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COMMENTARY

Gaps and opportunities in on-host winter tick (*Dermacentor albipictus*) surveillance in North America

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Abstract

The investigation and management of the impacts of winter tick (*Dermacentor albipictus*) infestations on moose (*Alces alces*) in North America necessitates coordinated surveillance and intervention efforts. However, variations in parasite surveillance methods and potential biases towards sampling specific host species for this generalist parasite can impede attempts to standardize observed disease patterns across vast regions and into the future. We collected and classified records of winter tick surveillance on ungulate hosts throughout North America to identify trends and biases in species, space, and time, with the aim of identifying gaps and suggesting improvements to existing practices. We conducted a literature review spanning a century of winter tick reports on free-roaming or wild ungulate hosts in North America, resulting in 125 relevant records. From this sample, we compiled information on host species and surveillance method details and categorized winter tick quantification techniques based on their perceived insight for analyses and interventions, assigned as an ecological information value (Eco-IV) ranging from 0 to 3. We examined variations in Eco-IV among free-roaming ungulates based on species, literature type, and data source. Among the 18 identified ungulate hosts, moose, white-tailed deer (*Odocoileus virginianus*),

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and elk (*Cervus canadensis*) were most frequently reported. We observed a higher Eco-IV for moose, indicating an abundance of species-specific information, and a lower Eco-IV (less information available) for methods focusing on white-tailed deer. Limited sample sizes prevented the identification of patterns of knowledge acquisition for elk. Eco-IVs in other ungulate species were consistently lower than moose, white-tailed deer, and elk, regardless of literature type or data source. Exotic and invasive species systematically lacked detailed methods (Eco-IV = 0). These findings highlight significant information gaps that impede the ability to compare winter tick infestation rates across studies, geographic regions, and host species, thus hindering coordinated management actions. We recommend standardizing winter tick quantification methods for all ungulate host species, specifically other common winter tick hosts such as white-tailed deer and elk, and increased communication among groups working on tick–host systems to address these gaps.

KEYWORDS

Alces alces, *Dermacentor albipictus*, moose, review, sampling, surveillance, ungulates, winter tick

Understanding and addressing the impacts of disease in multi-host systems of managed species presents considerable challenges to wildlife managers and disease researchers alike (Shaw and Dobson 1995, Dobson and Foufopoulos 2001, Joseph et al. 2013). The management of macroparasitic diseases in wildlife can be particularly challenging owing to complex system dynamics. These complexities may arise from unknown relationships between infestation burdens and host health, and sensitivities to environmental factors. Typical confounding components of wildlife disease systems like over-dispersed infestation distributions, limited host availability for sampling, and heterogeneity in clinical presentations across host species magnify challenges to research and management actions (Lachish and Murray 2018, Portier et al. 2019).

Comprehensive surveillance studies play a crucial role in developing effective management actions and analyzing parasite–host dynamics, including assessing invasion potential to new geographic regions and investigating ecological drivers for epizootic cycles (Stallknecht 2007, Lachish and Murray 2018). Such studies often quantify system characteristics like disease prevalence, infestation intensities, and host health outcomes, which are critical for analysis and decision-making but are often difficult to collect across large sample sizes and different host species. Additionally, limited surveys may suffer from several potential biases in wildlife disease monitoring. Surveys may focus on focal species with highly visible declines or disease symptoms, overlooking relevant reservoir species. For dose-dependent pathologies, as is the case for many parasite systems, some methods used for monitoring parasite loads and host health may have constrained analytical utility when infestation magnitudes are not appropriately measured. Additional biases can arise if individuals are sampled opportunistically, which may not align with the optimal parasite detection windows or draw from portions of the population with higher disease prevalence rates or burdens (Walton et al. 2016, Huyvaert 2018, Lachish and Murray 2018). For instance, Nusser et al. (2008) simulated disease surveillance studies for chronic wasting disease in white-tailed deer (*Odocoileus virginianus*) and found that convenience sampling (e.g., road-kill, hunter-shot sampling) can lead to biased or misleading results such as higher prevalence estimates in road-kill studies and lower prevalence in hunter-shot studies given a random disease model.

Imprecision or bias in surveillance data resulting from such limited monitoring studies can have a significant impact on estimates of infestation prevalence and intensity across hosts (Miller et al. 2012). This leads to increased uncertainty in determining appropriate management actions or conducting downstream analyses, especially in wildlife systems where baseline infestation data is typically scarce (Stephen and Berezowski 2022).

Concern over parasitic diseases and their impact on managed species has increased as interactions with threats posed by changes in land-use and climate become more evident (Hoberg et al. 2008, Weiskopf et al. 2019). Many parasite species, like certain tick species, spend a large proportion of their life cycle off-host, which increases their sensitivity to environmental changes like rising temperatures and fluctuating precipitation patterns in comparison to directly transmitted pathogens (Kutz et al. 2009). Shifts in host abundance and invasions of new host species caused by anthropogenic land-use and movement can also modify parasite life cycles for species with multiple definitive hosts or important reproductive life stages in multiple host species (Kutz et al. 2004, Hoberg et al. 2008). Providing a rigorous overview of how a parasite system has been monitored in the past and where biases and uncertainties persist can provide crucial information for developing effective surveillance program to address the impact parasites have on wildlife health, particularly in the context of global changes.

Winter ticks (*Dermacentor albipictus*) are obligate ectoparasites parasitizing several host species but are particularly notorious for their detrimental impact on moose (*Alces alces*). Moose can suffer from heavy tick burdens, often exceeding 50,000 ticks per animal, leading to significant hair loss (alopecia), blood loss, and even mortality in both adult moose and calves less than a year old (Samuel and Welch 1991, Samuel 2007). As one-host ticks, winter ticks spend a considerable portion of their life cycle on an individual host, attaching as larvae in the fall and remaining on-host throughout all 3 instars until fed adult female ticks drop off in spring (Samuel 2004). The dose-dependent nature of winter tick-induced disease and the timing of disease sampling on ungulates, which typically occurs during hunting seasons in the fall or capture seasons in the winter, have resulted in most studies reporting winter tick occurrence being focused on on-host studies rather than off-host surveys.

Hair loss, especially in late-stage winter tick infestations on moose, is a common symptom caused by the host's excessive grooming to remove engorging adult ticks (Glines 1983, Mooring and Samuel 1998*a*). The resulting distinctive, patchy appearance of moose, most visible in late winter and early spring, is coupled with other known or putative negative impacts on host health like reduced foraging time and decreased thermoregulation abilities (Musante et al. 2007, 2010). The combined effects of blood loss due to tick feeding and complications from grooming and hair loss can lead to poor nutritional condition, lower reproductive output or delayed reproductive timing, and even death (Scarpitti et al. 2005, Murray et al. 2006, Samuel 2007, Jones et al. 2017). Calves are especially susceptible to parasitism by winter ticks because of their relatively low body size and fast metabolism, making even moderate infestations problematic (Musante et al. 2007, Jones et al. 2017).

Additionally, susceptibility to complications from high winter tick infestation seems to differ significantly across host species, with symptoms from winter tick infestations infrequently reported in elk (*Cervus canadensis*), caribou (*Rangifer tarandus*), and white-tailed deer (Bondo et al. 2019, Calvente et al. 2020, Machtinger et al. 2021). Observed differences in infestation load and hair loss severity between moose and other ungulate species is hypothesized to be partially due to grooming behavior differences (Mooring and Samuel 1998*a* 1998*b* 1999; Addison et al. 2019; Normandeau et al. 2022; Mooring 2024). Under the programmed versus stimulus grooming hypothesis, moose are understood to be stimulus groomers where grooming activities are prompted by cutaneous irritation following adult female winter ticks engorging (Mooring 2024). Moose would therefore only begin removing large numbers of adult ticks by grooming from March-April, ultimately leading to hair loss. By contrast, programmed groomers, such as elk or white-tailed deer, regularly groom throughout the fall and winter months, reducing tick load throughout the on-host period. Although winter tick epizootics on non-moose hosts do not appear to be common or widespread, such hosts could still play an important role in overall winter tick dynamics across the landscape, especially in regions where they dramatically outnumber moose. Understanding the relative contributions of non-moose hosts to winter tick encounter rates with moose could help moose management and conservation agencies better address concerns with moose population trends. Additionally, species-specific pathologies from winter tick infestations highlight the need to validate and to develop winter tick surveillance in non-moose ungulates, especially considering that recent expansions of winter ticks (Kutz et al. 2009, Chenery et al. 2023) and moose (Chubbs and Schaefer 1997, Tape et al. 2016) northward into historically naive host populations.

Quantification methods for determining winter tick burdens on hosts are diverse and vary in the level of details they provide (Table 1). These methods include lethal or destructive techniques (e.g., hide digestions on hunter-harvested or roadkill carcasses), capture-specific methods (e.g., transect counts, timed counts, qualitative burden estimation), or non-invasive visual estimations of hair loss via photography, which is presumed to be correlated with tick burden (Glines and Samuel 1989, Sine et al. 2009, Wunschmann et al. 2015, Hoy et al. 2021). As with any disease surveillance metric, these methods generate data on important host–pathogen system characteristics like prevalence, infestation intensity, and correlated health outcomes on sampled hosts, which have varying utility for downstream analyses or for decision-making. For example, prevalence or occurrence data through hair loss can be helpful for analyzing spread or invasion, while transect counts can provide an estimation of burden and, when coupled with host health metrics, could be useful for analyzing host–parasite dynamics (Lachish and Murray 2018). For dose-dependent parasite systems in which pathology is known or theorized to result from infestation load, as opposed to simple occurrence, accurate burden estimations are crucial to linking load to health impacts and comparing infestation dynamics across species and areas.

TABLE 1 Methods and frequent synonyms commonly used to detect winter ticks on hosts for winter tick–ungulate host studies published in 1920–2021, including a non-exhaustive list of studies that either designed, validated, or used each method.

Method	Description	Uses	Example references
Transect Hair transect, hide transect, line transect, transect counts	Distance based method, counting the number of ticks per line of equal length (normally 10 cm). Sampling effort recorded (number of transects).	Tick count Burden estimation Density estimation	Sine et al. (2009)
Digestion Hide digestion	Count of tick exoskeletons following digestion of 10 × 10-cm hide samples (number of samples representing 15% of the total hide surface) into a potassium hydroxide solution.	Tick count Burden estimation Density estimation	Sine et al. (2009) Welch et al. (1989)
Timed sampling Carcasses were scanned for parasites during *x* minutes by one observer	Number of ticks counted per time unit, ideally by explicitly writing the number of persons involved and which body areas were scanned per host	Tick count Burden estimation Tick prevalence Tick occurrence	Durden et al. (1991) Amerasinghe et al. (1992)
Visual or *ad libitum* survey Visual inspection, scanned for parasites, collected ticks	Visual inspection of animals (e.g., during captures, or hunter registration stations), with effort not recorded (although often body areas scanned were cited).	Tick count Tick prevalence Tick occurrence	Wedincamp et al. (2016)
Hair loss quantification Hair damage, complete or partial hair damage, alopecia, hair breakage	Estimation of the area (or in rare case, volume) covered by hair loss or alopecia caused by winter ticks. Estimation either through continuous values (% of total area) or categories (variable, but mostly <5%; ~5–20%; ~20–40%; ~40–80%; >80%)	Index of tick burden Population-scale hair loss severity index Tick occurrence	Samuel and Barker (1979) Samuel et al.(1989) Samuel et al. (2004) Bergeron et al. (2014)

In the case of the winter tick–ungulate host system, data on disease severity and infestation burden are useful for managing and investigating disease dynamics and are often collected at various times of year. In moose particularly, most winter tick-related sampling takes the form of hunter-harvested sampling occurring around October-November and capture-related sampling occurring around January-February (Healy et al. 2020, Hoy et al. 2021, Rosenblatt et al. 2021). However, winter tick infestation intensity metrics are less frequently noted in other ungulates such as elk, caribou, and white-tailed deer despite studies describing incidental disease outcomes and notable infestation rates (Samuel and Welch 1991, Samuel 2004, Sine et al. 2009, Bondo et al. 2019, Calvente et al. 2020). Historically, winter ticks have been associated with moose declines in the northeastern United States and midwestern Canadian provinces, driven partially by moose density, earlier snow melt in spring, and later snowfall in fall, among other factors (Samuel 2007, Dunfey-Ball 2017, Healy et al. 2020). Recent observations of winter tick-related issues on moose populations in the western United States have raised concerns over winter tick impacts on western moose populations, specifically around regionally specific climate conditions associated with epizootics and interactions between winter ticks, moose, and overlapping host species like elk and mule deer (*Odocoileus hemionus*; Wunschmann et al. 2015, Idaho Department of Fish and Game [IDFG] 2017, Wyoming Game and Fish Department [WGFD] 2017, Bondo et al. 2019). The winter tick's broad geographic range (Chenery et al. 2023) and ability to parasitize a wide range of host species, including numerous ungulates, complicates consistent data collection and makes the winter tick system an ideal example for overviewing biases and uncertainties in monitoring.

We reviewed winter tick surveillance studies on ungulate hosts (ungulate species) and examined trends and biases in methods across host species, space, and time to assess critical gaps in current on-host surveillance methods. We discuss the resultant impacts on efforts to describe this disease system in the literature. By classifying and comparing methods of data collection across studies, we also explored the limitations of different survey designs and offer suggestions for best practices moving forward.

METHODS

Literature search

We assessed the available literature to examine how winter ticks are monitored across multiple ungulate host species in North America. Between 1 April and 15 April 2021, all co-authors separately launched search queries with the same combination of key words (see below) using their own institutional subscription to Web of Science (Clarivate Web of Science 2021). We performed subsequent searches on the institutional subscription that provided the highest number of records among co-authors. We collected published records of winter ticks on hosts (written in English or French) using a Boolean search query on 6 May 2021 on Web of Science (Clarivate Web of Science 2021). Our exact search string was TS = ("Dermacentor albipictus" OR "winter tick" OR "Ixodes albipictus" OR "Dermacentor albipictus kamschadalus" OR "Dermacentor kamschadalus" OR "Dermacentor erraticus albipictus" OR "Dermacentor nigrolineatus" OR "Ixodes oregonensis" OR "Dermacentor variegatus" OR "Dermacentor salmoni" OR "Cynorhaestes albipictus" OR "Dermacentor varius" OR "Elk tick" OR "Moose tick" OR "White fern winter tick" OR "White fern tick") AND TS = ("Alces" OR "Antilocapra" OR "Sus" OR "Tayassu" OR "Catagonus" OR "Pecari" OR "Rangifer" OR "Odocoileus" OR "Cervus" OR "Elaphus" OR "Ovis" OR "Oreamnos" OR "Ovibos" OR "Bison" OR "Equus"). We gathered 218 records dating from 1917 to 2021, primarily consisting of research articles published in scientific journals but also including a small number of records in the grey literature. To ensure grey literature studies were accurately represented in our data, we conducted targeted searches in ProQuest, Networked Digital Library of Theses and Dissertations, WorldCat, and EBSCO using the same key words as our initial search. Because several ungulate taxa are managed game species in North America, we also searched for records of winter ticks by searching for the term 'winter tick' in the provided search bar of Canadian, American, and Mexican provincial and state wildlife management agency websites. These searches yielded 48 additional records.

We screened all records for appropriateness based on the following eligibility criteria: 1) reports a novel record of winter tick occurrence on an ungulate host; 2) is not a synthesis, review, or modeling paper (may lead to double-counting or not real-world observation); 3) is not a laboratory study (only surveillance on species for which there are wild and free-roaming populations); and 4) is not an off-host survey or record on non-ungulate hosts (to exclude larval field collections studies and records on non-target hosts).

We ensured that there was an adequate author agreement for the assessment of record eligibility by estimating a Fleiss' kappa statistic (κ). A subset of 24 randomly selected records were assessed for appropriateness by all authors. We estimated agreement using the Fleiss' kappa statistic because it is a multi-rater statistic that is suitable to estimate agreement with categorical data (Gamer et al. 2021). Authors assessed appropriateness for inclusion for each study by classifying each of the 24 records as either yes (appropriate to be included for winter tick-surveillance methods), yes captive or experimental (appropriate to be included with the caveat that animals studied are not free-roaming), or no (not appropriate). We considered a pre-determined threshold of 0.6 or above as a benchmark for sufficient agreement, as in other reviews (Koricheva et al. 2013, de Raadt et al. 2021, Gamer et al. 2021). While studies on captive ungulates were retained at the appropriateness screening step, only studies on free-roaming ungulates moved on for data extraction and analysis.

Data extraction

We used a standardized questionnaire (Supporting Information S1), splitting literature item assessment across authors, to systematically record tick-load quantification techniques, tick identification methods, and information on host species and study context for the 125 records that met our criteria following our original search. In cases where an author was unsure if a record should be included or if they desired a second opinion on what methods were used, a second author was directed to read the record and discuss appropriate actions, which could include removing a record. We ensured that there was adequate author agreement on data extracted from literature items by estimating a Fleiss' kappa consensus statistic based on questionnaires for a subset of 5 randomly selected records. After screening and collecting data from all accepted records, we extracted information regarding the specific time periods when the methods were applied on hosts (e.g., fall hunting surveys, winter capture surveys).

To assess differences in the level of insight provided by different surveillance metrics across species, we classified methods into 4 ordered levels based on the authors' determination of ecological information value (Eco-IV). We assigned the lowest value as 0 (scarce or missing details) when authors reported winter ticks on a host species, with no quantitative measurements (e.g., "we found winter ticks on moose"), or when the methods were too poorly detailed and could not be appropriately understood. We assigned a value of 1 for tick occurrence when authors clearly reported winter tick occurrence (e.g., "we found winter ticks on a collared peccary") or prevalence on an ungulate host species (e.g., "winter ticks were found on 4/12 collared peccaries"). We assigned methods a 2 for counts or proxies (effort not measured) when authors specifically counted tick loads or used a proxy of tick load but did not account for sampling effort (e.g., "112 individual ticks counted along a white-tailed deer ear"). Finally, we gave the highest score (3) for quantification (effort measured) when winter ticks were counted while accounting for sampling effort, such as transect length or amount of time scanning for ticks (e.g., "112 individual ticks were counted along a 70-cm midline transect of a white-tailed deer").

Statistical analysis

We used a cumulative link model (with a logit link) using the ordinal package (Christensen 2019) in the R statistical software (R Core Team 2022) to investigate variations in method Eco-IV. Cumulative link models (i.e., proportional-odds models) are suitable for ranked categorical data, specially ordered categories with not necessarily equal intervals between ranks (Christensen 2019). Independent variables included data source (3 levels: unknown or unspecified source, citizen science, data collected by veterinary or wildlife professionals), type of publication (2 levels: grey literature, white literature) and host species (4 levels: moose, white-tailed deer, elk, other native species). We included a nominal effect of time period (1927–1988 or 1989–2021) on flexible thresholds to relax the proportional odds assumption (Christensen 2022). We chose 1989 to split time periods as this is when Welch and Samuel (1989) published a landmark manuscript on the hide digestion technique to quantify tick burden, a paper abundantly cited and used in following scientific publications. We categorized all native ungulate species besides white-tailed deer, elk, and moose into a combined group because of small sample sizes and to avoid complete separation. We restricted our analysis to native ungulate species because winter tick surveillance metrics were always poorly detailed in exotic or invasive species (Eco-IV = 0). If studies included a single surveillance method on multiple species, each unique combination of said surveillance method and host species was considered separately. When several methods were used for a species in a study, we kept the one with the highest score to avoid inflating our sample with methods to report ticks on hosts that had lower quantitative potential. For example, if a study estimated winter tick burden using the transect method (Sine et al. 2009; Eco-IV = 3) and hair loss occurrence (Eco-IV = 1) for 2 species (e.g., moose and white-tailed deer), our dataset included only 1 entry per species for the method with the highest score, which in this case are the transect counts.

RESULTS

We reviewed 266 literature items, of which 125 were deemed to contain relevant records of winter ticks on ungulate hosts (Figure 1). Fleiss' kappa estimating agreement on the appropriateness of a subset of 24 randomly selected literature items was $\kappa = 0.796$ ($z = 10.1$) for 4 reviewers and Fleiss' kappa for estimating agreement on questionnaire answers for 5 randomly selected relevant records was $\kappa = 0.828$ ($z = 78.8$) for 4 reviewers.

Data extraction from 125 relevant records yielded 153 unique reports of tick sampling method, host species, and literature item. These represented studies conducted over several states, provinces, and territories across the United States ($n = 107$), Canada ($n = 52$), and Mexico ($n = 1$) from 1917 to 2021, with 33.6% ($n = 42$) of the 125 records published in the last decade (Figure 2). Grey literature represented 20% ($n = 25$) of our screened records and was relatively more abundant in recent years than prior to 2010 (Figure 2B).

Ungulate hosts reported

From 125 records, we found 153 reports of winter ticks on 18 ungulate host species, of which moose (30.7%), white-tailed deer (26.8%), and elk (9.8%) were the most frequently cited hosts (Figure 3). Infestations on other native species included mule deer (*Odocoileus hemionus*; 7.2%), caribou (6.5%), and bighorn sheep (*Ovis canadensis*; 3.9%), and a small number of records of winter ticks on bison (*Bison bison*), pronghorn (*Antilocapra americana*), collared peccary (*Pecari tajacu*), mountain goat (*Oreamnos americanus*), and Stone's sheep (*Ovis dalli stonei*; cumulative 4.6%). Winter ticks were also reported on some instances of freely roaming non-native ungulate species such as barbary sheep (*Ammotragus lervia*), axis deer (*Axis axis*), fallow deer (*Dama dama*), Sika deer (*Cervus nippon*), red brocket deer (*Mazama americana*; cumulative 5.9%), horse (*Equus caballus*; 2.6%), llama (*Lama glama*; 0.7%), and feral pig (*Sus scrofa*; 2.6%). Overall, 78 records explicitly identified physical sampling locations on hosts. Sampling on moose was concentrated in 3 general areas: rump and croup, shoulders and withers, and neck (Table 2; Supporting Information S2). In white-tailed deer, sampling focused mainly on head, face, ears, and neck. General trends in quantification method by body area were not discernable in other ungulate species because of the low number of records with explicit details on body areas surveyed ($n = 14$).

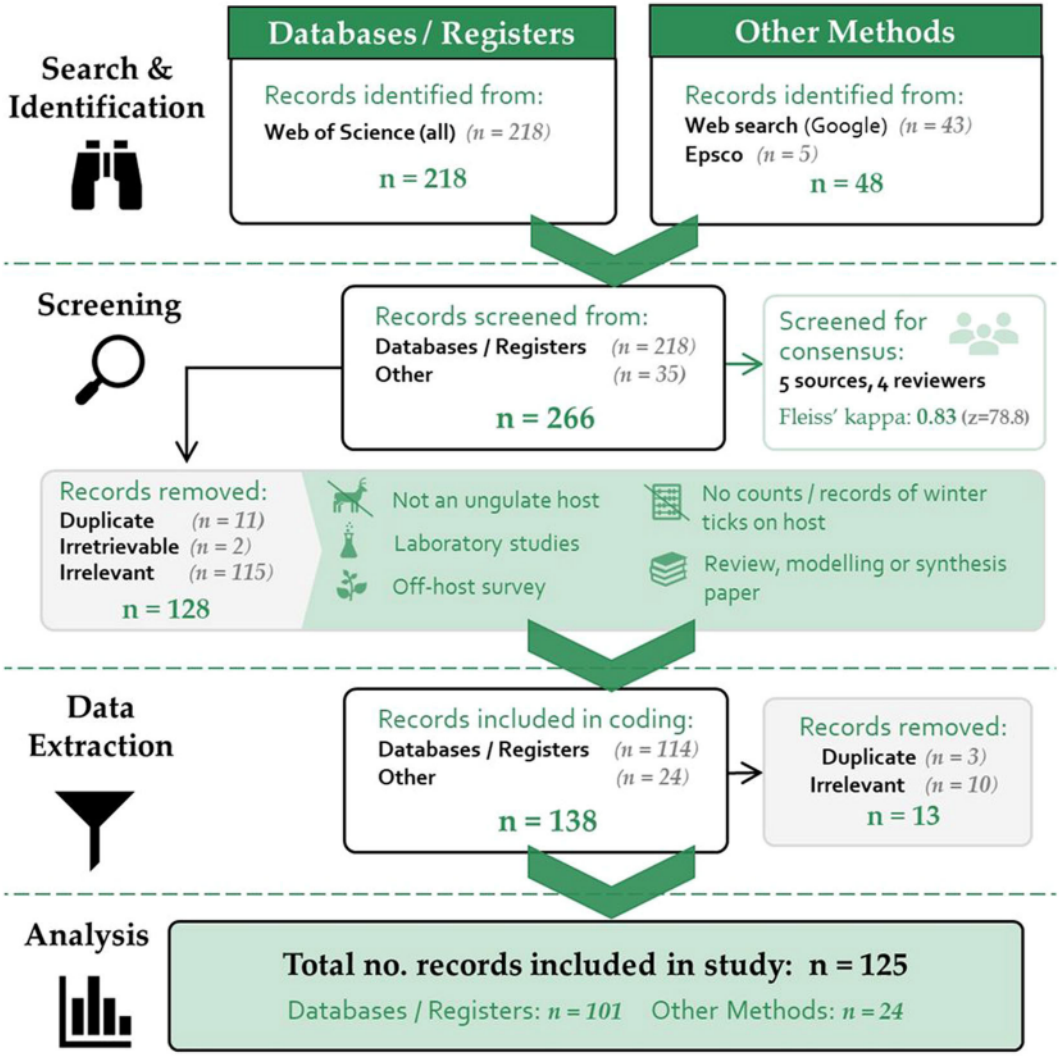

FIGURE 1 Diagram of the literature search and data extraction process used to obtain winter tick records on ungulate hosts.

Ecological information value (Eco-IV) across ungulate hosts

Winter tick surveillance metrics with some form of effort measured (transect counts, timed sampling, hide digestion) were more frequently recorded in studies on moose than for other ungulate species (Figures 3 and 4). Records noting winter tick infestations by prevalence or occurrence data only were more often found in white-tailed deer than other species (Figure 4C), while there was extensive variation in tick sampling method accuracy for records on elk (Figure 4). The number of records reporting winter tick sampling on moose increased in recent years (Figure 5A), while the peak in monitoring winter ticks occurred earlier around the 1990s in white-tailed deer (Figure 5B). The proportion of records using winter tick quantification methods with missing details on moose decreased until the 1990s but started to increase again afterward, reaching similar proportions in the 2000s as in the 1970s (Figure 5A). In white-tailed deer, studies between 1990–2010 tended to include higher Eco-IV methods, yet poorly detailed or imprecise methods of measuring winter tick burden still represented approximately 20–50% of records in the last

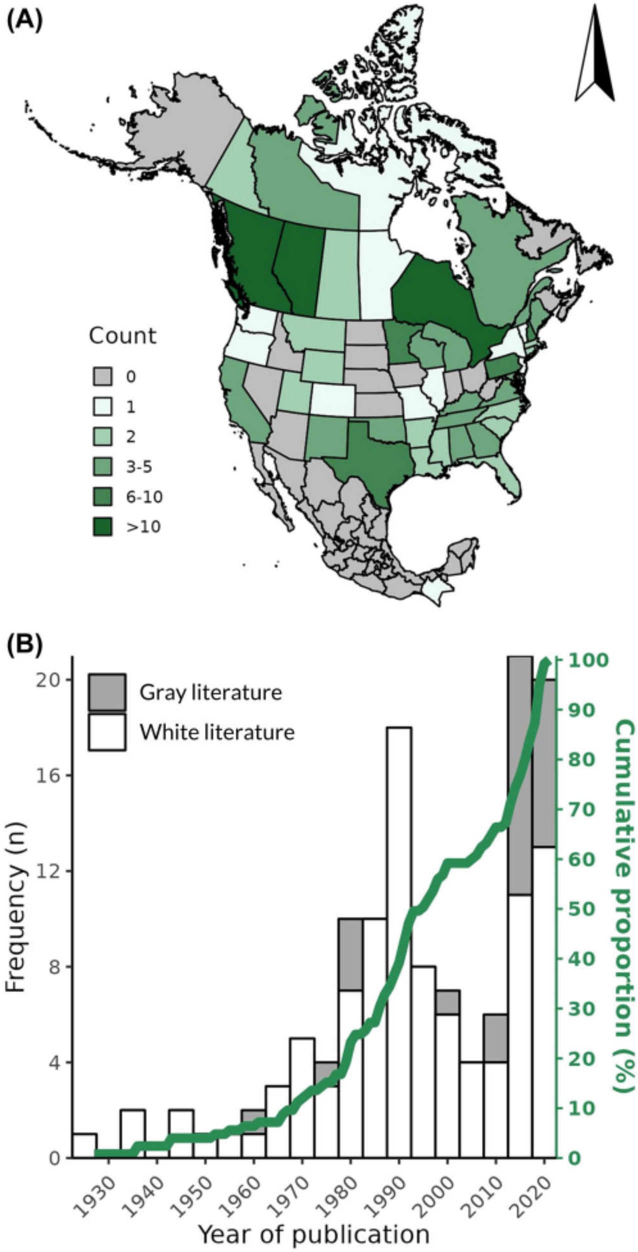

FIGURE 2 A) Geographical distribution of studies that reported winter ticks on at least one host species in North America from 1920–2021. B) Timeline of records broken by gray versus white literature (shaded) and by number per year (primary axis, bars) with cumulative proportion of the number of records in our dataset (secondary axis, green line).

40 years (Figure 5B). In elk, discontinuity in time and small sample size hindered any observation of clear patterns (Figure 5C).

Our cumulative link model revealed lower Eco-IV for winter tick infestation data from other native ungulate species compared to moose (Figure 6; Table 3). While odds ratios for white-tailed deer and elk were negative compared with moose, this trend was not as evident as with other native species. The odds of occurrence of a

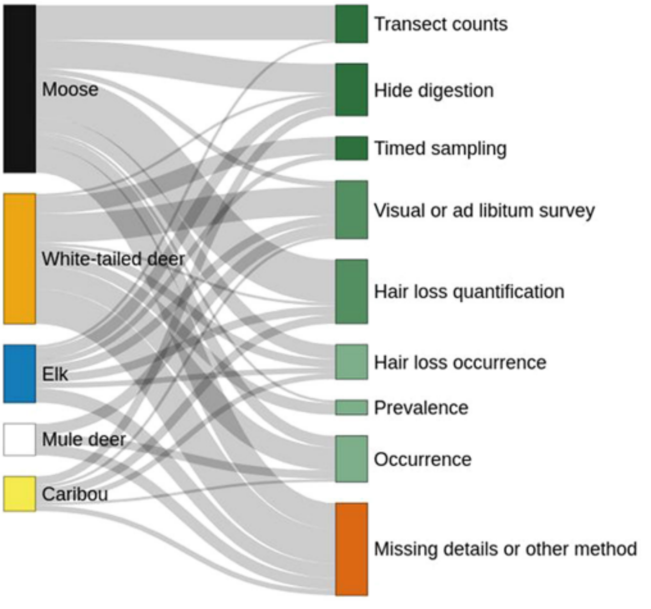

FIGURE 3 Sankey diagram displaying the relationships between tick monitoring methods (right) and the 5 most frequently reported host species in our data (left) for winter tick–ungulate host studies published in 1917–2021. Bar height and line width is proportional to the number of times a host has been reported for a given method. Methods are ranked from the highest ecological information value (Eco-IV; 3 [dark green]) to the lowest (1 [light green]), followed by missing information (0 [orange]).

higher value of Eco-IV for other ungulates were 0.10 (95% CI = 0.034–0.260) times that of moose (Figure 6A). When accounting for other factors, the decrease in predicted probabilities of observing a larger Eco-IV was more pronounced in other native species than in the 3 more commonly reported hosts species (Figure 6B). Our analysis did not reveal evidence of effects of literature type (white vs. grey literature) and data from professionals or from citizen science did not clearly affect Eco-IV (Figure 6A; Table 3).

Temporal distribution of methods and characterization of records

On a yearly basis, timed sampling methods were used most often in November and December, while hair loss methods were commonly reported in April and May (Figure 7). Historically, winter ticks were more often sampled on dead hosts than on living hosts (Figure 8), whether on hunter harvested hides or carcasses (as was commonly reported for white-tailed deer) or from necropsies. This trend shifted in 2010–2019 to include a larger number of reports of ticks on living hosts (Figure 8).

DISCUSSION

Developing an appropriate disease surveillance framework for multi-host parasite systems can be especially challenging in the absence of consistent collection protocols. In the winter tick–ungulate system, surveillance methods varied greatly across space, time, and host species, which can impede efforts to study epizootic trends and invasion patterns at larger scales. Our literature analysis revealed many instances in which records claiming

TABLE 2 Body areas scanned for ticks for all species mentioned in our dataset of winter tick–ungulate host studies published in 1920–2021. All sampling methods and accuracies were combined. Digits represent the number of studies that explicitly looked for ticks in given physical body area locations (e.g., 2 studies mentioned they looked for ticks at least on the head and face for moose). A study can thus be part of counts for several body areas. See Supporting Information S2 for body area locations.

	Body area																	
Host species	Head	Ears	Neck	Withers	Shoulder	Axilla	Chest	Ventral	Ribs	Flank	Inguinal	Ano-genital	Dorsal	Croup	Tail	Rump	Legs	Whole animal
Moose (*Alces alces*)	2	0	9	6	13	0	3	1	1	0	0	6	6	2	6	12	3	0
White-tailed deer (*Odocoileus virginianus*)	11	4	9	1	3	1	5	1	0	0	1	2	2	0	2	0	2	1
Elk (*Cervus canadensis*	2	1	1	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0
Mule deer (*Odocoileus hemionus*)	2	3	2	0	0	2	0	2	0	1	1	2	0	0	2	0	0	1
Caribou (*Rangifer tarandus*)	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0
Bighorn sheep (*Ovis canadensis*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stone's sheep (*Ovis dalli stonei*)	0	1	1	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0
Mountain goat (*Oreamnos americanus*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Collared peccary (*Pecari tajacu*)	1	1	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0
Bison (*Bison bison*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Barbary sheep (*Ammotragus lervia*)	2	2	2	0	0	2	0	2	0	0	0	2	0	0	2	0	0	0
Wild pig (*Sus scrofa*)	1	0	1	0	0	1	0	1	0	0	0	1	0	0	1	0	0	0
Horse (*Equus caballus*)	2	0	1	1	2	0	1	1	0	0	0	1	1	1	1	1	1	0
Llama (*Lama glama*)	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0

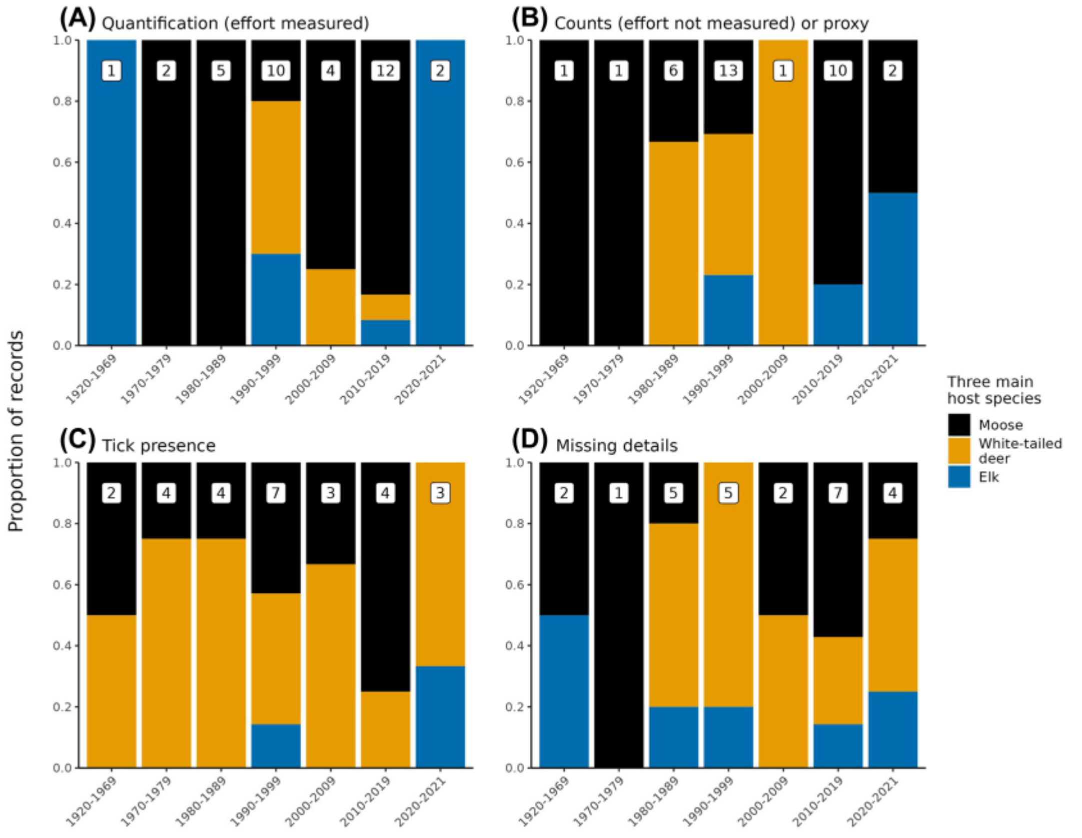

FIGURE 4 Distribution of ecological information value (Eco-IV) categories of sampling methods over time described among the 3 most frequently reported host species (moose, white-tailed deer and elk) for winter tick–ungulate host studies published in 1920–2021. We combined the methods hide digestion, transect counts, and timed sampling (A); visual *ad libitum* sampling and hair loss quantification (B); hair loss occurrence, winter tick prevalence, and winter tick occurrence (C), and those with a lack of precision or details in reported sampling methods (D). White labels with numbers indicate sample size per bar.

to use visual surveys or timed sampling failed to report sampling duration, number of persons involved, or the specific body areas examined. Such omissions limit the utility of collected data by impeding comparisons over time and space and between host species, and diminishes opportunities for managers to make use of existing information.

Trends and gaps in tick quantification across host species

Our study revealed variations in the type and ecological information value (Eco-IV) of winter tick surveillance metrics across ungulate hosts, with tick burden quantification studies with effort measured being less common on non-moose hosts. As mentioned above, moose are often targeted for winter tick monitoring studies because they experience more visible and serious complications from high infestations. However, other ungulates could contribute to the winter tick disease system as reservoirs and may transmit parasites to vulnerable hosts, like moose, when host habitats overlap during tick transmission seasons. When considering tick infestation rates reported in western systems thus far (DeCesare et al. 2024), there is potential that even low infestations with winter ticks could

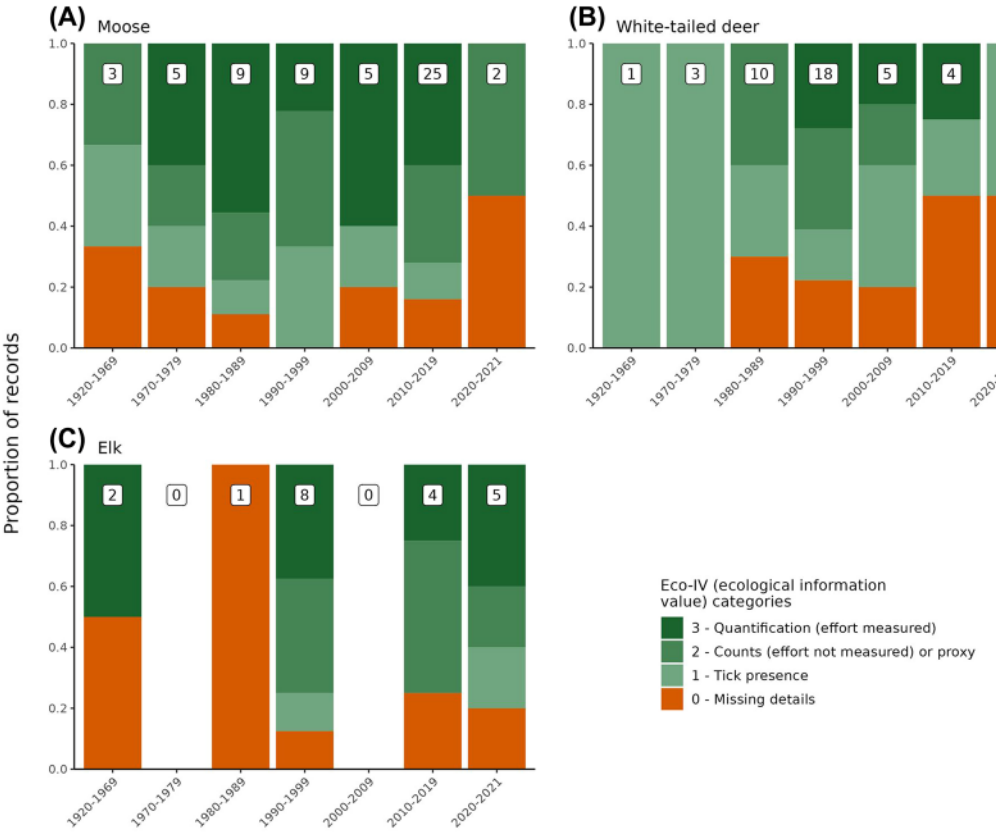

FIGURE 5 Ecological information value (Eco-IV) of sampling methods for winter tick–ungulate host studies by period within each of the 3 most-frequent host species: A) moose, B) white-tailed deer, and C) elk. Quantification (effort measured) includes hide digestion, transect counts, and timed sampling. Counts (effort not measured) or proxy combines visual *ad libitum* sampling and hair loss quantification. Tick presence combines hair loss occurrence, prevalence, and occurrence, and missing details includes studies with a lack of information or details in reported sampling methods. White labels with numbers indicate sample size per bar.

interact with coinfections and other stressors and lead to severe pathology (Debow et al. 2021). Thus, a lack of detailed data in non-moose species leaves critical gaps in the current understanding of winter tick infestation dynamics. In many western ecosystems, elk, mule deer, and caribou can outnumber moose by a factor of ≥10:1 (IDFG 2017, WGFD 2017). Even if other ungulates enter the spring season with fewer winter ticks than moose because they groom throughout the fall and winter, their comparative abundance implies a potentially important role in exposing moose to winter ticks (Samuel and Welch 1991, Mooring and Samuel 1998*a*). Because winter ticks are highly productive and modest infestations can include several hundred ticks per host, even fleeting overlap between the habitats of non-moose and moose hosts could constitute important transmission opportunities (Samuel 2007). For example, moose in the western United States tend to be sparsely distributed compared to northeastern moose and can share a high degree of overlap with other ungulate ranges, specifically elk (DeCesare et al. 2014, Timmerman and Rodgers 2017). Habitat overlap between moose and non-moose hosts is of concern especially during spring and fall, which are respectively drop-off and questing seasons for winter ticks. Researchers and managers in western moose–winter tick systems may wish to consider spatial overlap with non-moose ungulates like elk alongside known drivers of winter tick issues like moose density and warmer conditions in the spring and fall (Samuel 2007, Dunfey-Ball 2017, Healy et al. 2020, Hoy et al. 2021).

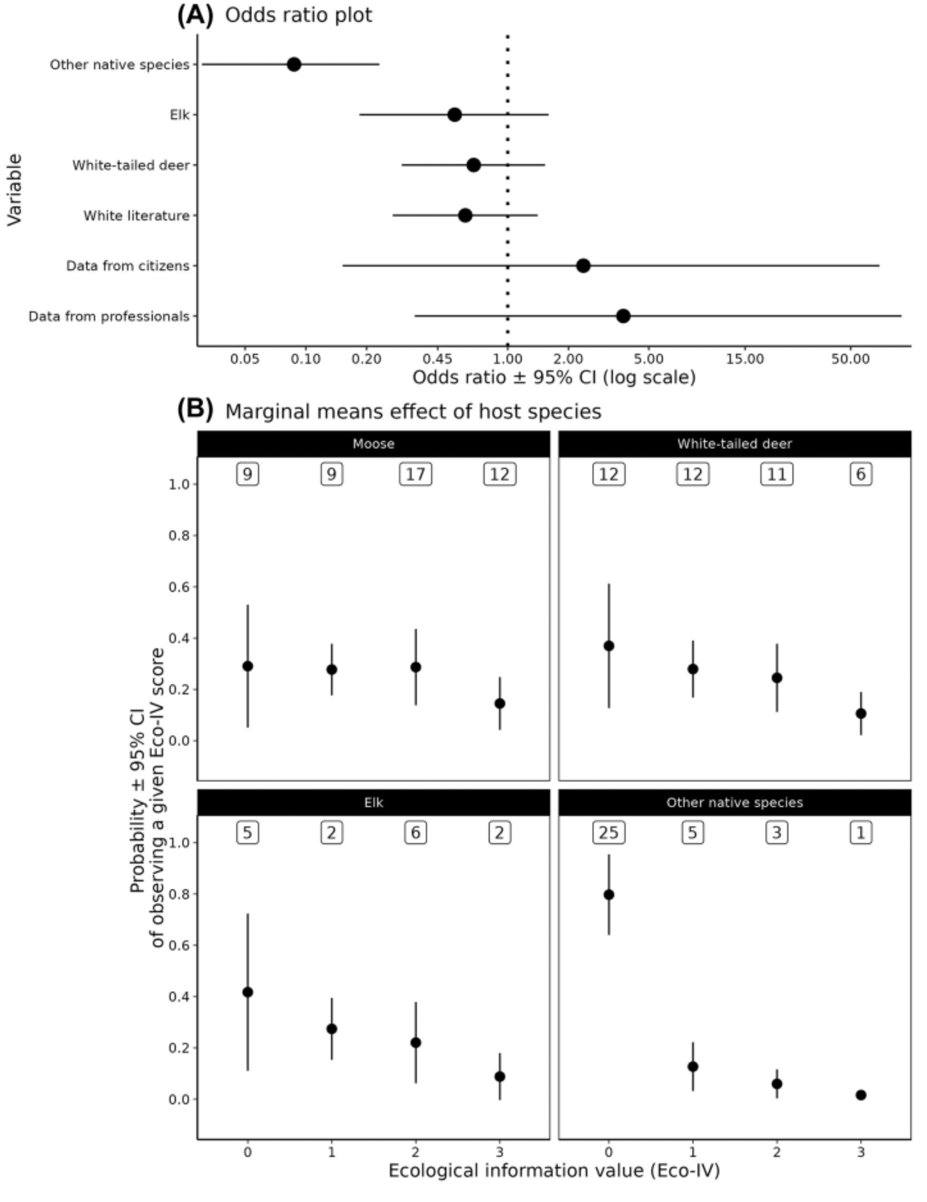

FIGURE 6 Influence of species, literature type, and data source on the probability of using a method with higher ecological information value (Eco-IV) for winter tick–ungulate host studies published in 1920–2021. We present odds ratios (A) of independent variables in the cumulative model (logit link) with method Eco-IV to estimate winter tick burden in hosts native to North America related to host species (reference level: moose), type of literature record (reference level: grey literature), and tick load data source (reference level: incomplete or unspecified source). Odds ratio for categorical variables can be interpreted as odds of an event occurring in one group to the odds of it occurring in another group. An odds ratio of 1 means that the event is equally probable for each group (no effect of this group). When the odds ratio is between 0 and 1, the event is less likely to occur in the reference group, whereas when it is greater than 1, the event is more likely to occur in the named group. We present predicted probabilities of observing a given Eco-IV score (B) for different native ungulate species. These predictions are marginal means, which are model predictions for the species effect while averaging over levels of other categorical variables included in the model. White labels with numbers indicate sample size in raw data that share the same conditions as the predictions.

TABLE 3 Results from a cumulative model (logit link) explaining the probability of authors reporting a method to estimate winter tick burden with higher levels of ecological information value (Eco-IV; an integer ranging from low [0] to high [3]) in relation to host species, tick load data source, and type of literature record for winter tick–ungulate host studies published in 1920–2021.

	Variable	Estimate (log-odds)	−95% CI	+95% CI
Species				
	Moose (reference level)			
	White-tailed deer	−0.39	−1.21	0.43
	Elk	−0.60	−1.69	0.47
	Other native species	−2.44	−3.49	−1.46
Data source				
	Incomplete information (reference level)			
	Data from citizen science	0.86	−1.88	4.24
	Data from professional	1.32	−1.06	4.49
Literature type				
	Grey literature (reference level)			
	White literature	−0.48	−1.31	0.34
Thresholds[a]				
	0 | 1 (Intercept)	−0.50		
	1 | 2 (Intercept)	1.33		
	2 | 3 (Intercept)	3.18		
	0 | 1 for 1989–2021	0.05		
	1 | 2 for 1989–2021	−1.05		
	2 | 3 for 1989–2021	−1.31		

[a]We allowed flexible thresholds to vary according to period (1927–1988 or 1989–2021), and used 1989 to split periods as this year is when Welch and Samuel (1989) published a manuscript on hide digestion technique to quantify tick burden, a method frequently cited and used in following research. Threshold number notation refers comparisons between Eco-IV levels (0-3).

A first feasible step towards standardization of surveillance should be consistent reporting of the number of individuals sampled, thus allowing accurate winter tick prevalence estimates. This simple information would help to model and fully understand the contribution of non-moose hosts to winter tick persistence and range expansion. This prevalence-based epidemiology approach is promising, as shown in a multi-host systems with 6 common parasites in multiple rodent species (Fenton et al 2015). Given the increasing winter tick surveillance efforts in all states and provinces that overlap with moose ranges (Figure 2), integrating all host surveillance data across a wide geographic scale remains an untapped and powerful way to predict winter tick dynamics upon which management practices could be based.

Eco-IV tended to be lower in other ungulate hosts, like white-tailed deer, because many tick-related studies had a wider scope to sample ectoparasites broadly or were specifically targeting occurrence records for the Lyme borreliosis vector, the black-legged tick (*Ixodes scapularis*). Greater communication among groups working on tick-host systems, such as the winter tick–ungulate and black-legged tick–white-tailed deer systems, may have allowed data collected incidentally to be used across more studies and for multiple purposes. As we are witnessing

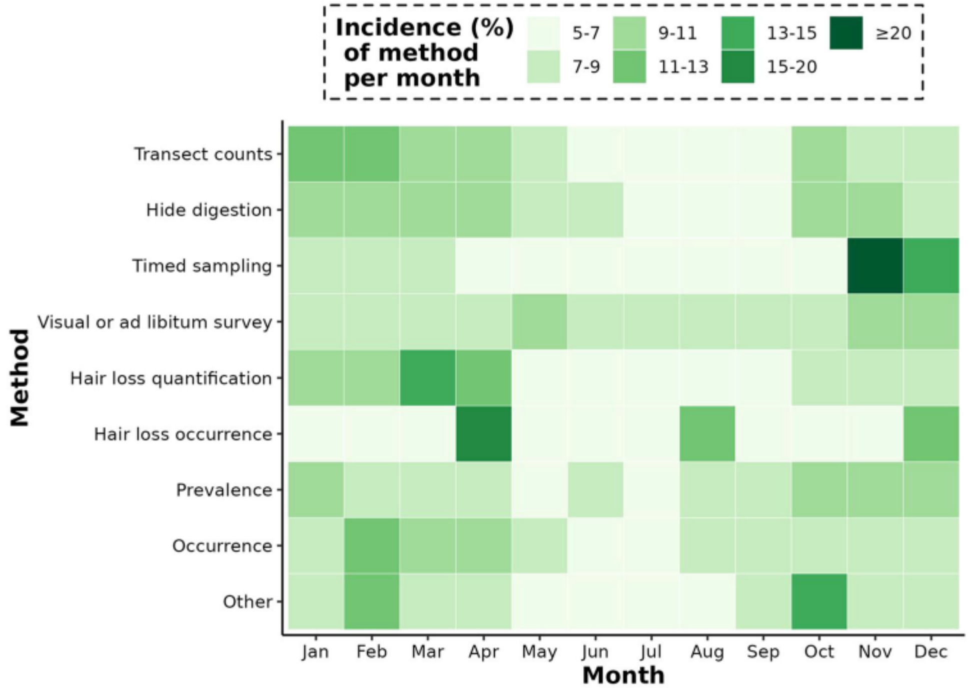

FIGURE 7 Temporal distribution of winter tick sampling methods for winter tick–ungulate host studies published in 1920–2021.

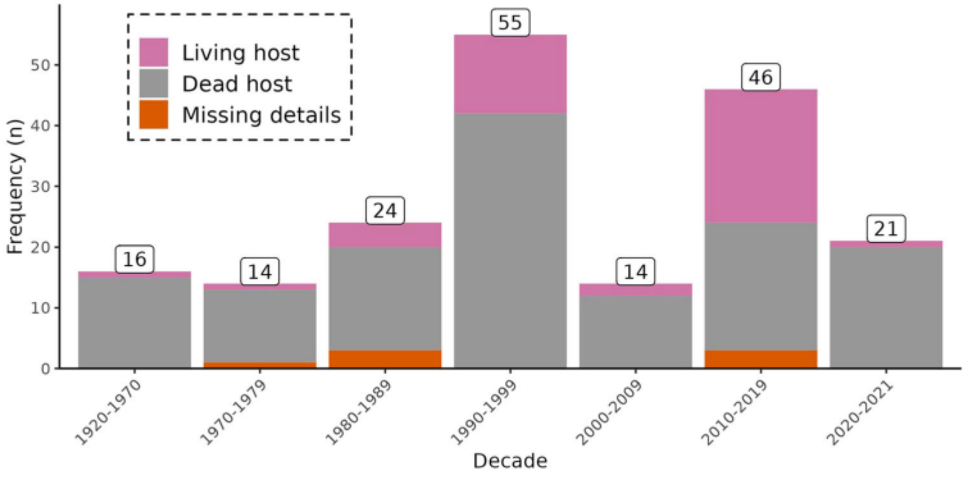

FIGURE 8 Temporal trends in host status (living [pink], dead [gray], missing data [orange]) during monitoring for winter tick–ungulate host studies. Bar height represents the number of records per decade by host status category (shaded) from 1920 to 2021.

climate-mediated expansion of geographic ranges of several host species into moose habitat, particularly white-tailed deer expansion northward (Kennedy-Slaney et al. 2018, Laurent et al. 2021), we need to develop and validate accurate methods for measuring winter tick load on ungulates other than moose. These non-moose hosts could also act as sentinels for winter tick surveillance and might help in predicting winter tick arrival into naive host populations. Researchers applying for funding involving routine ungulate capture or collaring operations could include winter tick quantification methods within their protocols and reference the potential for interspecific parasite transmission.

Spatiotemporal trends in winter tick surveillance metrics

Our study found differences in the reporting of winter tick surveillance studies across geographic space, which implies that winter tick monitoring on-host is not consistent across regions. We found very few studies (< 2 per state or province) describing monitoring methods for locations in the central United States or Mexico, with the greatest number of studies concentrated around the northeastern United States (Maine, Vermont, New Hampshire), eastern Canada (Ontario), and western Canadian provinces (British Columbia and Alberta). This finding is consistent with similar studies reporting the winter tick distribution (Samuel 2004, Lindquist et al. 2017, Chenery et al. 2023). Biases towards increased sampling in these geographic regions most likely arise because of prior management experience with winter ticks. For example, most of these locations have previously, or are currently, experiencing host die-offs in moose (e.g., Alberta [Pybus 1999], British Columbia [Watt 2021], Maine [Jones et al. 2019] New Hampshire [Dunfey-Ball 2017], Vermont [Debow et al. 2021]). The severity of host impact and the need for effective management or mitigation naturally imply a higher level of sampling effort for moose in these areas. However, the absence of a standardized approach to local or regional monitoring across geographic regions and host species complicates comparisons of host burdens, impacts, and tick numbers. This lack of standardization may hinder effective management action.

The increasing number of records in the grey literature reporting on-host winter tick surveillance in the past 2 decades matches trends found in previous studies (Chenery et al. 2023). As noted with regards to geographic trends, this could be due in part to a greater interest in monitoring by government and other wildlife management institutions who require such information to assess the degree of harm, mainly to moose, to make decisions regarding future winter tick management. However, most studies in our search are still primarily from the peer-reviewed, published literature. This has clear implications with respect to data accessibility for non-academic institutions responsible for wildlife management at local and regional scales and could be improved; for example, researchers could make the relevant data openly accessible via online data repositories to supplement the open-source data available from government agencies. By looking *a posteriori* at 19 records peer-reviewed and published after 2014, none had data availability statements, and as such only 5 provided raw data on which conclusions were drawn. These articles were descriptive, most of them being anecdotal events or case reports of necropsies with small sample sizes.

Although we found that the time of year when sampling took place aligned with the winter tick life cycle, most reports of surveys were during November and early spring, which could result in inaccurate measures of host burden. In particular, the relatively early surveys in November may suffer from a lower rate of winter tick detection due to the small size of larvae and nymphs, which comprise most life stages at this time of year (Addison and McLaughlin 1988, Samuel 2004), potentially resulting in misleading underestimates of total host burden. Moose could also still be encountering ticks in November depending on environmental conditions, leading to biased low estimates of tick infestation rates for fall on-host surveys. Similarly, surveys conducted on hosts in March and April may also result in lower tick counts because at this time of year gravid adult female ticks drop from the host to lay their eggs on the ground (Samuel 2004). Host grooming throughout the on-host season or in large bouts in late spring could also reduce tick loads up to the date of capture, underestimating the energetic consequences of tick feeding and irritation for late spring on-host surveys. Although it is unlikely that the level of sampling bias due to survey timing would drastically alter the total infestation count of ticks on individual hosts, such inaccuracies should be acknowledged as conservative estimates and noted as potential limitations depending on the expected use of the data. Efforts to validate the timing and on-host survey areas necessary to reach a reasonable approximation of infestation loads on non-moose host species like elk should be made, but in the near term researchers could acknowledge biases in quantification data based on sample timing and host species.

Climate change may exacerbate winter tick issues for moose in the near future. Winter ticks are sensitive to snow timing in spring and fall and to warm and dry conditions in summer, which are likely to fluctuate regionally under anthropogenic climate change (Pouchet et al. 2024). In the Greater Yellowstone Ecosystem, for example, more precipitation is expected to fall in spring versus winter as temperatures get warmer and overall snowpack volumes diminish (Hostetler et al. 2021). Meanwhile, summers are expected to lengthen, reach higher maximum temperatures, and have less precipitation throughout, creating hot and desiccating conditions for off-host winter tick eggs and larvae. How these conditions are likely to interact with the winter tick life cycle and affect overall population dynamics is unclear, but moose could be experiencing more variable and potentially extreme tick loads as they are also weathering direct metabolic impacts from fluctuating climate conditions. Additionally, overlap between moose and other winter tick hosts could increase in areas where migratory behaviors are in decline owing in part to declining winter severity, creating more opportunity for hosts dropping ticks in the spring to overlap with susceptible hosts the following fall (Cole et al. 2015).

Finally, understanding the benefits and limitations of collected information creates opportunities for data use in an otherwise data-limited system and new ways for researchers, biologists, and managers to work together in managing and monitoring wildlife diseases in the future. On-host surveillance will continue to be necessary to accurately assess winter tick infestation dynamics. However, consideration should also be given to non-invasive techniques that may be useful for monitoring winter ticks at broad scales at relatively low cost, such as camera trapping and public engagement projects. While some of these non-invasive methods were not necessarily calibrated for individual tick load quantification, these alternative methods have shown promise in aiding data collection in remote areas and challenging systems (Poh et al. 2022; Chenery et al. 2022, 2023). Fusing multiple data sources can also improve predictions on population dynamics (Dietze 2017), as exemplified in a Baltic salmon (*Salmo salar*) model combining over 10 data sources to produce predictions that help to guide salmon management (Kuikka et al. 2014). Walker et al. (2017) also fused data retrieved from a literature review on parasitic gastrointestinal nematodes in ungulates of southern Africa to predict parasite abundance in a wide range of hosts and understand how each host contributes to parasite persistence. Citizen science projects engaging multiple stakeholder groups could help reach non-moose hosts like elk with non-invasive survey techniques like early spring hair loss surveys, a form of engagement that has worked for other systems measuring hair loss such as with southern hairy-nosed (*Lasiorhinus latifrons*) and bare-nosed wombats (*Vombatus ursinus*) and sarcoptic mange (*Sarcoptes scabiei*) (Mayadunnage et al. 2024). We emphasize that broadening and standardizing winter tick surveillance efforts to a wider range of ungulate hosts would help researchers better understand winter tick dynamics across the landscape and give greater insight for management and conservation groups to make decisions about moose populations in the future.

MANAGEMENT IMPLICATIONS

Expanding quantification-based and other winter tick surveillance efforts to other hosts could not only clarify infestation severity and distribution dynamics for these hosts but also inform appropriate management actions for vulnerable hosts like moose. Multi-host surveillance might illuminate new management techniques available with the inclusion of other host species such as elk or white-tailed deer populations, which may be easier to implement using traditional methods such as hunting quotas (Lankester 2010, DeCesare et al. 2014, Timmerman and Rodgers 2017). Broadening winter tick surveillance studies to include voluntary non-moose hunter submissions of either winter tick counts or hide samples could serve as indicators for shifts in winter tick abundance or encounter rates within a given season. Citizen science projects surveying for early spring hair loss on moose are already used in British Columbia, Canada (BC Moose Winter Tick Surveillance Program; Watt 2021) and in the Yukon (Yukon Winter Tick Monitoring Project; Chenery et al. 2022). Such projects could be expanded to non-moose hosts and to include recording early spring hair loss from camera trap photographs or thermal imagery, as has been used in other species affected by hair loss, such as mange in red foxes (*Vulpes vulpes*; Carricondo-Sanchez et al. 2017) and wolves (*Canis lupus*; Cross et al. 2016).

Correlating tick loads on harvested non-moose ungulates in fall to tick loads on captured ungulates later in the year and either observed tick loads or hair loss on moose could give managers a larger toolset for understanding threats posed to moose and other ungulate hosts. Researchers investigating ticks and tick-borne diseases with important life stages on ungulate hosts could also help robust, routine, multi-host surveillance projects by applying partial funding to tick surveillance during capture operations, at check stations, and in hunter outreach initiatives.

The current absence of searching for winter ticks on other potential ungulate hosts, largely based on historical beliefs of predilection from limited captive studies almost 3 decades ago (Welch et al. 1991) has created a knowledge gap that likely impedes our understanding of winter tick–host dynamics at regional and landscape scales. Although challenges remain in the detection of winter ticks on non-moose hosts, such as deer and caribou, which are often less affected by the distinctive alopecia than moose, and to some degree, elk, the addition of fast and effective hair transect methods (Sine et al. 2009) to capture protocols for all ungulate species may be one of the most effective means of improving on-host detections.

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflicts of interest.

ETHICS STATEMENT

This manuscript reviewed research articles and thus did not involve capturing or handling of animals.

DATA AVAILABILITY STATEMENT

All data needed to reproduce analyses and figures of this manuscript are available on Figshare 10.6084/m9.figshare.c.7164970.

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REFERENCES

Addison, E. M., and R. F. McLaughlin. 1988. Growth and development of winter tick, *Dermacentor albipictus*, on moose, *Alces alces*. Journal of Parasitology 74:670–678.

Addison, E. M., D. J. H. Fraser, and R. F. McLaughlin. 2019. Grooming and rubbing behavior by moose experimentally infested with winter ticks (*Dermacentor albipictus*). Alces 55:23–35.

Amerasinghe, F. P., N. L. Breisch, A. F. Azad, W. F. Gimpel, M. Greco, K. Neidhardt, B. Pagac, J. Piesman, J. Sandt, T. W. Scott, and K. Sweeney. 1992. Distribution, density, and Lyme disease spirochete infection in Ixodes dammini (Acari: Ixodidae) on white-tailed deer in Maryland. Journal of Medical Entomology 29:54–61.

Bergeron, D. H., and P. J. Pekins. 2014. Evaluating the usefulness of three indices for assessing winter tick abundance in northern New Hampshire. Alces 50:1–15.

Bondo, K. J., B. Macbeth, H. Schwantje, K. Orsel, D. Culling, B. Culling, M. Tryland, I. H. Nymo, and S. Kutz. 2019. Health survey of boreal caribou (*Rangifer tarandus caribou*) in Northeastern British Columbia, Canada. Journal of Wildlife Diseases 55:544-562.

Calvente, E., S. Pelletier, J. Banfield, J. Brown, and N. Chinnici. 2020. Prevalence of winter ticks (*Dermacentor albipictus*) in hunter-harvested wild elk (*Cervus canadensis*) from Pennsylvania, USA (2017–2018). Veterinary Sciences 7:177.

Carricondo-Sanchez, D., M. Odden, J. D. C. Linnell, and J. Odden. 2017. The range of the mange: spatiotemporal patterns of sarcoptic mange in red foxes (*Vulpes vulpes*) as revealed by camera trapping. PLoS One 12:e0176200.

Chenery, E. S., M. Henaff, K. Magnussonn, N. J. Harms, N. E. Mandrak, and P. K. Molnar. 2022. Improving widescale monitoring of ectoparasite presence in northern Canadian wildlife with the aid of Citizen Science. Insects 13:380.

Chenery, E. S., N. J. Harms, H. Fenton, N. E. Mandrak, and P. K. Molnár. 2023. Revealing large-scale parasite ranges: An integrated spatiotemporal database and multisource analysis of the winter tick. Ecosphere 14:e4376.

Christensen, R. H. B. 2019. ordinal: regression models for ordinal data. <https://cran.r-project.org/package=ordinal>

Christensen, R. H. B. 2022. A tutorial on fitting cumulative link mixed models with clmm2 from the ordinal package. https://cran.r-project.org/web/packages/ordinal/vignettes/clmm2_tutorial.pdf

Chubbs, T. E., and J. A. Schaefer. 1997. Population growth of moose, *Alces alces*, in Labrador. Canadian Field-Naturalist 111: 238-242.

Cole, E. K., A. M. Foley, J. M. Warren, B. L. Smith, S. R. Dewey, D. G. Brimeyer, W. S. Fairbanks, H. Sawyer, and P. C. Cross. 2015. Changing migratory patterns in the Jackson elk herd. Journal of Wildlife Management 79:877-886.

Cross, P. C., E. S. Almberg, C. G. Haase, P. J. Hudson, S. K. Maloney, M. C. Metz, A. J. Munn, P. Nugent, O. Putzeys, D. R. Stahler, A. C. Stewart, and D. W. Smith. 2016. Energetic costs of mange in wolves estimated from infrared thermography. Ecology 97:1938-1948.

de Raadt, A., M. J. Warrens, R. J. Bosker, and H. A. Kiers. 2021. A comparison of reliability coefficients for ordinal rating scales. Journal of Classification 38:519-543.

Debow, J., J. Blouin, E. Rosenblatt, C. Alexander, K. Gieder, W. Cottrell, J. Murdoch, and T. Donovan. 2021. Effects of winter ticks and internal parasites on moose survival in Vermont, USA. Journal of Wildlife Management 85:1423-1439.

DeCesare, N. J., R. B. Harris, M. P. Atwood, E. J. Bergman, A. B. Courtemanch, P. C. Cross, G. L. Fralick, K. R. Hersey, M. A. Hurley, T. M. Koser, et al. 2024. Warm places, warm years, and warm seasons increase parasitizing of moose by winter ticks. Ecosphere 15:e4799.

DeCesare, N. J., T. D. Smucker, R. G. Garrott, and J. A. Gude. 2014. Moose status and management in Montana. Alces 50: 35-51.

Dietze, M. C. 2017. Ecological forecasting. (1st edition). Princeton University Press, Princeton, New Jersey, USA.

Dobson, A., and J. Foufopoulos. 2001. Emerging infectious pathogens of wildlife. Philosophical Transactions of the Royal Society of London Series B: Biological Sciences 356:1001-1012.

Dunfey-Ball, K. R. 2017. Moose density, habitat, and winter tick epizootics in a changing climate. Thesis, University of New Hampshire, Durham, USA.

Durden, L. A., S. Luckhart, G. R. Mullen, and S. Smith. 1991. Tick infestations of white-tailed deer in Alabama. Journal of Wildlife Diseases 27:606-614.

Fenton, A., D. G. Streicker, O. L. Petchey, and A. B. Pedersen. 2015. Are all hosts created equal? Partitioning host species contributions to parasite persistence in multihost communities. American Naturalist 186:610-622.

Gamer, M., J. Lemon, and I. F. P. Singh. 2021. irr: various coefficients of interrater reliability and agreement. R package version 0.84. 1. 2019. <https://cran.r-project.org/package=irr>

Glines, M. V. 1983. The winter tick, *Dermacentor albipictus* (Packard, 1869): its life history, development at constant temperatures and physiological effects on moose, *Alces alces*. Thesis, University of Alberta, Edmonton, Canada.

Glines, M. V., and W. M. Samuel. 1989. Effect of *Dermacentor albipictus* (Acari: Ixodidae) on blood composition, weight gain and hair coat of moose, *Alces alces*. Experimental and Applied Acarology 6:197-213.

Healy, C., P. J. Pekins, S. Atallah, and R. G. Congalton. 2020. Using agent-based models to inform the dynamics of winter tick parasitism of moose. Ecological Complexity 41:100813.

Hoberg, E. P., L. Polley, E. J. Jenkins, S. J. Kutz, A. M. Veitch, and B. T. Elkin. 2008. Integrated approaches and empirical models for investigation of parasitic diseases in northern wildlife. Emerging Infectious Diseases 14:10-17.

Hostetler, S., C. Whitlock, B. Shuman, D. Liefert, C. W. Drimal, and S. Bischke. 2021. Greater Yellowstone climate assessment: past, present, and future climate change in greater Yellowstone watersheds. Montana State University, Institute on Ecosystems, Bozeman, USA.

Hoy, S. R., L. M. Vucetich, R. O. Peterson, and J. A. Vucetich. 2021. Winter tick burdens for moose are positively associated with warmer summers and higher predation rates. Frontiers in Ecology and Evolution 9:758374.

Huyvaert, K. P. 2018. Filling the gaps: improving sampling and analysis of disease surveillance data in Galápagos. Pages 293-303 *in* P. G. Parker, editor. Disease ecology (1st edition). Springer, Cham, Switzerland.

Idaho Department of Fish and Game [IDFG]. 2017. State Wildlife Action Plan. IDFG, Boise, USA.

Jones, H., P. J. Pekins, L. E. Kantar, M. O'Neil, and D. Ellingwood. 2017. Fecundity and summer calf survival of moose during 3 successive years of winter tick epizootics. Alces 53:85-98.

Jones, H., P. Pekins, L. Kantar, I. Sidor, D. Ellingwood, A. Lichtenwalner, and M. O'Neal. 2019. Mortality assessment of moose (*Alces alces*) calves during successive years of winter tick (*Dermacentor albipictus*) epizootics in New Hampshire and Maine (USA). Canadian Journal of Zoology 97:22-30.

Joseph, M. B., J. R. Mihaljevic, A. L. Arellano, J. G. Kueneman, D. L. Preston, P. C. Cross, and P. T. J. Johnson. 2013. Taming wildlife disease: bridging the gap between science and management. Journal of Applied Ecology 50:702-712.

Kennedy-Slaney, L., J. Bowman, A. A. Walpole, and B. A. Pond. 2018. Northward bound: the distribution of white-tailed deer in Ontario under a changing climate. Wildlife Research 45:220–228.

Koricheva, J., J. Gurevitch, and K. Mengersen. 2013. Handbook of meta-analysis in ecology and evolution (1st edition). Princeton University Press, Princeton, New Jersey, USA.

Kuikka, S., J. Vanhatalo, H. Pulkkinen, S. Mäntyniemi, and J. Corander. 2014. Experiences in Bayesian inference in Baltic salmon management. Statistical Science 29:42–49.

Kutz, S. J., E. J. Jenkins, A. M. Veitch, J. Ducrocq, L. Polley, B. Elkin, and S. Lair. 2009. The Arctic as a model for anticipating, preventing, and mitigating climate change impacts on host–parasite interactions. Veterinary Parasitology 163:217-228.

Kutz, S. J., E. P. Hoberg, J. Nagy, L. Polley, and B. Elkin. 2004. "Emerging" parasitic infections in arctic ungulates. Integrative and Comparative Biology 44:109-118.

Lachish, S., and K. A. Murray. 2018. The certainty of uncertainty: potential sources of bias and imprecision in disease ecology studies. Frontiers in Veterinary Science 5:90.

Lankester, M. W. 2010. Understanding the impact of meningeal worm, *Parelaphostrongylus tenuis*, on moose populations. Alces 46:53-70.

Laurent, M., M. Dickie, M. Becker, R. Serrouya, and S. Boutin. 2021. Evaluating the mechanisms of landscape change on white-tailed deer populations. Journal of Wildlife Management 85:340–353.

Lindquist, E. E., T. Galloway, H. Artsob, L. Lindsay, M. Drebot, H. Wood, and R. Robbins. 2017. A Handbook to the ticks of Canada. Biological Survey of Canada Monograph Series, No. 7, Victoria, British Columbia, Canada.

Machtinger, E. T., H. R. Springer, J. E. Brown, and P. U. Olafson. 2021. Sudden mortality in captive white-tailed deer with atypical infestation of winter tick. Journal of Medical Entomology 58:1962-1965.

Mayadunnage, S., H. J. Stannard, P. West, and J. M. Old. 2024. Spatial and temporal patterns of sarcoptic mange in wombats using the citizen science tool, WomSAT. Integrative Zoology 19:387-399.

Miller, D. A., B. L. Talley, K. R. Lips, and E. H. Campbell Grant. 2012. Estimating patterns and drivers of infection prevalence and intensity when detection is imperfect and sampling error occurs. Methods in Ecology and Evolution 3:850-859.

Mooring, M. 2024. Programmed grooming after 30 years of study: a review of evidence and future prospects. Animals 14: 1266.

Mooring, M. S., and W. M. Samuel. 1998*a*. The biological basis of grooming in moose: programmed versus stimulus-driven grooming. Animal Behaviour 56:1561–1570.

Mooring, M. S., and W. M. Samuel. 1998*b*. Tick-removal grooming by elk (*Cervus elaphus*): testing the principles of the programmed-grooming hypothesis. Canadian Journal of Zoology 76:740–750.

Mooring, M. S., and W. M. Samuel. 1999. Premature loss of winter hair in free-ranging moose (*Alces alces*) infested with winter ticks (*Dermacentor albipictus*) is correlated with grooming rate. Canadian Journal of Zoology 77:148–156.

Murray, D. L., E. W. Cox, W. B. Ballard, H. A. Whitlaw, M. S. Lenarz, T. W. Custer, T. Barnett, and T. K. Fuller. 2006. Pathogens, nutritional deficiency, and climate influences on a declining moose population. Wildlife Monographs 166:1-30.

Musante, A. R., P. J. Pekins, and D. L. Scarpitti. 2010. Characteristics and dynamics of a regional moose *Alces alces* population in the northeastern United States. Wildlife Biology 16:185-204.

Musante, A. R., P. Pekins, and D. L. Scarpitti. 2007. Metabolic impacts of winter tick infestations on calf moose. Alces 43: 101-110.

Normandeau, J., C. Cassady St. Clair, S. J. Kutz, M. Hebblewhite, and E. H. Merrill. 2022. What makes elk tick: winter tick (*Dermacentor albipictus*) grooming behavior in wild elk (*Cervus canadensis*). Journal of Mammalogy 103:373-382.

Nusser, S. M., W. R. Clark, D. L. Otis, and L. Huang. 2008. Sampling considerations for disease surveillance in wildlife populations. Journal of Wildlife Management 72:52-60.

Poh, K. C., J. R. Evans, M. J. Skvarla, and E. T. Machtinger. 2022. All for One Health and One Health for All: considerations for successful citizen science projects conducting vector surveillance from animal hosts. Insects 13:492.

Portier, J., M.-P. Ryser-Degiorgis, M. R. Hutchings, E. Monchâtre-Leroy, C. Richomme, S. Larrat, W. H. M. van der Poel, M. Dominguez, A. Linden, P. T. Santos, et al. 2019. Multi-host disease management: the why and the how to include wildlife. BMC Veterinary Research 15:295.

Pouchet, C., C. Fernandez-Prada, C. Dussault, M. Leclerc, J. P. Tremblay, and S. D. Côté. 2024. Linking weather conditions and winter tick abundance in moose. Journal of Wildlife Management 88; e22551.

Pybus, M. J. 1999. Moose and ticks in Alberta: a dieoff in 1998/99. Alberta Environment Edmonton, Canada.

R Core Team. 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rosenblatt, E., J. DeBow, J. Blouin, T. Donovan, J. Murdoch, S. Creel, W. Rogers, K. Gieder, N. Fortin, and C. Alexander. 2021. Juvenile moose stress and nutrition dynamics related to winter ticks, landscape characteristics, climate-mediated factors and survival. Conservation Physiology 9:coab048.

Samuel, W. M. 1989. Locations of moose in Northwestern Canada with hair loss probably caused by the winter tick, *Dermacentor albipictus* (Acari: Ixodidae). Journal of Wildlife Diseases 25:436–439.

Samuel, W. M. 2004. White as a ghost: winter ticks and moose. Federation of Alberta Naturalists, Edmonton, Canada.

Samuel, W. M. 2007. Factors affecting epizootics of winter ticks and mortality of moose. Alces 43:39-48.

Samuel, W. M., and D. A. Welch. 1991. Winter ticks on moose and other ungulates: factors influencing their population size. Alces 27:169-182.

Samuel, W. M., and M. J. Barker. 1979. The winter tick, *Dermacentor albipictus* (Packard, 1869) on moose, *Alces alces* (L.), of central Alberta. Proceedings of the North American Moose Conference and Workshop 15:303–348.

Scarpitti, D., C. Habeck, A. R. Musante, and P. J. Pekins. 2005. Integrating habitat use and population dynamics of moose in northern New Hampshire. Alces 41:25-35.

Shaw, D. J., and A. P. Dobson. 1995. Patterns of macroparasite abundance and aggregation in wildlife populations: a quantitative review. Parasitology 111:S111-S133.

Sine, M., K. Morris, and D. Knupp. 2009. Assessment of a line transect method field method to determine winter tick abundance on moose. Alces 45:143-146.

Stallknecht, D. E. 2007. Impediments to wildlife disease surveillance, research, and diagnostics. Pages 445-461 *in* J. E. Childs, J. S. Mackenzie, and J. A. Richt, editors. Wildlife and emerging zoonotic diseases: the biology, circumstances and consequences of cross-species transmission. Springer, Berlin, Germany.

Stephen, C., and J. Berezowski. 2022. Wildlife health surveillance and intelligence. challenges and opportunities. Pages 99-111 *in* C. Stephen, editor. Wildlife population health (first edition). Springer International Publishing, Cham, Switzerland.

Tape, K. D., D. D. Gustine, R. W. Ruess, L. G. Adams, and J. A. Clark. 2016. Range expansion of moose in arctic Alaska linked to warming and increased shrub habitat. PLOS ONE 11:e0152636.

Timmerman, H. R., and A. R. Rodgers. 2017. The status and management of moose in North America - circa 2015. Alces 53: 1-22.

Walker, J. G., M. Plein, E. R. Morgan, and P. A. Vesk. 2017. Uncertain links in host–parasite networks: lessons for parasite transmission in a multi-host system. Philosophical Transactions of the Royal Society B: Biological Sciences 372:20160095.

Walton, L., G. Marion, R. S. Davidson, P. C. L. White, L. A. Smith, D. Gavier-Widen, L. Yon, D. Hannant, and M. R. Hutchings. 2016. The ecology of wildlife disease surveillance: demographic and prevalence fluctuations undermine surveillance. Journal of Applied Ecology 53:1460-1469.

Watt, K. 2021. Provincial Moose Winter Tick Surveillance Program. British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development, Fort St. John, Canada.

Wedincamp, J., and L. A. Durden. 2016. Ectoparasites of white-tailed deer (Artiodactyla: Cervidae) in Southeastern Georgia, USA. Journal of Entomological Science 51:113–121.

Weiskopf, S. R., O. E. Ledee, and L. M. Thompson. 2019. Climate change effects on deer and moose in the Midwest. Journal of Wildlife Management 83:769-781.

Welch, D. A., and W. M. Samuel. 1989. Evaluation of random sampling for estimating density of winter ticks (*Dermacentor albipictus*) on moose (*Alces alces*) hides. International Journal for Parasitology 19:691–693.

Welch, D. A., W. M. Samuel, and C. J. Wilke. 1991. Suitability of moose, elk, mule deer, and white-tailed deer as hosts for winter ticks (*Dermacentor albipictus*). Canadian Journal of Zoology 69:2300–2305.

Wunschmann, A., A. G. Armien, E. Butler, M. Schrage, B. Stromberg, J. B. Bender, A. M. Firshman, and M. Carstensen. 2015. Necropsy findings in 62 opportunistically collected free-ranging moose (*Alces alces*) from Minnesota, USA (2003-13). Journal of Wildlife Diseases 51:157-165.

Wyoming Game and Fish Department [WGFD]. 2017. State Wildlife Action Plan. Wyoming Game and Fish Department, Cheyenne, USA.

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SUPPORTING INFORMATION

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