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MOOSE HABITAT USE DURING CRITICAL PERIODS IN THE WINTER TICK LIFECYCLE AND AGENT-BASED MODELING OF MOOSE-WINTER TICK RELATIONSHIPS IN NORTHERN NEW HAMPSHIRE

Christine Healy
University of New Hampshire, Durham

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MOOSE HABITAT USE DURING CRITICAL PERIODS IN THE WINTER TICK LIFECYCLE AND AGENT-BASED MODELING OF MOOSE-WINTER TICK RELATIONSHIPS IN NORTHERN NEW HAMPSHIRE

BY

CHRISTINE LOUISE HEALY

B.S., Marist College, 2014

THESIS

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In

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This thesis has been examined and approved in partial fulfillment of the requirements for the degree of Master of Science in Natural Resources: Wildlife and Conservation Biology by:

Thesis Co-Director, Dr. Peter J. Pekins
Professor of Wildlife and Conservation Biology

Thesis Co-Director, Dr. Russell G. Congalton
Professor of Remote Sensing and Geographic Information Systems

Dr. Shadi Atallah
Assistant Professor of Environmental and Resource Economics

On May 10th, 2018

Original approval signatures are on file with the University of New Hampshire Graduate School.

DEDICATION

In dedication to my grandmothers, Sylvia Healy (1941-2017) and Louise Hoehman (1923-2018); two incredibly strong women who led by example and navigated this world with compassion and grace.

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ABSTRACT

MOOSE HABITAT USE DURING CRITICAL PERIODS IN THE WINTER TICK LIFECYCLE AND AGENT-BASED MODELING OF MOOSE-WINTER TICK RELATIONSHIPS IN NORTHERN NEW HAMPSHIRE

by

Christine Louise Healy

University of New Hampshire, September 2018

High calf mortality has been documented in North American moose (*Alces alces*) populations along the southern extent of their range; in New England, this has been attributed to winter tick (*Dermacentor albipictus*) parasitism. This research was conducted to better understand moose activity during critical periods in the winter tick life cycle, and to assess the potential of simulation models in managing moose against future epizootics. Seasonal habitat use was measured using geospatial analyses of locational data from radio-marked animals at 3 sites in New Hampshire and Maine. An agent-based model, spatially explicit to two subsections of the New Hampshire field site (Success and Jericho), was then constructed to simulate the role of moose density, weather events, winter tick abundance and aggregation, and proportion of available optimal habitat on % mortality and tick infestation level of dead calves.

The average size of home and core ranges generally increased from south to north, following the population gradient. Optimal habitat was the only land cover type used above its availability (1.1-2.1X availability in home range, 1.2-3.1X availability in core range), regardless of season or site, indicating that moose were selecting for this cover type during questing and

drop-off periods of winter ticks. The proportional overlap of cut habitat in home and core ranges exceeded the absolute proportion in home and core ranges. It is expected that temporal use of optimal habitat exceeds the geospatial estimates because 30-40% of the daily activity of moose is spent foraging. The high proportion of time spent foraging within optimal habitat that is available in disproportionately low proportion (< 20%) across the landscape suggests that high concentrations of winter ticks are available in this cover type.

The model was parameterized using empirical data acquired from the literature and results of the current field study. Of 58 combinations of variables, 17 produced epizootic events (calf mortality > 50%), of which 15 occurred in Jericho where the availability of optimal habitat was higher (28%) than the study site average (17%). Averages of the two sites under conditions representative of the current moose density and recent weather conditions yielded similar, albeit lower, calf mortality (53-66%) and infestation level (37,635 ticks/calf) than measured in the field study (~70% calf mortality, 48,600 ticks/calf). Winter tick abundance and aggregation both influenced the occurrence and severity of infestation and mortality at each site. While the model used a conservative approach with regard to several parameters (e.g., moose activity, winter tick abundance, % ticks that desiccate during drought, and moose density), it produced patterns and trends congruent with those calculated during the field study, and demonstrated the future management potential of this method.

INTRODUCTION

Moose populations along portions of the southern extent of their North American range have been receiving much attention in recent years, due to sightings of moose with severe alopecia and reports of high calf mortality. In New England, research has indicated that parasitism by winter ticks is the cause (Jones 2016, Jones et al. 2017). In response to this phenomenon, Maine, New Hampshire, and recently Vermont have established collaborative field- based research projects to monitor the productivity and mortality of moose throughout the region. Several hundred moose have been outfitted with GPS and VHF radio-collars between the three states from 2014-2018, contributing significantly to the understanding of moose-winter tick relationships. This research was completed using data collected through these field studies in New Hampshire and Maine.

The main objective of this project was to test whether empirical data could be used to parameterize a spatially explicit agent-based model that produced trends and results similar to those measured in the ongoing field study located in the same area. Much research on moose-winter tick epizootics indicate that winter tick abundance is driven by weather conditions and local moose density; late winter snow prolongs the questing period, allowing ticks several additional weeks to successfully attach to a host, while high moose density increases the number of available hosts. Global climate change is resulting in late winters becoming the new normal. Other studies have suggested that the most efficient means of managing the moose population for winter ticks and protecting against continued epizootics is to allocate additional hunting permits. Agent-based modeling could someday help aid wildlife managers in the determination of a sustainable moose population.

The research in this thesis is presented in two chapters (stand alone papers). Chapter 1 presents the research performed to gain a better understanding of moose movement and habitat use during critical periods in the winter tick lifecycle. Of particular interest was moose use of optimal habitat, or cut areas. Winter tick abundance estimates were available for this cover type, while unavailable for other habitats. This chapter justifies the assumption that moose likely acquire the bulk of their tick load in cut areas, an integral part of the model. Chapter 2 presents the construction and results of the agent-based model (ABM). The methods section conforms to the guidelines of the Overview, Design Concepts, and Details (ODD) protocol suggested for describing ABMs (Grimm et al. 2006, 2010).

Therefore, this document is organized as follows; an Introduction discussing the overall justification, objectives, and organization of the thesis. Chapter 1 details the GIS analysis of GPS locations transmitted by radio-marked female moose in northern New Hampshire and Maine during the drop-off and questing periods in 2014-2017. Appendix 1A and 1B at the end of this document provides information regarding the collar ID and age class of each moose during both seasons. Some collars were reassigned in the event that the original moose died and the battery life of the collar was sufficient for continued use. Because of this, the year the moose was collared is also included. Chapter 2 presents the agent-based model. Appendix 2 contains the code written to program the model in NetLogo 6.0.1 (Wilensky 1999). Appendix 3 shows the results of a preliminary analysis conducted to determine the number of model iterations needed to reduce variance in the outcome variables % calf mortality and infestation level of dead calves. Following the two chapters is a short Conclusions section that summarizes the contribution of this research in bullet form. Finally, a literature cited section divided by chapter completes the thesis.

CHAPTER 1:

Habitat Use of Moose during Critical Periods in the Winter Tick Lifecycle in Northern New England

INTRODUCTION

In recent years moose (*Alces alces*) populations in parts of New England have experienced high mortality of 10-12-month-old calves. In 3 of the past 5 years (2014-2016) mortality has exceeded 70% in northern New Hampshire and western Maine (Jones et al. 2017). The preponderance of this mortality is attributed to blood loss from excessively high loads of winter ticks (*Dermacentor albipictus*) (Jones 2016). Winter tick epizootics (mortality > 50%) occurred periodically in Canadian provinces during the late 20th century (Samuel 2004, Samuel 2007); however, their frequency has increased in the Northeastern United States in the last 15 years (Bergeron et al. 2013). Global climate change resulting in later onset of winter snow (Musante et al. 2010, Bergeron and Pekins 2014, Dunfey-Ball 2017) and high local moose density (Samuel 2004) are considered the primary reasons for the upsurge in winter tick parasitism.

Winter ticks range south of 60° N latitude throughout much of North America (Gregson 1956). They are monoxenous parasites found on a variety of vertebrate species, but are most commonly associated with ungulates, specifically moose, elk (*Cervus canadensis*), and white-tailed deer (*Odocoileus virginianus*) (Samuel et al. 2000). The life cycle of winter tick metamorphoses (3 stages - larvae, nymph, and adult) is consistent across their range (Lankester and Samuel 1998). Winter tick larvae ascend vegetation in early autumn and congregate at roughly shoulder height of large ungulates (McPherson 2000, Samuel 2004). Clusters of ticks seek hosts from mid-September to the first permanent snowfall, and engorged adults drop from their hosts from mid- to late-March through April. Because adult winter ticks, eggs, and larvae are relatively immobile, it is presumed that where adult females detach from their host in spring is where larvae quest the following fall.

Although moose are considered a generalist species, Peek (1997) argues that moose are “selective generalists” because they occupy early successional habitat more than proportionally available. Core ranges of moose in Sweden included cut areas with ~10% availability, twice that across the landscape (Cederlund and Okarma 1988), and moose in the Yukon consistently preferred shrub cover types over everything but conifers in all seasons (McCulley et al. 2017b). Peek et al. (1976) described high quality habitat in Minnesota as sites consisting of 40-50% early successional vegetation < 20 years old, but considered 1% annual rate of forest removal as very good moose habitat.

The proportion of available optimal habitat impacts moose movement across a landscape. They exhibit high fidelity to seasonal ranges between consecutive years (Gasaway et al. 1980, Cederlund et al. 1987, Cederlund and Sand 1994) and access to a sufficient quantity of quality forage minimizes movement (Timmerman and McNicol 1988); therefore, small home ranges are considered an indicator of good habitat for non-migratory moose populations (Scarpitti 2006). Ranges are also affected by other factors including sex and age, so large ranges do not necessarily point to poor habitat composition. Males typically use larger ranges than females, particularly during the rut when access to potential mates is more important than forage (Goddard 1970, Cederlund and Sand 1994). Females are generally not as active and continue to prioritize feeding with their calves throughout autumn. Males tend to have more exclusive, less social home ranges than females that often overlap with other females (Cederlund et al. 1987).

Additionally, yearlings and two-year-old moose are known to disperse, often long distances, from their natal home range (Roussel et al. 1975, Lynch and Morgantini 1984).

Many studies have compared moose movement and habitat use during approximate calendar seasons or biologically significant periods (e.g., calving and the rut) (Cederlund et al. 1987, Cederlund and Okarma 1988, Cederlund and Sand 1994, Thompson et al. 1995, Scarpitti 2006, Wattles and DeStefano 2013, Andreozzi et al. 2016, McCulley et al. 2017b). Terry (2015) analyzed movement paths of moose during the drop-off and questing periods of winter ticks, but did not delineate home and core ranges. No study has specifically investigated home range and habitat use during the critical questing and drop-off stages in the winter tick cycle, which generally spans the cusp of multiple seasons typically described in the literature. Given the sedentary nature of winter ticks, their off-host location in summer and fall is dependent on moose location during specific weeks in late winter and spring when adult female ticks drop from moose. Determining moose movement and habitat use during these weeks and in autumn when winter ticks quest for a host at the same location is critical to understanding the spatial ecology of winter tick epizootics.

The New Hampshire Fish and Game Department (NHFG) in collaboration with the University of New Hampshire (UNH) and the Maine Department of Inland Fisheries and Wildlife (MDIFW) began outfitting moose with VHF and GPS radio-collars in 2014 to monitor productivity and mortality in northern New Hampshire and western and northern Maine. These sites exhibit a range in moose density and seasonal weather, with the site in northern Maine typically experiencing earlier snow cover. Timber harvesting is widespread at all sites, and is the primary means by which optimal moose habitat is created. After the institution of the State Practices Act in 1989 which restricted commercial clearcutting, partial harvesting became the most common logging strategy in Maine, making up >90% of all statewide harvest in recent years (MFS 2016); in New Hampshire clearcutting remains common.

The objective of this study was to compare home/core ranges and seasonal habitat use by female moose during the two significant periods in the winter tick life cycle, at 3 sites in northern New England that exhibit different levels of tick-associated mortality, moose density, length of winter, and timber harvesting strategy. Only females were considered because their locations are representative of calves, the cohort at greatest risk of winter tick-related mortality. It was hypothesized that moose would preferentially include cut habitats within their home and core ranges during the questing and drop-off periods.

METHODS

Study Area- New Hampshire

The study area (Berlin) is located within Coos County and includes sections of Wildlife Management Units (WMUs) B, C1, and C2 in the towns of Berlin, Milan, Dummer, Success, Cambridge, Millsfield, Stark, and Second College Grant (Fig. 1). The landscape is bisected by the Androscoggin River and is relatively mountainous, bordered to the west by the Kilkenny Range and the south by the Mahoosuc Range. Landcover is predominately commercial forest in which deciduous areas are dominated by yellow (*Betula alleghaniensis*) and paper birch (*B. papyrifera*), American beech (*Fagus grandifolia*), and sugar maple (*Acer saccharum*), with softwood stands characterized by black spruce (*Picea mariana*), red spruce (*P. rubens*), balsam fir (*Abies balsamea*), and white cedar (*Thuja occidentalis*) (DeGraaf et al. 1992). Logging operations remove 1-3% of timber annually, and optimal moose habitat (4-16 year-old growth) increased 2.5X between 2001 and 2015 to equal > 17% of forest cover (Dunfey-Ball 2017). Habitat quality is considered good and not a limiting factor to the local moose population

(Bergeron 2011, Dunfey-Ball 2017). The average date of first snowfall is 14 November, with permanent snow typically beginning on 25 December (Dunfey-Ball 2017).

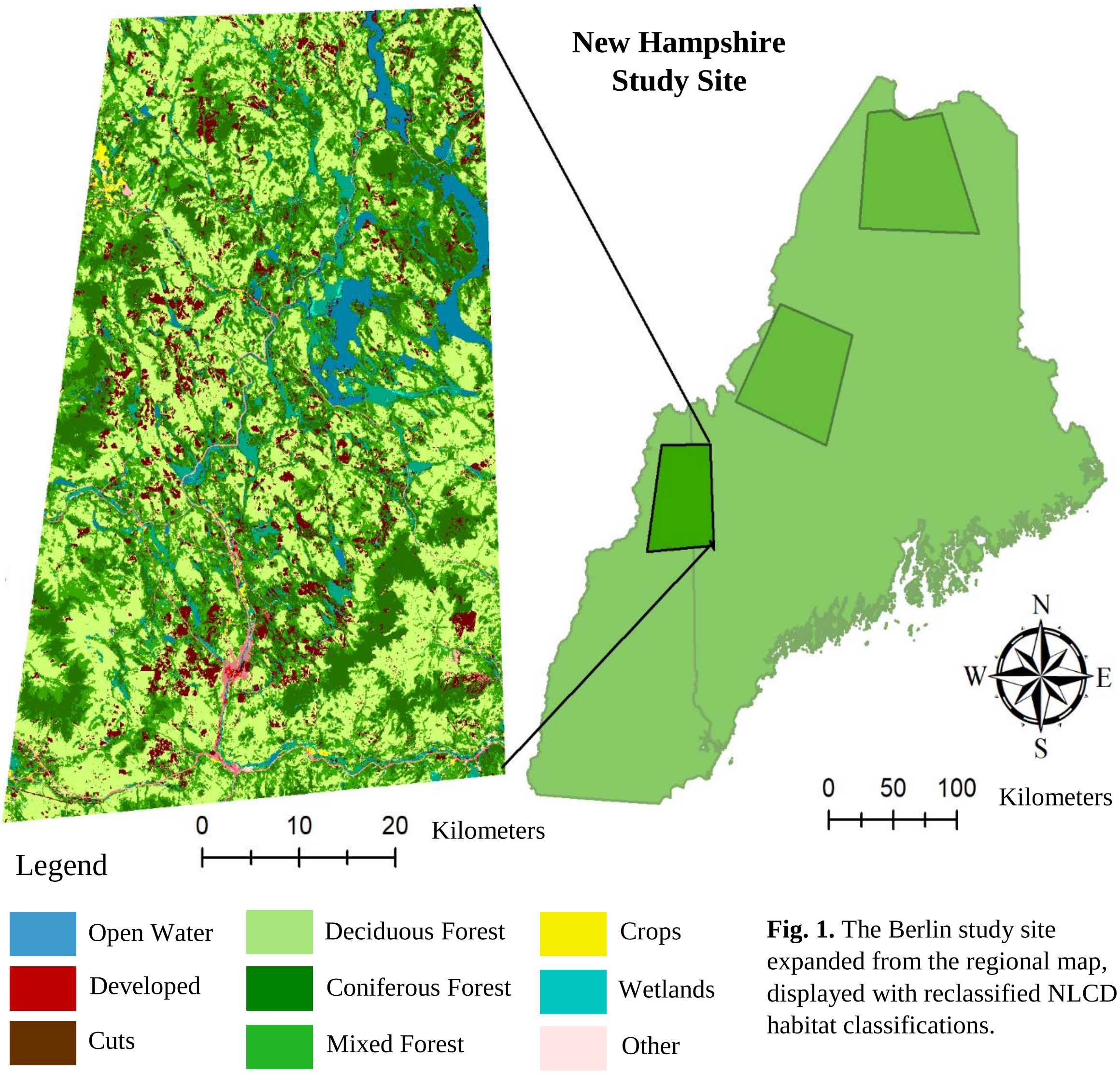

Fig. 1. The Berlin study site expanded from the regional map, displayed with reclassified NLCD habitat classifications.

The site is part of the NHFG North Region and was the location of a comprehensive study of moose population dynamics in 2001-2005 when density was estimated to be ~0.8 moose/km^2 (Musante et al. 2010). The most recent population estimate is ~0.6 moose/km^2 (NHFG 2017), and from 2014-2018, > 200 moose have been fit with radio-collars as part of the productivity and calf mortality study. Winter tick-related calf mortality was 62%, 74%, 77%, and 30% in 2014, 2015, 2016, and 2017, respectively (Jones 2016, unpublished data).

Study Area- Maine

The site in western Maine (Jackman) occupies portions of Somerset and Piscataquis Counties in Wildlife Management District (WMD) 8, surrounding the towns of Greenville and Jackman (Fig. 2). The eastern boundary is Moosehead Lake and the Maine-Quebec line borders the west; Golden Road and Route 27 are the northern and southern borders. The site is considered primarily a northern hardwood maple-beech-birch forest, with predominant hardwoods of red maple (*Acer rubrum*), sugar maple, yellow birch, and American beech, with balsam fir as the dominant softwood; portions of the site also include northern white-cedar and red spruce (McCaskill et al. 2016). Though clearcutting is limited in scale in Maine, ~32% of statewide clearcutting activity (14,531 total acres) in 2015 and 2016 occurred in Somerset and Piscataquis counties (MFS 2015, 2016). Optimal habitat has declined somewhat since 2001, but this decline may simply reflect the difficulty in discerning partial harvesting with Landsat imagery. Regardless, with 4-16 year-old cuts minimally representing > 17% of forest cover, it is considered excellent moose habitat (Dunfey-Ball 2017). Average dates of first and permanent snow are similar to the New Hampshire site.

Aerial surveys in 2013 estimated the average moose density as ~1.7 moose/km^2 (Kantar and Cumberland 2013); more recent estimates indicate a decline to 0.97-1.35 moose/km^2 (Jones et al. 2017). In 2014-2018 > 200 moose were GPS radio-collared as part of the collaborative study with New Hampshire. Calf mortality attributed to winter tick parasitism was 73%, 60%, 72%, and 53% in 2014, 2015, 2016, and 2017, respectively (Kantar, unpublished data).

The site in northern Maine (Aroostook) is located in Aroostook County within WMD 2 (Fig. 2). It includes the towns of Wheelock Mill and Winterville and is bordered the Allagash River to the west. The eastern boundary is Route 11, and the southernboundary is American

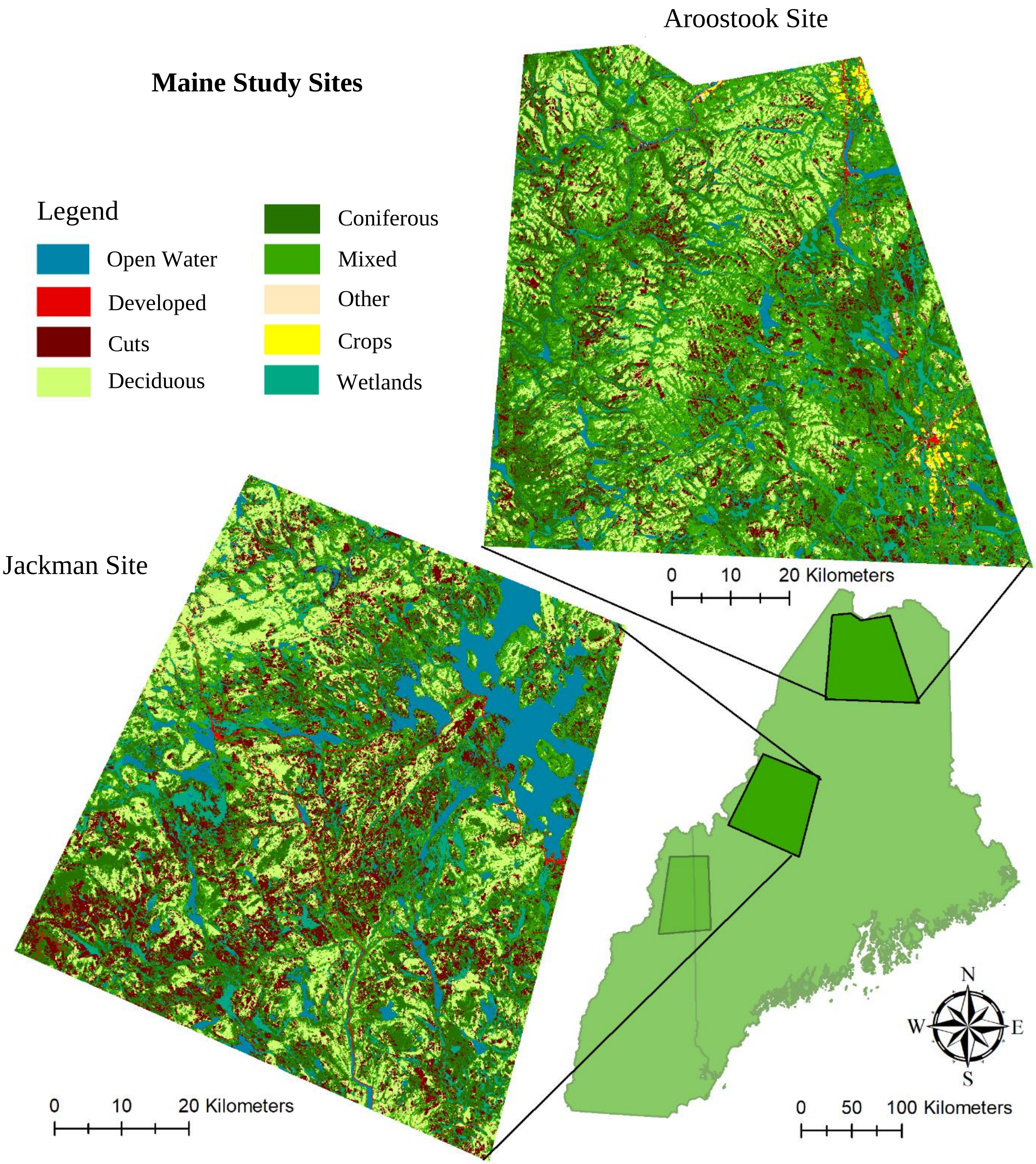

Fig. 2. The Jackman and Aroostook study sites expanded from the regional map, displayed with reclassified NLCD habitat classifications.

Realty Road. Spruce-fir and maple-beech-birch forest types categorize the site, with softwood stands dominated by balsam fir, northern white cedar, red spruce, and black spruce (McCaskill et al. 2016). About 1/3 of annual statewide clearcutting occurs in Aroostook County, with a total of 14,863 acres harvested in 2015 and 2016 combined (Maine Silviculture Activities Report 2015, 2016). Proportional availability of optimal habitat for moose was not available for this site, although it is considered excellent moose habitat (Andreozzi et al. 2016). Snow typically begins earlier at this site than at the other sites, and is thought to possibly limit the questing period and frequency of winter tick epizootics.

Moose density was estimated as 3.0-3.1 moose/km^2 during 2013 aerial surveys (Kantar and Cumberland 2013), and has since been adjusted to ~2.5 moose/km^2 in more recent surveys (Dunfey-Ball 2017, MDIFW unpublished data). This site was established in 2016 with > 120 GPS radio-collars deployed in 2016 - 2018. Winter tick-related calf mortality was 52% and 24% in 2016 and 2017, respectively (Kantar, unpublished data).

Landcover

National Land Cover Data (NLCD 2011) were used to estimate habitat composition at the three study sites (Berlin, Jackman, and Aroostook). Land cover categories of emergent and woody wetlands were combined to represent “general wetlands”. NLCD layers for New Hampshire and Maine were projected in UTM 19 N coordinates, and were clipped to polygons that had been digitized in ArcMap 10.3.1 (ESRI Redlands, CA) around locations of GPS transmissions in each site. The imagery dates ensured that new cuts (< 4 years since disturbance) were not included in the analysis.

Because the classification scheme categorizes early successional habitat as shrubland, herbaceous, and barren, these cover types were reclassified as “cuts”. This approach likely underestimates optimal habitat (4-16 year-old forest) for moose, as 16 year-old forest likely displays reflective properties more similar to mature forest than areas of recent disturbance. Additionally, partial cutting has proven more difficult to discern than larger clearcuts in Landsat imagery, as cut openings may be too small to be perceived as anything but noise at 30 x 30 m resolution. Change detection studies utilizing Landsat images to map forest disturbance have reported greater classification accuracy when the disturbance was clearcutting rather than partial harvesting (Wilson and Sader 2002: clearcuts = 79-96% accurate, partial cuts = 55-80% accurate; Jarron et al. 2017: clearcuts = 84% accurate, partial cuts = 64% accurate). The difficulty in identifying partial cuts is attributed to a more subtle and gradual change in spectral reflectance than evident with clearcuts (Jarron et al. 2017). Although this may yield a conservative estimate where partial harvesting is the predominant method of harvest, it was assumed that patterns of habitat use and selection would be evident.

The landcover composition at Berlin (3,405 km^2) was 82% forest comprised of deciduous (36%), mixed (27%), and coniferous (19%) types. Cuts represented ~9% of the landscape, and the remaining was wetlands (5%), open water (3%), and development (2%) (Fig. 1).

The Jackman site (5,535 km^2) was 65% forest cover: 23% coniferous and 21% deciduous and mixed forest each. Cuts were 19% and more prevalent than in Berlin or Aroostook; wetlands and open water (due to the inclusion of a portion of Moosehead Lake) were 8% (Fig. 2).

Aroostook (6,360 km^2) forest cover was mixed forest (38%), coniferous (22%), and deciduous (17%). Cuts were 11% with wetlands (8%), open water (2%), and cropland (1%) the remainder (Fig. 2).

Range Size

Two seasons were defined to account for 1) when adult female ticks drop from moose in spring, and 2) when larval ticks quest for a host in autumn: drop-off (15 March – 5 May) and questing (15 September – 26 November). GPS transmissions from female moose logged to GPS Plus X (Vectronic Aerospace GmbH) during drop-off (2014-2017) and questing (2014-2016) were exported to Microsoft Excel to summarize the number of locations per animal; radio-collars were programmed to transmit locations twice daily. Radio-collars that logged ≥ 50 locations during a season were used to calculate home and core ranges of individuals using kernel density estimation; a sample size of 50 is recommended with the kernel density method (Seaman et al. 1999**,** Scarpitti 2006). In 2014-2017, 49 animals in Berlin and 124 in Jackman were used during drop-off; 7 animals in Berlin and 75 in Jackman were used during questing (2014-2016). In 2016-2017 in Aroostook, 83 animals were used in the drop-off period and 26 were used during questing (2016 only). Certain moose were used in multiple seasons (Appendix 1).

The fixed kernel density estimation method produces a more accurate measure of landscape use than other techniques such as minimum-convex polygons (Worton 1995, Seaman et al. 1999). The smoothing factor chosen was least-squares cross-validation (LSCV) as it produces the least bias when sample sizes are sufficient (Seaman et al. 1999). Contours generated in this analysis highlight the areas in which an animal would theoretically be located a certain proportion of the time (Worton 1995). Home and core ranges were defined as the 95% and 50% probability densities since these are the most commonly reported in the literature (Worton 1995, Seaman et al. 1999, McCulley et al. 2017b). Ranges were calculated in the Geospatial Modelling Environment v. 0.7.4.0 (Beyer 2015) for each moose and imported to ArcMap.

Area (km^2) of home and core ranges was calculated using spatial statistics in ArcMap 10.3.1. Because kernel density estimation produces non-parametric results (Seaman et al. 1999), the comparison of mean ranges by season between sites was completed in R Studio 0.99.903 (RStudio Team 2015) using the Kruskal-Wallis test which does not assume normality of data. The ranges of calves during drop-off were combined with the adult cow age class, as calf ranges are presumed similar to their mother's range (Ballard et al. 1991); no questing period was available for calves captured in January. Where results were significant for multiple variables ($p < 0.05$), Dunn's test using Bonferroni adjustments (R package PMCMR) was used to determine which variables accounted for that significance.

Habitat Use

The NLCD layer for each site was clipped to and unioned with each home and core range polygon that fell within its boundary to measure the proportional availability of land cover types in ArcMap. The composition of core ranges was important because core range presumably reflects the area and habitats used most, whereas home range is a larger area that reflects less selective use. Comparing the composition of both ranges indicates if moose selected core ranges with specific habitat types less available within the home range. The Kruskal-Wallis test was used to compare the importance of each habitat type between seasons for adult cows and the composition of home and core ranges within each site. Because of a difference in proportional availability, significance testing between sites was not completed for habitat composition within home and core ranges.

Range Overlap

This analysis included female adults and calves that survived successive drop-off and questing periods in 2014, 2015, and 2016 in Berlin and Jackman, and 2016 in Aroostook. A total of 7 moose from Berlin, 76 moose from Jackman, and 26 moose from Aroostook fit this criterion. Home and core ranges for each moose measured during drop-off and questing of the same year were intersected using ArcMap 10.3.1 to determine where overlap occurred between seasons. The area of overlap was then divided by the total area covered by the drop-off and questing ranges to determine the proportion of habitat consistently used in both seasons. Non-parametric Kruskal-Wallis tests were performed in R Studio to determine if proportional overlap of home and core ranges differed by site. Where differences were significant ($p < 0.05$), Dunn's test was used to distinguish between sites.

National Landcover Data was clipped to each overlap to determine the proportion of cut areas consistently used between seasons. Spatial statistics within ArcMap were used to calculate the area of cuts within the overlaps, and this was divided by the total area of the overlaps for both home and core ranges. Non-parametric Kruskal-Wallis tests were performed in R Studio to determine if the proportion of cuts within overlaps of home and core ranges differed by site. Where differences were significant ($p < 0.05$), Dunn's test was used to distinguish between sites.

RESULTS

Range Size

Questing ranges were consistently larger than drop-off ranges, with the single exception of the core range at Berlin. Core ranges comprised 18-25% of home ranges regardless of season or site. Range size was consistently larger in Aroostook and smallest in Jackman. Home ($P = 0.39$) and core range ($P = 0.82$) size during drop-off was similar at all sites, ranging from 9.9-15.0 and 2.1-2.7 km^2, respectively. Conversely, size of home ($P = 0.02$) and core ranges ($P = 0.03$) was different during questing; Aroostook was larger than Berlin (>2.5 x larger) (Table 1). Individual variation in home and core range was high, ~4-5 fold.

Table 1. Home range (HR) and core range (CR) recorded for moose during the questing and drop-off periods at each site. Data for Berlin and Jackman were collected between 2014-2017 and for Aroostook 2016-2017. Where P values were significant, the results of Dunn's test indicating which sites were significantly different is listed, with sites abbreviated by first initial (A = Aroostook, B = Berlin, J = Jackman).

	Aroostook			Berlin			Jackman			
Seasonal Range	n	Mean ± SE (km^2)	range (km^2)	n	Mean ± SE (km^2)	range (km^2)	n	Mean ± SE (km^2)	range (km^2)	*P*
Home Range										
Drop-off	83	15.0 ± 2.0	0.3 - 117.6	49	13.0 ± 2.0	0.5 - 70.9	124	9.6 ± 0.7	0.2 - 43.9	0.39
Questing	26	34.1 ± 7.0	4.2 - 171.2	7	11.8 ± 2.6	3.7 - 23.2	75	23.2 ± 3.0	3.5 - 151.2	0.02 (A-B = 0.04)
Core Range										
Drop-off	83	2.7 ± 0.3	0.1 - 14.0	49	2.6 ± 0.4	0.1 - 11.6	124	2.1 ± 0.2	0.1 - 7.1	0.82
Questing	26	7.4 ± 1.2	1.1 - 22.7	7	2.9 ± 0.8	0.8 - 6.6	75	5.7 ± 0.8	0.9 - 43.9	0.03 (A-B = 0.04)

Habitat Use

Although available within each site, open water, developed, cropland, and “other” habitat types combined was < 2% of drop-off and questing ranges, and considered insignificant in the analysis. The proportional use of habitat types within home ranges was similar each season ($P > 0.05$). In core ranges during drop-off, deciduous forest was used more in Aroostook and Jackman ($P = 0.02, 0.05$), and coniferous forest was used more in Aroostook ($P = 0.03$). Cuts was the only habitat type consistently used more than its availability, regardless of site or season. Cuts were used 1.1-2.1 X their availability within home ranges, and 1.2-3.1 X their availability within core ranges (Fig. 3). Deciduous and coniferous forest types were consistently used less than available at Berlin and Jackman; mixed forest was used equal to or above its availability.

Few differences were found between home and core ranges within a site during the same season. Exceptions in core ranges during drop-off included less use of mixed forest in Aroostook ($P = 0.03$), deciduous forest in Aroostook and Jackman ($P = 0.02, 0.01$), and wetlands in Jackman ($P = 0.1$). Moose at all sites displayed 2-8% higher selection for cut areas within core ranges during questing, whereas use of cut areas was similar (within 2%) for home and core ranges during drop-off.

Range Overlap

Overall, 97% of moose had overlapping home ranges and 66% had overlapping core ranges. The proportion of home and core range overlaps varied from 0-73% and 0-43%, respectively; home range overlap in Berlin and Jackman was $\geq$20%. An increasing trend in overlap occurred from Aroostook to Berlin to Jackman; home ($P = 0.04$) and core range overlaps ($P = 0.01$) were higher in Jackman than Aroostook (Table 2). At all sites, the proportion of

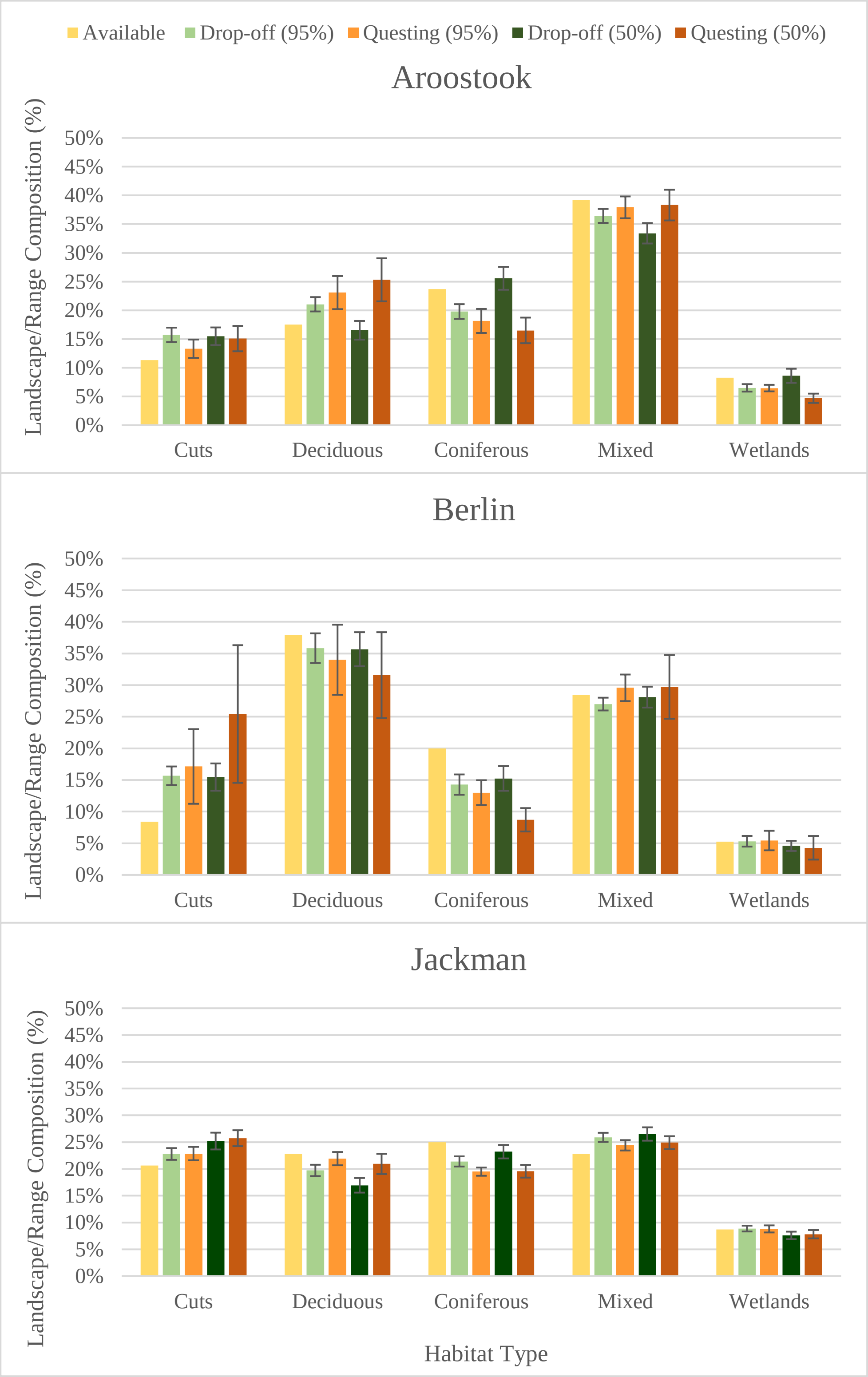

Fig. 3. Adult use of each of the 5 major habitat types. Yellow bars indicate landscape availability specific to each site, while green and orange bars represent drop-off and questing ranges. Lighter shades are 95% home range, darker shades are 50% core range. Error bars represent standard error.

overlap declined (~2-5 fold) from home to core ranges.

Table 2. Overlap of home (HR) and core (CR) ranges for moose that survived subsequent drop-off and questing seasons at each site.

	Aroostook			Berlin			Jackman		
Range	n	Mean (± SE) Overlap	Range Overlap	n	Mean (± SE) Overlap	Range Overlap	n	Mean (± SE) Overlap	Range Overlap
HR	25	15.1 ± 2.0%	1-40%	7	19.9 ± 6.0%	7-54%	75	24.3 ± 1.8%	0-73%
CR	13	3.1 ± 1.2%	0-24%	4	7.9 ± 4.2%	0-29%	56	8.8 ± 1.1%	0-43%

Across sites, the average proportion of cut habitat in seasonally overlapping home and core ranges was similar: 12.4-23% in home and 8-26% in core ranges. This proportion exceeded the proportional availability of cut habitat at each site (Table 3, Fig. 3). In contrast to seasonal overlap, the proportion of cut habitat overlap was similar between home and core ranges, except in Berlin. The proportion of cut habitat in home range overlap was 1.8x higher in Jackman than in Aroostook ($P < 0.00$); the proportion in Berlin was similar to that at both Maine sites. The proportion of cut habitat in core range was not different ($P < 0.05$) among sites, although the overlap in Jackman was 1.7-3.1x higher than at Aroostook and Berlin (Table 3). As with seasonal overlap, individual variation in overlap existed (0-75%).

Table 3. Proportion of home (HR) and core (CR) overlap that is composed of cut habitat.

	Aroostook		Berlin		Jackman	
Range	Mean (± SE) Cuts (%)	Range Cuts (%)	Mean (± SE) Cuts (%)	Range Cuts (%)	Mean (± SE) Cuts (%)	Range Cuts (%)
HR	12.4 ± 2.8	0-75.0	17.0 ± 5.7	1.7-46.3	23.0 ± 1.7	0-68.0
CR	14.8 ± 5.2	0-66.7	8.2 ± 4.7	0-18.9	25.8 ± 2.9	0-75.0

DISCUSSION

Range Size

Home and core range sizes during questing increased from south (Berlin) to north (Aroostook), a pattern likely reflecting the similar population density gradient at these sites. In general, the larger ranges during questing likely reflects higher movement and activity during breeding season. The ranges were generally similar to those reported in previous studies at the Berlin site and in Massachusetts (Table 4).

Table 4. A comparison of home range sizes for moose in New England during late winter, spring, and autumn.

Location	Drop-off HR Size (km^2)	Drop-off Dates	Questing HR Size (km^2)	Questing Dates	Method	Source
New Hampshire	14.23 ± 2.26	15 Mar. - 5 May	11.79 ± 2.63	15 Sept. - 26 Nov.	95% KDE	This study
Western Maine	9.35 ± 0.65	15 Mar. - 5 May	23.17 ± 3.03	15 Sept. - 26 Nov.	95% KDE	This study
Northern Maine	21.64 ± 6.13	15 Mar. - 5 May	36.98 ± 7.34	15 Sept. - 26 Nov.	95% KDE	This study
New Hampshire	~15.15	Late-winter + spring = 16 Feb. - 15 Jun.	24.7	Fall = 16 Sept. - 15 Dec.	90% KDE (VHF)	Scarpitti 2006
Massachusetts	~ 11.95	Late-winter + spring = 1 Jan. - 31 May	~11.4	Fall + early-winter = 1 Sept. - 31 Dec.	95% KDE	Wattles & DeStefano 2013

Habitat Use

Moose used cut habitat above its proportional availability within home and core ranges. This selective use is well documented regionally, year-round and in boreal forest at large (Belovsky 1981, Renecker and Hudson 1992, Scarpitti et al. 2005, Scarpitti 2006, Bjorneraas et al. 2011, Lenarz et al. 2011, Terry 2015). Although the relative difference between availability and use of cuts was lowest in Jackman, both availability and use of cuts was highest there, with use proportionally up to 25% higher than the other sites (Fig. 3). Moose generally displayed higher use of cut areas during questing than drop-off, despite larger home ranges during questing. This stronger habitat selection, despite larger home range, may ensure questing success and high tick abundance on moose despite their increased activity and movement during breeding. Overall, this analysis provides strong evidence of this selective use during the short and critical periods of drop-off and questing during the life cycle of winter ticks.

One limitation of describing habitat use from location data is that the GPS radio-collars were programmed to transmit coordinates only twice daily. Although home range composition can be reasonably defined, there is no estimate for the amount of time moose spend in each habitat type. Moose, like other ruminants, spend most time in three activities: feeding, resting, and ruminating (Renecker and Schwartz 1997). Daily activity budgets indicate that time spent per activity changes seasonally, but feeding generally occupies 30-40% of their time (Risenhoover 1987, Renecker and Hudson 1989a, Van Ballenberghe and Miquelle 1990). The bulk of forage consumption by moose is within cut areas, because optimal moose habitat provides highest quality forage and is concentrated spatially (Renecker and Schwartz 1997). Therefore, time spent in cuts is presumably higher than the proportional availability of cuts in the core range.

The high use of cut habitat by moose during drop-off and questing is important because the survival of winter tick larvae is highest in open cover types; tick density declines as canopy cover exceeds 60% closure (Drew and Samuel 1986a, Aalangdong 1994, Terry 2015) because restricted sunlight and cooler temperatures impacts the activity and efficiency of winter ticks during questing (Drew and Samuel 1986a, Aalangdong 1994). With the exception of years characterized by especially hot and dry conditions, open habitats are more conducive to successful larval transmission than closed habitats (Addison et al. 2016). In an assessment of randomly selected cover types crossing fall movement paths of GPS-collared moose, Terry (2015) found that 70% of locations categorized as regenerating habitat contained ticks; a greater proportion than any other cover type. In combination, selective habitat use by moose and higher survival of larval ticks provides favorable conditions to promote local abundance of winter ticks in optimal moose habitat.

Seasonal Overlap

Moose display seasonal range fidelity (Welch et al. 2000, Ofstad 2013), and unsurprisingly, all but 3 of 106 adult moose that survived consecutive questing and drop-off periods exhibited some degree of seasonal home range overlap. Average home range overlap in this study was 15-24%, with the greatest overlap in Jackman and the least in Aroostook. Core range overlap was lower at 3-9%, but followed the same site trend. Importantly, the seasonal proportional overlap of cut habitat in home and core ranges exceeded the absolute proportion in home and core ranges. The drop-off period in this study spanned portions of the late-winter and spring seasons as defined by Scarpitti (2006), who found 22% overlap in late-winter and fall home ranges, and 33% overlaps in spring and fall home ranges; core range overlaps were 10% and 16%, respectively.

Cut areas were 12-23% of the seasonal home range overlaps of 102 of 106 moose. Interestingly, core range overlaps contained a greater proportion of cut areas (15-26%) than home range overlaps at all sites except Berlin (8%) which had a small sample size (4 moose). These data indicate that moose not only select for cuts, but also use the same cuts during both the drop-off and questing seasons, and presumably identical feeding sites and paths within the same cuts. It is possible that moose contract offspring larvae in the fall from adult ticks that dropped from them the previous spring. This is consistent with Terry (2015) who found some degree of self-overlap on spring and fall movement paths of radio-collared moose (4.6%).

CONCLUSION

Understanding how and where moose acquire winter ticks is key to predicting the occurrence and relative severity of winter tick epizootics. This analysis indicates that moose in northern New England selectively use cut habitat more during the drop off and questing seasons of winter ticks. Importantly, this relationship was found despite cuts being underestimated due to the difficulty discerning smaller openings associated with partial harvesting in Landsat imagery, and possibly misclassifying older age classes of optimal habitat (4-16 years). Considering that moose spend 30-40% of daily activity feeding in optimal habitat that ranged from 9-19% availability at the study sites, it follows that winter tick abundance on the landscape is concentrated in a proportionally small, but selectively used optimal habitat. Again, this is a conservative conclusion as moose commonly bed in cuts during both seasons, presumably increasing the local abundance of gravid adult female ticks during drop off, and subsequently, tick loads on moose after questing. Winter tick abundance on the landscape is ultimately a function of multiple characteristics of the behavior, physiology, and local abundance of moose and winter ticks that are linked to dynamic processes of forest harvesting, weather events, and climate change. Assuming continuation of the current trend of sustained forest harvest in northern New England that produces near 20% availability of optimal moose habitat and high moose density, the near-term occurrence of winter tick epizootics will primarily be a function of annual weather events that limit survival of winter tick larvae in autumn.

CHAPTER 2:

Agent-Based Modeling of Moose-Winter Tick Relationships at Local and Regional Scales in Northern New Hampshire

INTRODUCTION

Widespread mortality of 10-month old moose (*Alces alces*) calves in the southern portion of their North American range has become increasingly frequent in the last decade. Ample research conducted in northern New England (New Hampshire, Maine, Vermont), Minnesota, Michigan (Isle Royale National Park), and several Canadian provinces (Alberta, Manitoba, Ontario, Saskatchewan, and Nova Scotia) has linked late winter mortality to parasitism by winter ticks (*Dermacentor albipictus*) (Samuel 2004, Musante et al. 2010, Bergeron and Pekins 2014, Jones et al. 2017, Dunfey-Ball 2017).

The life cycle of winter ticks differs from that of other common tick species (e.g., deer (*Ixodes scapularis*) and dog ticks (*Dermacentor variabilis*)), in that winter ticks are a one-host parasite; once they successfully attach to a host, they take all blood-meals and transition from larval to nymphal to adult stages on that animal (Samuel 2004). Winter ticks actively seek viable hosts (they quest) from mid-September through the onset of freezing temperatures, and drop off their hosts in late-March through mid-April (Drew and Samuel 1989). The drop-off period is when the bulk of calf mortality occurs because the final blood meal taken by adult female winter ticks depletes significantly more blood than previous blood meals, and calves are physically compromised by minimal/depleted fat stores (Samuel 2004). The smaller mass of calves versus adult moose puts them at greater risk of anemia and mortality (Musante et al. 2007).

Ongoing research projects have been established in New Hampshire, Maine, and Vermont to measure productivity and mortality of moose, and related epizootic trends. Winter tick epizootics are related to seasonal weather events and host population density. Multiple studies indicate that later onset of winter snow extends the questing period of winter ticks, allowing greater opportunity to contact a host (Aalangdong 1994, Bergeron and Pekins 2014). Dunfey-Ball (2017) predicted that late summer droughts, lasting for periods of ~18 days in late August - September, could cause substantial larval mortality from desiccation prior to the start of the questing period, and thus reduce the risk of epizootics. Observations in New Hampshire support this theory, as a widespread drought in September 2017 resulted in a ~50% reduction in October tick loads on calves, and calf mortality dropped from ~70% in 2014 – 2016 to ~30% (Jones 2016, Pekins, personal communication).

The impact of moose density and/versus the effects of weather on winter tick abundance has important management implications. Reducing the moose population through an increased harvest could theoretically reduce the prevalence of winter tick epizootics (>50% calf mortality) more quickly than allowing the system to balance itself. In order for the moose population in northern New Hampshire to stabilize, the frequency of epizootics must decline from 5 to 3 in 10 years (Jones 2016, Dunfey-Ball 2017). Population projections suggest that a lower density, sustainable moose population devoid of epizootics could be achieved in New Hampshire within the next 5 years by returning the number of moose hunting permits to the maximum issued; whereas ≥16 years would be required for an equivalent decline under the conservative current harvest levels.

Population density estimates are difficult to develop for wild animals, and commonly have wide margins of error. Such uncertainty makes it challenging for wildlife managers to implement specific harvest strategies to manage for a desired population density in a specific area. Population models are therefore useful to understand and predict the potential impacts of population management strategies.

Agent-based (individual-based) modeling is a form of population modeling that examines complex systems from a bottom-up perspective, rather than strictly at the population level. Individuals (agents) are given rules to follow that allow them to emulate their real-world counterpart within the confines of a model environment. Agents make decisions based on these rules that allow them to interact with other agents and their environment. Additionally, agents learn from their experiences, and adapt future behavior accordingly (Lane-deGraaf 2013). Agent-based models preserve heterogeneity and individuality within populations, rather than operating on the assumption that members will react in the same way to external stimuli.

Agent-based models have been used previously to explore host-parasite relationships. Wang et al. (2012) used an agent-based model to determine the impacts of host density, climate, and landscape variables on questing by lone-star ticks (*Amblyomma americanum*), and subsequent proliferation of vector-borne diseases. This study will evaluate those same parameters, but the primary interest lies in the impact of winter ticks on the survivorship of their hosts, rather than the impact of host density on tick density. Wang et al. (2015) also examined seasonality as it impacts the density of host populations. Conversely, in the winter tick model, seasonality determines the behavior of host agents, not the density of hosts. Models created for both of those studies (Wang et al. 2012, Wang et al. 2015) were spatially representative of a particular region within the United States, as with this winter tick model.

Agent-based modeling has been used in other studies focused on ungulate species. For example, Semeniuk et al. (2012) constructed a model to investigate the shift in woodland caribou (*Rangifer tarandus)* behavior during winter in response to environmental disturbance using GPS transmission data from 13 radio-collared animals. Similarly, GPS data from radio-collared moose were used to bind moose agents to realistic home ranges and compare movement of model moose with actual study animals. While this study does not allow for changes within the environment that could alter agent behavior, it could be adapted with snow to impede moose movement, or account for habitat modification related to forest harvesting. Grosman et al. (2009) used GPS data from radio-collared moose to inform moose movement and use of roadside salt licks.

Agent-based modeling was used to observe patterns and trends in calf mortality and average infestation level of dead calves resulting from interactions among winter ticks, moose, climate, and landscape variables representative of a study area in an explicit moose habitat in Berlin, New Hampshire where a mortality and productivity study has been ongoing since 2014. Specifically, the model was built to assess how moose density, date of snowfall, drought, winter tick aggregation, and winter tick abundance influence the occurrence and severity of epizootics.

Background Information and Modeling Considerations

While agent-based modeling originated in the early 1970s with Thomas Schelling's segregation model (Singh et al. 2009), it has only recently become a popular tool across numerous fields, including the natural sciences. It is an effective technique for simulating interactions in complex systems, and is useful when modelers are interested in trends that result from relationships between heterogenous individuals that are capable of sensing stimuli and learning within a spatially explicit environment. This model type was chosen to investigate the impact of winter tick epizootics on moose populations because the key agents (moose and winter ticks) are independently driven to accomplish their goals, and individually susceptible to consequences based both on their own actions, and other actions influencing the environment. Additionally, the environment itself (represented by distribution and availability of clearcuts) plays an important role in individual decision-making, which can be addressed in an agent-based model.

The original plan for the model was modified due to practical limitations of the software in which the model was designed. NetLogo (Wilensky 1999), a program designed specifically for agent-based modeling, allows for the allocation of a finite amount of computer memory to be utilized for model runs (1 GB). Once this threshold has been reached, the model will not run simulations in BehaviorSpace, the application in which experiments are processed. The usage of relatively high resolution (30 x 30 m) GIS data layers and the necessity for many thousands of winter tick agents to be present on the landscape exceeded the memory allotment for simulations of the study area as a whole. It was important to preserve the spatial resolution of the GIS data layers because the location and distribution of clearcuts within the study area was an integral component of the model; changing the resolution of the data layers would have resulted in increased error in land cover classification. Therefore, the study area was divided into subsections to provide for localized differences throughout the study area, with subsequent averaging to identify trends across the study area.

Additionally, winter ticks were originally intended to be adaptive agents that would remain in the system as they cycled through their life stages. Because of the quantity of winter ticks needed to reach the abundance levels used in the model, their presence significantly increased the simulation time. Therefore, unattached winter tick agents were eliminated at the conclusion of the questing period after which tick agents equated the infestation number unique to each moose agent; in actuality, unattached ticks eventually perish in winter and have no effect on the hosts. The infestation number was used to calculate blood loss which is a sufficient and computationally efficient means of understanding winter tick impact (i.e., death). The only stage of the life cycle that is represented by a blood meal in the model is adult female engorgement which occurs just before winter ticks detach from their host. Only this stage was used because the amount of blood lost during the other blood meals (larval, nymphal) is insignificant in comparison to the final blood meal, and less likely to have measured consequence on the host moose (Samuel 2004). Importantly, this approach maintains a conservative approach to calculating mortality.

Finally, although moose have an adaptive strategy of grooming to remove ticks, no reliable estimate exists to calculate the removal rate, and many calves show no symptoms of hair loss indicating tick removal. Overall, the estimates of winter tick abundance on the landscape and their accumulation by host moose were conservative as the parasite was restricted only to cut (optimal) habitat.

METHODS

2.1. Study area

The study area used in the model was within the towns of Berlin and Success in Coos County, New Hampshire (Fig. 4). These towns are included in the current field study between the University of New Hampshire and the New Hampshire Fish and Game Department that has been monitoring mortality and productivity of moose (n > 200) in portions of wildlife management units (WMU) B, C1, C2 since 2014. The study area is composed of large tracts of privately-owned forest where commercial logging actively occurs. In 2001, ~12% of the study area was considered optimal moose habitat (4-16 years post-harvest) and by 2016 this estimate had increased to 17.5% (Dunfey-Ball 2017); habitat quality is considered excellent and not a limiting factor to moose survival (Bergeron 2011, Dunfey-Ball 2017).

Motorized outdoor recreation is a common leisure activity in the study area with all-terrain vehicles (ATVs) permitted on designated roads connecting Berlin and Success. Jericho Mountain State Park (Park) in Berlin is a popular tourist destination for ATV riders, containing > 100 miles (160 km) of trail system. The Berlin study site (referred to as "Jericho") covers ~41 km^2 of the Park to the west of Route 110 and north of Route 2, surrounding Jericho Lake. The study site at Success (~110 km^2) is located just east of Route 16 and bounded to the east by the Mahoosuc Range and Maine border, the south by the Appalachian Trail, and the north by French Hill Road/Chickwolnepy Stream.

These sites were selected for the model because each contained a high concentration of GPS-locations of radio-marked moose, which allowed for the validation of moose movement rules within the model. Additionally, the sites displayed differing levels of optimal moose habitat; Success is representative of the larger study area with ~17% cut area, whereas Jericho included ~28% cuts. Cut area was calculated using National Landcover Data (NLCD 2011, USGS). Because early successional habitat is represented as shrubland, herbaceous, or barren in the NLCD classification scheme, these habitats were reclassified as cuts and used to represent optimal moose habitat.

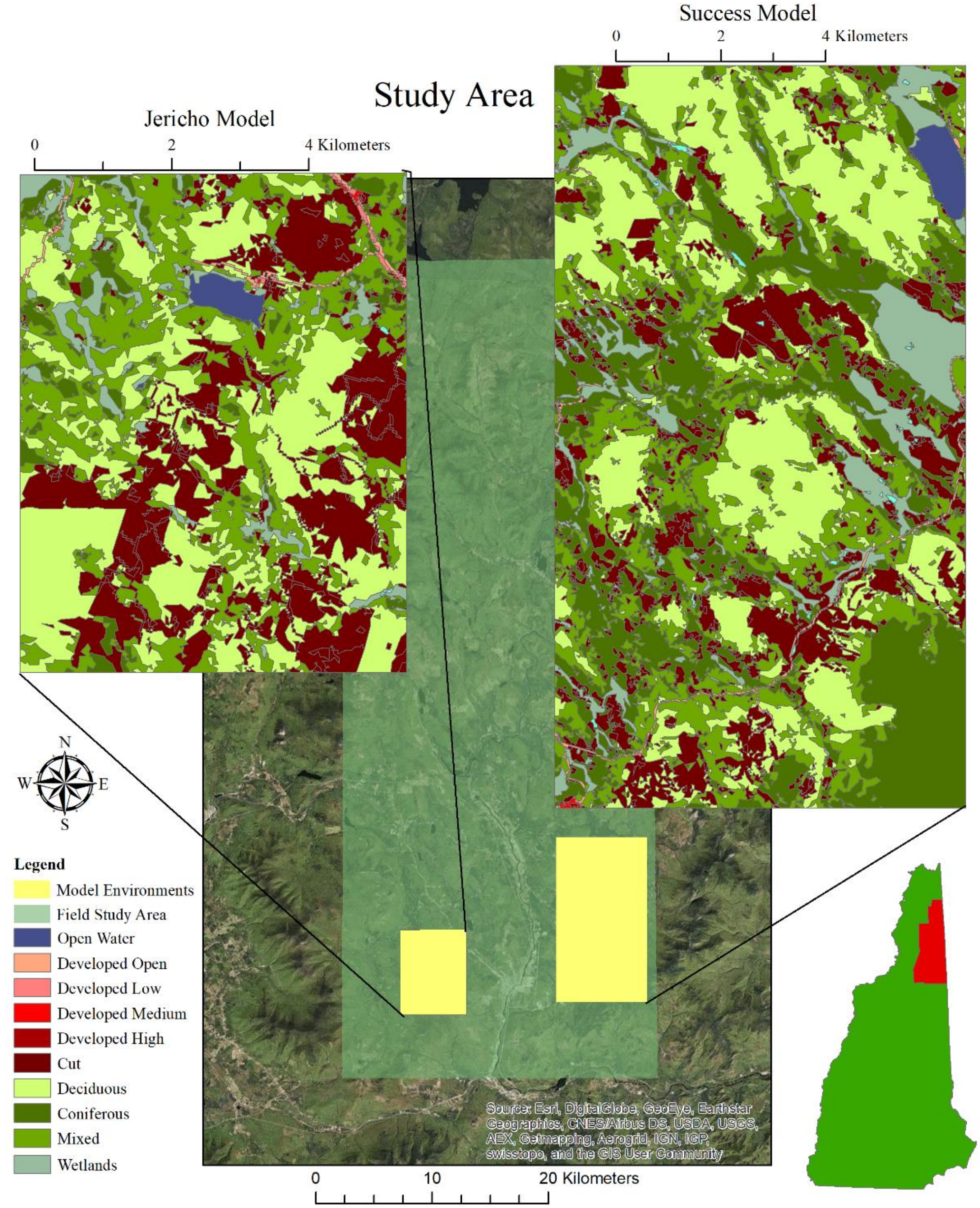

Fig. 4. Yellow rectangles show the sections of the field study area (large green rectangle) considered in the model. The enlargements display the habitat composition of Jericho (left) and Success (right) as determined by the most recent (2011) reclassified National Land Cover Data. The area in red on the map of New Hampshire indicates the location of the field study area.

2.2. Model description

The description for this model follows the ODD (Overview, Design Concepts, and Details) protocol recommended for describing agent-based models (Grimm et al. 2006, 2010). The model was implemented in the open-source program NetLogo, version 6.0.1 (Wilensky 1999) and R Studio (RStudio Team 2015) was used to analyze simulation results. The code used to construct this model is available in Appendix 2.

Overview

2.2.1. Purpose

The purpose of this model was to simulate the role of moose density and weather events, among other variables, in the occurrence and severity of winter tick epizootics at localized spatial scales. The model was designed to test whether the frequency and severity of epizootics were related to forest harvest rates by using two sites with different availability of optimal habitat: Success (17%) was equal to the larger study area estimate and Jericho (28%) exceeded (1.6 X) the study area estimate.

2.2.2. Entities, state variables, and scales

Two types of agents were used: moose and winter ticks. Moose were mobile agents that persisted in the model regardless of season, with ticks as primitive agents present only during the questing season. State variables for moose were age cohort, weight (kg), blood volume (L), and a winter tick infestation level. An initialization point was randomly designated and used to determine their home range. Winter tick agents represented clusters of ticks, as opposed to individuals. State variables included the number of ticks questing in a cluster and a home patch (Table 5).

The Jericho environment was comprised of a grid of 183 x 237 patches, and the Success grid was 263 x 473 patches. Each patch was an area of 30 x 30 m to correspond with the spatial resolution of NLCD pixels. Model boundaries were finite. A model run simulated one year, with each of 8,766 time steps representing one hour. Model days were divided into morning (3 time steps), daytime (9 time steps), evening (3 time steps), and night (9 time steps). The model cycled through 5 seasons: questing, winter, drop-off, calving, and summer. The length of questing and winter seasons varied with the date of the first snowfall set prior to initialization.

2.2.3. Process overview and scheduling

Moose follow a sequence of simplified activity rules that are representative of actual moose in the study region; they move across the landscape, acquire winter ticks, lose blood, drop winter ticks, and potentially die of blood loss during a simulation (Fig. 5). Adult moose rarely suffer mortality from winter tick parasitism due to their large mass, although their overall body condition is impacted (Musante et al. 2007, Jones et al. 2017). Because of this, model moose of the adult cohort do not die during a simulation; their function is to create a realistic distribution of ages within the population and to acquire a portion of the available winter ticks. Data were collected on moose location at each time step. Because they are immobile, winter ticks were dependent on moose behavior to secure a host. Ticks contacted by a moose during the questing period successfully quested, increasing the infestation number of their moose host. Unsuccessful questing ticks died on the first day of winter.

Table 5. Empirical data used to calibrate the model; parameters, parameter values, and source in the literature.

Parameters	**Value**	**Source**
Regional Moose Density	0.86[1], 0.60[2], 0.46[1] moose/km^2	Rines 2015[1], NHFG 2017[2]
Calf weight	176 kg (109-225 kg)	Pekins, personal communication
Adult ♀ (moose) weight	268 kg (dressed) -- 391 kg (live)	NHFG 2016
Blood volume	~8% body weight (kg) = L	Samuel 2004
Daily activity	4, 6*, 8, 10 (hours)	Risenhoover 1987
Questing Home Range	~12 km^2 (4-23 km^2)	This study
Movement/hour	30, 60*, 90, 120, 150 m	This study
Tick abundance in cuts (mean)	0.07, 0.16 ticks/m^2	Bergeron 2011
Tick abundance in cuts (max)	0.40, 0.64 ticks/m^2	Bergeron 2011
Proportion adult ♀ winter ticks	~25% ticks on calves	Samuel 2004
Size of blood meal	2x blood fed weight	Samuel 2004
Engorged weight	0.61 g, 0.5 g	Glines 1983, Drew and Samuel 1989
% ticks that desiccate during drought	25%, 30%*, 35%	See section 2.2.6

* indicates baseline for models

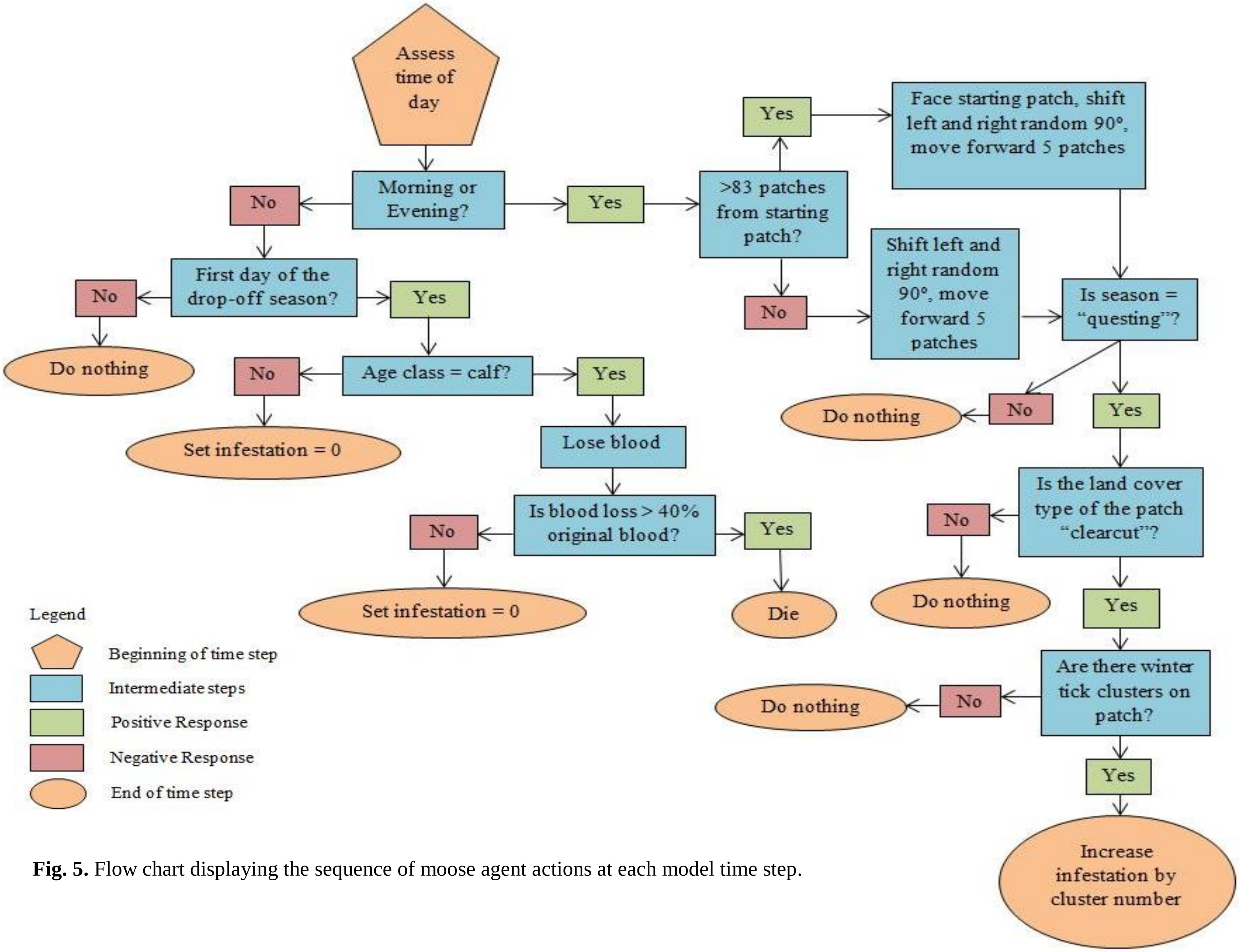

Fig. 5. Flow chart displaying the sequence of moose agent actions at each model time step.

Design concepts

Objectives, learning, prediction, and collectives were not applicable to this preliminary version of the moose-winter tick model.

2.2.4.1. Basic Principles

This model is principally based on the assumption that winter ticks are primarily acquired by moose within cut areas. Previous analysis demonstrated that moose in the study area selectively use (use exceeds availability) cut habitat within home and core ranges during the winter tick questing and drop-off periods (Chapter 1). Regenerating cuts (4-16 years) supply moose with palatable and digestible forage and moose spend 30-40% of each day foraging for maintenance and growth (Risenhoover 1987, Renecker and Hudson 1989a, Van Ballenberghe and Miquelle 1990). Although moose spend a disproportionate amount of time foraging in cuts which leads to local concentration of winter ticks, cut areas compose only ~20% of the local home range.

Additionally, winter ticks are highly sensitive to weather conditions; slight changes in air temperature and moisture impact their activity and questing ability (Aalangdong 1994, Samuel 2004, 2007, Dunfey-Ball 2017). The microclimate of cut areas is more conducive to winter tick survival than closed canopy forest, where temperatures are often lower during the questing season (Drew and Samuel 1986a, Aalangdong 1994, Addison et al. 2016). While it is acknowledged that winter ticks are not restricted to cut areas, the concentrated amount of time moose spend in this habitat type, compounded with the comparatively higher rate of survival and success observed in larval questing beneath an open canopy, justifies the basic assumption for the purpose of this exploratory model.

2.2.4.2. Emergence

Infestation and calf mortality emerge based on weather and density settings which influence the number of winter tick clusters that moose agents may interact within cut openings.

2.2.4.3. Adaptation

There is implicit adaptation in moose movement rules; moose are restricted by the boundary of their home range, which limits the number of cut patches that a moose can access during a simulation. This indirectly aids in individual success as it may limit total infestation.

2.2.4.4. Sensing

All agents were capable of discerning land cover type, to some extent. Winter ticks could sense if a patch was cut, whereas moose could distinguish between cuts, deciduous forest, coniferous forest, mixed forest, and patches that fit none of these categories (“other”). All agents were responsive to seasonality within the model; winter ticks recognized the questing period and the first day of winter, and moose recognized all seasons. Winter ticks were programmed to sense if a drought occurred and moose could sense the time of day and the boundaries of their home range. Agents had no information on the locations of other agents (of their own species or the opposite) operating within the model.

2.2.4.5. Interaction

Agents could interact with other agents of their own species by temporarily sharing the same patch, which had no impact on their fitness or decision-making. The frequency of intraspecies interactions was limited by the immobility of winter ticks and the constriction of moose to a home range. Winter ticks interacted with moose that shared their patch during a time step by increasing the infestation level of that moose.

2.2.4.6. Stochasticity

The direction of moose movement was determined randomly; individuals were instructed to shift to the right and left between 0 - 90° before proceeding forward. The size of individual home ranges was also random, based on the origin point. Moose could have home ranges up to ~20 km^2, but the finite boundaries of the model made this impossible in many cases, reducing home range size to ~7 km^2 in certain cases. This impacted the likelihood of agents picking up ticks, as the proportional availability of cut areas differed between home ranges. Additionally, if the simulation indicated the occurrence of drought, 30% of winter ticks were randomly eliminated from the model environment.

2.2.4.7. Observation

Model runs could be observed in the NetLogo graphical user interface (GUI) which allowed for the creation of plots and monitors to track state variables and the progression of the simulation through time. Agents could also be tracked throughout model runs to view their individual variables.

Details

2.2.5. Initialization

Each simulation began at 00:00 hr (night) on the first day of the questing period (15 September). The values of the test variables (moose density, winter tick abundance, winter tick cluster size, date of snowfall, and presence of drought) and the study site differed at initialization, as they were dependent upon the intended experiment (Section 2.2.5). All moose began each simulation on a patch with “cut” as the landcover type; this became the center of their home range and encouraged a selection for this habitat type, which is observed in nature (Thompson et al. 1995, Peek 1997, Scarpitti 2006). Winter tick clusters were also concentrated on “cut” patches where they remained for the duration of the questing period. Moose were assigned a weight between 150 and 400 kg at initialization which determined their age class (adult = ≥ 200 kg, calves = < 200 kg) and blood volume (L); each individual began with a winter tick infestation = 0.

2.2.6. Input data

Initial values of variables were calculated using parameters from the literature (Table 5). The number of moose agents (n) was determined using the equation (n = rounded (A * d)), where A = the total area of the study site (Success = 110.65 km^2, Jericho = 40.80 km^2), and d = the experimental moose density (0.86, 0.60, 0.46, 0.40, 0.35, and 0.30 moose/km^2). Densities of 0.86, 0.60, and 0.46 are representative Connecticut Lakes Region (NHFG), the study area, and the North Region, respectively (Rines 2015, NHFG 2017). The remaining densities were selected because an earlier prototype of the model suggested that epizootic events may become infrequent at densities within this range.

A weight of 200 kg was designated as the threshold for age class because the average weight of calves collared in January 2016 and 2017 in New Hampshire for the field study was ~174 kg, with a range of 109-227 kg (Pekins, personal communication). The weight range for model calves encouraged the replication of this mean. The upper bound of adult weight was determined based on data reported in the 2016 harvest assessment (NHFG 2016); the average dressed weight of cows was 590 lb (268 kg) which would equate to a live weight of ~861 lb (391 kg), assuming dressed weight is 69% of live weight (NHFG 2016). Blood volume (L) is ~8% of body weight (kg) (Samuel 2004).

The number of winter tick agents (wt) populating the model at initialization was derived using the equation: $(wt = ((Ac * L)/c)*n$, where:

Ac = the area of cuts within the study site (Success = 18.40 km^2, Jericho = 11.44 km^2),
L = winter tick abundance level (converted to ticks/km^2),
c = the number of winter ticks questing together (100, 300, 500, 700 ticks/tick agent), and
n = the number of moose agents.

Winter tick abundance was previously measured in autumn 2008 and 2009 in local cut areas; mean tick density was 0.16 ticks/m^2 in 2008 and 0.07 ticks/m^2 in 2009, and maximum density was 0.64 ticks/m^2 and 0.40 ticks/m^2, respectively (Bergeron 2011). These densities were used to represent low (0.07 ticks/m^2), medium (0.16 ticks/m^2), high (0.40 ticks/m^2), and severe (0.64 ticks/m^2) abundance levels (L).

Blood loss (B_L) was calculated using the equation: $B_L = (I * 0.25) * 0.001$, where:

I = infestation,
0.25 represents the proportion of winter ticks that are adult females (Samuel 2004), and
0.001 is the amount of blood (L) consumed by each adult female (2X engorged weight, Samuel 2004; weight = 0.5-0.6 g, Glines 1983, Drew and Samuel 1989).

An individual blood loss > 40% of the original blood volume resulted in mortality of that calf (McGuill & Rowan 1989, Samuel 2004).

The dates of first snowfall were estimated from local weather trends recorded in Berlin. The date of early snow (12 Nov) is close to the mean date of snowfall occurring during non-epizootic years; late snow (10 Dec) was a mid-range estimate as permanent snow can delay until late December in epizootic years (Dunfey-Ball 2017).

Bergeron and Pekins (2014) estimated winter tick infestation of moose in New Hampshire by performing tick counts on 10 cm x 10 cm squares at the shoulder and rump of harvested moose during the October hunt. This method has been used at check stations in the North region during each year of the field study. Average winter tick loads measured during questing seasons preceding epizootic years (2013-2015) were 34-50 ticks/harvested moose; the average measured in 2016 after a drought was 19 (Dunfey-Ball 2017, Pekins, personal communication), suggesting winter tick desiccation rates of 44-62% during late summer-early fall droughts. However, because only one winter tick estimate was available following drought conditions, the model was programmed conservatively with a lower desiccation rate of 30%.

The distance moose agents traveled during each active hour was approximated using GPS locations from the New Hampshire field study. Five radio-collared females that transmitted ≥ 50 locations during the 2015 or 2016 questing periods (15 Sept. through 26 Nov.) were selected at random. Five dates within the questing period were then chosen at random for each moose, and the Euclidean distance was taken between the two locations recorded during selected days. The resulting distances were averaged and divided by 3, as the time between transmissions was 12 h, and the model assumed moose were active for 6 h per day (Risenhoover 1987). With the inclusion of an outlier, moose were estimated to move 113 m/active h; however, with the removal of this value, the estimate was reduced to 62 m/active h. Because each patch in the model grid was representative of Landsat resolution, movements were bound to 30 m increments, and 60 m was used to represent travel distance. This is likely a conservative estimate, as Euclidean distance represents the most direct path between two points and does not account for random wandering.

2.2.7. Submodels

2.2.7.1. Moose density and weather experiment

This submodel tested the relationship between epizootic occurrence (> 50% calf mortality), moose density, date of snowfall, and occurrence of drought. Winter ticks are prone to desiccation in dry conditions and freezing temperatures limit questing activity (Aalangdong 1994, Samuel 2004, 2007); it was therefore expected that epizootics would be uncommon when weather conditions within the model were cold and dry. Snowfall and drought were paired to create 4 weather scenarios: worst case (late snow, no drought), best case (early snow, drought), intermediate 1 (early snow, no drought), and intermediate 2 (late snow, drought) (Table 6). The effect of a drought was represented by elimination of 30% of the winter tick agents at the first

Table 6. Weather scenarios used for the moose density and weather models. The "best case" scenario refers to the combination of weather conditions least likely to result in epizootic events, whereas the "worst case" scenario is the most likely to result in epizootics. The two intermediate scenarios were used to investigate the impact of date of snowfall and occurrence of drought separately on epizootic events.

Weather Scenario	Date of Snow	Drought
Best Case	12-Nov	Yes
Intermediate 1	12-Nov	No
Intermediate 2	10-Dec	Yes
Worst Case	10-Dec	No

time step in the simulation. Each weather scenario was tested at 6 possible moose densities (0.86, 0.60, 0.46, 0.40, 0.35, 0.30 moose/km^2), with winter tick abundance and cluster size held constant at “high” and 500, respectively. A total of 200 simulations were completed using each combination of variables in both study sites.

ANOVAs and Tukey HSD tests were completed in R Studio (RStudio Team 2015) and used to determine the individual and combined impact that moose density and weather scenario had on the outcome variables average % calf mortality and average infestation level of dead calves (log-transformed); significance was set at $P < 0.05$. Simulations that failed to generate calves at initialization were tallied, but not included in statistical analyses. Simulations in which calf mortality was zero were included in analyses to calculate % calf mortality; however, because they yielded null values for infestation level, they were eliminated from analyses for this outcome variable. To approximate the regional mortality and infestation level predicted by the model, the results from the two sites were averaged; averages were weighted to account for the size (area) difference that dictated the difference in the number of moose agents within each site. It was hypothesized that calf mortality and infestation level would be highest when worst and intermediate 1 weather scenarios were conducted at high moose densities (0.86 and 0.60 moose/km^2).

2.2.7.2. Winter tick abundance experiments

The aim of this submodel was to test which winter tick abundance levels produced epizootic events at each study site (Table 7). We measure the effect of a change in this parameter on model outcomes, holding all other parameters constant: 500 ticks/cluster, 0.60 moose/km^2, worst case weather conditions. As in the previous submodel, 75 simulations were conducted at each winter tick abundance level in both study sites.

Table 7. Winter tick abundance levels in ticks/m^2 and ticks/km^2 used in the winter tick abundance model experiments.

Abundance Level	Ticks/m^2	Ticks/km^2
Low	0.07	70,000
Medium	0.16	160,000
High	0.40	400,000
Severe	0.64	640,000

The impact of winter tick abundance on the outcome variables was assessed using ANOVA and TukeyHSD tests ($P < 0.05$). Because the winter tick abundance estimates were compiled during questing seasons that preceded non-epizootic years, it was hypothesized that low and medium winter tick abundances (calculated using the mean abundance values collected in 2009 and 2008, respectively) would not result in epizootics at either site, while high and severe abundances (derived from maximum abundances) were likely to cause epizootic events. Weighted averages were used to approximate regional totals.

2.2.7.3. Winter tick aggregation experiment

This submodel was designed to test the impact of winter tick aggregation on moose acquisition of and infestation by ticks. Winter ticks quest in clusters, rather than individually; however, reliable estimates of cluster size are not available in the literature. Aalangdong (1994) reported clusters of "very few (< 20) to several hundred" winter ticks during field observations. For this experiment, the total number of individual ticks represented by clusters was maintained across simulations, but the number of tick agents present on the landscape differed as the infestation value changed. Within a simulation, all winter tick agents contained the same infestation value (100, 300, 500, or 700 winter ticks/agent). Each infestation value was tested using a moose density of 0.60 moose/km^2, "high" winter tick abundance, an intermediate date of snowfall (26 November), and an absence of drought. A total of 75 simulations was conducted using each cluster size in both study sites. ANOVA and Tukey HSD tests were used to determine the significance ($P < 0.05$) of cluster size on average % calf mortality and average infestation level of dead calves. It was hypothesized that cluster size of 500 would produce the highest % calf mortality and infestation level. Weighted averages between sites were used to approximate the regional impact of this variable.

2.3. Validation

Moose populations within model simulations averaged 22% calves and 78% adults, a ratio reasonably similar to aerial survey estimates in Minnesota (13-19% calves; DelGiudice 2017) and Michigan (17-23% calves; Largent et al. 2015). The movement rules of moose were validated by comparing the proportion of time moose agents spent in each habitat type in the model to empirical GPS locations of actual moose in the study area. Each time step a model moose spent within one of the 4 defined habitat types, it reported its location to a habitat log that recorded the cumulative time steps spent by all moose within each habitat. This was divided by the number of time steps multiplied by the number of moose agents. The proportion of time steps that were unaccounted for were considered time spent in “other”.

GPS radio-collared moose in the field study transmit their locations twice daily, and this information is logged in GPS Plus X software (Vectronic Aerospace GmbH). Locations logged within digitized polygons representing the Success and Jericho study sites during the questing season (15 September – 26 November in 2014, 2015, and 2016) were classified by habitat type using NLCD 2011 data in ArcMap 10.3.1 (ESRI, Redlands, CA). Proportional time spent in each habitat type was calculated and compared to habitat availability at both sites.

Table 8. Proportion of time spent by model and GPS moose in recognized habitat types, compared to availability within Jericho and Success.

Habitat	Model Use	GPS Moose	Availability
Cuts			
Success	24%	22%	17%
Jericho	33%	32%	28%
Deciduous			
Success	25%	22%	26%
Jericho	36%	29%	33%
Coniferous			
Success	25%	24%	25%
Jericho	5%	5%	6%
Mixed			
Success	24%	27%	23%
Jericho	26%	28%	26%
Other			
Success	2%	5%	9%
Jericho	0%	6%	7%

The proportional time that model moose spent in the 4 defined habitat types (plus "other") in Success was within 3% of the calculated habitat use based on GPS locations of actual moose in Success. Model and GPS moose in Jericho only differed > 3% in proportional time spent in 2 habitats: deciduous forest (+ 7%) and "other" (- 6%). GPS-moose selected for cut areas (Chapter 1) and this trend was replicated in model moose (Table 8).

2.4. Experimental Design

Experiments were designed to compute the infestation level and calf mortality under varying biological and environmental conditions within two spatially explicit landscapes in northern New Hampshire. The number of simulations used in each experiment was based on results of preliminary trials. Simulations were completed in increments of 25, from 25 to 200 iterations at all moose density and weather conditions possible for submodel 1. The resulting average infestation level and % calf mortality at each number of iterations were compared; when variation was < 2,000 ticks for infestation level (< 10% under the best weather conditions) and 5% for calf mortality, the variance between simulations was considered insignificant (Appendix

3). Two-hundred iterations were necessary to meet these criteria for the weather and moose density experiments. Iterations of 75 were sufficient to stabilize the outcome variables for winter tick abundance and aggregation submodels.

RESULTS

3.1 Moose density and weather experiment

Of 24 possible weather/density scenarios, only 1 produced an epizootic event (> 50% calf mortality) in Success (Fig. 6), whereas 11 epizootics occurred in Jericho (Fig. 7). Percent calf mortality was consistently lower (2-47%) in Success than Jericho, though more apparent during epizootic events in Jericho (34-47%). The epizootic in Success characterized by 56% mortality was under the worst-case weather conditions and moose density of 0.86 moose/km^2; the same conditions in Jericho yielded 90% calf mortality. Combined averages ranged from 17-66% calf mortality for conditions closest to those in the field study (Table 5).

Infestation level in Success was 0-25% lower than that in Jericho under corresponding conditions (Fig. 8). As density decreased, infestation level of model moose became more similar; for example, at densities of 0.30 and 0.35 moose/km^2, infestation levels in Success and Jericho were within 3% under all weather scenarios except the worst case. The maximum infestation recorded by any calf agent was 84, ,500 and 74,500 ticks in Jericho and Success, respectively, and occurred under worst-case weather conditions at a density of 0.86 moose/km^2. The combined infestation levels were 31,874 and 36,381 ticks at densities of 0.60 and 0.86 moose/km^2 for worst-case weather.

At densities > 0.40 moose/km^2, the weather scenario generally had a significant ($P <$ 0.05) impact on % calf mortality and infestation level at both sites, with the intensity of both

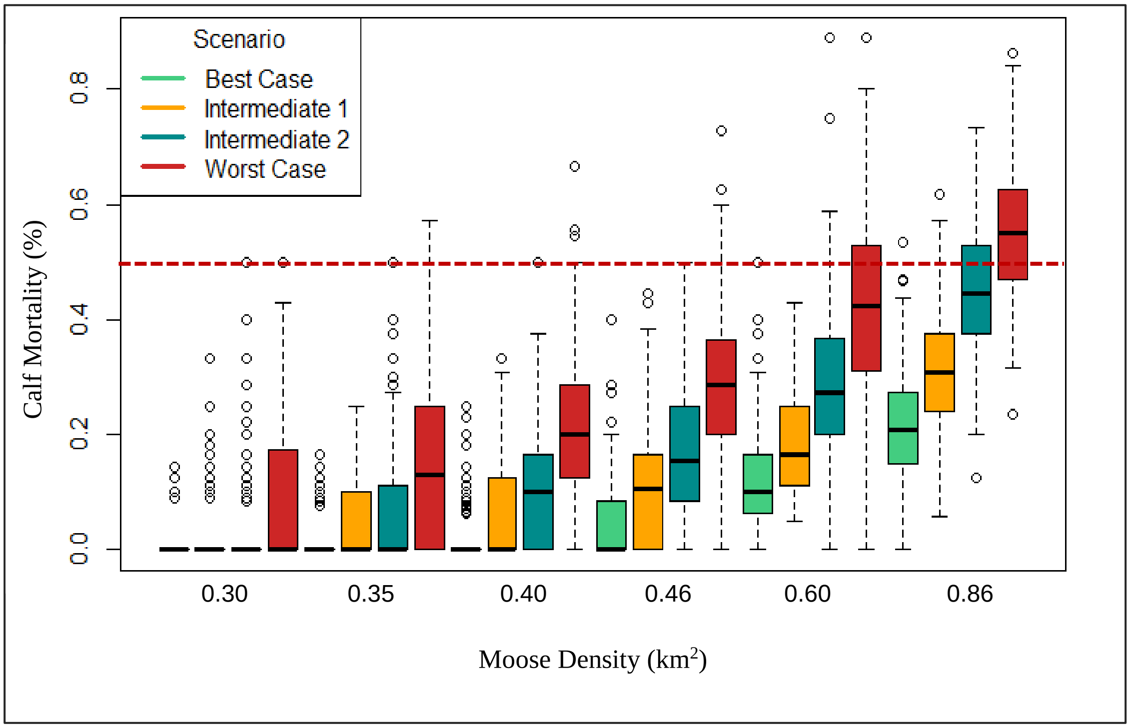

Fig. 6. Boxplot of average % calf mortalities occurring under each weather condition at all densities in Success. The dashed red line indicates 50% mortality; results above this line are considered epizootic events.

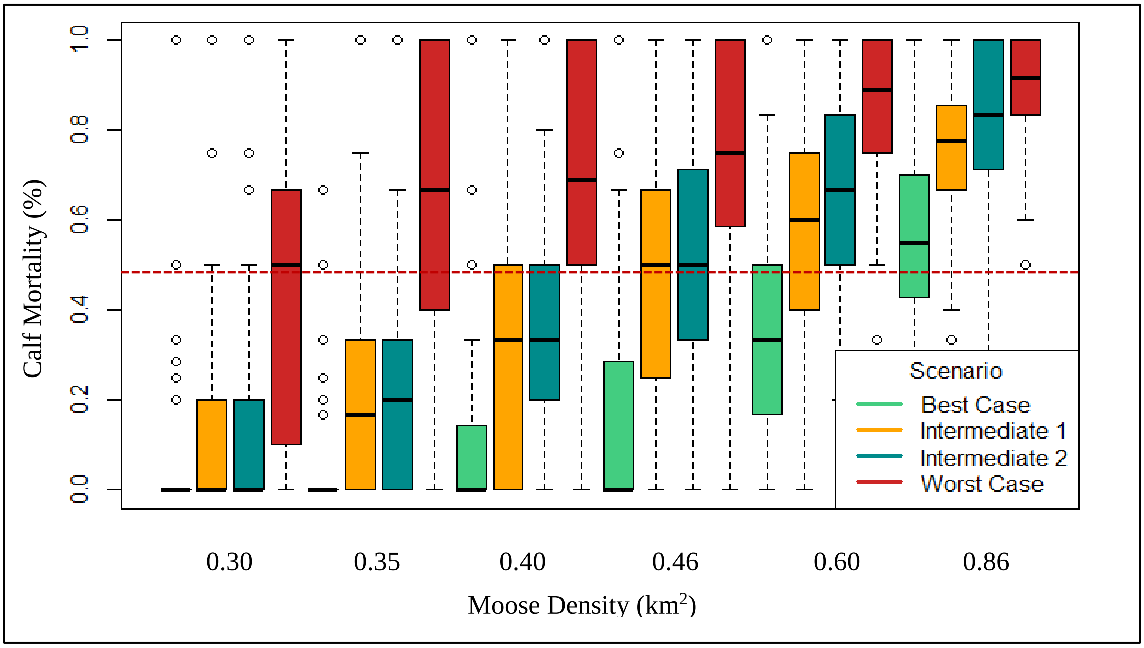

Fig. 7. Boxplot of average % calf mortalities occurring under each weather condition at all densities in Jericho. The dashed red line indicates 50% mortality; results above this line are considered epizootic events.

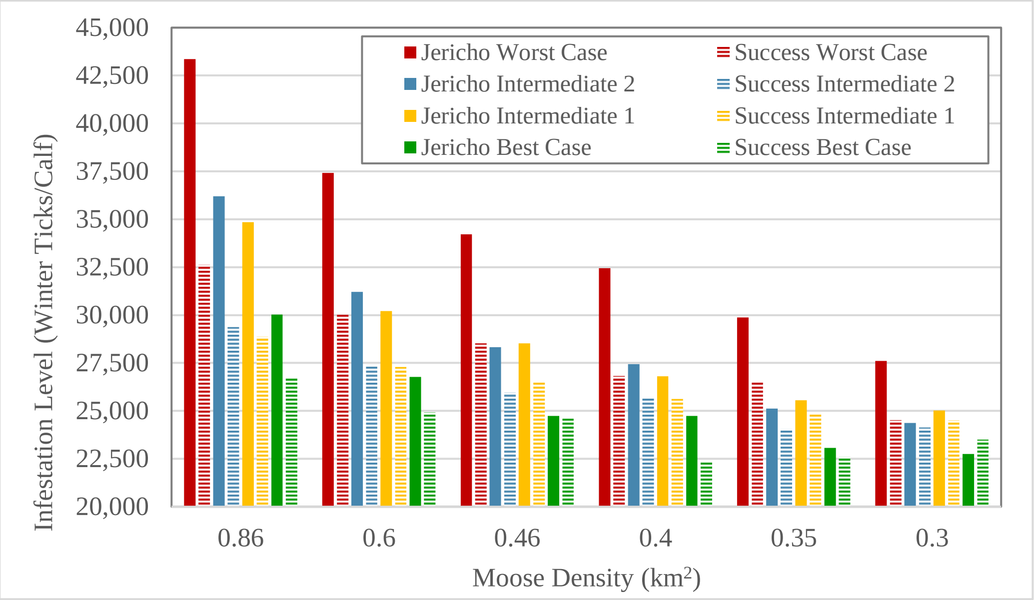

Fig. 8. Bar chart of average infestation level of dead calves in Success and Jericho under all moose density/weather scenarios. Solid bars indicate results from Jericho, while striped bars represent Success.

Table 9. The weighted % calf mortality found between Success and Jericho, under weather and density conditions most similar to those recorded during the field study.

Conditions	% Calf Mortality
0.60 moose/km^2	
Worst-Case	53
Intermediate 2	32
Best-Case	19
0.86 moose/km^2	
Worst-Case	66
Intermediate 2	52
Best-Case	31

outcome variables declining across the following progression of weather scenarios: worst case, intermediate 2, intermediate 1, best case (Table 10). An exception to this trend occurred with the two intermediate weather scenarios; percent calf mortality under these conditions in Jericho was not different at any density, nor was infestation level at densities ≤ 0.60 moose/km^2. In Success, the intermediate 2 weather conditions yielded higher % calf mortality than at intermediate 1

Table 10. Impact of moose density on outcome variables average % mortality and average infestation level between weather scenarios in both model environments.

Weather Scenario	0.86 (*P*)	0.60 (*P*)	0.46 (*P*)	0.40 (*P*)	0.35 (*P*)	0.30 (*P*)
Best-Intermediate 1						
Success						
% Calf Mortality	0.0000	0.0000	0.0000	0.0138	0.9897	0.9804
Infestation level	0.0000	0.0019	0.0046	0.0010	0.5405	0.9568
Jericho						
% Calf Mortality	0.0000	0.0000	0.0000	0.0000	0.9843	0.1343
Infestation level	0.0000	0.0000	0.0000	0.0089	0.0058	0.1393
Best-Intermediate 2						
Success						
% Calf Mortality	0.0000	0.0000	0.0004	0.0817	0.9943	0.9959
Infestation level	0.0000	0.0000	0.0928	0.0008	0.8223	0.9925
Jericho						
% Calf Mortality	0.0000	0.0000	0.0000	0.0000	0.8631	0.9021
Infestation level	0.0000	0.0000	0.0000	0.0000	0.0535	0.3522
Best-Worst						
Success						
% Calf Mortality	0.0000	0.0000	0.0000	0.0000	0.2242	0.9886
Infestation level	0.0000	0.0000	0.0000	0.0000	0.0824	0.9685
Jericho						
% Calf Mortality	0.0000	0.0000	0.0000	0.0000	0.0000	0.0009
Infestation level	0.0000	0.0000	0.0000	0.0000	0.0000	0.0001
Intermediate 1-2						
Success						
% Calf Mortality	0.0000	0.0042	0.9512	0.6987	0.9992	0.9768
Infestation level	0.2194	0.9792	0.5941	0.9996	0.6778	0.9336
Jericho						
% Calf Mortality	0.9981	0.0683	0.2699	0.9129	0.9198	0.0881
Infestation level	0.0046	0.0928	0.9467	0.1643	0.6366	0.8585
Intermediate 1-Worst						
Success						
% Calf Mortality	0.0000	0.0000	0.0000	0.0000	0.0000	0.1057
Infestation level	0.0000	0.0000	0.0000	0.0616	0.0150	0.9962
Jericho						
% Calf Mortality	0.0033	0.0000	0.0000	0.0000	0.0000	0.0306
Infestation level	0.0000	0.0000	0.0000	0.0000	0.0000	0.0009
Intermediate 2-Worst						
Success						
% Calf Mortality	0.0000	0.0000	0.0000	0.0000	0.0001	0.3086
Infestation level	0.0000	0.0000	0.0000	0.0862	0.0003	0.9515
Jericho						
% Calf Mortality	0.0089	0.0011	0.0000	0.0000	0.0000	0.0000
Infestation level	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000

Table 11. Significance of moose density on average % calf mortality and average infestation level when weather scenarios are pooled.

Moose Density (km^2)	% Calf Mortality (*P*)	Infestation level (*P*)
0.30-0.35		
Success	0.9850	0.0502
Jericho	1.0000	0.4059
0.30-0.40		
Success	0.9602	0.0002
Jericho	0.5307	0.0000
0.30-0.46		
Success	1.000	0.0000
Jericho	0.0193	0.0000
0.30-0.60		
Success	0.0383	0.0000
Jericho	0.0000	0.0000
0.30-0.86		
Success	0.0000	0.0000
Jericho	0.0000	0.0000
0.35-0.40		
Success	1.000	0.5772
Jericho	0.3516	0.0003
0.35-0.46		
Success	0.8719	0.0000
Jericho	0.0033	0.0000
0.35-0.60		
Success	0.0001	0.0000
Jericho	0.0000	0.0000
0.35-0.86		
Success	0.0000	0.0000
Jericho	0.0000	0.0000
0.40-0.46		
Success	0.7023	0.0044
Jericho	0.4895	0.0375
0.40-0.60		
Success	0.0000	0.0000
Jericho	0.0000	0.0000
0.40-0.86		
Success	0.0000	0.0000
Jericho	0.0000	0.0000
0.46-0.60		
Success	0.0003	0.0013
Jericho	0.0000	0.0000
0.46-0.86		
Success	0.0000	0.0000
Jericho	0.0000	0.0000
0.60-0.86		
Success	0.0000	0.0000
Jericho	0.0000	0.0000

conditions only at the highest densities (0.60 and 0.86 moose/km^2), and there was no difference in infestation level. When moose density was ≤ 0.40 moose/km^2, worst-case weather conditions continued to yield significantly higher % calf mortality versus other weather scenarios in Jericho and Success. Few differences were found at low densities between the other weather scenarios (Table 10).

When weather scenarios were pooled, % calf mortality was positively correlated with moose density ≥ 0.46 moose/km^2 in Jericho and ≥ 0.60 moose/km^2 in Success ($P < 0.05$), with few exceptions. No differences were found in % calf mortality at moose densities of 0.40 and 0.46 moose/km^2 in Jericho. Infestation level was positively correlated with all moose densities except 0.30-0.35 moose/km^2 in Jericho and 0.35-0.40 moose/km^2 in Success (Table 11).

3.2 Winter Tick Abundance Experiment

Winter tick abundance had a significant ($P = 0.00$) influence on both outcome variables, with severe abundance resulting in the highest % calf mortality and infestation level at each site. Epizootic events occurred in Jericho at high (83%) and severe (92%) winter tick abundances, and in Success at severe abundance (65%). Medium abundance caused relatively low calf mortality at each site, and was insufficient to create epizootics (Fig. 9). The largest difference in % calf mortality between sites occurred at high winter tick abundance. Combined average % calf mortality between sites was 7%, 52%, and 72% at medium, high, and severe tick abundances, respectively.

The disparity in infestation level between sites increased with increasing tick abundance; infestations in Success were 5%, 20%, and 27% lower than in Jericho at medium, high, and severe winter tick abundances, respectively (Fig. 10). The maximum infestation recorded by any

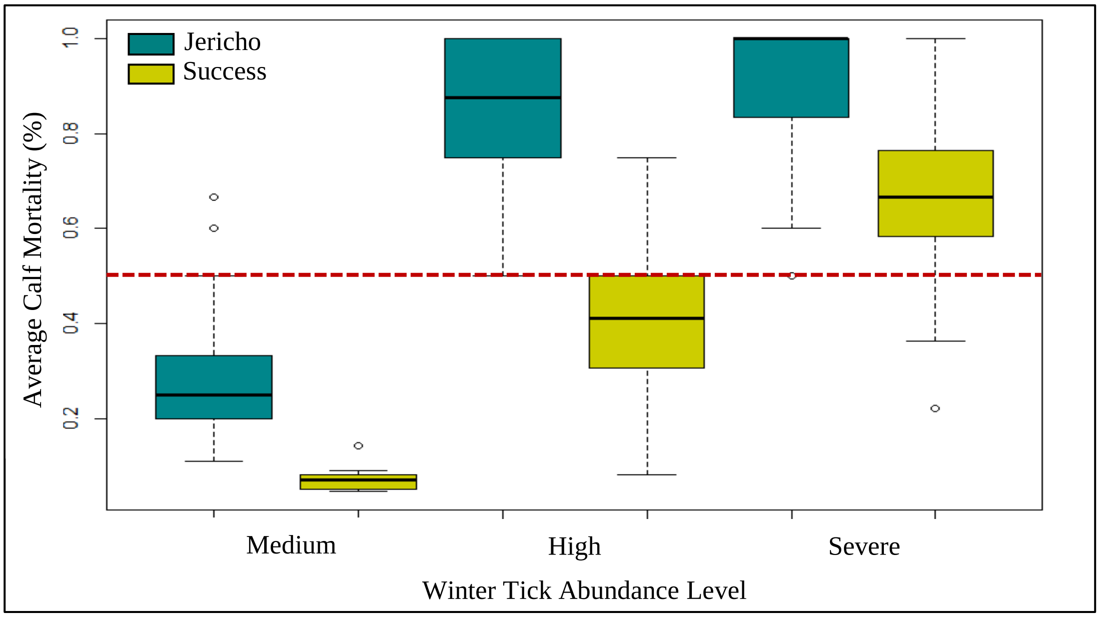

Fig. 9. Boxplots of averages % calf mortality at medium, high, and severe winter tick abundance levels. The red dashed line indicates 50% mortality- the threshold for epizootics.

individual calf agent was 90,500 in Jericho and 76,000 in Success; both occurred when winter tick abundance was severe. Combined infestations resulting from medium, high, and severe tick abundances were 23,794, 31,927, and 37,635 ticks/individual.

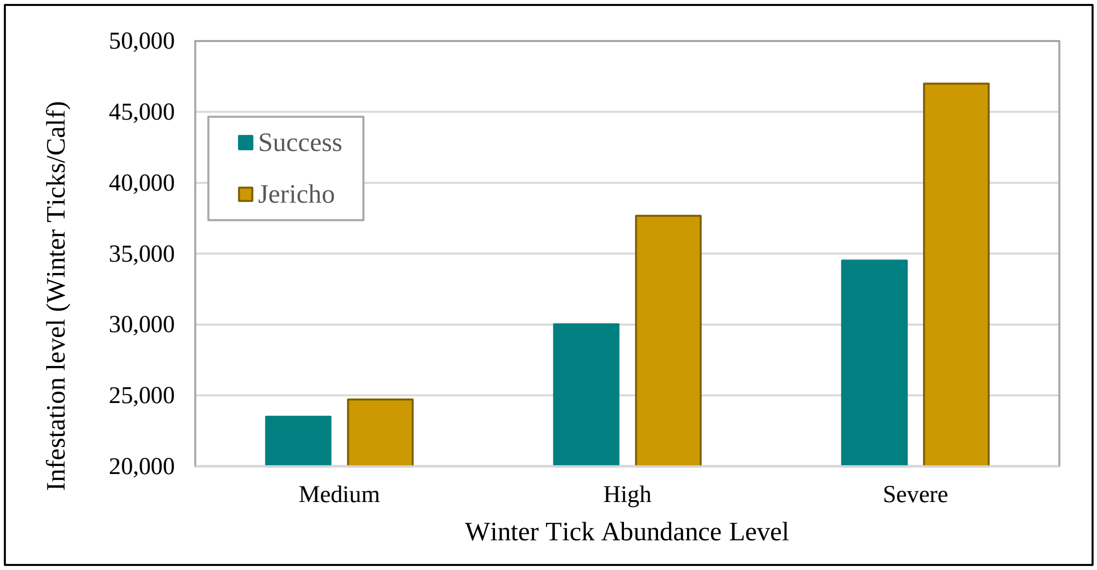

Fig. 10. Bar chart of average infestation level of dead calves in both environments at medium, high, and severe winter tick abundance.

3.3 Winter tick aggregation experiment

Percent calf mortality and infestation level at both sites was lower ($P < 0.05$) at cluster size of 300 than clusters of 500 or 700. No differences were found in % calf mortality between cluster sizes of 500 and 700 in Jericho, or for infestation level in Success (Table 12).

Table 12. Impact of cluster size on outcome variables average % calf mortality and average infestation level of dead calves in Success and Jericho.

Cluster Size	% Calf Mortality (*P*)	Infestation level (*P*)
300-500		
Success	0.0000	0.0000
Jericho	0.0000	0.0000
300-700		
Success	0.0000	0.0000
Jericho	0.0000	0.0000
500-700		
Success	0.0022	0.7667
Jericho	0.3013	0.0000

Epizootic events occurred in Jericho regardless of cluster size, and mortality rate increased as cluster size increased. Percent calf mortality in Success was also positively correlated with cluster size, but mortality never reached epizootic level (Fig. 11). The relative difference in % mortality between sites was similar (42-44%) at each cluster size. Combined mortality was 27%, 42%, and 49% at cluster sizes of 300, 500, and 700.

Infestation level increased with cluster size, though more rapidly in Jericho; infestation in Success was 11%, 15%, and 20% lower than in Jericho at cluster sizes of 300, 500, and 700, respectively (Fig. 12). The maximum infestation at cluster size 700 was 70,000 ticks/individual in Jericho and 56,700 ticks/individual in Success. Combined infestation of dead calves was 27,278, 30,214, and 31,314 for cluster sizes 300 – 700, respectively.

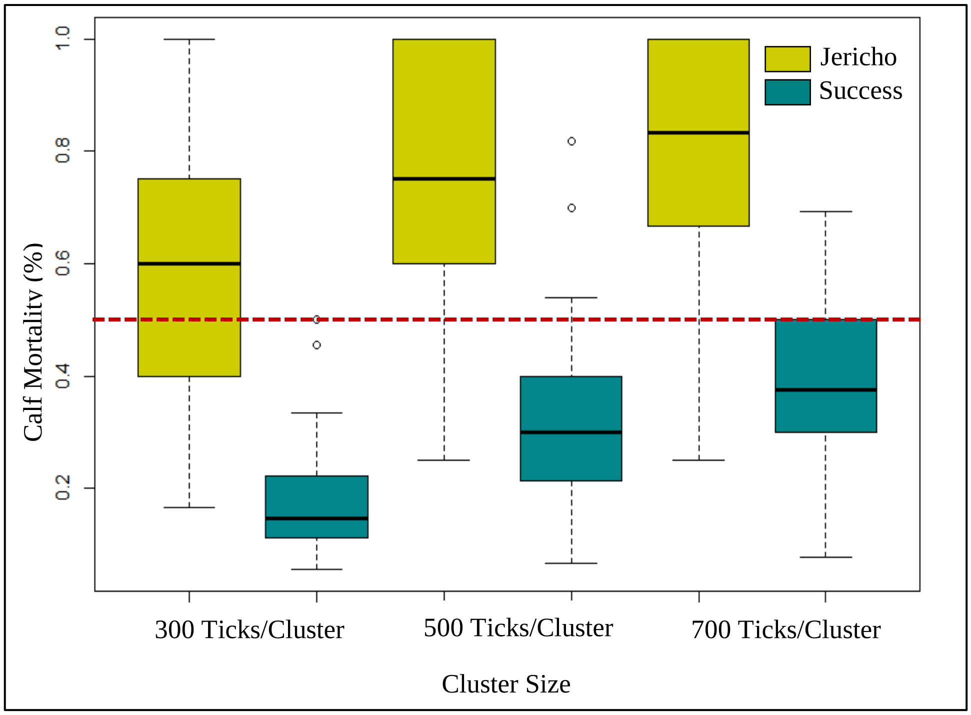

Fig. 11. Boxplots of average % calf mortalities in both model environments when winter tick agents represent clusters of 300, 500, and 700 ticks. The red dashed line represents 50% mortality- the threshold for epizootic events.

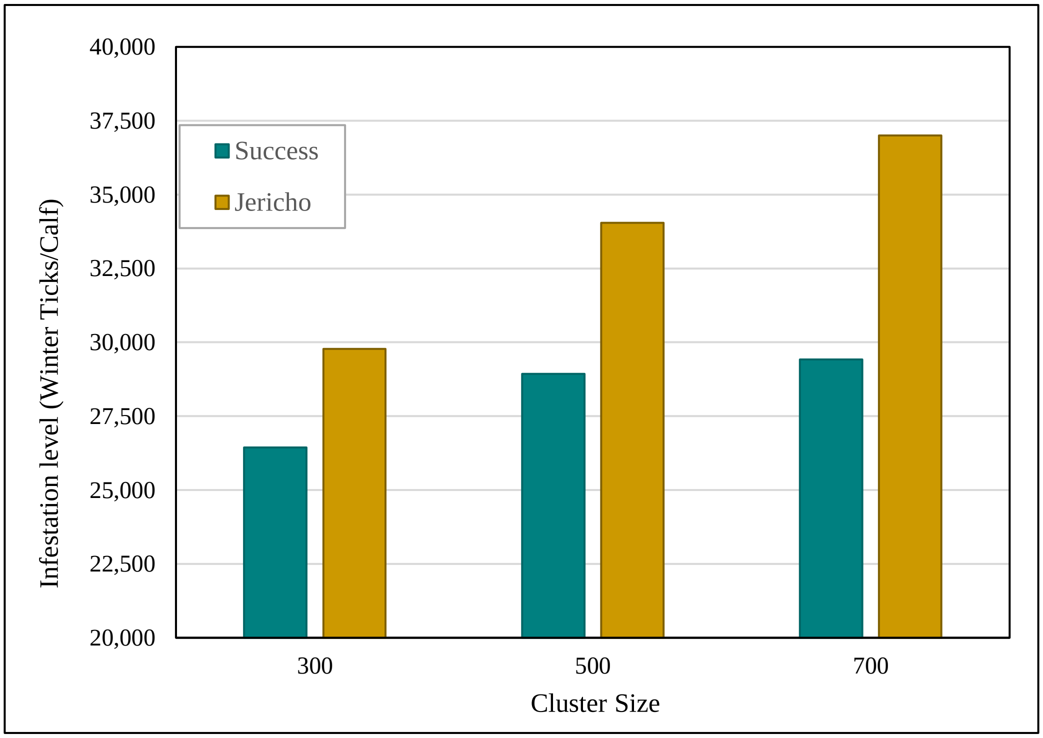

Fig. 12. Bar chart of average infestation level of dead calves in both model environments at each cluster size.

3.4 Sensitivity Analysis

A series of sensitivity analyses examined the effect of modifying the baseline values of the model parameters on % calf mortality, average infestation level, maximum infestation level, and % time spent in cut habitat present in each study site (Table 13). The primary goal was to test the impact of small changes in parameter values that were not explicit in the literature, or for which it was expected that model settings were conservative. The proportion of time spent in cuts was included in the list of outcome variables to ensure that the model was valid relative to habitat use.

3.4.1 Model Sensitivity to Movement Rules

The first parameter analyzed was moose activity (h) that varies seasonally relative to forage availability. Estimates range from ~6-10 h (Risenhoover 1987, Renecker and Hudson 1989a, Van Ballenberghe and Miquelle 1990), hence the baseline value in the model was conservative (6 h). Model sensitivity to active hours was tested under conditions representative of worst-case weather, the study site moose density, and for conditions similar to the cluster experiments where tick agents represented 700 winter ticks. The proportion of time moose agents spent within cuts was consistent (± 1%) regardless of active hours. The remaining outcome variables increased with active time, indicating that they were sensitive to this parameter, however, the degree of sensitivity varied by study site. Percent calf mortality was more influenced by active hours in Success, and average and maximum infestation levels increased more in Jericho.

The impact of distance traveled per time step was also considered in the analysis. Both sites revealed some sensitivity to variations in this parameter, with outcome variables negatively

Table 13. Results of model sensitivity analysis. Rows highlighted in grey represent baseline values. Active hours were tested under conditions representative of the worst-case weather at site density (10 Dec), and under conditions representative of the winter tick aggregation experiment, when snows occurred at a median date (26 Nov) and winter tick agents represented 700 ticks.

Parameter	Calf Mortality (%)	Infestation level	Max Infestation	Time in Cuts (%)
Active Hours				
Success (10 Dec)				
4	18.5	27,276	46,000	18.9
6	42.0	30,025	62,500	19.3
8	61.0	32,796	72,000	19.7
10	74.0	35,747	83,000	20.0
Jericho (10 Dec)				
4	58.0	30,857	52,000	33.2
6	86.0	37,421	56,000	34.3
8	92.6	45,313	85,500	34.7
10	96.0	52,005	93,500	35.0
Success (26 Nov)				
4	25.3	30,996	54,600	19.2
6	37.7	28,713	53,900	19.1
8	54.3	36,628	90,300	19.7
10	64.8	39,739	102,200	19.9
Jericho (26 Nov)				
4	60.0	32,886	65,100	33.7
6	85.7	37,334	68,600	34.0
8	86.7	46,345	100,100	34.6
10	89.1	54,307	104,300	34.3
Distance/time step (m)				
Success				
30	44.7	33,909	75,000	19.6
60	42.0	30,025	62,500	19.3
90	38.4	27,835	52,000	19.1
120	35.8	26,958	49,000	19.1
150	35.5	26,285	43,000	19.0
Jericho				
30	78.3	40,969	86,000	34.0
60	86.0	37,421	56,000	34.3
90	85.3	35,807	59,500	33.9
120	85.4	33,691	56,000	34.2
150	84.1	32,909	58,500	34.1
Drought (%)				
Success				
25%	24.7	27,444	51,500	18.9
30%	20.0	27,394	49,500	18.8
35%	15.5	26,141	48,500	18.7
Jericho				
25%	70.6	33,053	58,000	33.5
30%	68.0	31,215	54,000	33.2
35%	63.4	30,123	51,000	33.4

correlated with distance traveled. The percent calf mortality deviated ±8% from the baseline when distance traveled was reduced to 30 m or increased to 90-150 m per time step, and infestation level fell within ± 9 winter tick clusters. Maximum infestation when moose movement was 30 m/time step was > 10,000 above the maximum infestations at the baseline in both study sites. When movement distance increased, Jericho displayed little variation in maximum infestation level, whereas Success had larger variation. The proportion of time moose agents spent in cut habitat remained consistent (± 0.4%).

3.4.2 Model Sensitivity to Drought

The sensitivity to the proportion of ticks that desiccated during drought conditions indicated that all outcomes were somewhat negatively correlated with % drought. The % calf mortality increased or decreased by 3-5% with 5% increments from the baseline. The variation in infestation level was relatively low, and the proportion of time spent in cut habitats was not sensitive to drought.

DISCUSSION

Fifty-eight combinations of 6 variables (moose density, drought, date of snow, winter tick abundance, winter tick aggregation, and study site) were simulated using this model. Of these, 17 produced epizootic events, of which 15 occurred in Jericho. Infestation levels < 19,500 winter ticks were insufficient to cause calf mortality.

4.1 Moose Density and Weather Experiment

During the epizootic years of 2014-2016, all calves collared in Jericho (n=17) and Success (n=16) as part of the field study died, presumably due to winter tick parasitism (unpublished data). These mortality rates exceeded those generated in the model under similar density and weather conditions. At both sites, the differences % calf mortality and infestation level were positively correlated with the proportion of optimal moose habitat available. Jericho had disproportionately more optimal moose habitat (28%) within the larger field study that averaged 17%; Success matched the average proportion. Importantly, these proportions were likely underrepresented in the model for 2 reasons: 1) the difficulty in discerning small cuts at Landsat resolution (Wilson and Sader 2002, Jarron et al. 2017), and 2) the method by which the NLCD classification scheme was adapted to approximate cuts which likely did not account for older optimal habitat (>15 years).

Despite this, the combined % calf mortality and infestation level that most closely represented autumn weather conditions and moose density (0.60 moose/km^2) in the study area in 2013-2016 generated a regional epizootic (53%), albeit lower than measured in the field study (~70%). Dunfey-Ball (2017) suggested that concentrated optimal habitat may result in elevated local moose density and that regional epizootics may reflect high mortality within these areas. It is plausible that the high concentration of optimal habitat in Jericho and Success elevated local moose density above the regional estimate. The combined % calf mortality at the highest density (0.86 moose/km^2) was 66.5%, slightly above that measured in 2014 (62%; Jones et al. 2017).

Epizootics in Jericho were predicted at all weather scenarios at high moose density (0.86). Conversely, only at the worst case scenario did an epizootic occur at <0.40 moose/km^2, and the threshold for 3 of 4 weather scenarios was at 0.46 moose/km^2, about 25% lower than the current moose density (0.60). What is perhaps more significant is that mortality occurred at all weather scenarios at both sites because infestation level was sufficient to induce mortality; essentially, tick abundance on the landscape was sufficient to cause mortality. Focus on epizootics (>50 % mortality) is somewhat arbitrary given that sustained, measurable annual mortality would be considered abnormal relative to winter tick parasitism; it is typically pulsed in annual frequency, rarely occurring in consecutive years (Samuel 2004), as in the previous study in 2002-2005 (Musante et al. 2010). In Success where optimal habitat availability was equal to the area average (17%), the combination of moderate moose density, extended questing period, and high tick abundance was sufficient to cause ~30% mortality (Fig. 3). Either "best case/intermediate" weather, lower moose density, or both would be required to reduce mortality to <20%.

4.2 Winter Tick Abundance Experiment

Low and medium winter tick abundances were insufficient to produce epizootics at either site. This was expected as the values used to estimate winter tick abundance were collected during questing seasons preceding non-epizootic years; low and medium abundances were calculated from the average tick density measured across all cuts (Bergeron and Pekins 2014).

High winter tick abundance produced epizootics in Jericho but not Success, though the average calf mortality represented a regional epizootic (53%). The most similar outcome to field data was the combined average mortality of 72% at severe winter tick abundance, similar to that measured in 2015 (74%). Additionally, the infestation level under these conditions in Jericho (46,995) was within 200 ticks of the average measured on calf hides in the field study (46,800), although those measurements are considered conservative (Jones et al. 2017). The average infestation level in Success was slightly less than the lower extent measured on calf hides in the field study (34,800), but the combined average was reasonable (37,635), though lower than average. Extrapolation of these infestation levels and mortality rates should account for the lower regional distribution and concentration of optimal habitat; nonetheless, it is likely that the model estimates of tick abundance under severe settings were conservative. Of consequence is that at low and medium tick abundance epizootics, or even average mortality > 20% did not occur; again, limiting tick abundance on the landscape is the optimal approach to limiting mortality.

4.3 Winter Tick Aggregation Experiment

The total number of questing winter ticks was maintained throughout this experiment; however, the aggregation clusters vary the number of tick agents effectively increasing the tick number per encounter as cluster size increases. At clusters of 100, mortality did not occur in either environment, despite the high concentrations within cuts; calves were unable to accumulate an infestation level that caused ≥ 40% loss of blood volume. At cluster size ≥ 300, the occurrence of epizootics was unchanged within each site, but the severity of % calf mortality and infestation level was impacted. Combined average estimates of % mortality at cluster size 700 was 22% higher than at cluster size 300, and nearly reached the epizootic threshold (49%).

The assumption that winter ticks quest in groups of a consistent size is clearly unrealistic; field observations indicate wide variation from < 20 to 100s of ticks per cluster (Aalangdong 1994). This experiment indicates that aggregation size and their distribution likely play a significant role in the infestation level, specifically in this model, and accurate estimates of cluster size and tick abundance (density) would improve both parameter and model accuracy.

4.4 Future studies

It is likely that the daily activity of moose used in the model was also a conservative estimate. Moose agents were programmed to be active (feeding) only 6 h daily (Risenhoover 1987), yet activity varies seasonally in response to weather conditions and forage quality (Risenhoover 1987, Renecker and Hudson 1989a, Van Ballenberghe and Miquelle 1990). For example, the questing period of winter ticks coincides with the moose breeding period when moose are more active than in other seasons, and moose may spend 10 h foraging daily (Renecker and Hudson 1989a, Van Ballenberghe and Miquelle 1990). Presumably, the combination of longer foraging time and increased activity associated with breeding during the questing period would increase exposure to ticks, and elevate infestation levels and presumably mortality, as indicated in the sensitivity analysis.

Moose are limited in their ability to rid themselves of winter ticks, given their lack of programmed grooming behavior. However, many moose do react to feeding nymphal and adult ticks as evidenced by hair loss; any tick removal is unaccounted for in the model. Additionally, the model does not consider blood volume lost to nymphs that is spread over 2-3 months, or adult male winter ticks during March-April. The 40% estimate of blood loss causing death is likely reached earlier than predicted, further evidence that the model is conservative.

CONCLUSIONS

Moose-winter tick epizootics are complex to model because numerous variables influence moose and winter tick populations, and accurate density estimates of moose, and particularly winter tick abundance on the landscape, are difficult to measure accurately. This model was constructed with empirical data compiled from multiple studies, and yielded calf mortality rates reasonably similar to those measured in an ongoing field study.

The parameters and related assumptions used to build the model were conservative overall, yet the model produced reasonable predictions and trends expected under variable conditions. It is likely that the estimate of winter tick abundance, moose movement, and availability of optimal habitat were low, and Jericho with its concentrated availability of optimal habitat likely had a local density exceeding the regional estimate. It is also possible that the tick cluster estimates were high. Tick infestation estimates did not account for stimulus grooming that reduces infestation, albeit blood loss to cohorts of ticks other than adult females was unaccounted for. Despite these discrepancies, the model produced reasonably similar calf mortality rates and infestation levels as those measured in the field study, generated an average infestation level within 200 ticks of the conservative estimate in the field study, and the combined averages under plausible weather and density conditions yielded mortality rates representative of epizootics in 2014 and 2015.

This exercise with agent-based modeling identified a number of important relationships in the moose-winter tick relationship. Mortality was predicted under a number of different combinations of weather scenarios, tick abundance, cluster size, and moose density; however, the key parameter in this relationship is abundance of winter ticks on the landscape. Only autumn weather can affect mortality substantially at moderate-high moose density; otherwise, an epizootic or abnormally high mortality occurred. It is probably not coincidental that the low and medium tick abundances, measured when epizootics were less frequent, did not cause mortality in the model. Without favorable weather through either drought and/or early snow, lower moose density is probably required to reduce mortality, ostensibly by reducing tick abundance on the landscape. More accurate moose and winter tick density estimates would be invaluable to improve this model’s use and reliability, and most importantly, to assess any management strategy to reduce moose density.

THESIS CONCLUSIONS

I. Moose exhibit selection for optimal habitat during the critical ecological periods of questing and drop-off in the life cycle of winter ticks across northern New England.

II. High fidelity to home and core ranges indicate that moose use cut habitat, and for individuals, overlapping use of the same locations in sequential questing and drop-off periods. This behavior explains how moose consistently acquire winter ticks and perpetuate a self-sustained system.

III. Comparatively low availability yet high selective use of optimal habitat, compounded by the fact that 30-40% of moose daily activity is devoted to foraging, indicates that locally high winter tick abundance may be concentrated in proportionally small, but selectively used optimal habitat. Such areas, that theoretically would shift across the landscape in concert with forest harvesting patterns, may play a disproportionate role in the frequency of epizootics.

IV. The model, under similar moose density and environmental conditions, produced reasonably similar, albeit, conservative results for calf mortality and infestation level compared to an ongoing field study in the same area.

V. Epizootics did not occur in the model when winter tick abundance was parameterized using average winter tick abundance estimates measured during questing seasons preceding non-epizootic years.

VI. Infestations < 19,500 winter ticks were insufficient to cause calf mortality in the model. This level of infestation is considered less than that associated with an epizootic.

VII. Winter tick aggregation was an important variable in the model; moose were unable to acquire enough ticks to produce mortality when tick agents equated to infestations of 100. Clusters ≥ 300 did not impact the occurrence of epizootics, but did influence the severity of mortality within the population. Cluster size has not been adequately measured in the field.

VIII. High calf mortality and epizootics occurred under variable model settings representative of empirical estimates in the field study unless either 1) favorable weather conditions (early fall drought, early snow) reduced tick abundance or shortened the questing period, or 2) moose density was < 0.46 moose/km^2.

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APPENDICES

APPENDIX 1A: GPS MOOSE USED TO CALCULATE QUESTING HOME AND CORE RANGES

Collar ID	Age	Year Collared	Site	Questing Year
14239	Adult	2015	Berlin	2015
17807	Adult	2015	Berlin	2015
17809	Adult	2015	Berlin	2015
17810	Adult	2015	Berlin	2015
14241	Adult	2015	Berlin	2016
17807	Adult	2015	Berlin	2016
17809	Adult	2015	Berlin	2016
14335	Adult	2014	Jackman	2014
14336	Adult	2014	Jackman	2014
14343	Adult	2014	Jackman	2014
14350	Adult	2014	Jackman	2014
14353	Adult	2014	Jackman	2014
14354	Adult	2014	Jackman	2014
14357	Adult	2014	Jackman	2014
14360	Adult	2014	Jackman	2014
14363	Adult	2014	Jackman	2014
14364	Adult	2014	Jackman	2014
14365	Adult	2014	Jackman	2014
14369	Adult	2014	Jackman	2014
14370	Adult	2014	Jackman	2014
14372	Adult	2014	Jackman	2014
14373	Adult	2014	Jackman	2014
14382	Adult	2014	Jackman	2014
14384	Adult	2014	Jackman	2014
14387	Adult	2014	Jackman	2014
14390	Adult	2014	Jackman	2014
14335	Adult	2014	Jackman	2015
14336	Adult	2014	Jackman	2015
14340	Adult	2015	Jackman	2015
14341	Adult	2014	Jackman	2015
14343	Adult	2014	Jackman	2015
14347	Adult	2015	Jackman	2015
14349	Adult	2015	Jackman	2015
14350	Adult	2014	Jackman	2015
14353	Adult	2014	Jackman	2015
14354	Adult	2014	Jackman	2015
14356	Adult	2014	Jackman	2015
14360	Adult	2014	Jackman	2015
14362	Adult	2014	Jackman	2015
14363	Adult	2014	Jackman	2015

14365	Adult	2014	Jackman	2015
14369	Adult	2014	Jackman	2015
14370	Adult	2014	Jackman	2015
14372	Adult	2014	Jackman	2015
14373	Adult	2014	Jackman	2015
14382	Adult	2014	Jackman	2015
14383	Adult	2014	Jackman	2015
14384	Adult	2014	Jackman	2015
14386	Adult	2014	Jackman	2015
14389	Adult	2014	Jackman	2015
14390	Adult	2014	Jackman	2015
14331	Adult	2015	Jackman	2016
14335	Adult	2014	Jackman	2016
14336	Adult	2014	Jackman	2016
14339	Adult	2015	Jackman	2016
14340	Adult	2015	Jackman	2016
14343	Adult	2014	Jackman	2016
14345	Adult	2015	Jackman	2016
14346	Adult	2015	Jackman	2016
14349	Adult	2015	Jackman	2016
14350	Adult	2014	Jackman	2016
14356	Adult	2014	Jackman	2016
14359	Adult	2015	Jackman	2016
14360	Adult	2014	Jackman	2016
14362	Adult	2014	Jackman	2016
14363	Adult	2014	Jackman	2016
14365	Adult	2014	Jackman	2016
14366	Adult	2015	Jackman	2016
14369	Adult	2014	Jackman	2016
14370	Adult	2014	Jackman	2016
14371	Adult	2015	Jackman	2016
14372	Adult	2014	Jackman	2016
14373	Adult	2014	Jackman	2016
14376	Adult	2015	Jackman	2016
14377	Adult	2015	Jackman	2016
14382	Adult	2014	Jackman	2016
14383	Adult	2014	Jackman	2016
14384	Adult	2014	Jackman	2016
14385	Adult	2015	Jackman	2016
14386	Adult	2014	Jackman	2016
14389	Adult	2014	Jackman	2016
14390	Adult	2014	Jackman	2016
19119	Adult	2016	Aroostook	2016
19121	Adult	2016	Aroostook	2016

19123	Adult	2016	Aroostook	2016
19125	Adult	2016	Aroostook	2016
19128	Adult	2016	Aroostook	2016
19131	Adult	2016	Aroostook	2016
19134	Adult	2016	Aroostook	2016
19137	Adult	2016	Aroostook	2016
19139	Adult	2016	Aroostook	2016
19141	Adult	2016	Aroostook	2016
19142	Adult	2016	Aroostook	2016
19146	Adult	2016	Aroostook	2016
19148	Adult	2016	Aroostook	2016
19149	Adult	2016	Aroostook	2016
19153	Adult	2016	Aroostook	2016
19156	Adult	2016	Aroostook	2016
19159	Adult	2016	Aroostook	2016
19162	Adult	2016	Aroostook	2016
19164	Adult	2016	Aroostook	2016
19165	Adult	2016	Aroostook	2016
19166	Adult	2016	Aroostook	2016
19169	Adult	2016	Aroostook	2016
19171	Adult	2016	Aroostook	2016
19174	Adult	2016	Aroostook	2016
19177	Adult	2016	Aroostook	2016
19184	Adult	2016	Aroostook	2016
19204	Adult	2016	Aroostook	2016

APPENDIX 1B: GPS MOOSE USED TO CALCULATE DROP-OFF HOME AND CORE RANGES

Collar ID	Age	Year Collared	Site	Drop-off Year
14239	Adult	2015	Berlin	2015
14241	Calf	2015	Berlin	2015
14243	Calf	2015	Berlin	2015
14244	Adult	2015	Berlin	2015
14245	Calf	2015	Berlin	2015
17806	Calf	2015	Berlin	2015
17807	Adult	2015	Berlin	2015
17808	Calf	2015	Berlin	2015
17809	Adult	2015	Berlin	2015
17810	Adult	2015	Berlin	2015
17813	Calf	2015	Berlin	2015
14239	Calf	2015	Berlin	2016
14241	Calf	2015	Berlin	2016
17807	Calf	2015	Berlin	2016
17809	Calf	2015	Berlin	2016
17810	Calf	2015	Berlin	2016
20315	Calf	2016	Berlin	2016
20318	Adult	2016	Berlin	2016
20331	Calf	2016	Berlin	2016
20336	Calf	2016	Berlin	2016
20341	Calf	2016	Berlin	2016
20342	Calf	2016	Berlin	2016
20348	Adult	2016	Berlin	2016
14241	Adult	2015	Berlin	2017
17807	Adult	2015	Berlin	2017
20315	Calf	2017	Berlin	2017
20317	Adult	2017	Berlin	2017
20318	Calf	2017	Berlin	2017
20319	Adult	2017	Berlin	2017
20320	Calf	2017	Berlin	2017
20321	Calf	2017	Berlin	2017
20322	Calf	2017	Berlin	2017
20325	Adult	2017	Berlin	2017
20326	Calf	2017	Berlin	2017
20328	Adult	2017	Berlin	2017
20330	Adult	2017	Berlin	2017
20333	Calf	2017	Berlin	2017
20334	Calf	2017	Berlin	2017
20335	Calf	2017	Berlin	2017
20337	Adult	2017	Berlin	2017

20338	Adult	2016	Berlin	2017
20339	Adult	2017	Berlin	2017
20341	Calf	2017	Berlin	2017
20342	Calf	2017	Berlin	2017
20343	Calf	2017	Berlin	2017
20344	Adult	2017	Berlin	2017
20346	Calf	2017	Berlin	2017
20347	Adult	2017	Berlin	2017
20348	Adult	2017	Berlin	2017
22633	Adult	2017	Berlin	2017
14330	Calf	2014	Jackman	2014
14331	Adult	2014	Jackman	2014
14332	Adult	2014	Jackman	2014
14335	Adult	2014	Jackman	2014
14336	Adult	2014	Jackman	2014
14343	Adult	2014	Jackman	2014
14345	Adult	2014	Jackman	2014
14346	Adult	2014	Jackman	2014
14347	Adult	2014	Jackman	2014
14350	Adult	2014	Jackman	2014
14353	Adult	2014	Jackman	2014
14354	Adult	2014	Jackman	2014
14356	Calf	2014	Jackman	2014
14360	Adult	2014	Jackman	2014
14362	Calf	2014	Jackman	2014
14363	Adult	2014	Jackman	2014
14364	Adult	2014	Jackman	2014
14365	Adult	2014	Jackman	2014
14369	Adult	2014	Jackman	2014
14370	Adult	2014	Jackman	2014
14371	Adult	2014	Jackman	2014
14372	Adult	2014	Jackman	2014
14373	Adult	2014	Jackman	2014
14375	Calf	2014	Jackman	2014
14376	Adult	2014	Jackman	2014
14377	Adult	2014	Jackman	2014
14382	Adult	2014	Jackman	2014
14383	Calf	2014	Jackman	2014
14384	Adult	2014	Jackman	2014
14385	Adult	2014	Jackman	2014
14386	Calf	2014	Jackman	2014
14387	Adult	2014	Jackman	2014
14389	Calf	2014	Jackman	2014
14390	Adult	2014	Jackman	2014

14329	Calf	2015	Jackman	2015
14330	Calf	2015	Jackman	2015
14331	Calf	2015	Jackman	2015
14332	Calf	2015	Jackman	2015
14337	Calf	2015	Jackman	2015
14339	Calf	2015	Jackman	2015
14342	Calf	2015	Jackman	2015
14343	Adult	2014	Jackman	2015
14345	Calf	2015	Jackman	2015
14346	Calf	2015	Jackman	2015
14347	Adult	2015	Jackman	2015
14349	Adult	2015	Jackman	2015
14350	Adult	2014	Jackman	2015
14353	Adult	2014	Jackman	2015
14354	Adult	2014	Jackman	2015
14357	Adult	2015	Jackman	2015
14359	Calf	2015	Jackman	2015
14360	Adult	2014	Jackman	2015
14363	Adult	2014	Jackman	2015
14364	Adult	2014	Jackman	2015
14365	Adult	2014	Jackman	2015
14366	Calf	2015	Jackman	2015
14368	Calf	2015	Jackman	2015
14370	Adult	2014	Jackman	2015
14371	Calf	2015	Jackman	2015
14372	Adult	2014	Jackman	2015
14373	Adult	2014	Jackman	2015
14376	Calf	2015	Jackman	2015
14377	Calf	2015	Jackman	2015
14379	Calf	2015	Jackman	2015
14382	Adult	2014	Jackman	2015
14384	Adult	2014	Jackman	2015
14385	Calf	2015	Jackman	2015
14387	Adult	2014	Jackman	2015
14390	Adult	2014	Jackman	2015
14333	Calf	2016	Jackman	2016
14335	Adult	2014	Jackman	2016
14340	Adult	2015	Jackman	2016
14342	Calf	2016	Jackman	2016
14343	Adult	2014	Jackman	2016
14349	Adult	2015	Jackman	2016
14350	Adult	2014	Jackman	2016
14354	Adult	2014	Jackman	2016
14356	Adult	2014	Jackman	2016

14360	Adult	2014	Jackman	2016
14362	Adult	2014	Jackman	2016
14363	Adult	2014	Jackman	2016
14364	Calf	2016	Jackman	2016
14365	Adult	2014	Jackman	2016
14369	Adult	2014	Jackman	2016
14370	Adult	2014	Jackman	2016
14372	Adult	2014	Jackman	2016
14373	Adult	2014	Jackman	2016
14382	Adult	2014	Jackman	2016
14383	Adult	2014	Jackman	2016
14384	Adult	2014	Jackman	2016
14386	Adult	2014	Jackman	2016
14389	Adult	2014	Jackman	2016
14390	Adult	2014	Jackman	2016
19190	Calf	2016	Jackman	2016
19193	Calf	2016	Jackman	2016
19195	Calf	2016	Jackman	2016
19197	Calf	2016	Jackman	2016
19200	Calf	2016	Jackman	2016
14329	Calf	2017	Jackman	2017
14330	Calf	2017	Jackman	2017
14331	Calf	2017	Jackman	2017
14339	Adult	2015	Jackman	2017
14340	Adult	2015	Jackman	2017
14342	Calf	2017	Jackman	2017
14345	Adult	2015	Jackman	2017
14346	Adult	2015	Jackman	2017
14347	Calf	2017	Jackman	2017
14349	Adult	2015	Jackman	2017
14350	Adult	2014	Jackman	2017
14353	Adult	2017	Jackman	2017
14359	Adult	2015	Jackman	2017
14360	Adult	2014	Jackman	2017
14365	Adult	2014	Jackman	2017
14366	Adult	2015	Jackman	2017
14368	Calf	2017	Jackman	2017
14369	Adult	2014	Jackman	2017
14370	Adult	2014	Jackman	2017
14371	Adult	2015	Jackman	2017
14372	Adult	2014	Jackman	2017
14373	Adult	2014	Jackman	2017
14376	Adult	2015	Jackman	2017
14377	Adult	2015	Jackman	2017

14379	Calf	2017	Jackman	2017
14382	Adult	2014	Jackman	2017
14384	Adult	2014	Jackman	2017
14385	Adult	2015	Jackman	2017
14389	Adult	2014	Jackman	2017
14390	Adult	2014	Jackman	2017
19119	Adult	2016	Aroostook	2016
19120	Calf	2016	Aroostook	2016
19121	Adult	2016	Aroostook	2016
19122	Calf	2016	Aroostook	2016
19123	Adult	2016	Aroostook	2016
19124	Calf	2016	Aroostook	2016
19125	Adult	2016	Aroostook	2016
19127	Calf	2016	Aroostook	2016
19128	Adult	2016	Aroostook	2016
19130	Calf	2016	Aroostook	2016
19131	Adult	2016	Aroostook	2016
19133	Adult	2016	Aroostook	2016
19134	Adult	2016	Aroostook	2016
19135	Calf	2016	Aroostook	2016
19136	Adult	2016	Aroostook	2016
19137	Adult	2016	Aroostook	2016
19138	Calf	2016	Aroostook	2016
19139	Adult	2016	Aroostook	2016
19140	Calf	2016	Aroostook	2016
19141	Adult	2016	Aroostook	2016
19142	Adult	2016	Aroostook	2016
19143	Calf	2016	Aroostook	2016
19146	Adult	2016	Aroostook	2016
19147	Calf	2016	Aroostook	2016
19148	Adult	2016	Aroostook	2016
19149	Adult	2016	Aroostook	2016
19151	Calf	2016	Aroostook	2016
19153	Adult	2016	Aroostook	2016
19155	Calf	2016	Aroostook	2016
19156	Adult	2016	Aroostook	2016
19157	Calf	2016	Aroostook	2016
19159	Adult	2016	Aroostook	2016
19161	Calf	2016	Aroostook	2016
19162	Adult	2016	Aroostook	2016
19164	Adult	2016	Aroostook	2016
19165	Adult	2016	Aroostook	2016
19166	Adult	2016	Aroostook	2016
19167	Calf	2016	Aroostook	2016

19169	Adult	2016	Aroostook	2016
19170	Calf	2016	Aroostook	2016
19171	Adult	2016	Aroostook	2016
19173	Calf	2016	Aroostook	2016
19174	Adult	2016	Aroostook	2016
19177	Adult	2016	Aroostook	2016
19180	Adult	2016	Aroostook	2016
19181	Calf	2016	Aroostook	2016
19184	Adult	2016	Aroostook	2016
19203	Calf	2016	Aroostook	2016
19121	Adult	2016	Aroostook	2017
19123	Adult	2016	Aroostook	2017
19125	Adult	2016	Aroostook	2017
19127	Calf	2017	Aroostook	2017
19128	Adult	2016	Aroostook	2017
19130	Calf	2017	Aroostook	2017
19131	Adult	2016	Aroostook	2017
19134	Adult	2016	Aroostook	2017
19135	Calf	2017	Aroostook	2017
19137	Adult	2016	Aroostook	2017
19139	Adult	2016	Aroostook	2017
19141	Adult	2016	Aroostook	2017
19142	Adult	2016	Aroostook	2017
19146	Adult	2016	Aroostook	2017
19147	Adult	2017	Aroostook	2017
19148	Adult	2016	Aroostook	2017
19149	Adult	2016	Aroostook	2017
19151	Calf	2017	Aroostook	2017
19152	Calf	2017	Aroostook	2017
19153	Adult	2016	Aroostook	2017
19154	Calf	2017	Aroostook	2017
19156	Adult	2016	Aroostook	2017
19161	Calf	2017	Aroostook	2017
19162	Adult	2016	Aroostook	2017
19164	Adult	2016	Aroostook	2017
19165	Adult	2016	Aroostook	2017
19166	Adult	2016	Aroostook	2017
19167	Calf	2017	Aroostook	2017
19169	Adult	2016	Aroostook	2017
19170	Calf	2017	Aroostook	2017
19171	Adult	2016	Aroostook	2017
19174	Adult	2016	Aroostook	2017
19176	Calf	2017	Aroostook	2017
19180	Calf	2017	Aroostook	2017

19183	Calf	2017	Aroostook	2017
19184	Adult	2016	Aroostook	2017
19204	Adult	2017	Aroostook	2017
24239	Calf	2017	Aroostook	2017
24241	Calf	2017	Aroostook	2017
24243	Calf	2017	Aroostook	2017
24245	Calf	2017	Aroostook	2017
24247	Calf	2017	Aroostook	2017
24250	Calf	2017	Aroostook	2017
24256	Calf	2017	Aroostook	2017

APPENDIX 2A: JERICHO MODEL CODE

```
extensions [gis]

;; Create Breeds

breed [moose a-moose] ;; establishes moose as a group of agents

breed [wticks wtick] ;; establishes winter ticks as agents NOTE: called wticks because ticks is a primitive relating to model time in NetLogo

moose-own [starting-patch

      infestation
      num-clusters
      weight
      total-blood
      remaining-blood
      age
      weight-loss
      original-weight
      critical-fat] ;; all variables that are specific to the moose cohort

wticks-own [cluster] ;; all variables specific to winter ticks

patches-own [land-cover-type ] ;; variables that are unique to the environment

globals [NLCDJerichoQuarter

     land-cover
     season
     month
     time-of-day
     num-moose
     ticks-in-cuts
     ticks-in-decid
     ticks-in-conif
     ticks-in-mixed
     infestation-number
     calf-mortality
     adult-mortality
     total-calves
     fatal-infestation
     length-of-winter
     max-total-calf-infest
     mean-total-calf-infest] ;; variables that exist within the global environment, and are thus accessible to all agents (moose, wticks, patches, links)
```

```
to set-GIS

  ca ;; always start a model by clearing the environment
  set NLCDJerichoQuarter gis:load-dataset "C:/Users/Christine/Dropbox/NLCDJerichoQuarter.shp"
  gis:set-world-envelope (gis:envelope-of NLCDJerichoQuarter)

end

to setup

;;color-patches
;; Establish moose and wticks as agents, assign physical properties
  set-default-shape moose "cow"
  populate-moose
  ask moose [
    symbolize-moose
    set num-moose (count moose)
    move-to one-of patches with [ land-cover-type = 31 or land-cover-type = 52 or land-cover-type = 71 ]
    set starting-patch patch-here
    set weight ((random 251.00) + 149.00) ;; assigns a random weight to each moose agent, which will be used to determine their age class
    set original-weight weight
    set critical-fat original-weight * 0.75
    set total-blood weight * 0.08     ;; the amount of blood each individual has is determined as 8% of total body weight
      setup-age
    set total-calves (count moose with [age = "calf"])]

    populate-wticks
    ask wticks [ ;; number of clusters is variable by slider on the interface
    set shape "circle"
    set size 1
    set color black
    cluster-in-cuts]

 reset-ticks
end

to go



;; Tick procedures: if it is questing season and they contact a moose, they attach- questing successful
```

```
   ;; if questing season ends and moose has not made contact with tick cluster, ticks have failed to
quest, and they will die
ask wticks [
    quest]
;; Moose procedures: Look into % of time spent in certain habitat types per season- this will
define their movement
   ;; movement will be determined by time of day (bedded or active)
   ;; could look into energetics so that eating restores strength- last priority
  ask moose [
    move
    pick-up-wticks
    report-environment
    adjust-weight
    lose-blood
    update-meanmax-infest]
 ;; check-fat]
set-seasonality
set-time-of-day
set-month
update-meanmax-infest
   if season = "winter" [
    set length-of-winter length-of-winter + 1]
  if remainder ticks 8766 = 1 [
   if drought? [
    let %wt 0.30
    let n count wticks
    ask n-of (%wt * n) wticks
      [die]
  ]]
if ticks = 8766 [ stop ]
 tick
end

;;;;;;;;;;;;;;;;;;;;;;; Environmental Settings ;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to display-land-cover

  gis:draw NLCDJerichoQuarter 1

end

to display-land-cover-in-patches

  gis:apply-coverage NLCDJerichoQuarter "GRIDCODE" land-cover-type
  ask patches
  [if land-cover-type = 11
    [set pcolor blue
```

```
      set land-cover "open-water"]
    if land-cover-type = 21
    [set pcolor 18
      set land-cover "developed-open"]
    if land-cover-type = 22
    [set pcolor 17
      set land-cover "developed-low"]
    if land-cover-type = 23
    [set pcolor 15
      set land-cover "developed-medium"]
    if land-cover-type = 24
    [set pcolor 14
      set land-cover "developed-high"]
    if land-cover-type = 31
    [set pcolor brown
      set land-cover "cut"]
    if land-cover-type = 41
    [set pcolor 58
      set land-cover "deciduous"]
    if land-cover-type = 42
    [set pcolor 53
      set land-cover "coniferous"]
    if land-cover-type = 43
    [set pcolor green
      set land-cover "mixed"]
    if land-cover-type = 52
    [set pcolor brown
      set land-cover "shrub"]
    if land-cover-type = 71
    [set pcolor brown
      set land-cover "herbaceous"]
    if land-cover-type = 82
    [set pcolor yellow
      set land-cover "crops"]
    if land-cover-type = 90
    [set pcolor turquoise
      set land-cover "wetlands"]
    if land-cover-type = 95
    [set pcolor turquoise
      set land-cover "wetlands"]
  ]

end

;; Create seasons and time of day

to set-seasonality
```

```
  if snow = "12Nov" [
    if remainder ticks 8766 <= 1392 [
      set season "questing" ]]
  if snow = "26Nov" [
    if remainder ticks 8766 <= 1728 [
      set season "questing"]]
  if snow = "10Dec" [
    if remainder ticks 8766 <= 2064 [
      set season "questing" ]]
  if snow = "12Nov" [
    if remainder ticks 8766 >= 1393 and remainder ticks 8766 <= 4351 [
      set season "winter" ]]
  if snow = "26Nov" [
    if remainder ticks 8766 >= 1729 and remainder ticks 8766 <= 4351 [
      set season "winter"]]
  if snow = "10Dec" [
    if remainder ticks 8766 >= 2065 and remainder ticks 8766 <= 4351 [
      set season "winter"]]
  if remainder ticks 8766 >= 4352 and remainder ticks 8766 <= 5744 [
    set season "drop-off"]
  if remainder ticks 8766 >= 5745 and remainder ticks 8766 <= 6513 [
    set season "calving" ]
  if remainder ticks 8766 >= 6714 and remainder ticks 8766 <= 8766 [
    set season "summer" ]

end

to set-month

  if remainder ticks 8766 <= 360 or remainder ticks 8766 >= 8425 [
    set month "September" ]
  if remainder ticks 8766 >= 361 and remainder ticks 8766 <= 1104 [
    set month "October" ]
  if remainder ticks 8766 >= 1105 and remainder ticks 8766 <= 1824 [
    set month "November" ]
  if remainder ticks 8766 >= 1825 and remainder ticks 8766 <= 2568 [
    set month "December" ]
  if remainder ticks 8766 >= 2569 and remainder ticks 8766 <= 3312 [
    set month "January" ]
  if remainder ticks 8766 >= 3313 and remainder ticks 8766 <= 4008 [
    set month "February" ]
  if remainder ticks 8766 >= 4009 and remainder ticks 8766 <= 4752 [
    set month "March" ]
  if remainder ticks 8766 >= 4753 and remainder ticks 8766 <= 5472 [
    set month "April" ]
  if remainder ticks 8766 >= 5473 and remainder ticks 8766 <= 6216 [
    set month "May" ]
```

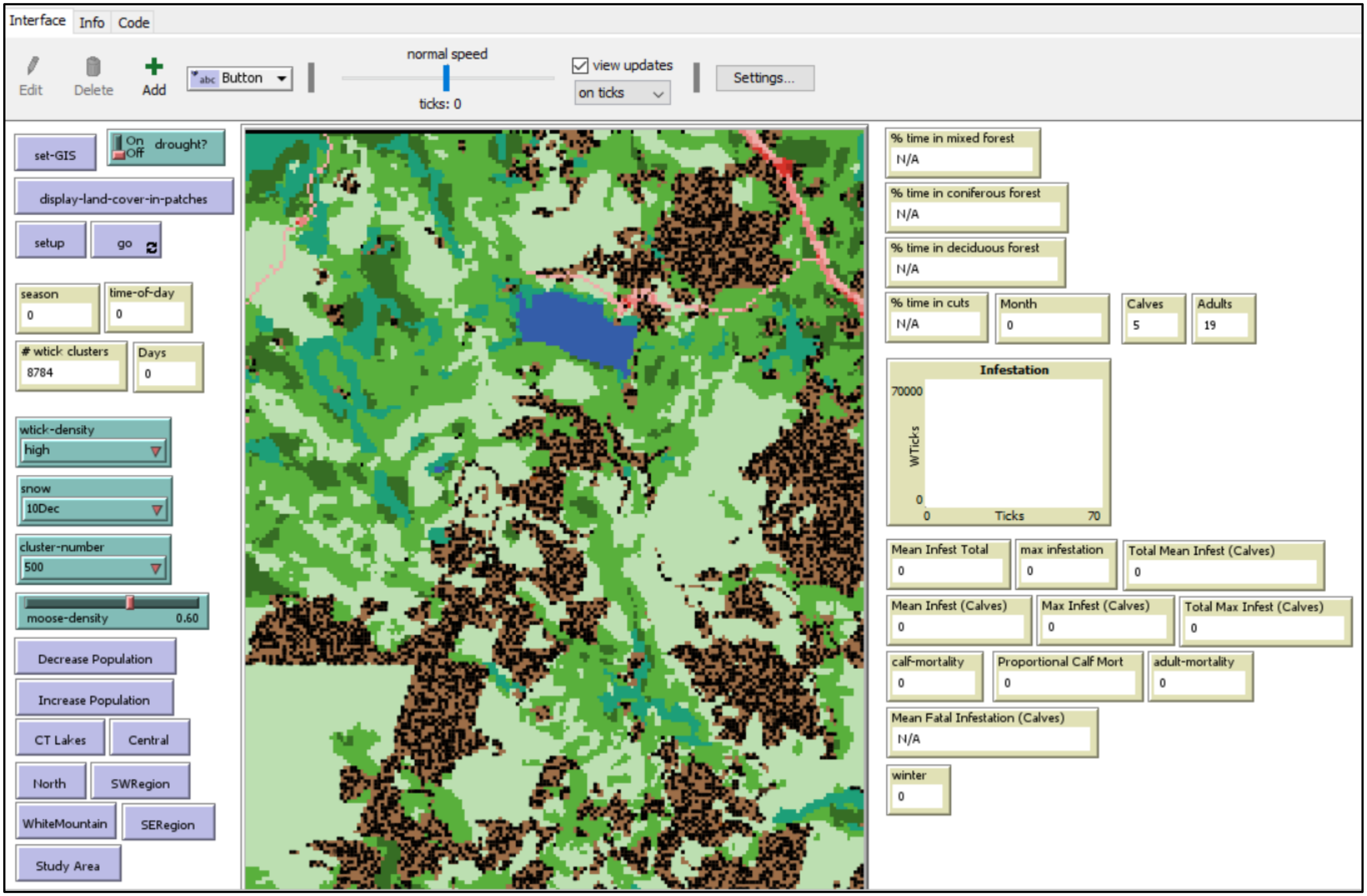
```
  if remainder ticks 8766 >= 6217 and remainder ticks 8766 <= 6936 [
    set month "June" ]
  if remainder ticks 8766 >= 6937 and remainder ticks 8766 <= 7680 [
    set month "July" ]
  if remainder ticks 8766 >= 7681 and remainder ticks 8766 <= 8424 [
    set month "August" ]

end

;; Establish time of day to control moose movement

to set-time-of-day

  if remainder ticks 24 < 6 or remainder ticks 24 > 20 [ ;; 9 non-active hours
    set time-of-day "night"]
  if remainder ticks 24 >= 6 and remainder ticks 24 <= 8 [ ;; 3 active hours in the morning
    set time-of-day "morning" ]
  if remainder ticks 24 >= 9 and remainder ticks 24 < 18 [ ;; 9 (mostly) non-active hours during
the day
    set time-of-day "day" ]
  if remainder ticks 24 >= 18 and remainder ticks 24 <= 20 [  ;; 3 active hours in the evening
    set time-of-day "evening" ]

end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;; Winter Tick Actions ;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to populate-wticks

  if wtick-density = "low" and cluster-number = "100" [
    create-wticks (num-moose * 320)
    set infestation-number 100 ]
  if wtick-density = "low" and cluster-number = "300" [
    create-wticks (num-moose * 107)
    set infestation-number 300 ]
  if wtick-density = "low" and cluster-number = "500" [
    create-wticks (num-moose * 64)
    set infestation-number 500 ]
  if wtick-density = "low" and cluster-number = "700" [
    create-wticks (num-moose * 46)
    set infestation-number 700 ]  ;; 16 if clusters have 300, 10 if clusters have 500, 7 if clusters
have 700
 if wtick-density = "medium" and cluster-number = "100" [
    create-wticks (num-moose * 732)
    set infestation-number 100 ]
  if wtick-density = "medium" and cluster-number = "300" [
    create-wticks (num-moose * 244)
  set infestation-number 300 ]
```

```
  if wtick-density = "medium" and cluster-number = "500" [
    create-wticks (num-moose * 146)
    set infestation-number 500 ]
  if wtick-density = "medium" and cluster-number = "700" [
    create-wticks (num-moose * 105)
    set infestation-number 700 ] ;; 37 if clusters have 300, 22 if clusters have 500, 16 if clusters
have 700
  if wtick-density = "high" and cluster-number = "100" [
    create-wticks (num-moose * 1831)
    set infestation-number 100 ]
  if wtick-density = "high" and cluster-number = "300" [
    create-wticks (num-moose * 610)
    set infestation-number 300 ]
  if wtick-density = "high" and cluster-number = "500" [
    create-wticks (num-moose * 366)
    set infestation-number 500 ]
  if wtick-density = "high" and cluster-number = "700" [
    create-wticks (num-moose * 262)
    set infestation-number 700 ] ;; 91 if clusters have 300, 55 if clusters have 500, 39 if clusters
have 700
  if wtick-density = "severe" and cluster-number = "100" [
    create-wticks (num-moose * 2838)
    set infestation-number 100 ]
  if wtick-density = "severe" and cluster-number = "300" [
    create-wticks (num-moose * 946)
    set infestation-number 300 ]
 if wtick-density = "severe" and cluster-number = "500" [
    create-wticks (num-moose * 567)
    set infestation-number 500 ]
  if wtick-density = "severe" and cluster-number = "700" [
    create-wticks (num-moose * 405)
    set infestation-number 700 ] ;; 142 if clusters have 300, 85 if clusters have 500, 61 if clusters
have 700
end

to cluster-in-cuts

  move-to one-of patches with [ land-cover-type = 31 or land-cover-type = 52 or land-cover-type
= 71 ]  ;; simple fix found on stack exchange

end

to quest

  if season = "questing" [
   let host one-of moose-here
   if host != nobody
```

```
    [die]
  ]
  if ticks > 1 and season != "questing"
  [die]

end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;; Moose Actions ;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to populate-moose

  create-moose (round(40.7919 * moose-density))
;;  if moose-density = "singular" [
;;    create-moose 1 ]
;;  if moose-density = "SERegion" [
;;    create-moose 2 ]
;;  if moose-density = "SWRegion/Central" [
;;    create-moose 4]
;;  if moose-density = "WhiteMountain" [
;;    create-moose 6 ]
;;  if moose-density = "North" [
;;    create-moose 19 ]
;;  if moose-density = "CTLakes" [
;;    create-moose 35 ]

end

to symbolize-moose

  ask moose with [age = "calf"] [     ;; calves will be symbolized differently than adults- they will
be an orangey brown and smaller
    set size 3
    set color 23]
  ask moose with [age = "adult"] [
    set size 4
    set color 32]

end

to setup-age          ;; how a moose agent determines its age class

  ask moose
  [ifelse weight < 200   ;; if a moose weighs under 200 kg, it is considered a calf for the purpose
of the model. If it weighs over 200 kg, it is an adult
    [set age "calf"]
    [set age "adult"]
  ]

end
```

```
to move

  if (time-of-day = "morning" or time-of-day = "evening") and age = "calf" [
    ifelse distance starting-patch > 83 [
      face starting-patch] [
      rt random 90
      lt random 90 ]
      fd 1 ]
  if (time-of-day = "morning" or time-of-day = "evening") and age = "adult" [
    ifelse distance starting-patch > 83 [
      face starting-patch] [
      rt random 90
      lt random 90 ]
      fd 5 ]

end

to pick-up-wticks     ;; procedure for how to become infested

  if season = "questing" [
  let infest one-of wticks-here
  if infest != nobody    ;; if a moose moves to occupy the same square as a cluster of ticks
    [set infestation infestation + infestation-number  ;; 300 or 500 or 700
      set num-clusters (num-clusters + 1) ]]  ;; the moose's infestation level is increased by 1000 (a
placeholder for the number of ticks questing together
end

to report-environment

  let occupied one-of moose-here
  if (land-cover-type = 71 or land-cover-type = 52 or land-cover-type = 31) and occupied !=
nobody [
    set ticks-in-cuts ticks-in-cuts + 1 ]
  if land-cover-type = 41 and occupied != nobody [
    set ticks-in-decid ticks-in-decid + 1 ]
  if land-cover-type = 42 and occupied != nobody [
    set ticks-in-conif ticks-in-conif + 1 ]
  if land-cover-type = 43 and occupied != nobody [
    set ticks-in-mixed ticks-in-mixed + 1 ]

end

to update-meanmax-infest

  if season = "questing" [
    set max-total-calf-infest (max [infestation] of moose with [age = "calf"])
    set mean-total-calf-infest (mean [infestation] of moose with [age = "calf"])
  ]
```

```
end

to adjust-weight

  ask moose [
    set weight-loss one-of [true false]
    if weight-loss and season = "winter" [
      set weight (weight - ((weight * one-of [0.07 0.25]) / length-of-winter) / 24) ]]

end

to lose-blood

  if season = "drop-off" [  ;; if all the ticks have successfully quested, and there are no more clusters remaining on the landscape
    set remaining-blood total-blood - ((0.25 * infestation)* 0.001)   ;; total number of infestation * .25 = number of adult females, each female takes 0.001 L of blood
  if remaining-blood < total-blood * 0.60 AND age = "calf" [
      set calf-mortality calf-mortality + 1
      set fatal-infestation fatal-infestation + (infestation)
    die]  ;; if the remaining blood after questing is less than 3/4 of the total blood at the beginning of the model, that moose dies
    stop   ;; don't lose any more blood after ticks have taken this blood meal
    ;; adults do not typically die from winter tick infestation, so they have been programmed not to die.
   ]
 ;if season = "calving" [
  ;  set infestation 0]

end
```



season
0

time-of-day
0

wtick clusters
8784

Days
0

wtick-density
high

snow
10Dec

cluster-number
500

moose-density 0.60

% time in mixed forest
N/A

% time in coniferous forest
N/A

% time in deciduous forest
N/A

% time in cuts
N/A

Month
0

Calves
5

Adults
19

Mean Infest Total
0

max infestation
0

Total Mean Infest (Calves)
0

Mean Infest (Calves)
0

Max Infest (Calves)
0

Total Max Infest (Calves)
0

calf-mortality
0

Proportional Calf Mort
0

adult-mortality
0

Mean Fatal Infestation (Calves)
N/A

winter
0

Fig. Jericho model interface in NetLogo

APPENDIX 2B: SUCCESS MODEL CODE

```
extensions [gis]

;; Create Breeds

breed [moose a-moose] ;; establishes moose as a group of agents

breed [wticks wtick] ;; establishes winter ticks as agents NOTE: called wticks because ticks is a primitive relating to model time in NetLogo

moose-own [starting-patch

        infestation
        num-clusters
        weight
        total-blood
        remaining-blood
        age
        weight-loss
        original-weight
        critical-fat] ;; all variables that are specific to the moose cohort

wticks-own [cluster] ;; all variables specific to winter ticks

patches-own [land-cover-type ] ;; variables that are unique to the environment

globals [NLCDSuccess

      land-cover
      season
      month
      time-of-day
      num-moose
      ticks-in-cuts
      ticks-in-decid
      ticks-in-conif
      ticks-in-mixed
      infestation-number
      calf-mortality
      adult-mortality
      total-calves
      fatal-infestation
      length-of-winter
      max-total-calf-infest
      mean-total-calf-infest] ;; variables that exist within the global environment, and are thus accessible to all agents (moose, wticks, patches, links)
```

```
to set-GIS

  ca ;; always start a model by clearing the environment

  set NLCDSuccess gis:load-dataset "C:/Users/Basal/Dropbox/NLCDSuccess.shp"

  gis:set-world-envelope (gis:envelope-of NLCDSuccess)

end

to setup

;;color-patches

;; Establish moose and wticks as agents, assign physical properties
  set-default-shape moose "cow"
  populate-moose
  ask moose [
    symbolize-moose
    set num-moose (count moose)
    move-to one-of patches with [ land-cover-type = 31 or land-cover-type = 52 or land-cover-
type = 71 ]
    set starting-patch patch-here
    set weight ((random 251.00) + 149.00) ;; assigns a random weight to each moose agent, which
will be used to determine their age class
    set original-weight weight
    set critical-fat original-weight * 0.75
    set total-blood weight * 0.08     ;; the amount of blood each individual has is determined as 8%
of total body weight
      setup-age
    set total-calves (count moose with [age = "calf"])]

    populate-wticks
    ask wticks [ ;; number of clusters is variable by slider on the interface
    set shape "circle"
    set size 1
    set color black
    cluster-in-cuts]
reset-ticks

end

to go

;; Tick procedures: if it is questing season and they contact a moose, they attach- questing
successful

   ;; if questing season ends and moose has not made contact with tick cluster, ticks have failed to
quest, and they will die
```

```
ask wticks [
    quest]
;; Moose procedures: Look into % of time spent in certain habitat types per season- this will define their movement
   ;; movement will be determined by time of day (bedded or active)
   ;; could look into energetics so that eating restores strength- last priority
  ask moose [
    move
    pick-up-wticks
    report-environment
    adjust-weight
    lose-blood
   update-meanmax-infest]
 ;; check-fat]
set-seasonality
set-time-of-day
set-month
   if season = "winter" [
    set length-of-winter length-of-winter + 1]
  if remainder ticks 8766 = 1 [
   if drought? [
    let %wt 0.20
    let n count wticks
    ask n-of (%wt * n) wticks
      [die]
  ]]
if ticks = 8766 [ stop ]
 tick

end

;;;;;;;;;;;;;;;;;;;;;;;; Environmental Settings ;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to display-land-cover

  gis:draw NLCDSuccess 1

end

to display-land-cover-in-patches

  gis:apply-coverage NLCDSuccess "GRIDCODE" land-cover-type
  ask patches
  [if land-cover-type = 11
    [set pcolor blue
      set land-cover "open-water"]
    if land-cover-type = 21
    [set pcolor 18
```

```
    set land-cover "developed-open"]
   if land-cover-type = 22
   [set pcolor 17
    set land-cover "developed-low"]
   if land-cover-type = 23
   [set pcolor 15
    set land-cover "developed-medium"]
   if land-cover-type = 24
   [set pcolor 14
    set land-cover "developed-high"]
   if land-cover-type = 31
   [set pcolor brown
    set land-cover "cut"]
   if land-cover-type = 41
   [set pcolor 58
    set land-cover "deciduous"]
   if land-cover-type = 42
   [set pcolor 53
    set land-cover "coniferous"]
   if land-cover-type = 43
   [set pcolor green
    set land-cover "mixed"]
   if land-cover-type = 52
   [set pcolor brown
    set land-cover "shrub"]
   if land-cover-type = 71
   [set pcolor brown
    set land-cover "herbaceous"]
   if land-cover-type = 82
   [set pcolor yellow
    set land-cover "crops"]
   if land-cover-type = 90
   [set pcolor turquoise
    set land-cover "wetlands"]
   if land-cover-type = 95
   [set pcolor turquoise
    set land-cover "wetlands"]
  ]

end

;; Create seasons and time of day

to set-seasonality

  if snow = "12Nov" [
   if remainder ticks 8766 <= 1392 [
```

```
    set season "questing" ]]
  if snow = "26Nov" [
    if remainder ticks 8766 <= 1728 [
      set season "questing"]]
  if snow = "10Dec" [
    if remainder ticks 8766 <= 2064 [
      set season "questing" ]]
  if snow = "12Nov" [
    if remainder ticks 8766 >= 1393 and remainder ticks 8766 <= 4351 [
      set season "winter" ]]
  if snow = "26Nov" [
    if remainder ticks 8766 >= 1729 and remainder ticks 8766 <= 4351 [
      set season "winter"]]
  if snow = "10Dec" [
    if remainder ticks 8766 >= 2065 and remainder ticks 8766 <= 4351 [
      set season "winter"]]
  if remainder ticks 8766 >= 4352 and remainder ticks 8766 <= 5744 [
    set season "drop-off"]
  if remainder ticks 8766 >= 5745 and remainder ticks 8766 <= 6513 [
    set season "calving" ]
  if remainder ticks 8766 >= 6714 and remainder ticks 8766 <= 8766 [
    set season "summer" ]

end

to set-month

  if remainder ticks 8766 <= 360 or remainder ticks 8766 >= 8425 [
    set month "September" ]
  if remainder ticks 8766 >= 361 and remainder ticks 8766 <= 1104 [
    set month "October" ]
  if remainder ticks 8766 >= 1105 and remainder ticks 8766 <= 1824 [
    set month "November" ]
  if remainder ticks 8766 >= 1825 and remainder ticks 8766 <= 2568 [
    set month "December" ]
  if remainder ticks 8766 >= 2569 and remainder ticks 8766 <= 3312 [
    set month "January" ]
  if remainder ticks 8766 >= 3313 and remainder ticks 8766 <= 4008 [
    set month "February" ]
  if remainder ticks 8766 >= 4009 and remainder ticks 8766 <= 4752 [
    set month "March" ]
  if remainder ticks 8766 >= 4753 and remainder ticks 8766 <= 5472 [
    set month "April" ]
  if remainder ticks 8766 >= 5473 and remainder ticks 8766 <= 6216 [
    set month "May" ]
  if remainder ticks 8766 >= 6217 and remainder ticks 8766 <= 6936 [
    set month "June" ]
```

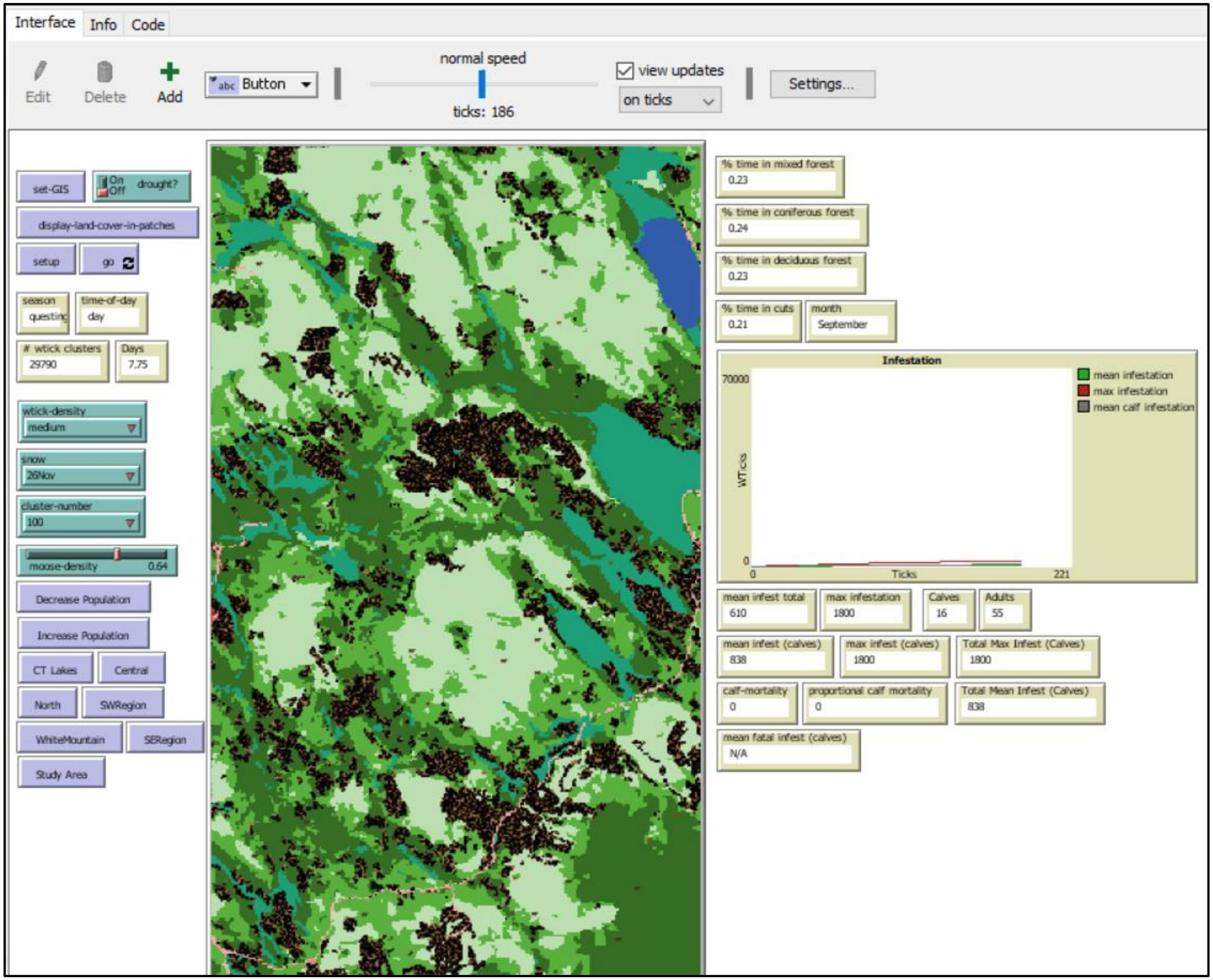
```
  if remainder ticks 8766 >= 6937 and remainder ticks 8766 <= 7680 [
    set month "July" ]
  if remainder ticks 8766 >= 7681 and remainder ticks 8766 <= 8424 [
    set month "August" ]

end

;; Establish time of day to control moose movement

to set-time-of-day

  if remainder ticks 24 < 6 or remainder ticks 24 > 20 [ ;; 9 non-active hours
    set time-of-day "night"]
  if remainder ticks 24 >= 6 and remainder ticks 24 <= 8 [ ;; 3 active hours in the morning
    set time-of-day "morning" ]
  if remainder ticks 24 >= 9 and remainder ticks 24 < 18 [ ;; 9 (mostly) non-active hours during
the day
    set time-of-day "day" ]
  if remainder ticks 24 >= 18 and remainder ticks 24 <= 20 [  ;; 3 active hours in the evening
    set time-of-day "evening" ]

end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;; Winter Tick Actions ;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to populate-wticks

  if wtick-density = "low" and cluster-number = "100" [
    create-wticks (num-moose * 189)
    set infestation-number 100 ]
  if wtick-density = "low" and cluster-number = "300" [
    create-wticks (num-moose * 63)
    set infestation-number 300 ]
  if wtick-density = "low" and cluster-number = "500" [
    create-wticks (num-moose * 38)
    set infestation-number 500 ]
  if wtick-density = "low" and cluster-number = "700" [
    create-wticks (num-moose * 27)
    set infestation-number 700 ]  ;; 16 if clusters have 300, 10 if clusters have 500, 7 if clusters
have 700
 if wtick-density = "medium" and cluster-number = "100" [
    create-wticks (num-moose * 433)
    set infestation-number 100 ]
  if wtick-density = "medium" and cluster-number = "300" [
    create-wticks (num-moose * 144)
  set infestation-number 300 ]
  if wtick-density = "medium" and cluster-number = "500" [
    create-wticks (num-moose * 87)
```

```
    set infestation-number 500 ]
  if wtick-density = "medium" and cluster-number = "700" [
    create-wticks (num-moose * 62)
    set infestation-number 700 ] ;; 37 if clusters have 300, 22 if clusters have 500, 16 if clusters have 700
  if wtick-density = "high" and cluster-number = "100" [
    create-wticks (num-moose * 1083)
    set infestation-number 100 ]
  if wtick-density = "high" and cluster-number = "300" [
    create-wticks (num-moose * 361)
    set infestation-number 300 ]
  if wtick-density = "high" and cluster-number = "500" [
    create-wticks (num-moose * 217)
    set infestation-number 500 ]
  if wtick-density = "high" and cluster-number = "700" [
    create-wticks (num-moose * 155)
    set infestation-number 700 ] ;; 91 if clusters have 300, 55 if clusters have 500, 39 if clusters have 700
  if wtick-density = "severe" and cluster-number = "100" [
    create-wticks (num-moose * 1678)
    set infestation-number 100 ]
  if wtick-density = "severe" and cluster-number = "300" [
    create-wticks (num-moose * 559)
    set infestation-number 300 ]
 if wtick-density = "severe" and cluster-number = "500" [
    create-wticks (num-moose * 336)
    set infestation-number 500 ]
  if wtick-density = "severe" and cluster-number = "700" [
    create-wticks (num-moose * 240)
    set infestation-number 700 ] ;; 142 if clusters have 300, 85 if clusters have 500, 61 if clusters have 700
end

to cluster-in-cuts

  move-to one-of patches with [ land-cover-type = 31 or land-cover-type = 52 or land-cover-type = 71 ]  ;; simple fix found on stack exchange

end

to quest

  if season = "questing" [
   let host one-of moose-here
   if host != nobody
    [die]
  ]
```

```
  if ticks > 1 and season != "questing"
  [die]

end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;; Moose Actions ;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to populate-moose

  create-moose (round(110.652 * moose-density))

end

to symbolize-moose

  ask moose with [age = "calf"] [     ;; calves will be symbolized differently than adults- they will
be an orangey brown and smaller
    set size 3
    set color 23]
  ask moose with [age = "adult"] [
    set size 4
    set color 32]

end

to setup-age          ;; how a moose agent determines its age class

  ask moose
  [ifelse weight < 200   ;; if a moose weighs under 200 kg, it is considered a calf for the purpose
of the model. If it weighs over 200 kg, it is an adult
    [set age "calf"]
    [set age "adult"]
  ]

end

to move

  if (time-of-day = "morning" or time-of-day = "evening") and age = "calf" [
    ifelse distance starting-patch > 83 [
      face starting-patch] [
      rt random 90
      lt random 90 ]
      fd 2 ]
  if (time-of-day = "morning" or time-of-day = "evening") and age = "adult" [
    ifelse distance starting-patch > 83 [
      face starting-patch] [
      rt random 90
      lt random 90 ]
```

```
      fd 5 ]

end



to pick-up-wticks     ;; procedure for how to become infested

  if season = "questing" [
  let infest one-of wticks-here
  if infest != nobody    ;; if a moose moves to occupy the same square as a cluster of ticks
    [set infestation infestation + infestation-number  ;; 300 or 500 or 700
      set num-clusters (num-clusters + 1) ]]  ;; the moose's infestation level is increased by X
end



to report-environment

  let occupied one-of moose-here
  if (land-cover-type = 71 or land-cover-type = 52 or land-cover-type = 31) and occupied !=
nobody [
    set ticks-in-cuts ticks-in-cuts + 1 ]
  if land-cover-type = 41 and occupied != nobody [
    set ticks-in-decid ticks-in-decid + 1 ]
  if land-cover-type = 42 and occupied != nobody [
    set ticks-in-conif ticks-in-conif + 1 ]
  if land-cover-type = 43 and occupied != nobody [
    set ticks-in-mixed ticks-in-mixed + 1 ]

end

to update-meanmax-infest

  if season = "questing" [
    set max-total-calf-infest (max [infestation] of moose with [age = "calf"])
    set mean-total-calf-infest (mean [infestation] of moose with [age = "calf"])
  ]

end

to adjust-weight

  ask moose [
    set weight-loss one-of [true false]
    if weight-loss and season = "winter" [
      set weight (weight - ((weight * one-of [0.07 0.25]) / length-of-winter) / 24) ]]

end
```

```
to lose-blood

  if season = "drop-off" [  ;; if all the ticks have successfully quested, and there are no more clusters remaining on the landscape
    set remaining-blood total-blood - ((0.25 * infestation)* 0.001)   ;; total number of infestation * .25 = number of adult females, each female takes 0.001 L of blood
  if remaining-blood < total-blood * 0.60 AND age = "calf" [
      set calf-mortality calf-mortality + 1
      set fatal-infestation fatal-infestation + (infestation)
    die]  ;; if the remaining blood after questing is less than 3/4 of the total blood at the beginning of the model, that moose dies
    stop   ;; don't lose any more blood after ticks have taken this blood meal
    ;; adults do not typically die from winter tick infestation, so they have been programmed not to die.
   ]
 ;if season = "calving" [
  ;  set infestation 0]

End
```



ticks: 186

☑ view updates: on ticks

season: questing

time-of-day: day

wtick clusters: 29790

Days: 7.75

wtick-density: medium

snow: 26Nov

cluster-number: 100

moose-density: 0.64

% time in mixed forest: 0.23

% time in coniferous forest: 0.24

% time in deciduous forest: 0.23

% time in cuts: 0.21

month: September

mean infest total: 610

max infestation: 1800

Calves: 16

Adults: 55

mean infest (calves): 838

max infest (calves): 1800

Total Max Infest (Calves): 1800

calf-mortality: 0

proportional calf mortality: 0

Total Mean Infest (Calves): 838

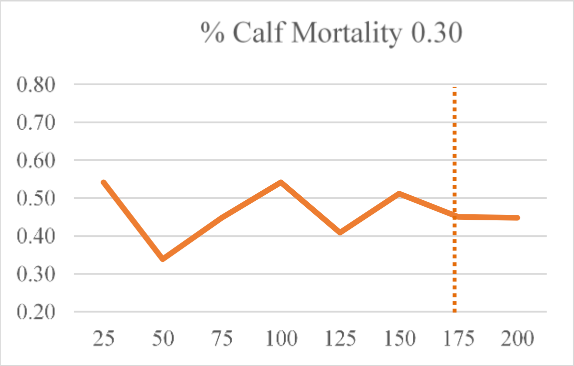
mean fatal infest (calves): N/A

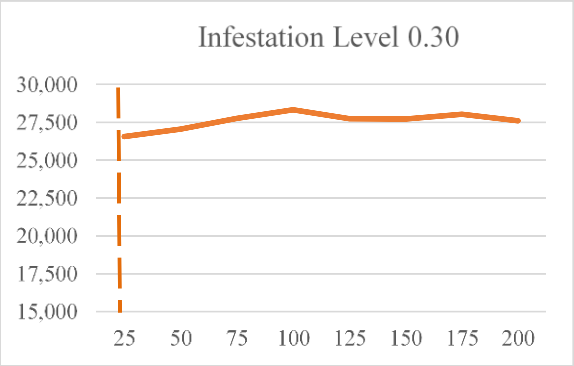
Fig. Success Model Interface in NetLogo

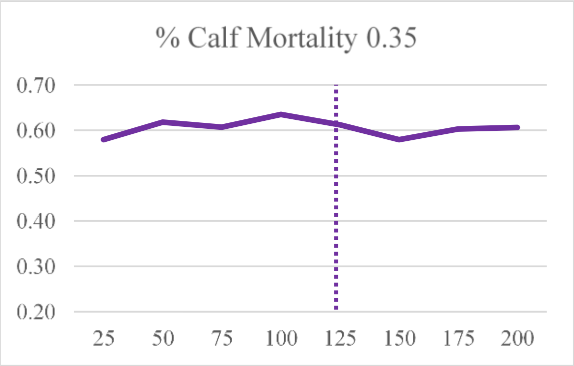
APPENDIX 3A: PRELIMINARY SIMULATIONS FOR JERICHO MODEL

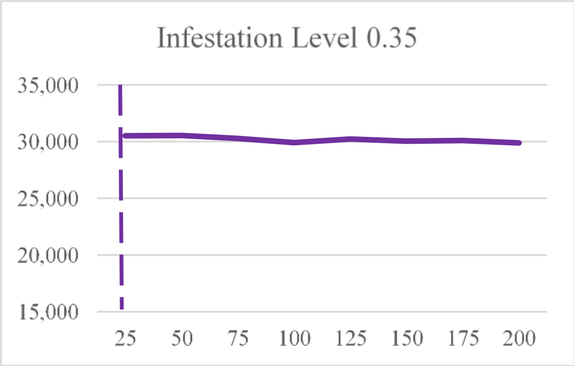
Dashed lines represent where variance meets 5% mortality or 2000 winter tick threshold. Numbers next to outcome variables show moose density. The X-axis shows the number of model iterations.

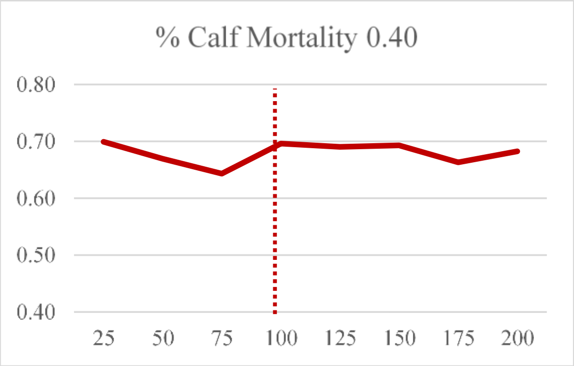
WORST CASE WEATHER

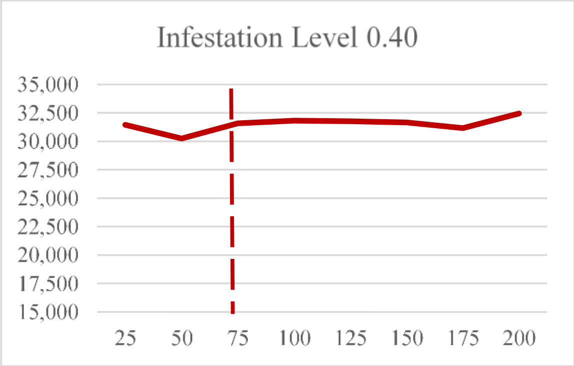

% Calf Mortality 0.30

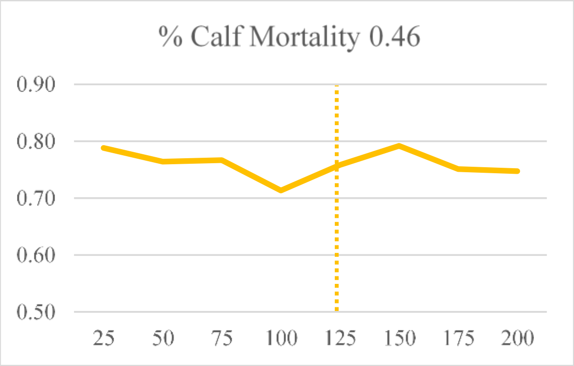

Infestation Level 0.30

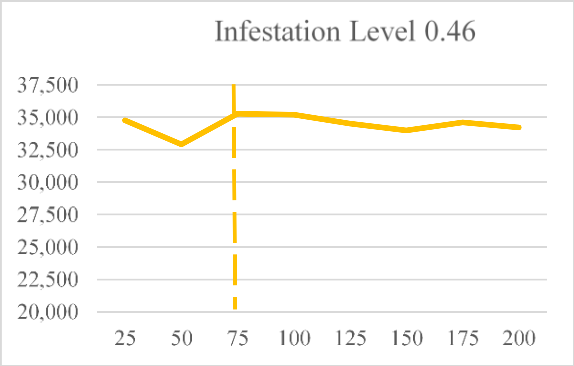

% Calf Mortality 0.35

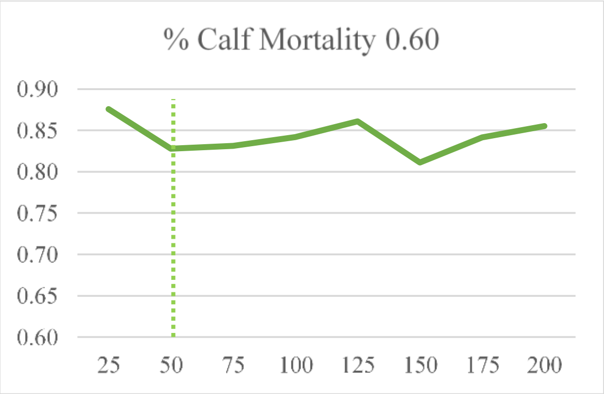

Infestation Level 0.35


% Calf Mortality 0.40

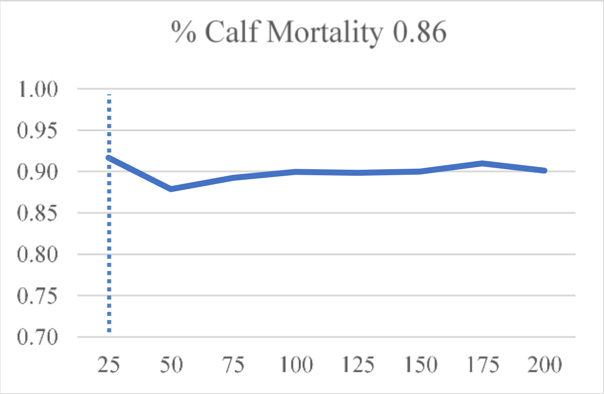

Infestation Level 0.40

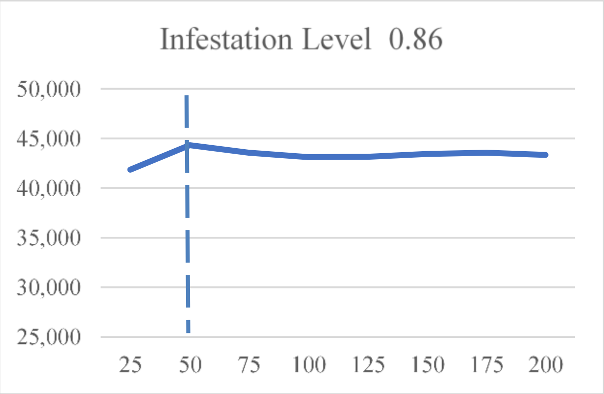

% Calf Mortality 0.46


Infestation Level 0.46

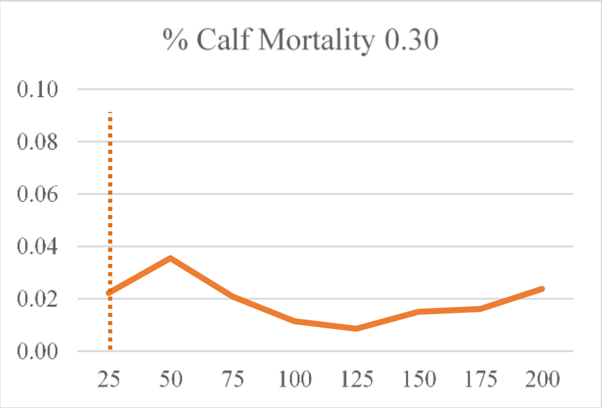

% Calf Mortality 0.60


Infestation Level 0.60

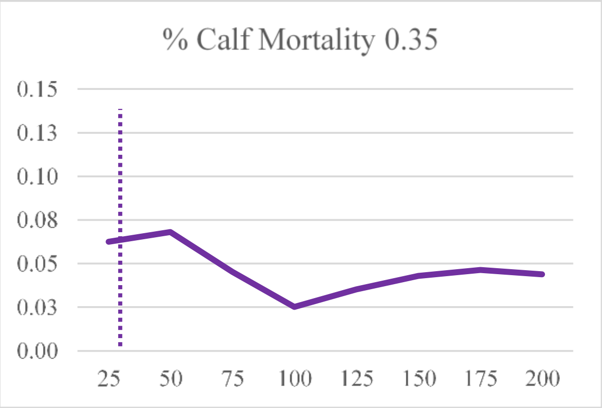

% Calf Mortality 0.86

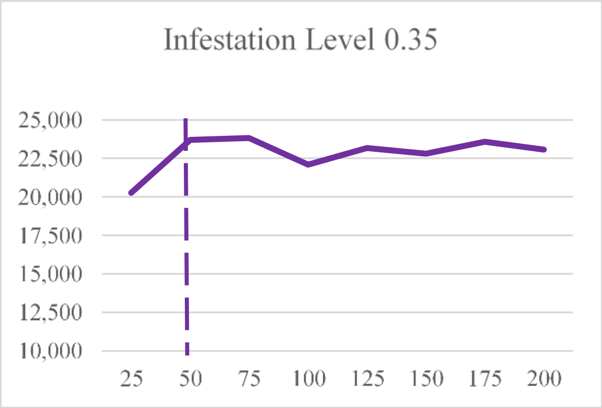

Infestation Level 0.86

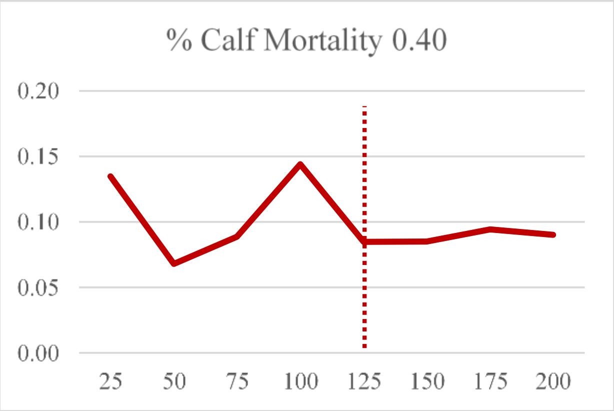
BEST CASE WEATHER

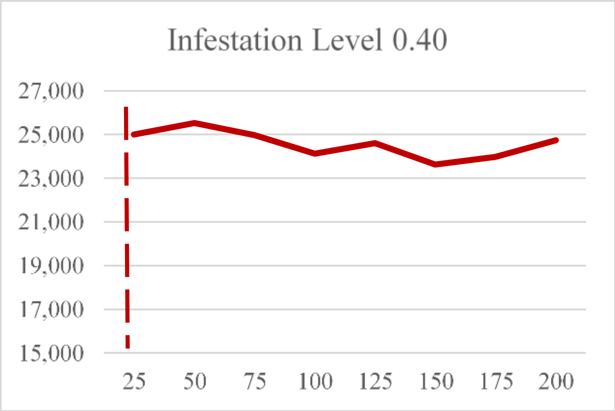

% Calf Mortality 0.30


Infestation Level 0.30


% Calf Mortality 0.35


Infestation Level 0.35


% Calf Mortality 0.40
0.20
0.15
0.10
0.05
0.00
25
50
75
100
125
150
175
200


Infestation Level 0.40
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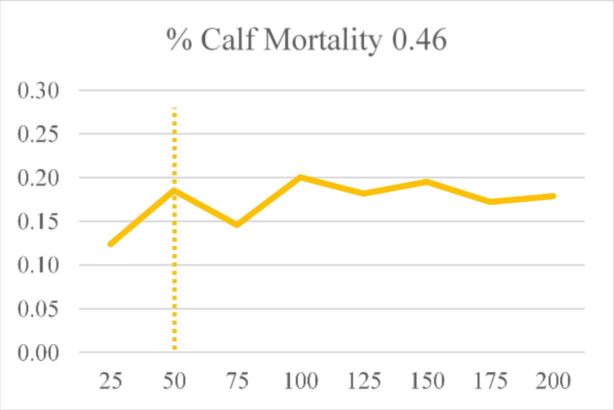
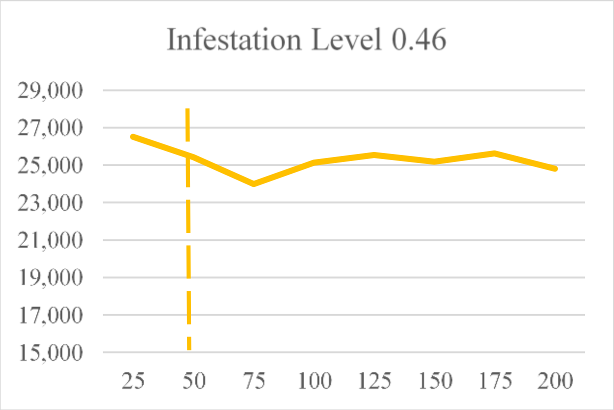
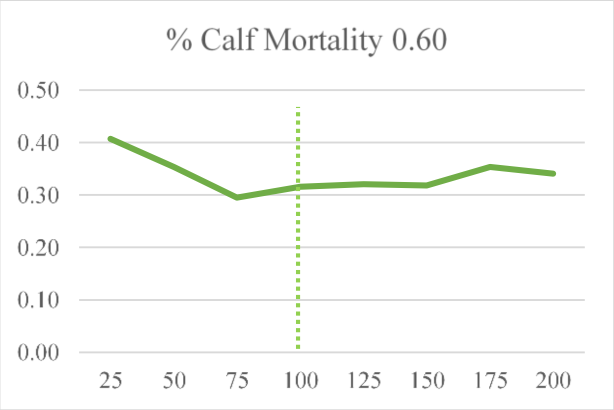
25,000
23,000
21,000
19,000
17,000
15,000
25
50
75
100
125
150
175
200


% Calf Mortality 0.46
0.30
0.25
0.20
0.15
0.10
0.05
0.00
25
50
75
100
125
150
175
200


Infestation Level 0.46
29,000
27,000
25,000
23,000
21,000
19,000
17,000
15,000
25
50
75
100
125
150
175
200


% Calf Mortality 0.60
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0.40
0.30
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0.10
0.00
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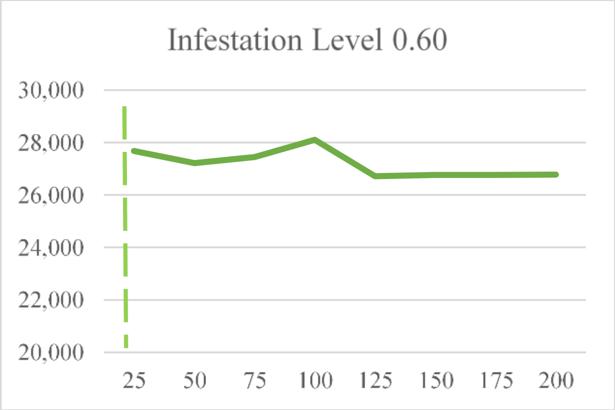
50
75
100
125
150
175
200


Infestation Level 0.60
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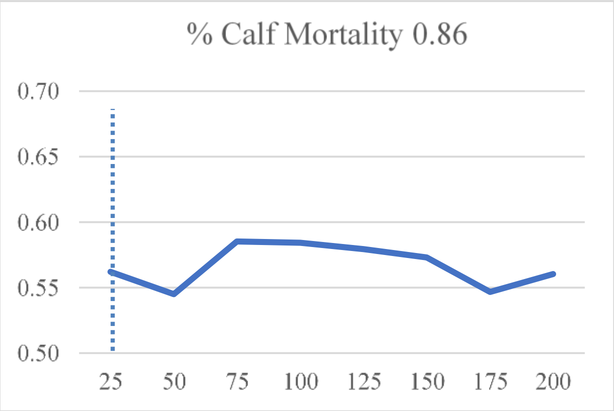
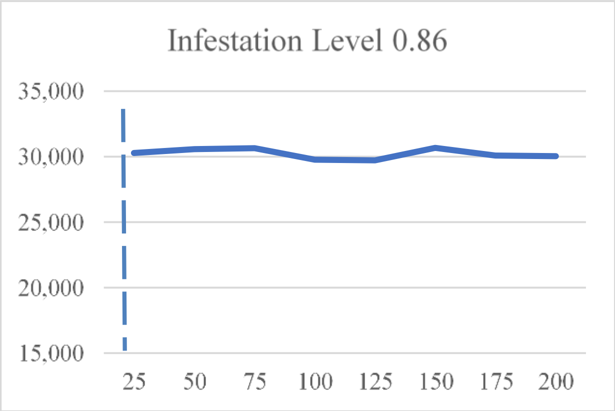
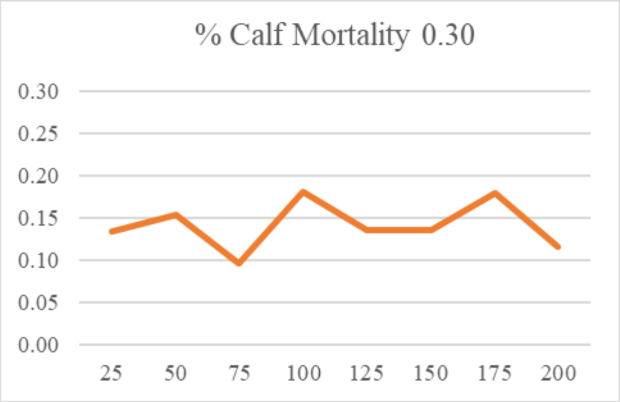
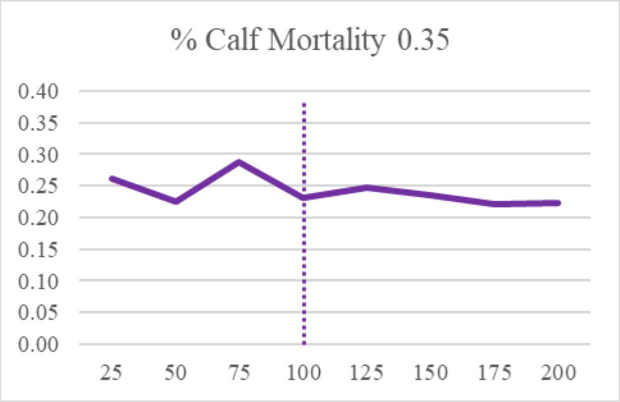
26,000
24,000
22,000
20,000
25
50
75
100
125
150
175
200

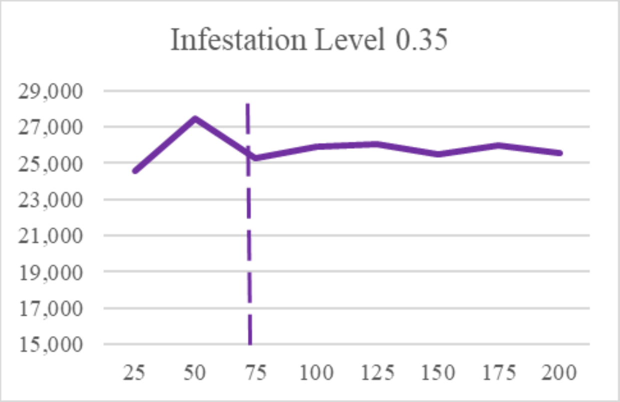

% Calf Mortality 0.86
0.70
0.65
0.60
0.55
0.50
25
50
75
100
125
150
175
200

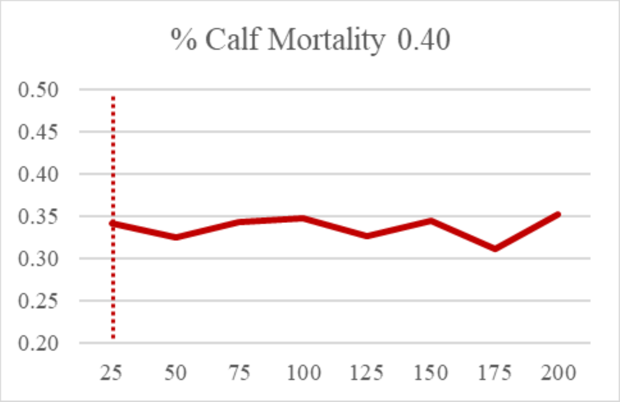

Infestation Level 0.86
35,000
30,000
25,000
20,000
15,000
25
50
75
100
125
150
175
200

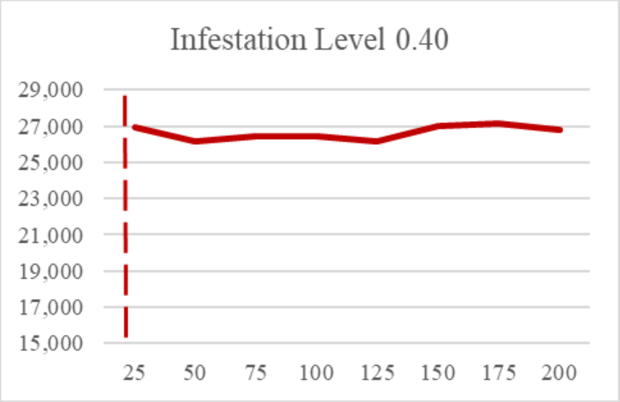
INTERMEDIATE 1 WEATHER

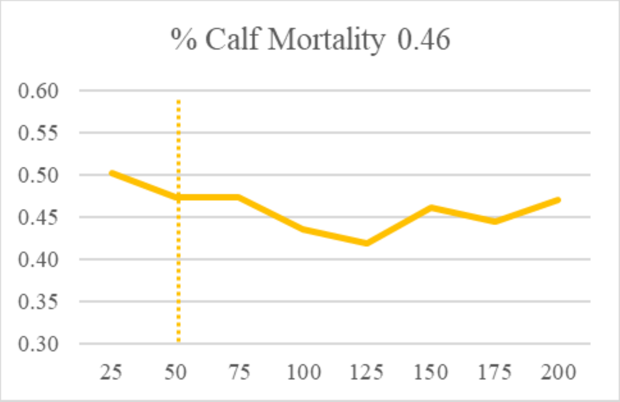


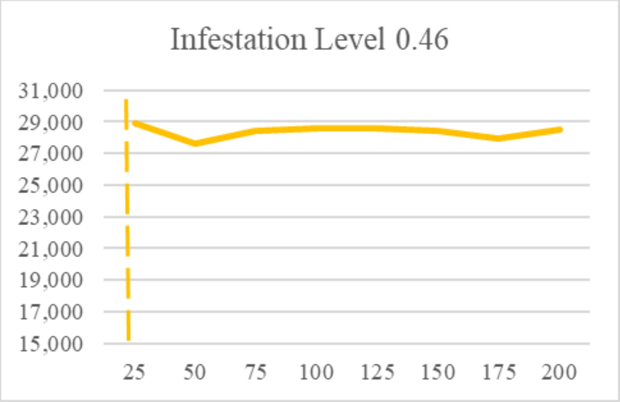


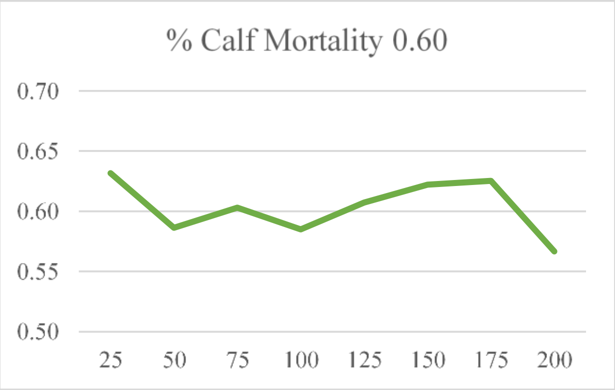


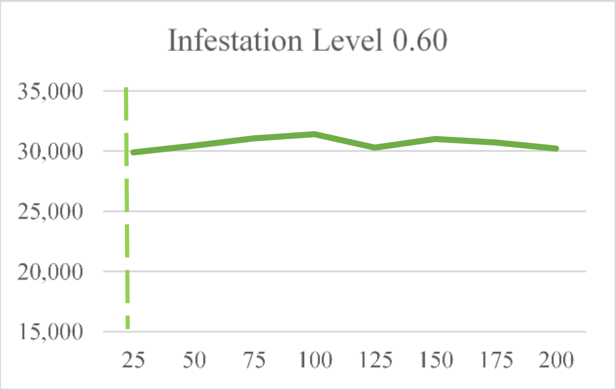


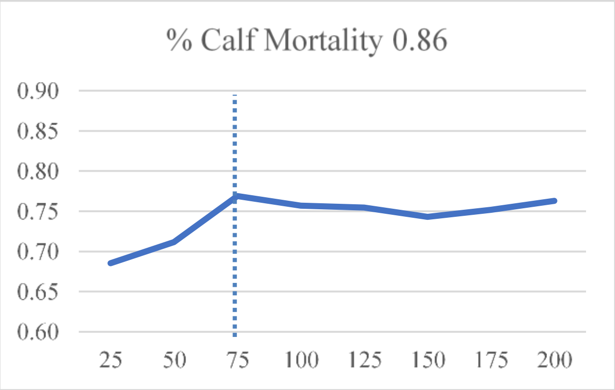


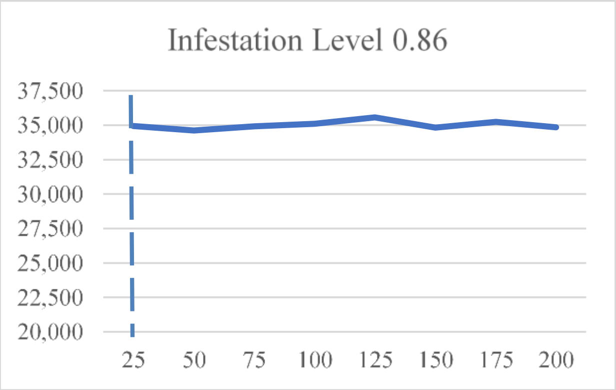




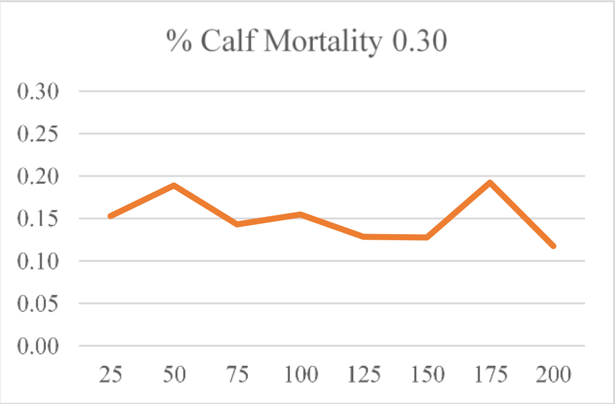


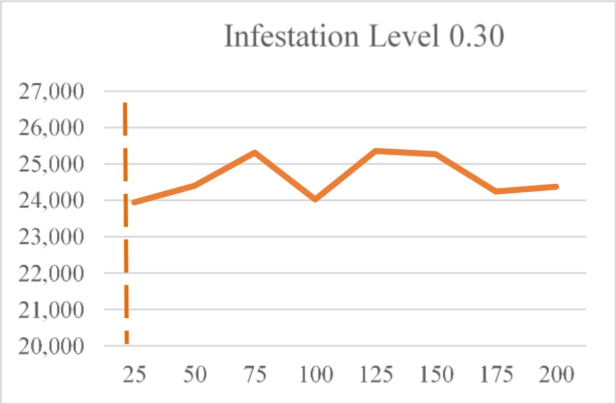


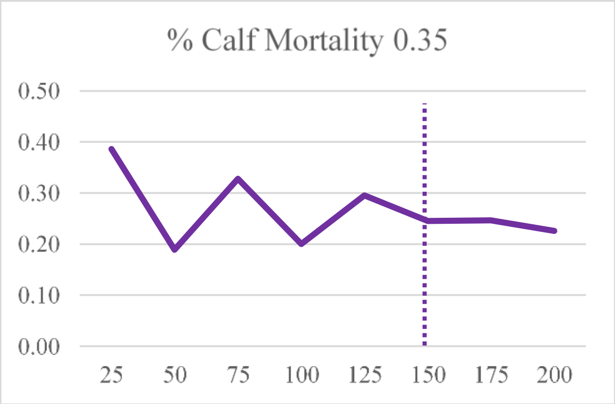


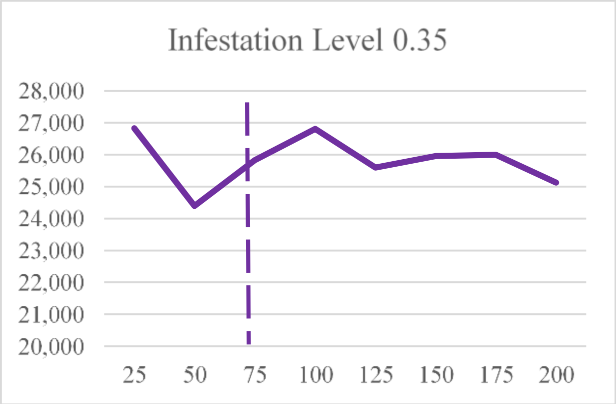


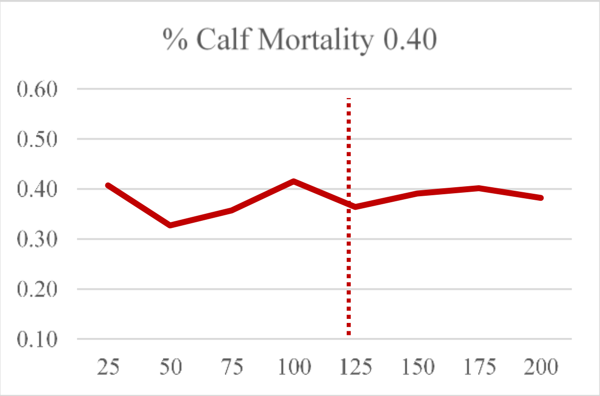
INTERMEDIATE 2 WEATHER

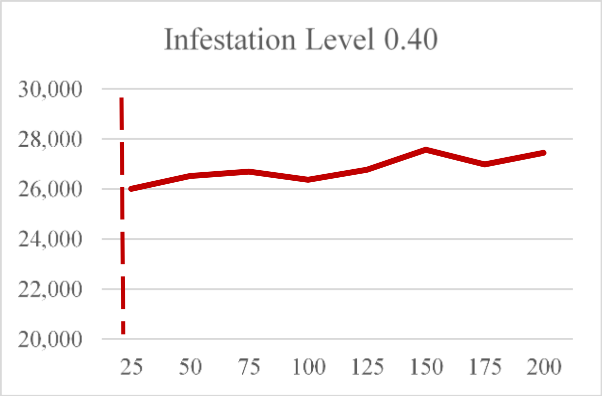


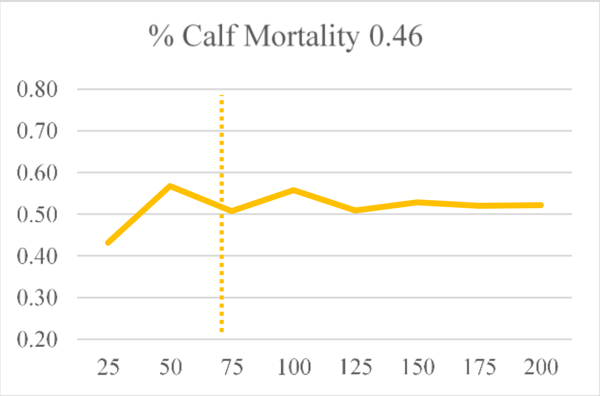


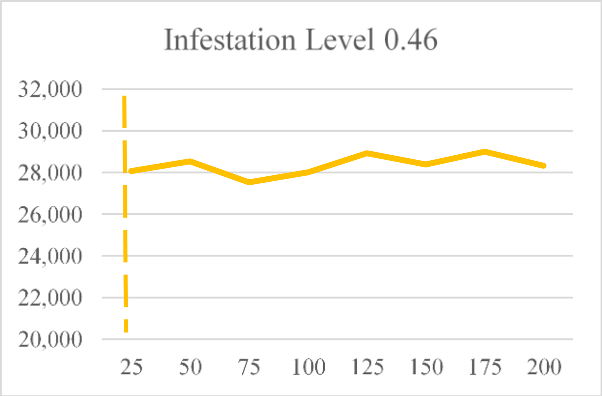


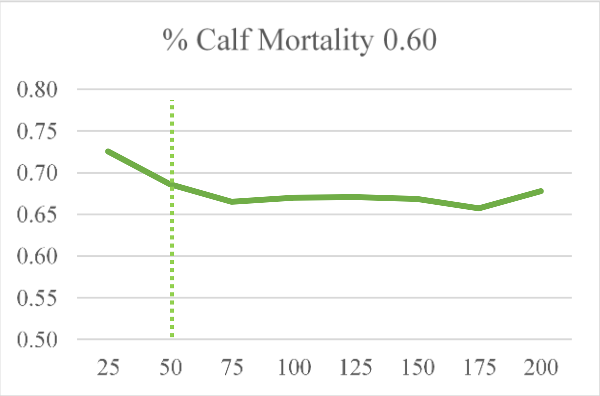



% Calf Mortality 0.40

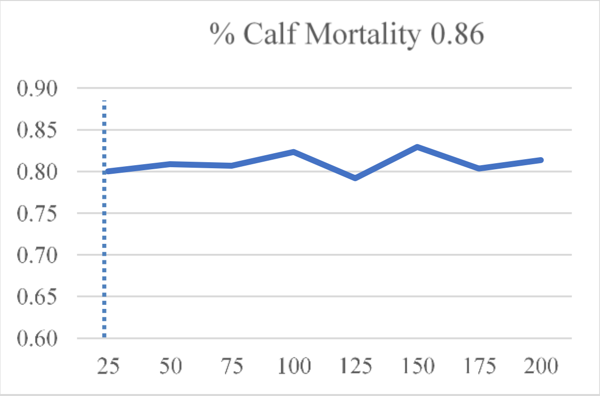

Infestation Level 0.40

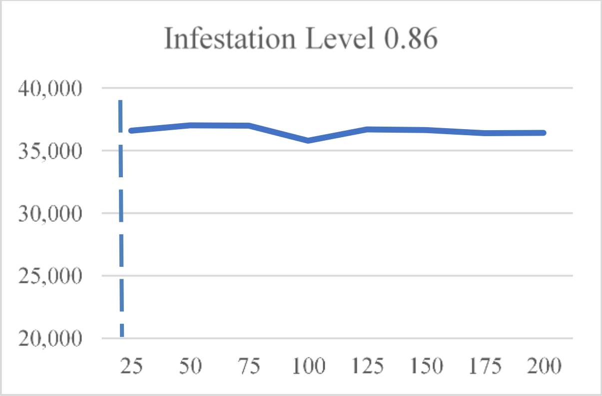

% Calf Mortality 0.46


Infestation Level 0.46


% Calf Mortality 0.60


Infestation Level 0.60

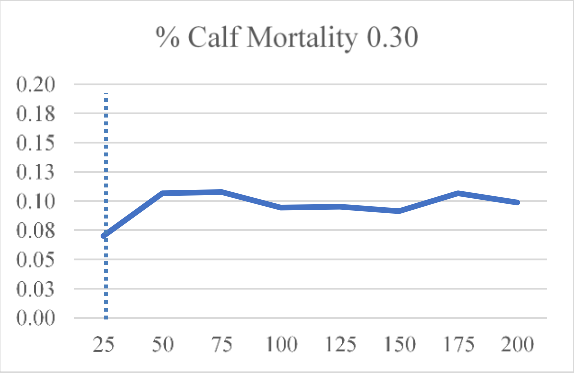

% Calf Mortality 0.86

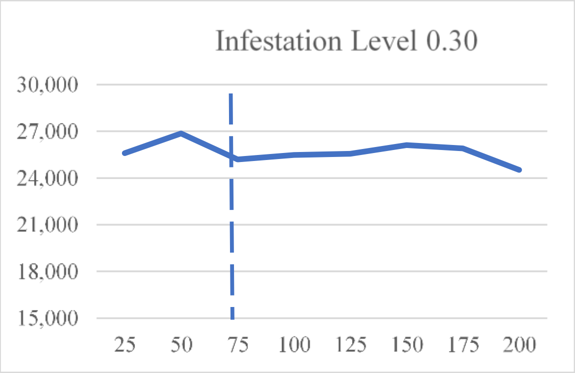

Infestation Level 0.86

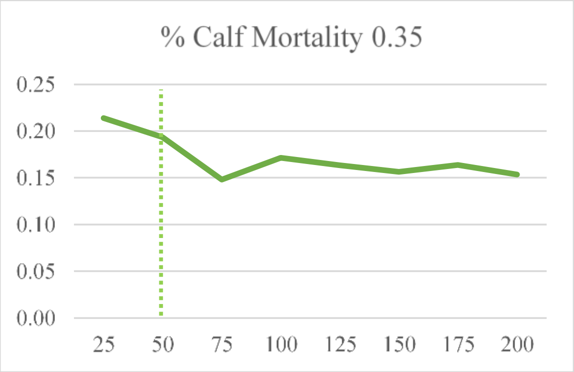
APPENDIX 3B: PRELIMINARY SIMULATIONS FOR SUCCESS MODEL

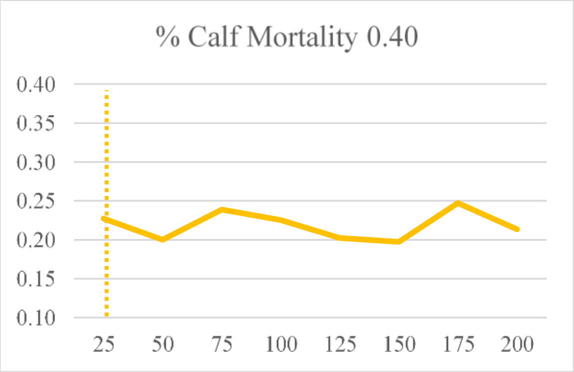
Dashed lines represent where variance meets 5% mortality or 2000 winter tick threshold. Numbers next to outcome variables show moose density. The X-axis shows the number of model iterations.

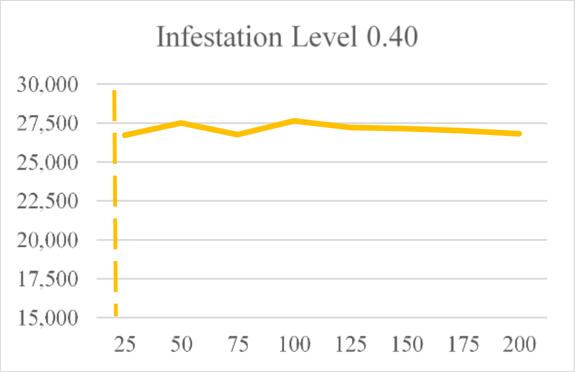
WORST CASE WEATHER

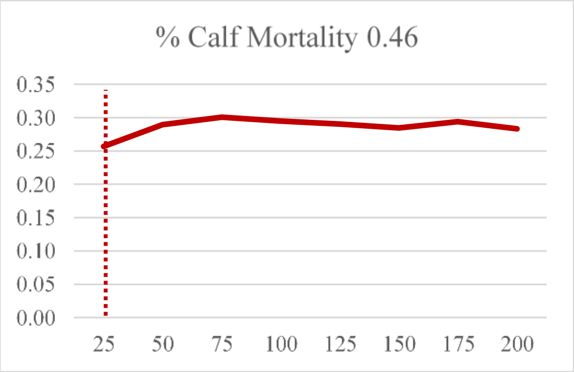


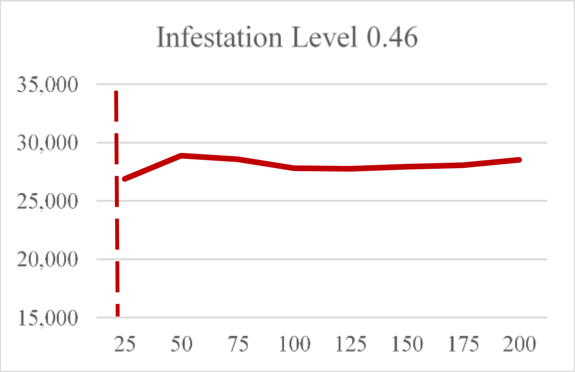


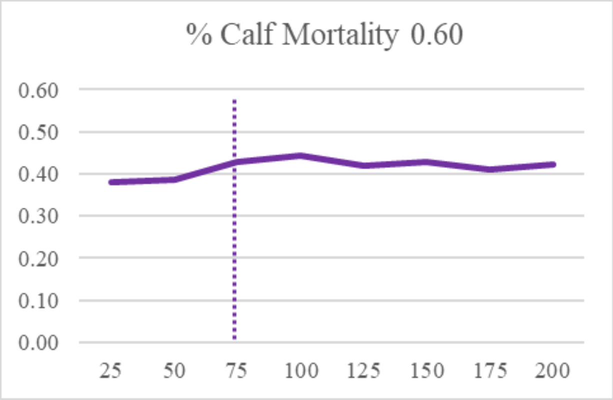


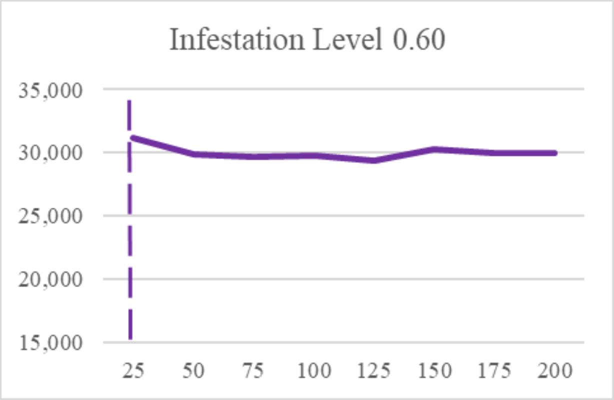


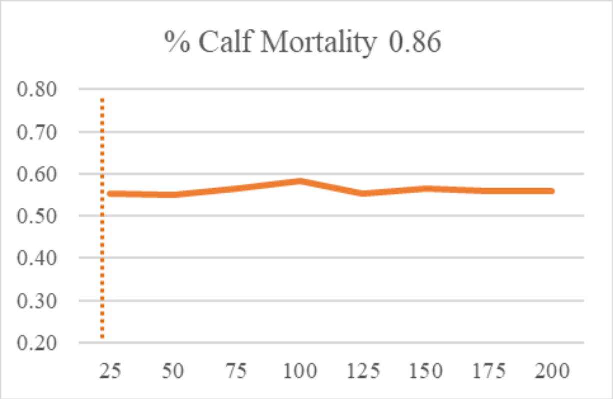


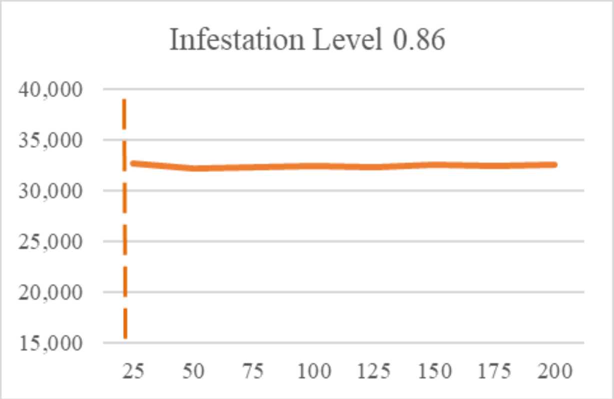




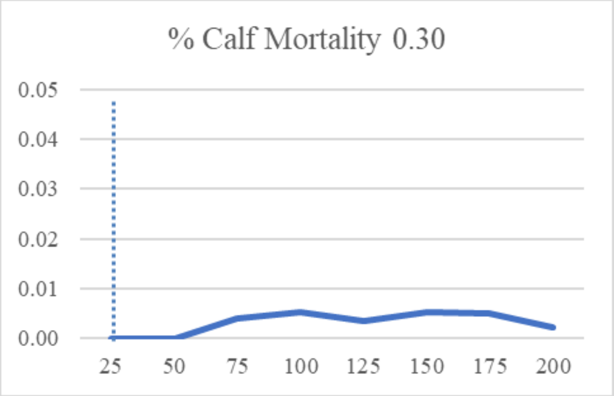


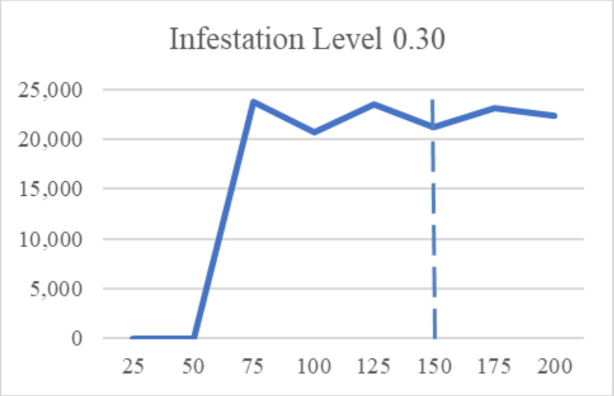


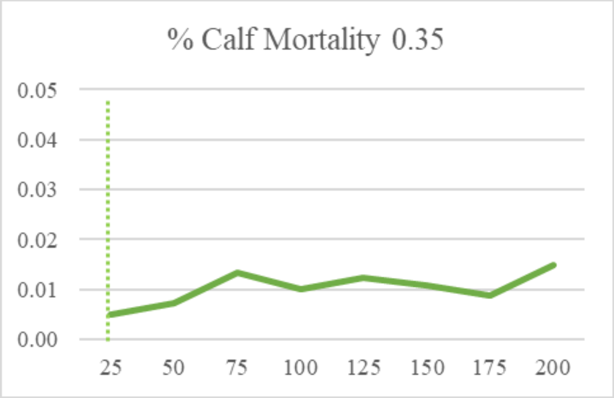


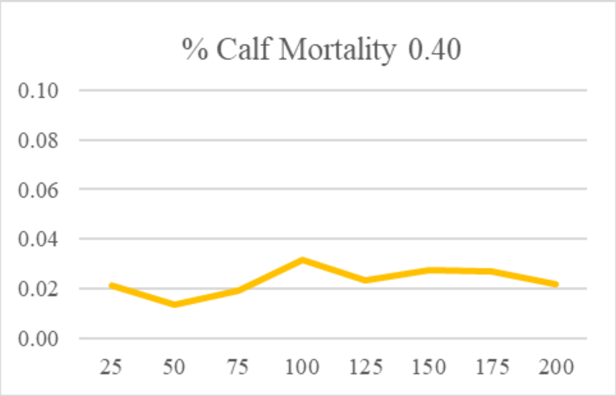


BEST CASE WEATHER

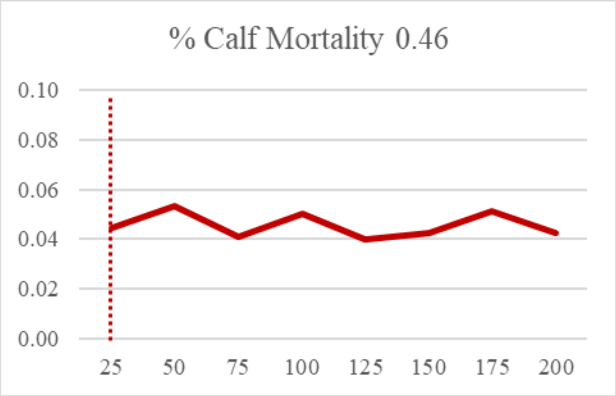


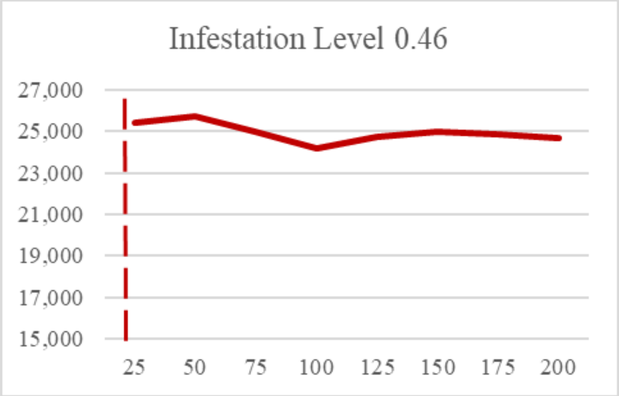


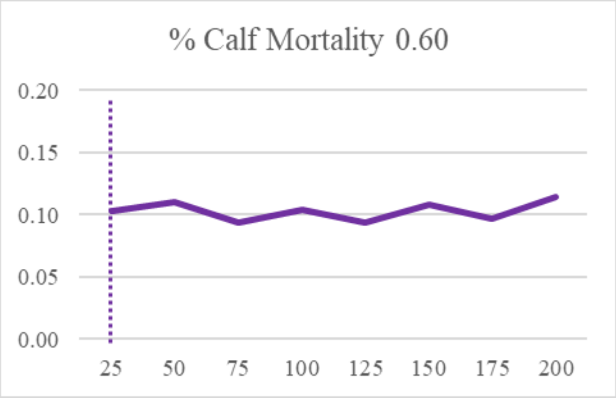


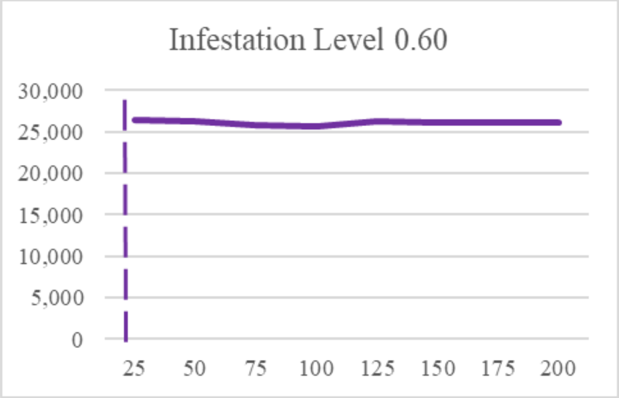

% Calf Mortality 0.40

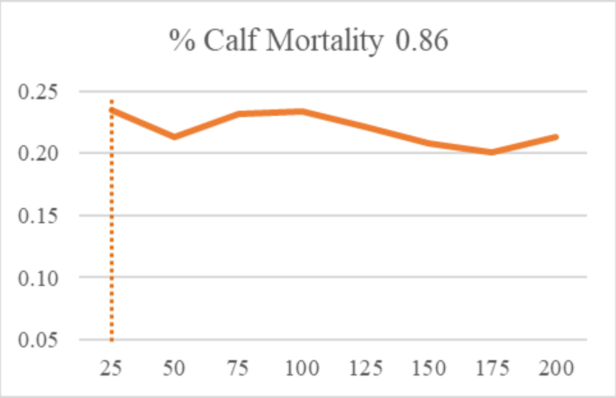

Infestation Level 0.40

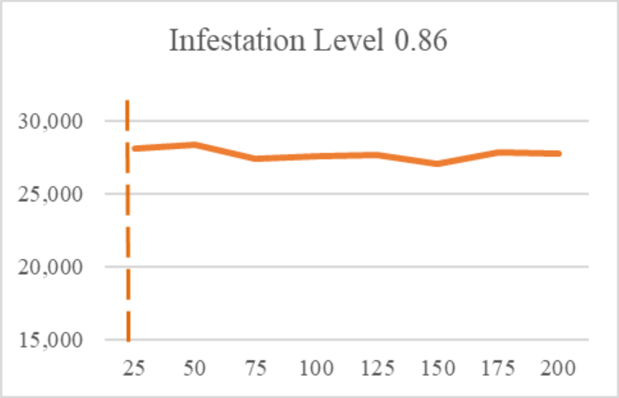

% Calf Mortality 0.46


Infestation Level 0.46

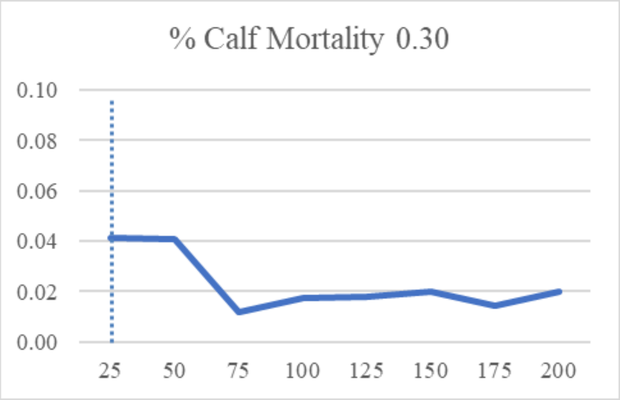

% Calf Mortality 0.60

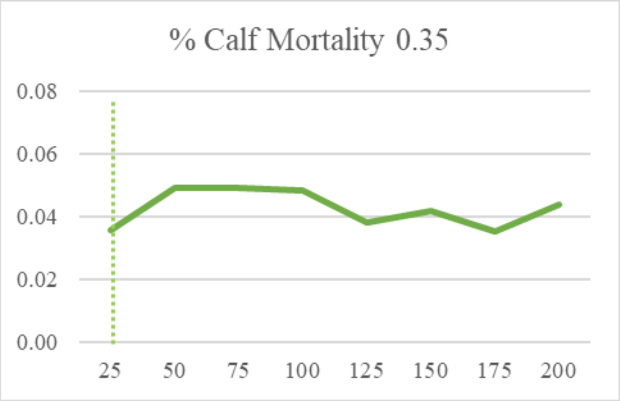

Infestation Level 0.60

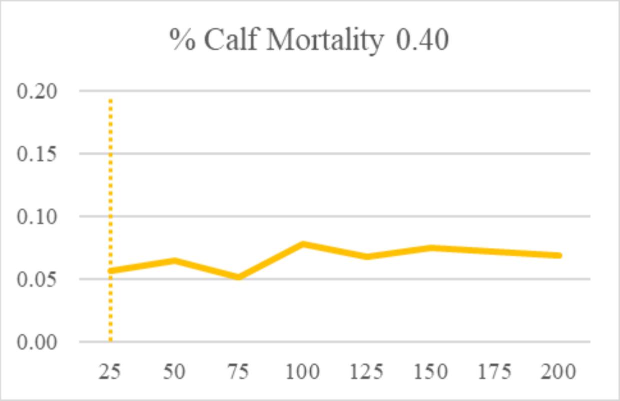

% Calf Mortality 0.86

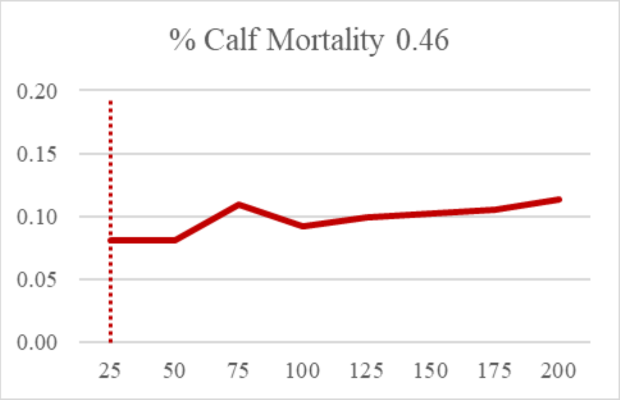

Infestation Level 0.86

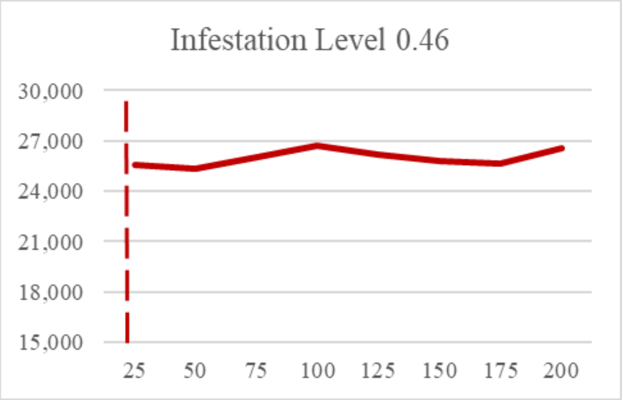
INTERMEDIATE 1 WEATHER

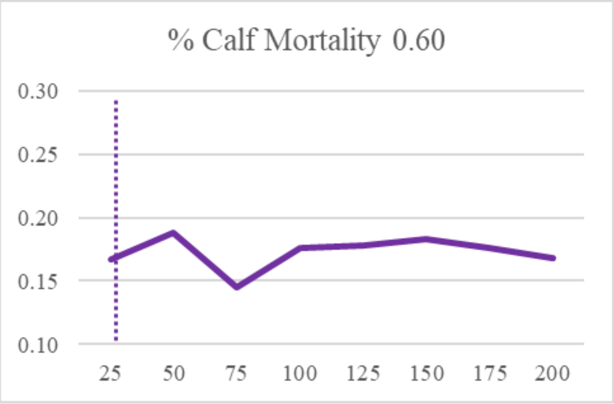


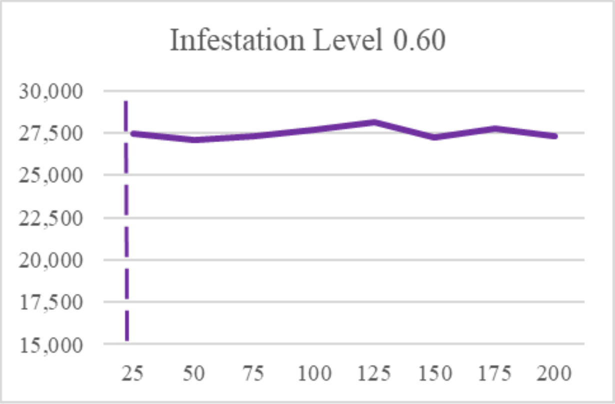


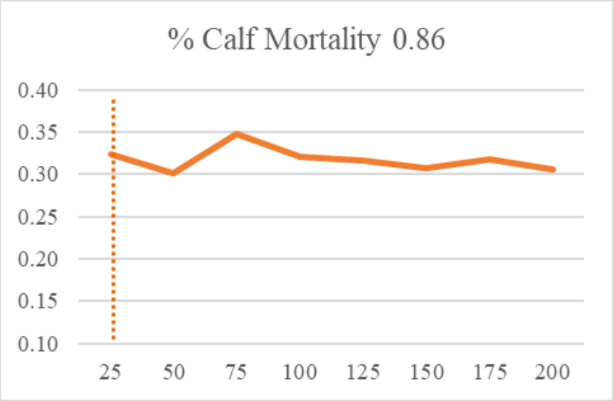


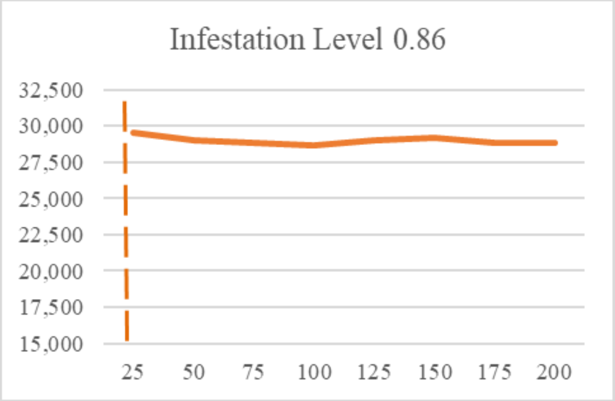




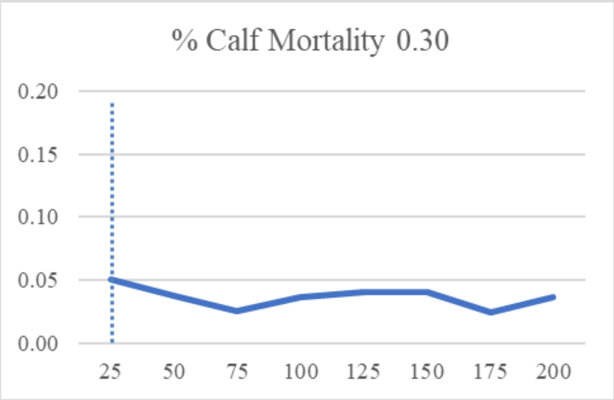


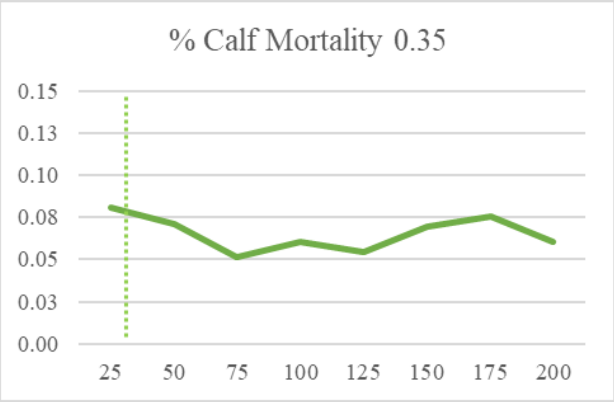


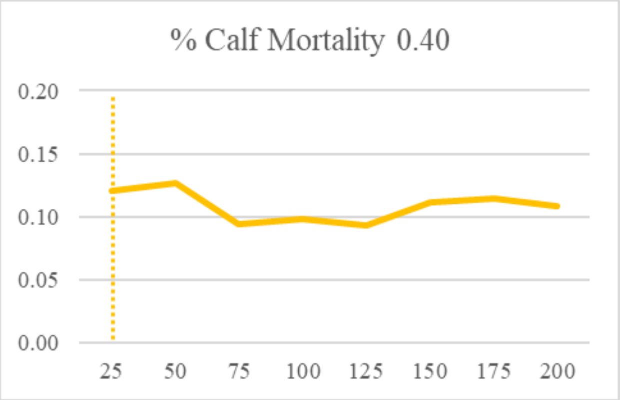




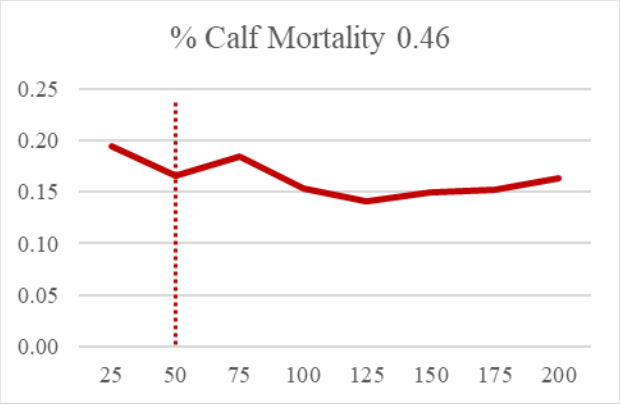
INTERMEDIATE 2 WEATHER






% Calf Mortality 0.40


Infestation Level 0.40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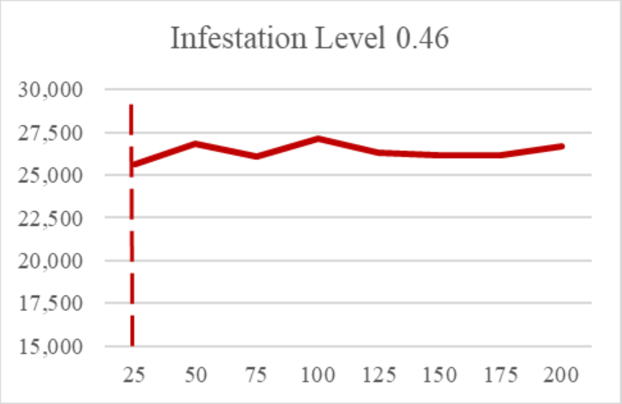
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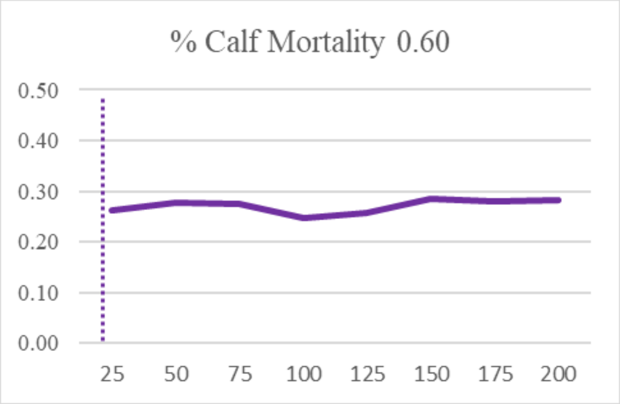
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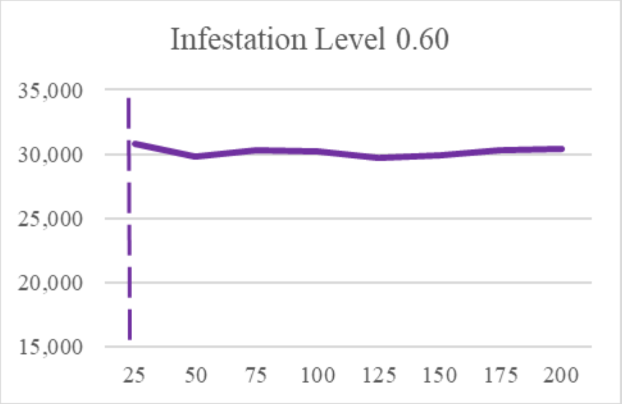
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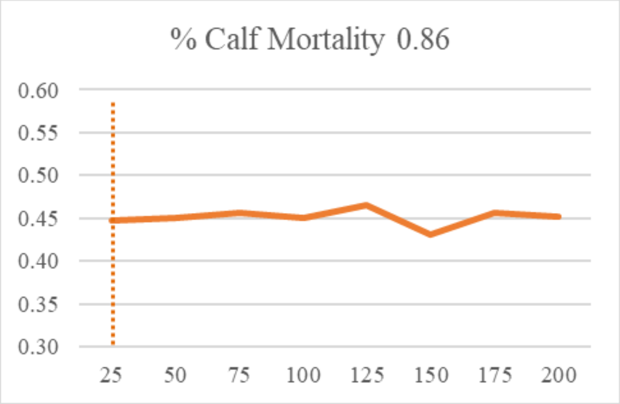
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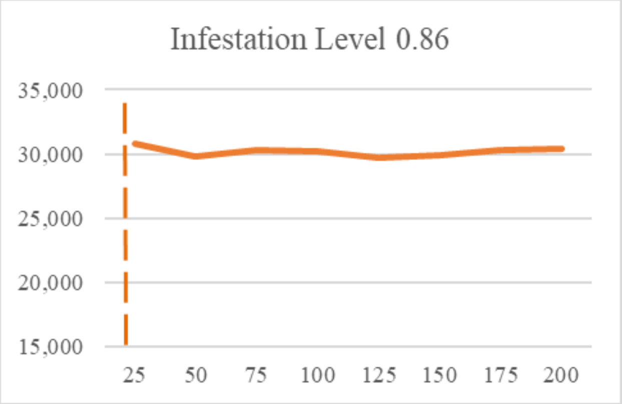
Infestation Level 0.86