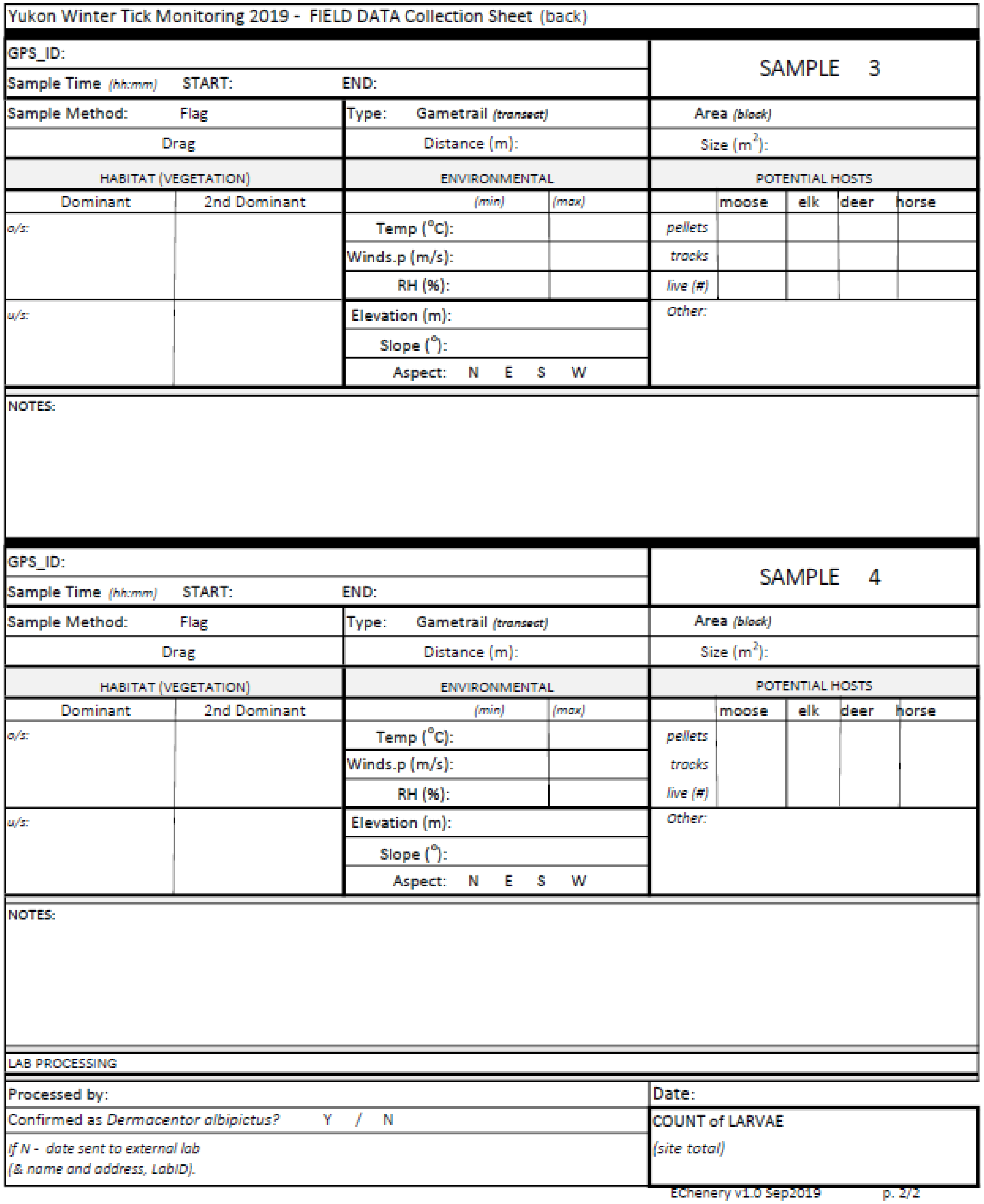

Yukon Winter Tick Monitoring 2019 - FIELD DATA Collection Sheet (back)

GPS_ID:			SAMPLE 3
Sample Time *(hh:mm)*	START:	END:	
Sample Method: Flag		Type: Gametrail *(transect)*	Area *(block)*
Drag		Distance (m):	Size (m^2):

HABITAT (VEGETATION)		ENVIRONMENTAL			POTENTIAL HOSTS				
Dominant	2nd Dominant		*(min)*	*(max)*		moose	elk	deer	horse
o/s:		Temp (°C):			*pellets*				
		Winds.p (m/s):			*tracks*				
		RH (%):			*live (#)*				
u/s:		Elevation (m):			*Other:*				
		Slope (°):							
		Aspect: N E S W							

NOTES:

GPS_ID:			SAMPLE 4
Sample Time *(hh:mm)*	START:	END:	
Sample Method: Flag		Type: Gametrail *(transect)*	Area *(block)*
Drag		Distance (m):	Size (m^2):

HABITAT (VEGETATION)		ENVIRONMENTAL			POTENTIAL HOSTS				
Dominant	2nd Dominant		*(min)*	*(max)*		moose	elk	deer	horse
o/s:		Temp (°C):			*pellets*				
		Winds.p (m/s):			*tracks*				
		RH (%):			*live (#)*				
u/s:		Elevation (m):			*Other:*				
		Slope (°):							
		Aspect: N E S W							

NOTES:

LAB PROCESSING

Processed by:	Date:
Confirmed as *Dermacentor albipictus?* Y / N	COUNT of LARVAE
If N - date sent to external lab *(& name and address, LabID).*	*(site total)*

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TICK DETECTION DATA

Yukon Winter Tick Monitoring 2019 - FIELD DATA Collection Sheet

TICK_GPS_ID	Date	Time *(measure taken)*	Temp (oC)		Wind (m/s)		RH (%)		Distance to nearest Gametrail (cm)	Approx. questing height (cm)	PHOTOS	FLAG TAPE	GPS MARK
			min	*max*	*min*	*max*	*min*	*max*					
Vegetation on:			Dominant o/s & u/s:				Elevation:		**Host evidence?**				
Vegetation on:			Dominant o/s & u/s:				Elevation:		**Host evidence?**				
Vegetation on:			Dominant o/s & u/s:				Elevation:		**Host evidence?**				
Vegetation on:			Dominant o/s & u/s:				Elevation:		**Host evidence?**				
Vegetation on:			Dominant o/s & u/s:				Elevation:		**Host evidence?**				
Vegetation on:			Dominant o/s & u/s:				Elevation:		**Host evidence?**				
Vegetation on:			Dominant o/s & u/s:				Elevation:		**Host evidence?**				

B.4 Field equipment checklist

This list comprises most items that are needed for flagging/dragging per full-day sampling (1-3 sites) with a field team of two. Quantities of items are the minimum, and spares are recommended for contingencies. Note that additional equipment that might be required for sample processing in the lab are not listed (e.g. -20oC freezer for sample storage).

Table S2. Field Equipment Checklist

Item description	Purpose	Nº. / amount
Prepare in advance		
Waterproof copier paper (white)	Print Field Data sheets	1 per site + spares
Label tape / label sheets	Sample labelling in the field. Can be pre-printed with site details or blank	1 roll / full sheet
Ethanol (95%)	Add to spray bottle, for killing larval ticks. (Ensure bottle refilled)	As needed
Field equipment list		
Tick drag and flag assembly	For tick sampling. *See Section B3*. Clean and dry, stored in own labelled Ziploc bag	1 per person, per transect + spare
Duct tape	For assembling flag/drag; repairs in the field	2
Storage clipboard	Hold and write datasheets in field	1
Field data sheets	To record data	1 per site + spares
Pencils	Completing datasheets	3
Forceps	To help with larval removal, or for removing other large insects from material	1
Larval tick collection materials	For larval tick collection and storage. *See Section B3.*	1 per site + spares
Lint rollers	To collect larval ticks from sampling cloth / personnel.	2
Label tape / label sheets	For sample labelling	1
Handheld GPS	To navigate to and from sampling site	1
Field camera (Olympus Tough TG5)	To take site and sample photos	1
AA Lithium ion batteries	Spares for camera and GPS	5
Hand lens / Magnifier	Checking sampling cloth for larval ticks	1 per person
Sharpie marker	Sample labelling.	2
Measuring tape (50m)	For measuring transects in field	1

Item description	**Purpose**	**Nº· / amount**
Field equipment list (cont.)		
Kestrel Environmental Meter	For taking and recording environmental measurements at each sampling site.	1
Stopwatch	Timing sampling effort	2
Pigtail pegs / wire rods	For marking out start and end of transect; location of any larvae found	8
Neon flagging tape	To tie on pegs and rods for location marking	1 roll
Scissors	To cut flagging tape and labels	1
*Field and personnel safety **		
Whistle	For emergency communication	1 per person
First Aid Kit (field)	For small injuries through to field emergencies. Ensure is restocked before each sampling event.	1
Bear spray	For personnel safety	1 per person
Bear bangers	For personnel safety	1 set per person
Bug jacket / bug head net	For personnel protection from biting insects	1 per person
Neon vest	Maximum visibility, for personnel safety particularly during hunting season.	1 per person
Garmin InReach	To check in with Whitehorse office every 4 hours; emergency communication	1
Topographic site map	Navigation to and from sampling site	As many as sites
Compass	Navigation to and from sampling site	1
Foil blanket, matches	Emergency survival equipment - warmth	1 per person
Overnight survival kit (in vehicle)	Sleeping bag, food, water	1 set, in vehicle
Lab processing		
White copier paper/ tray	To aid visibility of larvae for counting	1
Microscope	For tick identification	1
Field data sheets	Record tick numbers	1 per site
Pencil	Record tick numbers	1
Perfume-free laundry liquid	Wash used sampling cloths	1
Ziploc freezer bag	Organise and store tick samples	1 per site

Appendix C

Supporting information for Parasites at the edge: Abiotic factors associated with larval *Dermacentor albipictus* occurrence and abundance at a northern range boundary in Yukon, Canada.

Emily S. Chenery, Louise. C. Archer, N. Jane Harms, Nicholas E. Mandrak, Péter K. Molnár

In prep.

Contents:

C.1 Site and variable information

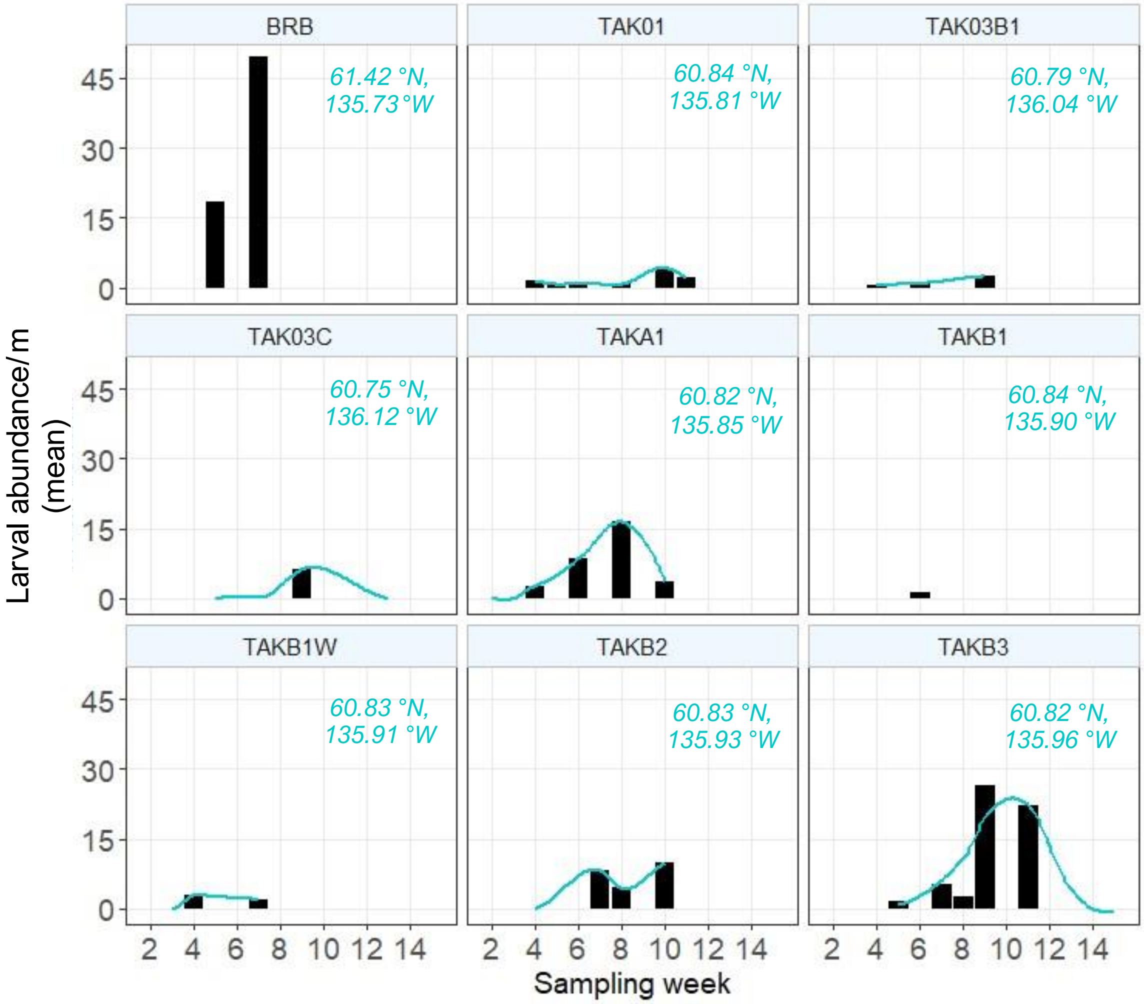


Figure C1 Mean abundance of larval *Dermacentor albipictus* per metre of transect sampled, by sampling week (2019), and grouped within sites. Trendlines given as LOWESS smoothed curves. Only sites where larvae were detected for one or more weeks are shown here, but all were used in analysis (see main text); site latitude and longitude are given per panel. Sampling weeks in 2019 covered the following dates: 2 = 26th- 30th August, 3 = 2nd – 6th September, 4 = 9th – 13th September, 5 = 16th – 20th September, 6 = 23rd – 27th September, 7 = 30th September – 4th October, 8 = 7th – 11th October, 9 = 14th – 18th October, 10 = 21st – 25th October, 11 = 28th October – 1st November, 12 = 4th – 8th November, 13 = 11th – 14th November, 14 = 18th – 22nd November, 15 =25th – 29th November.

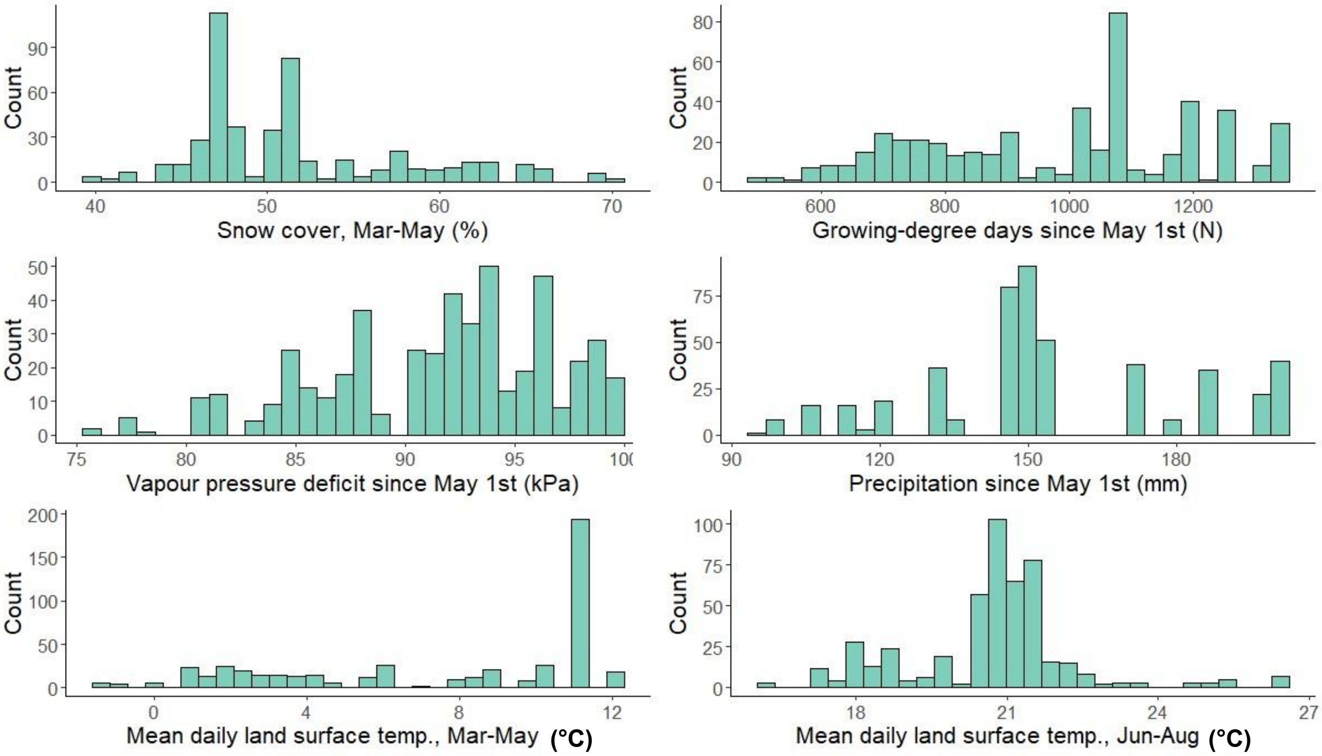
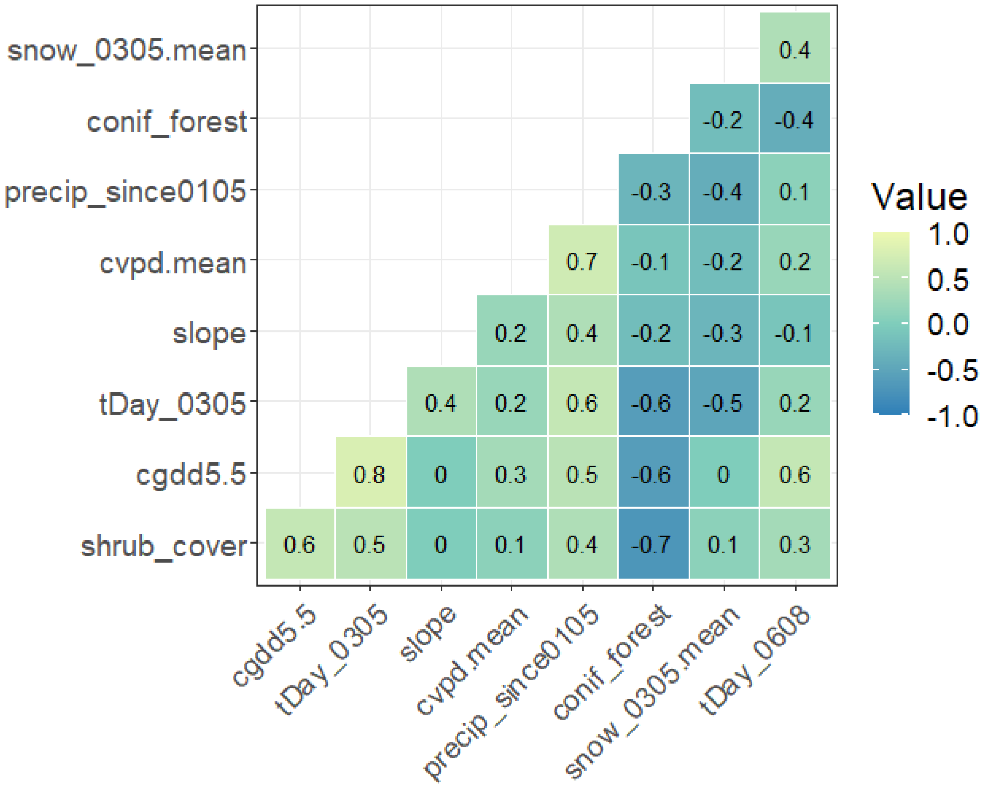


Figure C2 Distribution of observed values for predictor variables across all sampling sites.

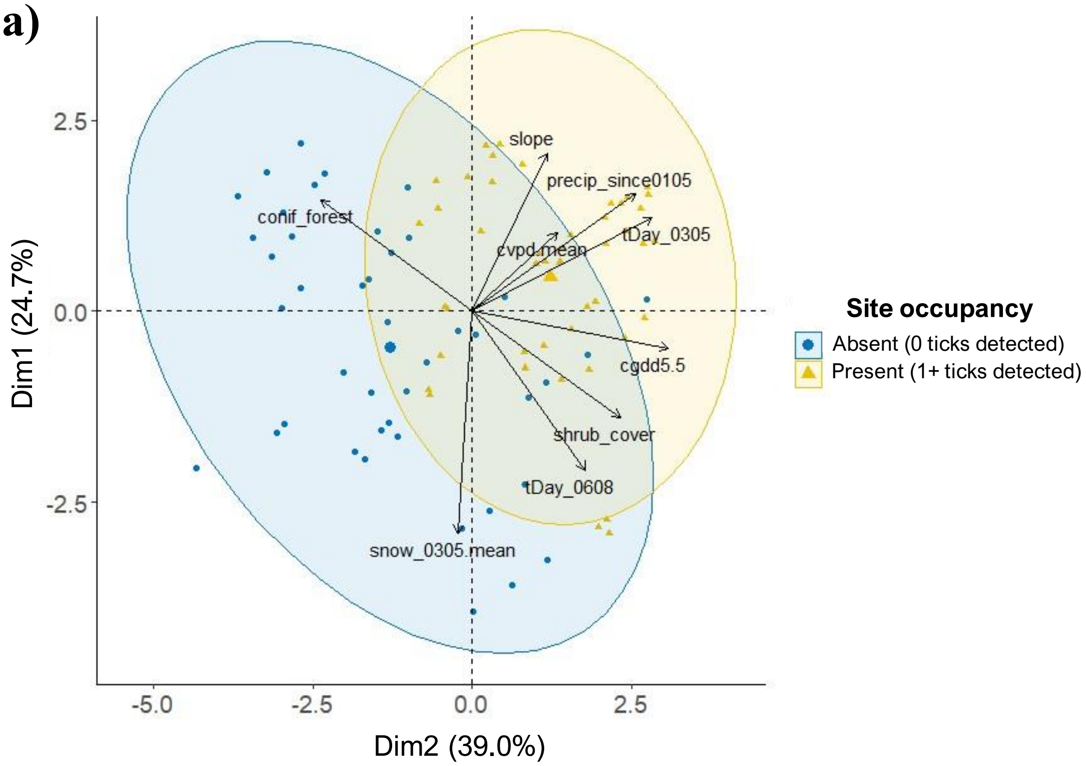


	cgdd5.5	tDay_0305	slope	cvpd.mean	precip_since0105	conif_forest	snow_0305.mean	tDay_0608
snow_0305.mean								0.4
conif_forest							-0.2	-0.4
precip_since0105						-0.3	-0.4	0.1
cvpd.mean					0.7	-0.1	-0.2	0.2
slope				0.2	0.4	-0.2	-0.3	-0.1
tDay_0305			0.4	0.2	0.6	-0.6	-0.5	0.2
cgdd5.5		0.8	0	0.3	0.5	-0.6	0	0.6
shrub_cover	0.6	0.5	0	0.1	0.4	-0.7	0.1	0.3

Figure C3 Correlation matrix of the predictor variables considered important for *D. albipictus* presence or abundance. Note, not all variables were subsequently included in final model formulations (see main text for details). Variables: cgdd5.5 = accumulated growing-degree days above 5.5°C; tDay_0305 = mean daily land surface temperature between 1 March and 31 May; tDay_0608 = mean daily land surface temperature between 1 June and 31 August; slope = hillslope of terrain (degrees); cvpd.mean = mean cumulative vapour pressure deficit (kPa); precip_since0105 = accumulated precipitation (mm) since 1 May; conif_forest = proportion of coniferous forest cover (%) calculated per 1 km^2 site; shrub_cover = proportion of shrub cover (%) calculated per 1 km^2 site; snow_0305.mean = mean proportion of site covered in snow (%) between 1 March and 31 May; tDay_0608 = mean daily land surface temperature between 1 June and 31 August.

C.2 Principal Component Analysis

a)



b)

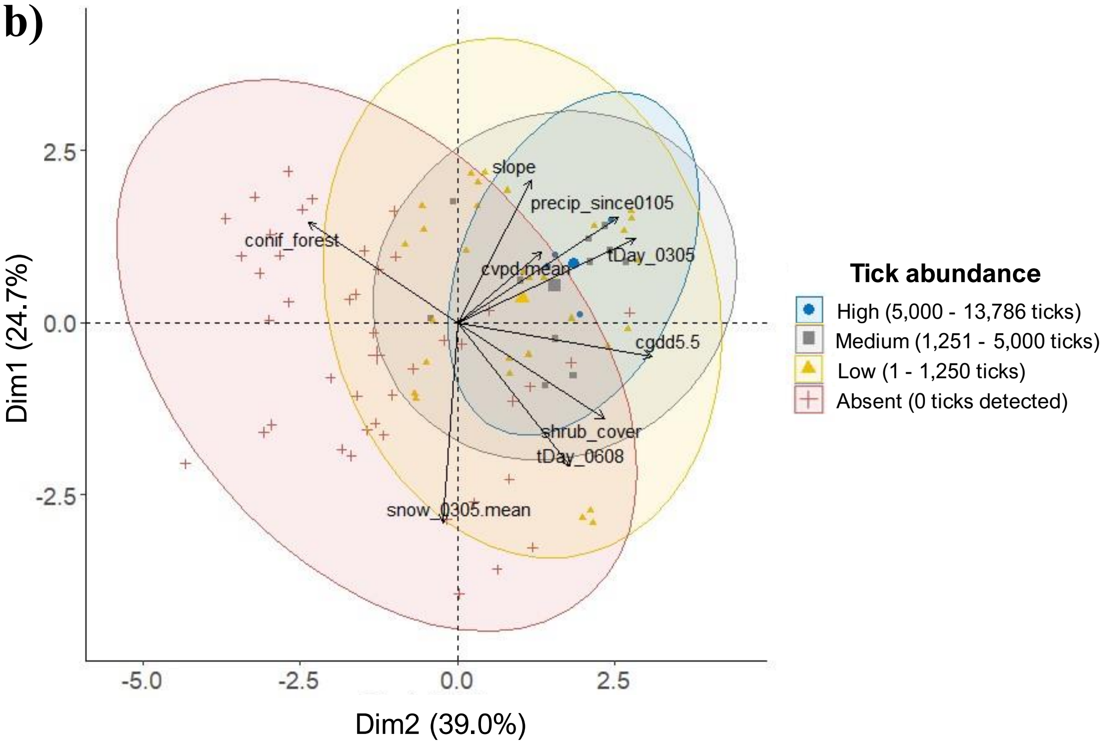


Figure C4 a) Biplot of the first two principal components (PCs) (Dim1, Dim2) of PCA, accounting for >60% total variation. Points have been labelled according to the presence/ absence of larval ticks detected at each site (shaded ellipses). **b)** Biplot of first two PCs with points labelled according to larval tick abundance category at each site (shaded ellipses). Variables: cgdd5.5 = accumulated growing-degree days above 5.5°C; tDay_0305 = mean daily land surface temperature between 1 March and 31 May; tDay_0608 = mean daily land surface temperature between 1 June and 31 August; slope = hillslope of terrain (degrees); cvpd.mean = mean cumulative vapour pressure deficit (kPa); precip_since0105 = accumulated precipitation (mm) since 1 May; conif_forest = proportion of coniferous forest cover (%) calculated per 1 km2 site; shrub_cover = proportion of shrub cover (%) calculated per 1 km2 site; snow_0305.mean = mean proportion of site covered in snow (%) between 1 March and 31 May; tDay_0608 = mean daily land surface temperature between 1 June and 31 August.

Table C1. Pearson's correlation coefficients (*r*) between individual variables included in PCA analysis and the first three principal components (PCs) and their variance explained (%). Variables contributing to above average variance in the PCA are given in **bold,** these are also the most highly correlated with that PC. Variables: cgdd5.5 = accumulated growing-degree days above 5.5°C; tDay_0305 = mean daily land surface temperature between 1 March and 31 May; slope = hillslope of terrain (degrees); cvpd.mean = mean cumulative vapour pressure deficit (kPa); precip_since0105 = accumulated precipitation (mm) since 1 May; conif_forest = proportion of coniferous forest cover (%) calculated per 1 km2 site; shrub_cover = proportion of shrub cover (%) calculated per 1 km2 site; snow_0305.mean = mean proportion of site covered in snow (%) between 1 March and 31 May; tDay_0608 = mean daily land surface temperature between 1 June and 31 August.

Variable	PC1 (39.0%)	PC2 (24.7%)	PC3 (13.5%)
cgdd5.5	**0.89**	-0.14	0.13
tDay_0305	**0.82**	0.35	-0.33
precip_since0105	**0.74**	0.45	0.22
shrub_cover	**0.67**	-0.04	-0.22
tDay_0608	0.52	**-0.60**	**0.36**
cvpd.mean	0.38	0.29	**0.80**
slope	0.34	**0.60**	-0.23
snow_0305.mean	-0.06	**-0.85**	0.11
conif_forest	**-0.68**	0.42	**0.40**

C.3 Model structure

a) Occurrence models

The models predicting larval *D. albipictus* occurrence (presence/absence) all followed the same hierarchical model structure (Eq.1):

$$Occurrence_{ijk} \sim \text{Bernoulli}(p_{ijk})$$

$$logit(p_{ijk}) = (\beta_0 + s_{0,j} + w_{0,k}) + \beta_m x_{m,ijk}$$

$$\beta_0 \sim Normal(0, 1.5)$$

$$\beta_m \sim Normal(0, 0.5)$$

$$s_{0,j} \sim Normal(0, \tau_s)$$

$$w_{0,k} \sim Normal(0, \tau_w)$$

$$\tau_s \sim Student\ t(3, 0, 2.5)$$

$$\tau_w \sim Student\ t(3, 0, 2.5)$$

where p_{ijk} is the probability of larval tick presence (ranging from 0 to 1) at site *j* for sampling week *k* given a combination of predictor variables, x_m, whose slopes β_m, are drawn from a normal distribution with a mean of 0 and standard deviation of 0.5, with the global intercept β_0 drawn from a normal distribution with a mean of 0 and standard deviation of 0.5, adjusted by $s_{0,j}$ and $w_{0,k}$ to give intercepts for each site and sampling week, respectively.

b) Abundance models

Models predicting larval *D. albipictus* abundance all followed the same hierarchical structure (Eq.2):

$$Abundance_{ijk} \sim ZINB(\lambda_{ijk}, \kappa, z_j)$$

$$\log(\lambda_{ijk}) = (\beta_0 + s_{0,j} + w_{0,k}) + \beta_m x_{m,ijk}, logit(z_j) = \beta_z + s_{z,j}$$

$$\beta_0 \sim Normal(2.5, 0.5)$$

$$\beta_i \sim Normal(0, 0.25)$$

$$s_{0,j} \sim Normal(0, \tau_s)$$

$$w_{0,k} \sim Normal(0, \tau_w)$$

$$\tau_s \sim Student\ t(3, 0, 2.5)$$

$$\tau_w \sim Student\ t(3, 0, 2.5)$$

$$\kappa \sim \ gamma(0.01, 0.01)$$

$$\beta_z \sim Normal(0, 1.5)$$

$$s_{z,j} \sim Normal(0, \tau_z)$$

$$\tau_z \sim Student\ t(3, 0, 2.5)$$

where the predicted abundance is drawn from a zero-inflated negative binomial distribution, with the probability of zero having a mean of z_j , and all other values a mean of $\lambda_{ijk},$ and shape κ . The mean λ_{ikk} is modelled as a linear function of predictor variables, x_m, whose slopes β_m, are drawn from a normal distribution with a mean of 0 and standard deviation of 0.25, with the global intercept β_0 drawn from a normal distribution with a mean of 1 and standard deviation of 0.5, adjusted by $s_{0,\,j}$ and $w_{0,\,k}$ to give intercepts for each site and sampling week, respectively. The mean z_j , is also modelled as a linear function with slope β_z, drawn from a normal distribution with a mean of 0 and standard deviation of 1.5, and adjusted by $s_{j,\,z}$ to give the intercept for site, which is adjusted by the probability of drawing excess zeroes.

C.4 Prior predictive simulations

Prior selection is a critical component of the Bayesian modelling process, particularly in the case of small datasets whereby prior choices can have a large impact on model results (van de Schoot et al., 2021; Wesner & Pomeranz, 2021). To examine if our specified priors generated reasonable prior predictions, we used prior predictive simulation (Gabry et al., 2019), simulating 100 draws across the range of our standardized variables for both occurrence (Figure S5(a)) and abundance models (Figure S5(b)). For both models, simulations show a wide range of variation across slopes, allowing for varying strengths of relationship with the predictor.

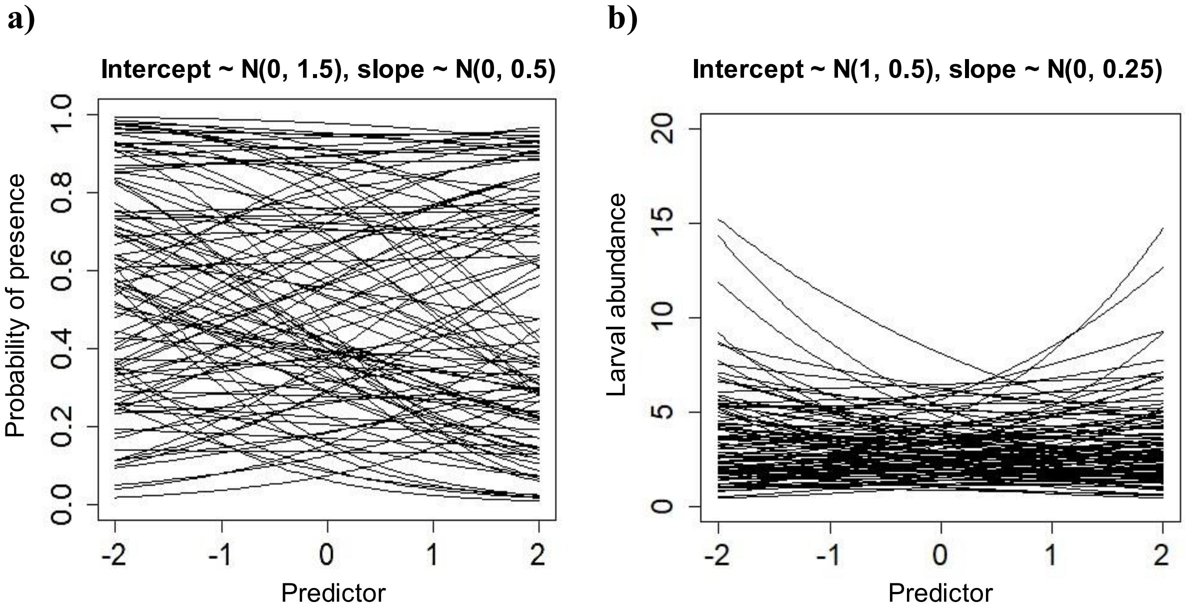
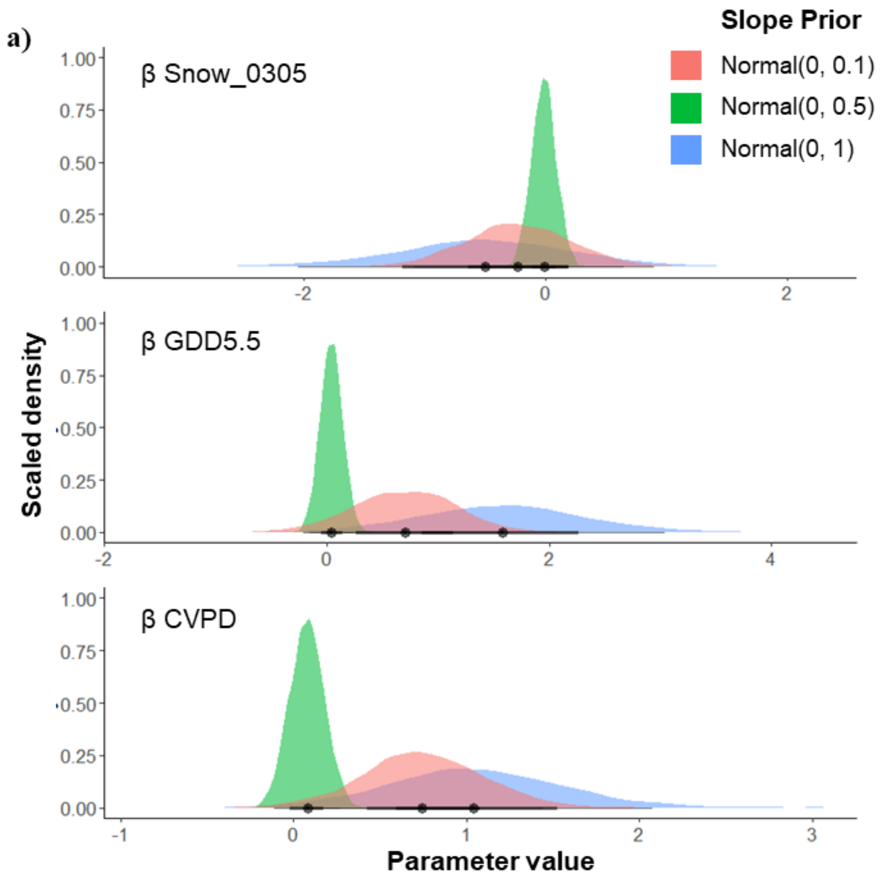


Figure C5. Prior predictive distributions for a) occurrence and b) abundance models, based on 100 draws. Both models incorporated weakly informative priors to allow for the full range of relationships between predictors and response variables to be sampled.

C.5 Prior sensitivity

Following best practice, we conducted a sensitivity analysis to understand the influence of prior settings on the posterior outcomes of both our occurrence (a) and abundance (b) models (van Erp et al., 2018; van de Schoot et al., 2021). Models were re-run after adjusting the standard deviation (SD) of the slope β prior within defined lower and upper thresholds that represented more or less informative priors. Intercept priors were kept fixed throughout (occurrence: Normal(0, 1.5); abundance: Normal(1, 0.5), zero-inflated Normal(0, 1.5)). Occurrence models were run with a lower SD of 0.1 and an upper SD of 1, and abundance models run with adjusted SD values of 0.1 and 0.5, respectively.

The prior sensitivity analysis (Figure S6(a) and (b)) indicates that both models were sensitive to prior specification, likely due to small sample size. Nonetheless, the posterior distribution density was highest for the weakly informative priors selected for our main models.



b)

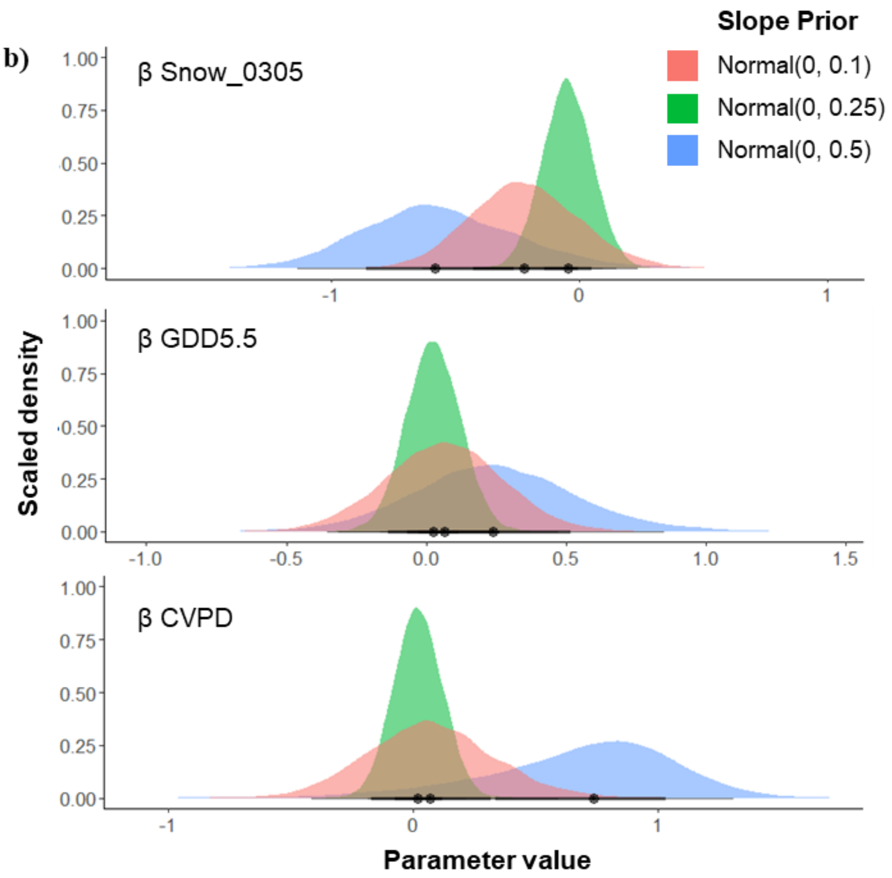


Figure C6. Posterior distributions for each predictor included in a) occurrence and b) abundance (count) models. The final model included in the main text is shown in green, with variations on this model adjusting the standard deviation of the slope prior within lower (red) and upper (blue) bounds. Mean (black dot) and 95% credible intervals (black line) are also shown for each distribution.

C.6 Posterior predictive checks

Predictive checks of the posterior distribution are recommended to examine model fit (Gelman et al., 2014; Hobbs & Hooten, 2015). In R, we used the function *pp_check()* from the package *brms* (Bürkner, 2017) to sample 10 draws from new data for both occurrence (Figure S7(a)) and abundance models (Figure S7(b)). A fit is considered ‘good’ if the predicted distributions, generated from the joint posterior distribution, are visually similar to those observed in the original dataset. Both our occurrence and abundance models appear to generate similar datasets to the original, suggesting sufficient model fit for inference.

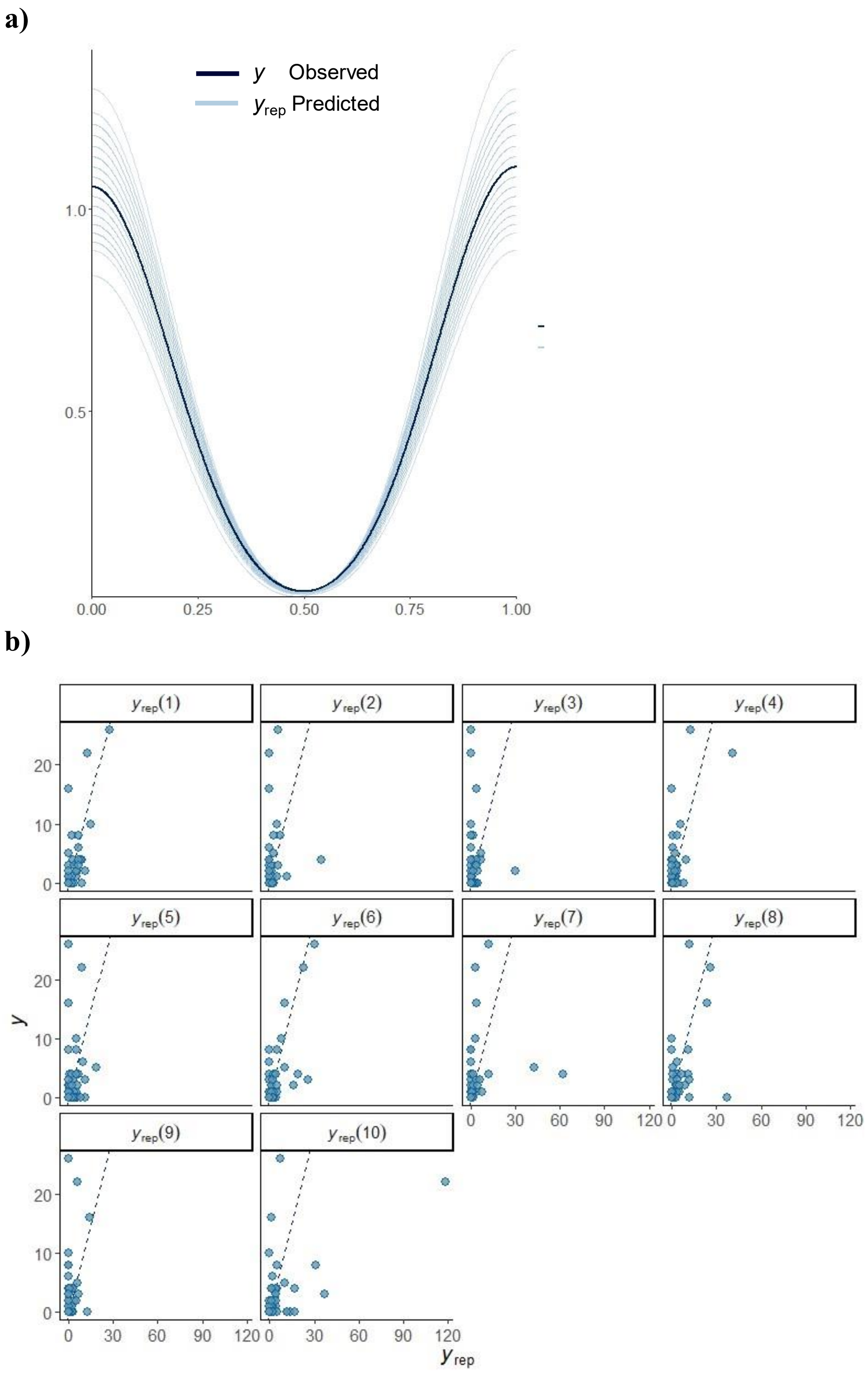


Figure C7. Posterior predictive distributions for global models of a) occurrence and b) abundance, based on 100 draws. Dark blue lines in **(a)** show the distribution of model data (*y*), with individual light blue lines showing each of the 10 simulated data sets from the posterior predictive distribution (y_{rep}). Blue dashed lines in **(b)** show the distribution of model data (y), and light blue points show the data for each repeated simulation (separate panels) (y_{rep}(n)).

References

Bürkner, P. (2017). brms: An R Package for Bayesian Multilevel Models Using Stan. Journal of Statistical Software, 80(1), 1–28. https://doi.org/doi:10.18637/jss.v080.i01

Gabry, J., Simpson, D., Vehtari, A., Betancourt, M., & Gelman, A. (2019). Visualization in Bayesian workflow. Journal of the Royal Statistical Society Series A-Statistics in Society, 182(2), 389-402. https://doi.org/10.1111/rssa.12378

Gelman, A., Carlin, J. B., Stern, H. S., Dunson, D. B., Vehtari, A., & Rubin, D. B. (2014). Bayesian data analysis. (Third edition). Chapman and Hall/CRC.

Hobbs, N. T., & Hooten, M. B. (2015). Bayesian models: A statistical primer for ecologists. Princeton University Press.

van de Schoot, R., Depauli, S., King, R., Kramer, B., Märtens, K., Tadesse, M. G., Vannucci, M., Gelman, A., Veen, D., Willemsen, J., & Yau, C. (2021). Bayesian statistics and modelling. Nat Rev Methods Primers, 1(1). https://doi.org/10.1038/ s43586-020-00001-2

van Erp, S., Mulder, J., & Oberski, D. L. (2018). Prior Sensitivity Analysis in Default Bayesian Structural Equation Modeling. Psychological Methods, 23(2), 363–388.

Wesner, J. S., & Pomeranz, J. P. F. (2021). Choosing priors in Bayesian ecological models by simulating from the prior predictive distribution. Ecosphere, 12(9), e03739. https://doi.org/10.1002/ecs2.3739

Appendix D

Supporting information for - Improving Widescale Monitoring of Ectoparasite Presence in Northern Canadian Wildlife with the Aid of Citizen Science

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Insects 13(4),380

DOI: 10.3390/insects13040380

Contents:

D.1 Yukon Winter Tick Monitoring Project sample kit

Description and template materials for the Yukon Winter Tick Monitoring Project (YWTMP) hide sample kit.

Collecting a sample from the areas of known high tick-abundance on an animal, namely the neck and shoulder region or rump, is a common means of assessing winter tick presence (Samuel, 2004; Sine et al., 2009). This kit is designed to obtain a 40 x 20cm section of moose or caribou hide from the right shoulder of the animal, so that it can be visually assessed for winter ticks (*Dermacentor albipictus*).

Note that full host burden (full body tick density estimate) cannot be assessed from this method, which provides a coarse approximation of relative tick numbers per host and presence only data.

Materials needed

- Large Ziploc™ bag (26.8 x 27.3cm)
- Submission details label (*Appendix A)*
- Nitrile gloves (x1 pair, Large size)
- Paper template: sample location template & instructions (*Appendix B)*

Kit assembly

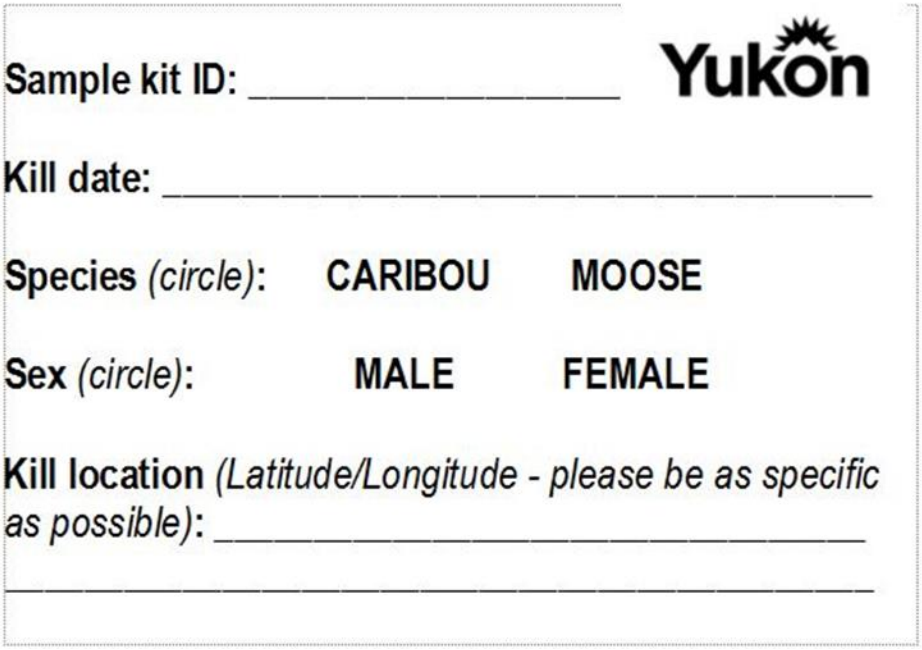
1. Label Ziploc™ bag with submission label. Ensure that unique identifier is written into the Sample Kit ID field, and recorded in the lab spreadsheet.
2. Print double-sided paper instructions and template and trim excess paper following guidelines.
3. Place template and one pair of nitrile gloves inside the bag and seal.

Literature cited:

Samuel, W. M. (2004). White as a Ghost: Winter ticks and moose. Natural History Series. Alberta: Federation of Alberta Naturalists.

Sine, M., K. Morris and D. Knupp. (2009). Assessment of a line transect field method to determine winter tick abundance on moose. Alces 45: 143–46.

Section 1. Submission Kit Label



Yukon

Sample kit ID: ____________________

Kill date: ____

Species *(circle)*: **CARIBOU** **MOOSE**

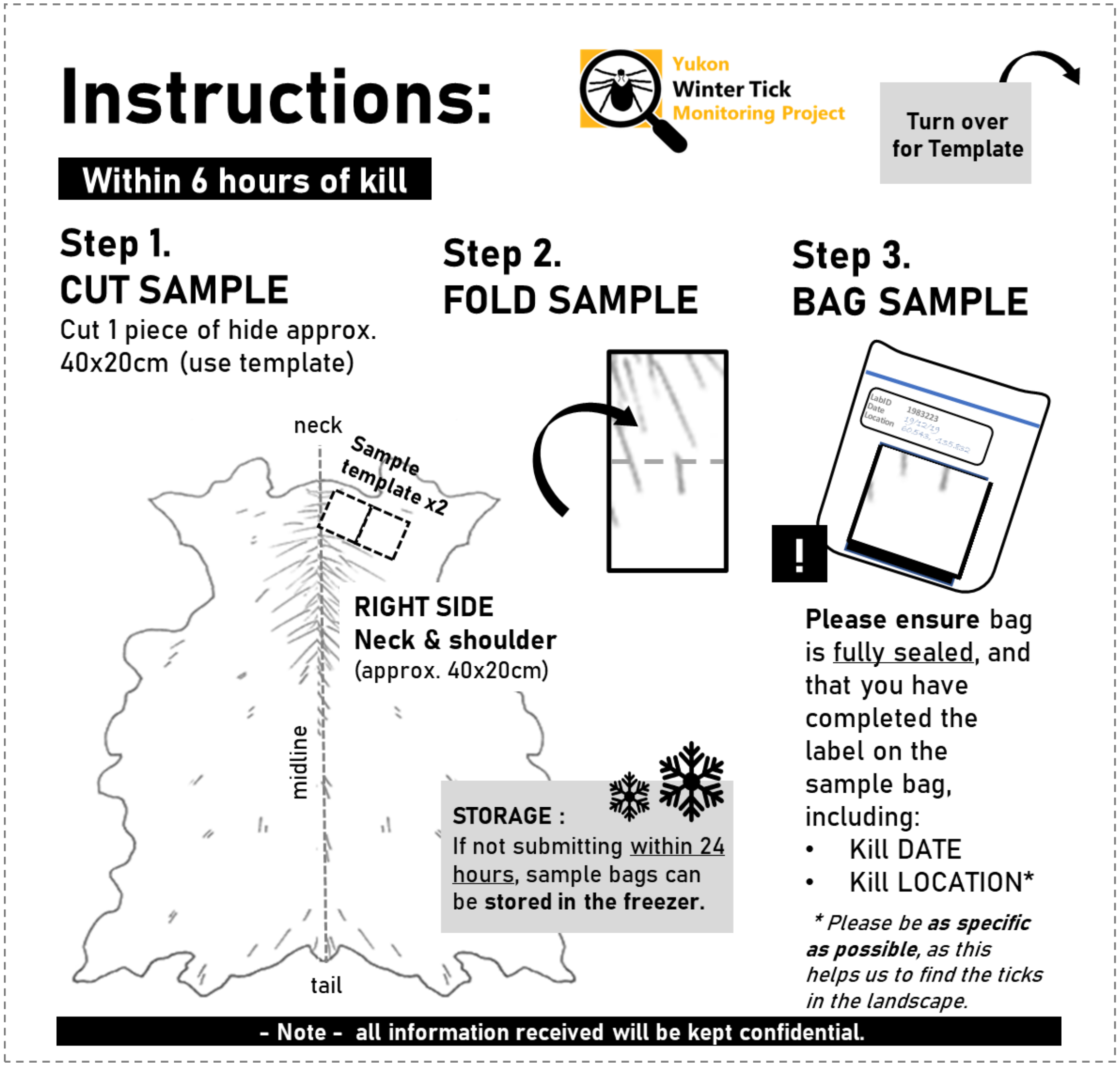
Sex *(circle)*: **MALE** **FEMALE**

Kill location *(Latitude/Longitude - please be as specific as possible)*: ____________________________________

____

Section 2. Hide sample kit template and instructions

(side 1)



Instructions:

Yukon
Winter Tick
Monitoring Project

Turn over for Template

Within 6 hours of kill

Step 1.
CUT SAMPLE

Cut 1 piece of hide approx. 40x20cm (use template)

RIGHT SIDE
Neck & shoulder
(approx. 40x20cm)

Step 2.
FOLD SAMPLE

STORAGE :
If not submitting within 24 hours, sample bags can be **stored in the freezer.**

Step 3.
BAG SAMPLE

!

Please ensure bag is fully sealed, and that you have completed the label on the sample bag, including:

- Kill DATE
- Kill LOCATION*

** Please be **as specific as possible**, as this helps us to find the ticks in the landscape.*

- Note - all information received will be kept confidential.

[OFFICE USE]

Printing instructions :

- print double-sided
- cut this edge off
- fold so that “Instructions” title is clearly visible
- place leaflet in sample bag.

(side 2)

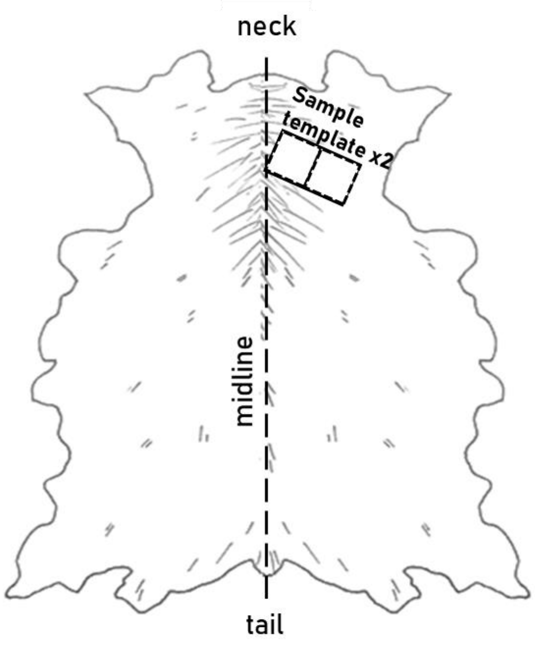
Yukon Winter Tick Monitoring Project

Turn over for full instructions

Sample Template

Cut approx.
2x size
(40 x 20cm)

RIGHT SIDE
neck & shoulder
region



Approx. 20cm

Approx. 20cm

D.2 Yukon Winter Tick Monitoring Project sampling protocol

Sampling methodology to assess winter tick presence and count from samples submitted as part of the Yukon Winter Tick Monitoring Project Hide Submissions Scheme 2019 and 2020.

This method adapts the sub-sampling method used by Sine et al. (2009) to assess hide samples of moose for winter ticks by building on the existing process used by Environment Yukon’s Animal Health Unit (Kuba et al., 2016). An intensive visual hide transect method is used on a smaller hide sample (approximately 20cm x 40cm) taken from the right midline and shoulder of the hide. It allows greater maneuverability of the hide sample piece to include assessment under a dissecting microscope or using a magnifying sheet.

Equipment / materials needed

- Defrosted hide sample to be processed (note: defrosting takes approximately 8-12 hours)
- Hide sample processing datasheet & pen for notetaking *(Section A)*
- Measuring tape or metre ruler
- Printed hide sample transect template (optional, *Section B*)
- Plain white paper (A3)
- Knitting needle
- 10x magnifier or microscope
- Headlamp or other bright overhead light
- Personal Protective Equipment (lab coat, nitrile gloves)

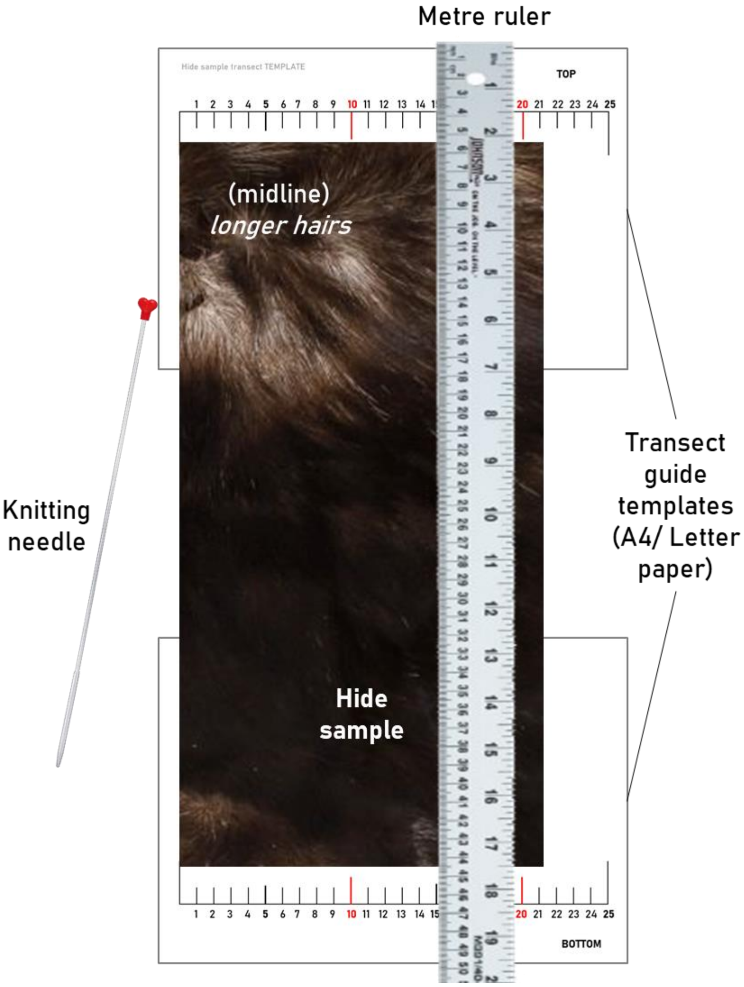
Methods

1. Collect all materials and equipment needed for processing. Hide samples should be removed from the freezer and thoroughly defrosted, 24 hours in advance. It is important to leave the hide sample in its original bag during defrost so that the bag and hide piece can be processed together.
2. Remove sample from Ziplock™ bag, taking care to note the collection information from the bag label on your datasheet. Set aside for step 4.
3. Lay the sample on a flat surface in a well-lit area, hair side up, with the midline on the left (if visible – see Figure S1). Note the midline should be identifiable by longer hairs along one edge or corner of the sample). Use the transect templates under the top and bottom edges of the sample. This will help to keep transect sampling effort consistent.

Figure D1.

Suggested set up for processing hide sample pieces.

Using the transect guide templates helps to ensure transects are straight, so that the sampling is of equal effort throughout. The same gauge (width) knitting needle should be used for all samples each season.



4. Next, lay the Ziplock™ bag over a piece of plain white paper to improve visibility. Carefully check for any loose ticks – especially under the Ziplock™ fastening, bag corners or any other creases. Note the number of loose ticks on the datasheet, if applicable.
5. Using the measuring tape or ruler, measure the width and length of the hide sample piece and note on the datasheet.
6. Now complete a visual hide transect check, starting 1cm in from the left-hand edge of the sample. Use a headtorch if necessary, to ensure the sample is fully visible. Each transect should be for the full length of the sample, taking care to part the hair with the knitting needle to expose the skin beneath (see Kuba et al., 2016 for a full description of method). A magnifying sheet or microscope can also be used to ensure larvae are not missed. Cross off transect numbers on the datasheet as they are completed, to help keep a track of each line. Add extra numbers as necessary.
7. If ticks are found, note the transect number, life stage and engorgement status of the tick (Figure S2) on the relevant line of the datasheet.

8. Continue sampling each transect line at 1cm intervals until the whole hide piece has been completed.

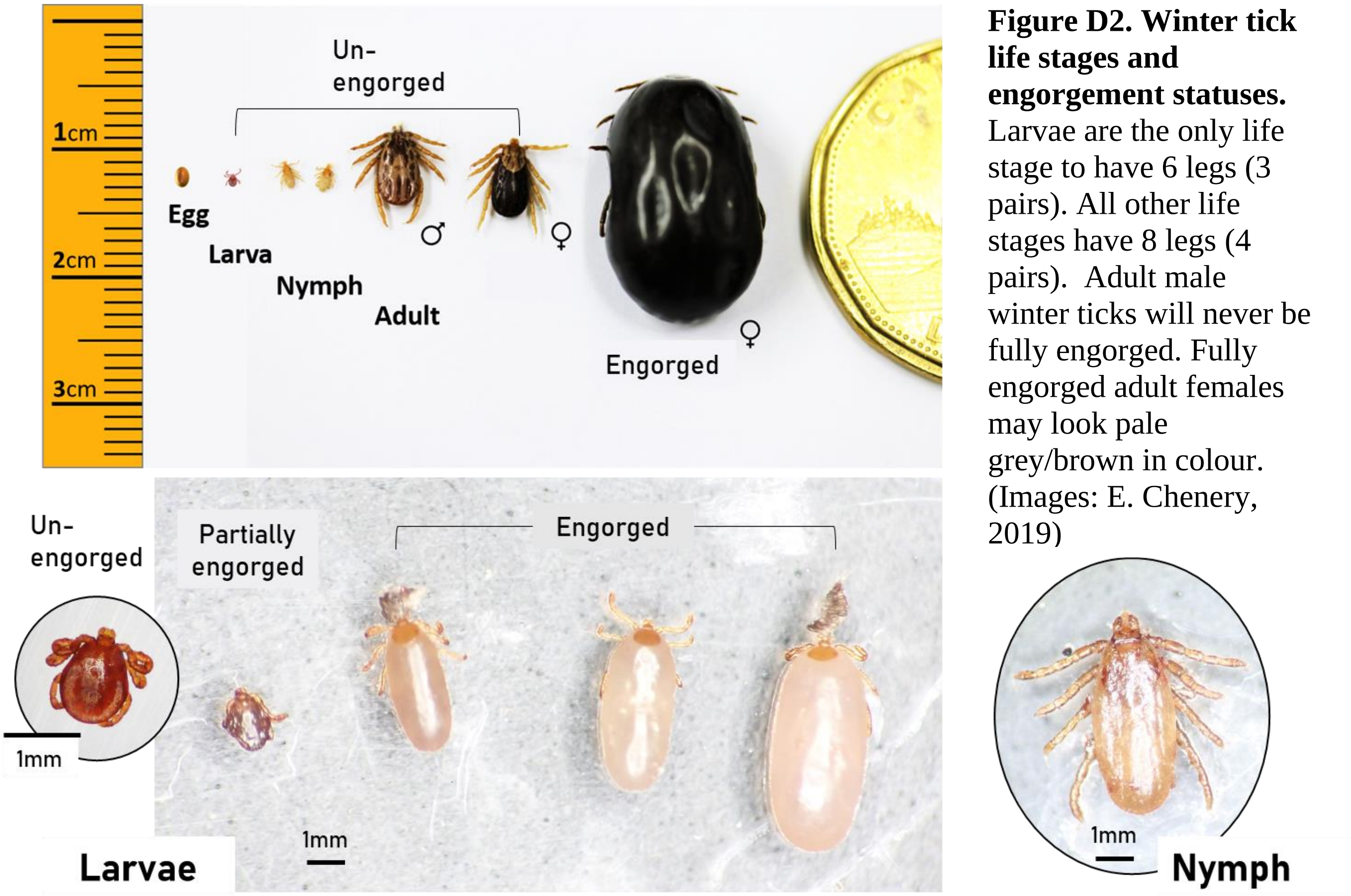


Figure D2. Winter tick life stages and engorgement statuses. Larvae are the only life stage to have 6 legs (3 pairs). All other life stages have 8 legs (4 pairs). Adult male winter ticks will never be fully engorged. Fully engorged adult females may look pale grey/brown in colour. (Images: E. Chenery, 2019)

9. Complete the datasheet with the total number of transects used and total the number of ticks across transects, including the 5 transect table on the back of the sheet. If no ticks were detected, make sure to write “0” in the total ticks column (do <u>not</u> leave blank).
10. Hide pieces and bags can be disposed of. Keep tick specimens in ethanol if uncertain of their identification. Be sure to label any specimens clearly with the HIDE and Lab-ID number.

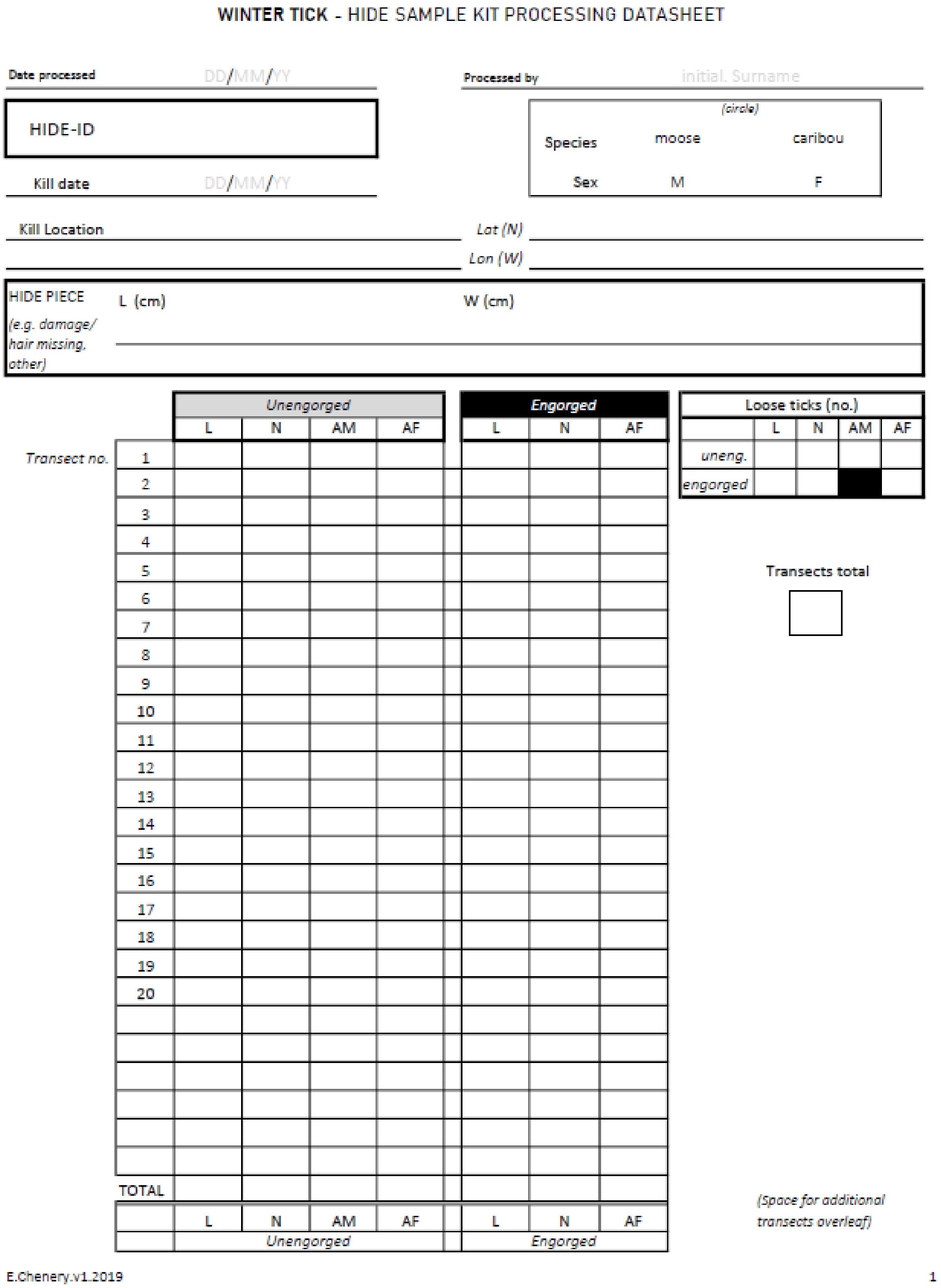
The datasheet should be entered electronically, updating tick totals on the Winter_Tick_Hide_Samples_2011-present.xls using the <u>5 transect</u> totals, and the full dataset on the Hide_Samples tab of the workbook.

References

Kuba, K., M. Larivee, E. Kloppers, R. Ward, R. Florkiewicz, M. VanderKop, & N. J. Harms. (2016). Hair transect sampling method trials for monitoring winter tick (*Dermacentor albipictus*) burdens on elk (*Cervus elaphus*) hides in Yukon. Yukon Fish and Wildlife Branch Report TR-16. Whitehorse, Yukon, Canada.

Sine, M., K. Morris, & D. Knupp. (2009). Assessment of a line transect field method to determine winter tick abundance on moose. *Alces*, *45*(October), 143–146.

Section 1. Hide Sample processing datasheet



WINTER TICK - HIDE SAMPLE KIT PROCESSING DATASHEET

Date processed DD/MM/YY

Processed by initial. Surname

HIDE-ID

Kill date DD/MM/YY

(circle)

Species moose caribou

Sex M F

Kill Location

Lat (N)

Lon (W)

HIDE PIECE *(e.g. damage/ hair missing, other)* L (cm) W (cm)

	Unengorged				*Engorged*		
Transect no.	L	N	AM	AF	L	N	AF
1							
2							
3							
4							
5							
6							
7							
8							
9							
10							
11							
12							
13							
14							
15							
16							
17							
18							
19							
20							
TOTAL							
	L	N	AM	AF	L	N	AF
	Unengorged				*Engorged*		

Loose ticks (no.)				
	L	N	AM	AF
uneng.				
engorged			■	

Transects total

☐

(Space for additional transects overleaf)

E.Chenery.v1.2019

1

WINTER TICK - HIDE SAMPLE KIT PROCESSING DATASHEET

(Continued from p1. additional transects if needed)

	Unengorged				*Engorged*		
	L	N	AM	AF	L	N	AF
Transect no.							
TOTAL							
	L	N	AM	AF	L	N	AF
	Unengorged				*Engorged*		

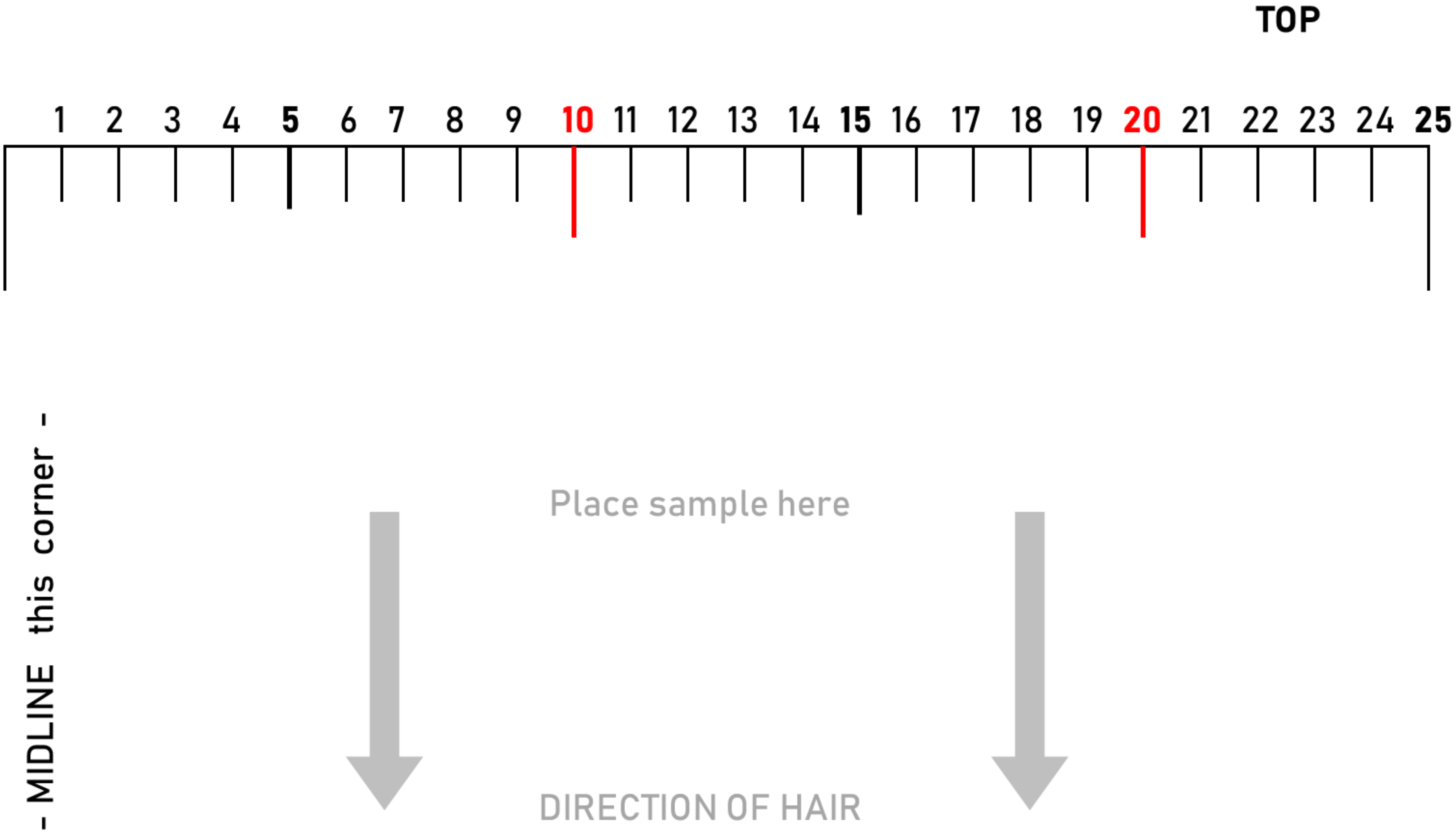
For Winter_Tick_Hide_Submissions.xls

Number of transects from p1 ☐
Divide by 5
Round down <.5
Round up >=.5 ☐

Using totals from the full transect list overleaf, sum ticks to create 5, even transects.
e.g. For a total of 20 transects, (20/5=4) sum ticks in transects in groups of 4:
1-4, 5-8, 9-12, 13-16 and 14-20.

Sum transect no.			*Unengorged*				*Engorged*		
	from	to	L	N	AM	AF	L	N	AF
R1									
R2									
R3									
R4									
R5									

Section 2. Hide sample transect template



- MIDLINE this edge -

BOTTOM

D.3 Hide sample map 2011-2020: all species

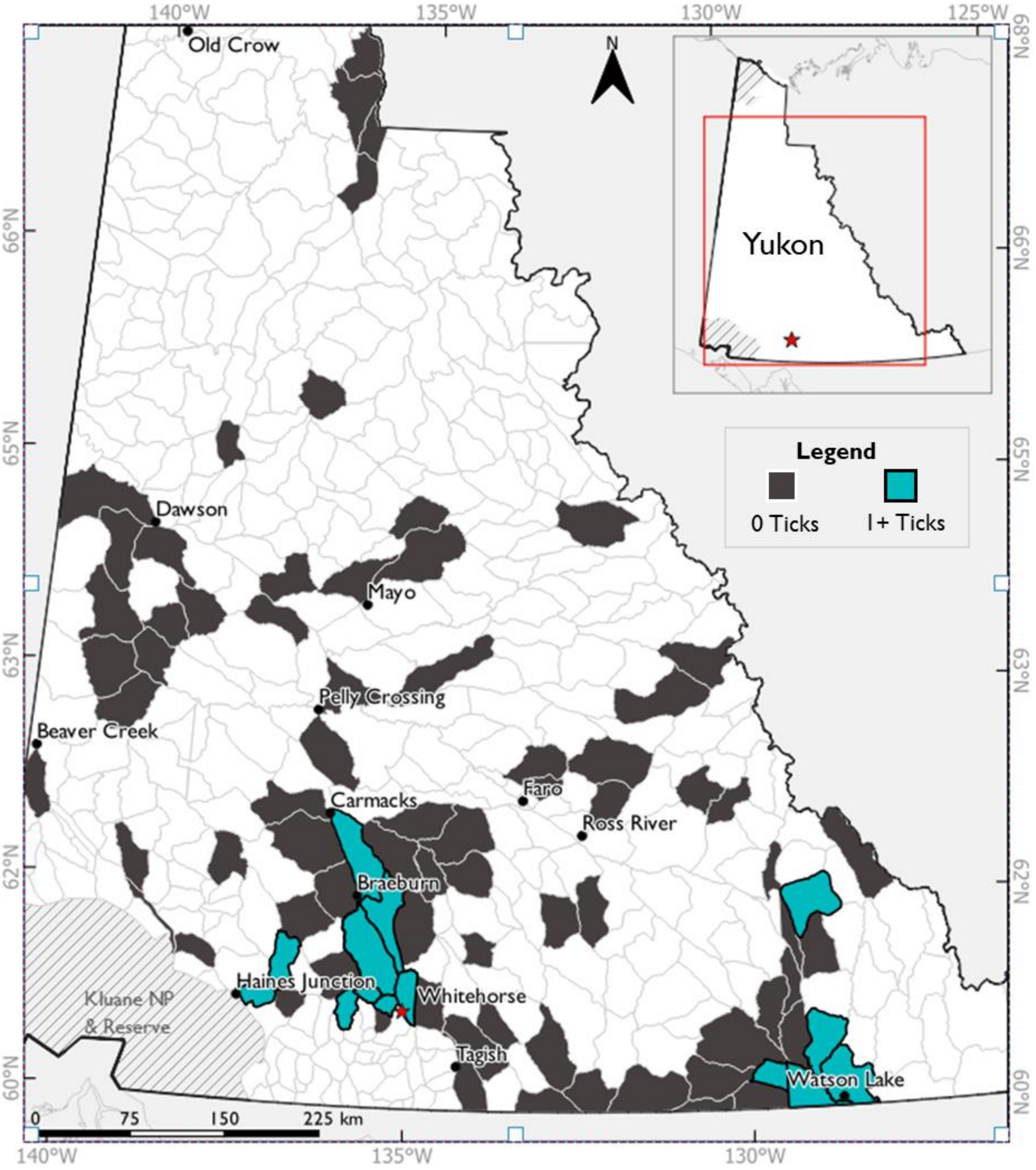


Figure D3. Map of Yukon Game Management Subzones (GMS) where hide samples have been received from cervid hunters (moose, elk, caribou, mule deer), 2011 – 2020 seasons. Subzones where one or more winter ticks (*Dermacentor albipictus)* have been found on one or more hides are shown in blue, all hides on which ticks have not yet been detected are given in dark grey. GMS that have not been sampled are shown in white.