

Burden-structured population models for moose

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Purpose

Epizootics of winter ticks (*Dermacentor albipictus*) on moose (*Alces alces*) have caused high calf mortality and population declines in the New England area (Musante, Pekins, and Scarpitti 2010; Jones et al. 2017; Jones et al. 2018). Increased hunter harvests have been proposed as a management strategy, following from a hypothesis that reduced moose populations will decrease questing tick abundances and facilitate recovery of moose populations (Samuel 2004). This management strategy relies on the existence of a host population threshold for tick persistence. Yet, field observations do not indicate a clear moose population threshold for tick persistence (table 4-1 in Jones 2016). This uncertainty about moose population thresholds for tick persistence is a challenge for management, since it is unclear how low moose populations must be reduced and how long it would take for populations to recover. Since these uncertainties are similar to those faced in the control of disease in humans we could use tools from epidemiology to estimate thresholds for the moose-tick system and evaluate the feasibility of harvesting to control tick epizootics.

Mathematical models of host-parasite interactions have a long history in epidemiology and have been used to to guide disease control policy for human diseases (Fine, Eames, and Heymann 2011). Models have also since applied to wildlife disease control and have been used to estimate host thresholds for disease persistence (Campbell, Henke, and Fedynich 2007; McCallum 2016; Lloyd-Smith et al. 2005). To facilitate the application of epidemiological tools towards the study of the moose-tick system, I developed a model which describes the population dynamics of moose and ticks (burden-structured model) which is similar to matrix models commonly used for moose population projection. In the following sections I provide the rationale and structure of the proposed model, data requirements for estimation of model parameters, and examples of model output under different harvesting strategies.

Rationale for burden-structured model

The simplest population models describe how population-average birth and death rates dictate changes in a population over time. However, differences between individuals causes variation in survival and reproduction (vital rates) among individuals in a population. For instance, vital rates of a particular animal commonly depend on characteristics like stage (e.g., calf, yearling, adult), age, and/or size. This is the motivation behind matrix population models which structure populations into discrete classes which may each have different vital rates. By accounting for realistic variation in survival and reproduction among individuals, structured models can be connected to empirical data and used to generate data-driven population projections.

Since tick-burden varies among moose and the fitness consequences suffered by each moose varies depending on the numbers of ticks it carries, we need to explicitly model variation in tick-burden. By connecting burden-structured models with fields estimates of moose survival and fecundity across different tick-burdens we could make population projections for both moose and ticks. Populations of ticks can be modeled because the numbers of questing larvae each fall depends on the numbers of ticks feeding on moose the previous year, which is obtained in the model by summing the tick-burdens over the moose population from the previous year. Modeling tick populations is needed because it allows for the calculation of the population growth

rate of tick, R_0 , which can be used to calculate host population thresholds for disease persistence (Allen and Driessche 2008).

R_0 has the same interpretation as the population growth rate (λ) estimated using matrix projection models, i.e., tick epizootics can occur when $R_0 > 1$ and epizootics won't occur when $R_0 < 1$. Similar to how sensitivity analysis of λ can be used to evaluate how management actions might impact the population growth of moose, sensitivity analysis of R_0 can be used to evaluate how alternative management actions could be used to control winter tick epizootics (Klepac and Caswell 2011). Uncertainty in parameter estimates for moose and tick population growth can also be propagated into the uncertainty of moose population thresholds estimated using the R_0 approach. R_0 can be calculated using standard methods from mathematical epidemiology (Allen and Driessche 2008; Klepac and Caswell 2011). Overall, this means that parameterized burden-structured models could be used to estimate moose population thresholds for tick control and calculate the uncertainty of the estimated threshold which would be useful for managers seeking to control tick epizootics.

Model structure and assumptions

The model tracks two state variables over time, the abundance of ticks in the environment (questing larvae) and numbers of adult moose cows. Events in the model follow a simplified version of the annual sequence of interactions between moose and winter ticks. The following five events happen in order during each annual time step of the model. A mathematical description of the model is given in the appendix.

1. *Moose acquire ticks from the environment.*

- The resulting distribution of burdens is assumed to be have a negative binomial distribution; the negative binomial distribution is used because it allows for high variation in burden (over-dispersion) which is common for parasites like ticks (Shaw and Dobson 1995). This assumption is observable in histograms (figure 5.2 in Samuel 2004) and summary statistics of moose tick burdens (e.g., table 2-2 in Jones 2016) and was used in a statistical model for tick abundance for these reasons (Ball 2017).
- The mean of the burden distribution was assumed to increase with questing larval abundance, i.e., if there are many questing larvae in the environment moose will acquire more ticks which increases the average tick-burden among the moose population. This is consistent with findings from Samuel's comparison of flagged larvae and tick burdens on moose (Samuel 2007). The functional form relating abundance of questing larvae and the mean moose burden should be determined from empirical data.

2. *A proportion of moose is harvested.*

- The probability of being harvested is assumed to be independent of burden. This assumption may be violated if current tick burden has an observable impact of moose condition during the harvesting season and if hunters preferentially harvest moose that have good body condition.

3. *Moose die from natural mortality or tick feeding.*

- There is a constant probability of dying from non-tick related causes.
- The effect of ticks on the probability of dying is in addition to the constant probability of death in the absence of tick infestation.

4. *Ticks detach from moose and lay eggs.*

- The expected proportion of ticks that are engorged females lay eggs. Of the laid eggs, some proportion successfully eclose and will be recruited as questing larvae in the subsequent year.

5. *Moose give birth to calves.*

- The current model includes two stages, calf and adult (only females are tracked).
- Moose recruitment is currently density-independent in this model, so moose population in this model grows or declines exponentially when ticks are absent similar to previous models of moose population dynamics (Jones 2016).

Data requirements

To model both tick and moose population dynamics we need to know three properties of this host-parasite system:

1. *How variation in tick burden affects moose survival and reproduction.*

This can be determined from measurements of tick-burden, survival, and reproduction of individuals over time by regressing tick-burden onto survival and calving. These estimates can then be used to construct population projection matrices for the burden-structured model. An example of this is shown in the following section for simulated data.

2. *The expected number of larval ticks recruited per moose with a certain tick-burden.*

Previous work on tick recruitment could be used to inform estimates of larval tick recruitment. While the studies tend to be small, and have little replication or control, they will still be useful as a starting place for preliminary modeling and later on as priors for Bayesian estimation of parameters (Hobbs and Hooten 2015).

3. *How density/abundance of questing larvae impacts the acquisition and distribution of tick burdens among moose.*

This is the most challenging question to answer, but is critical for modeling tick epidemiology (Healy et al. 2020) and important for estimation of tick control thresholds (Lloyd-Smith et al. 2005). Adaptation of existing parameter estimation techniques (Ghosh, Gelfand, and Clark 2012; González, Martorell, and Bolker 2016) could be used to estimate tick attachment parameters given longitudinal data of moose population abundances and “snapshots” of tick burdens, e.g., tick counts from harvested moose (Bergeron and Pekins 2014). By combining these data with the proposed burden-structured model, tick transmission parameters could be estimated using Bayesian techniques (Hobbs and Hooten 2015) which would also allow for inclusion of prior information and other data about tick attachment (e.g., Healy et al. 2020; Ball 2017).

Parameterization

Estimating impact of tick-burden on survival and calving

I use a simulated data set to demonstrate how parameters could be estimated from individual-level observations of cow and calf moose. The data set consists of measurements of tick-burden, survival, and calving. Tick burden was simulated following a negative binomial distribution (mean = 33,000 ticks/moose, dispersion parameter (k) = 3). The parameters were chosen to qualitatively match a histogram of winter tick burdens among moose presented by Samuel (2004). Each of the moose in the simulated data set were then assigned a survival outcome and number of calves produced. Survival outcomes and number of calves were assigned from binomial and multinomial distributions, respectively. Probabilities of survival and calving were assumed to be decreasing functions of tick burden.

Parameter estimates were obtained from the simulated data by regressing survival or number of calves onto moose burden. I used logistic regression to estimate survival probabilities and multinomial regression to estimate the expected number of calves. The parameter estimates were used to parameterize projection matrices for the burden-structured model. The simulated data and model fits for the data are shown in the following figures.

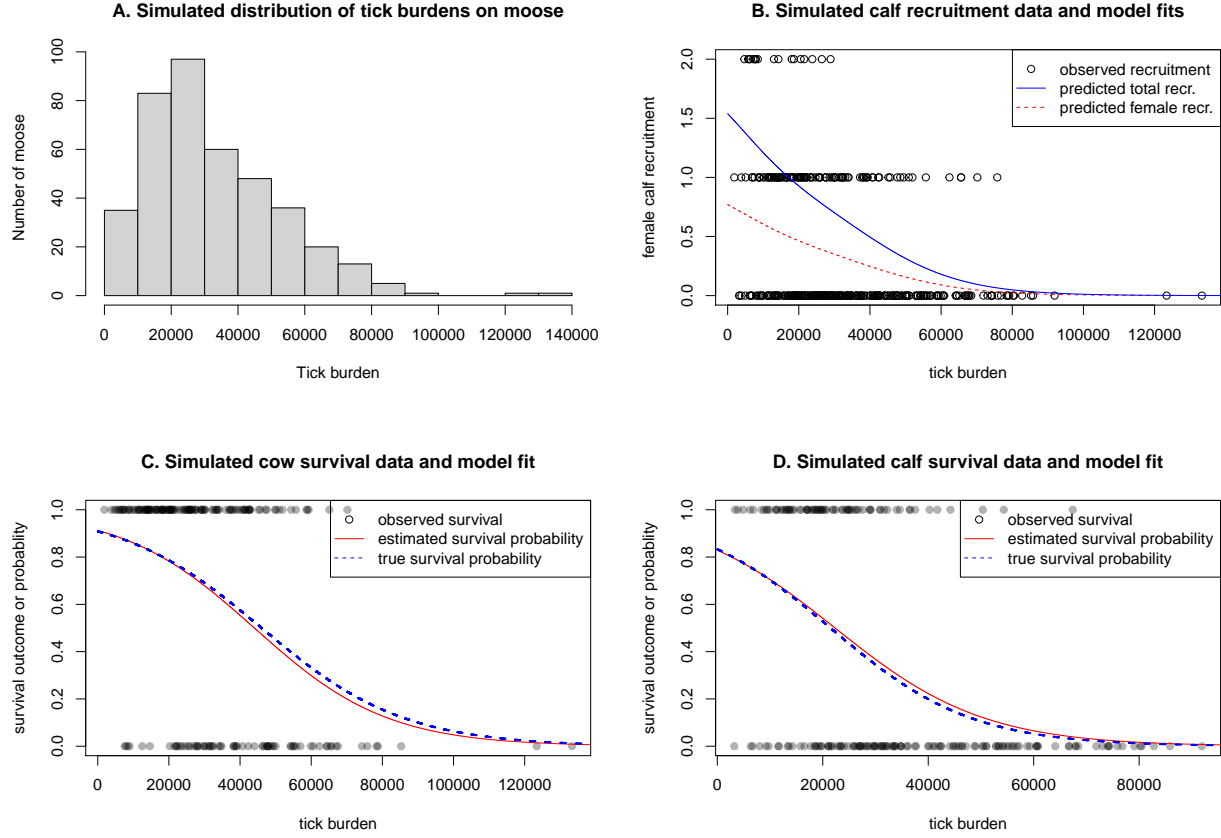


Fig. 1. Simulated vital rates and parameter estimation.

Parameters for larval tick recruitment

To determine the number of larvae that are recruited from each moose, we need to take the product of the following quantities: the proportion of ticks on a moose that are engorged females, the average number of eggs each engorged female lays, and the expected proportion of those eggs from which larvae eclose and survive until the fall questing season. For the model shown here, I assumed that 25 % of the ticks on a moose survived to become engorged females based on a point estimate reported by Samuel (2004). These surviving engorged females each lay an expected 5,000 eggs which is the upper-bound of winter tick egg-laying (Drummond et al. 1969). I arbitrarily set larval eclosion and survival at 30 % of total eggs, since the controlled studies I have read did not measure eclosion success. These rough estimates and assumptions result in 375 larvae recruited per infesting tick. Below is a plot showing how larval recruitment per moose increases with the moose's tick-burden.

Note that I'm assuming that larval recruitment is density-independent. That is, there is no difference when comparing the expected number of larvae produced from an engorged female tick from a lightly-infested moose to one from a heavily-infested moose. Previous work has shown no evidence of density-dependence for tick-burdens ranging between 20,000-40,000 (Addison and McLaughlin 1988), however, this may not be true when infestations are heavier. The assumption of density-independent larval recruitment may bias the model by making tick control harder to achieve.

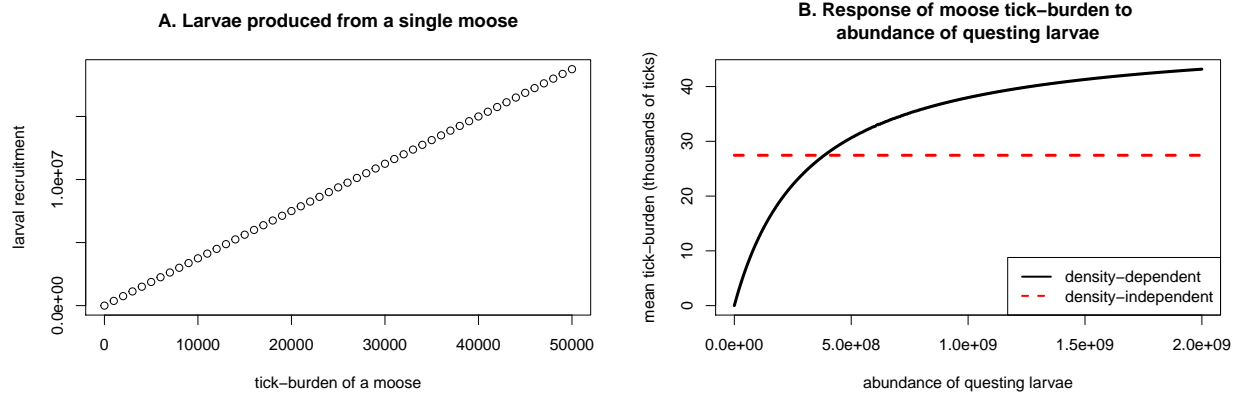


Fig. 2. Assumed functional forms of tick recruitment and tick attachment.

Parameters for tick-attachment to moose

For the tick-attachment process there are at least 3 parameters that need to be estimated. The first two are the mean and shape parameters of the negative binomial distribution which controls the distribution of ticks among moose in this model. At least one or more additional parameters is needed to describe the relationship between the abundance of questing larvae in the environment and the mean tick-burden. For the model shown here, I assume a simple functional form which only has one additional parameter. Since I have no data and I haven't found relevant findings in the literature I just chose parameter values that seemed reasonable based on model output. Ideally, the functional form and parameters would be determined from empirical data meeting the conditions outlined previously in *Data Requirements*.

Example model outputs

In this section, I present some model projections for different levels of harvesting. These projections use the model structure, assumptions, and parameterizations presented above. Of course, it wouldn't be appropriate to make any claims about how harvesting might impact an actual moose-tick system until the model is parameterized with real data. However, these theoretical results demonstrate how this model can be used to assess alternative winter tick management strategies if it were parameterized with additional empirical data.

In all simulations I initialize the system with 10^6 questing larvae and 100 moose. I then examined how different proportions of constant harvesting impacted moose populations and tick persistence. I have not yet written the code for calculating tick population growth rates (R_0) so those results and the derived moose population thresholds for tick persistence are not included in this document.

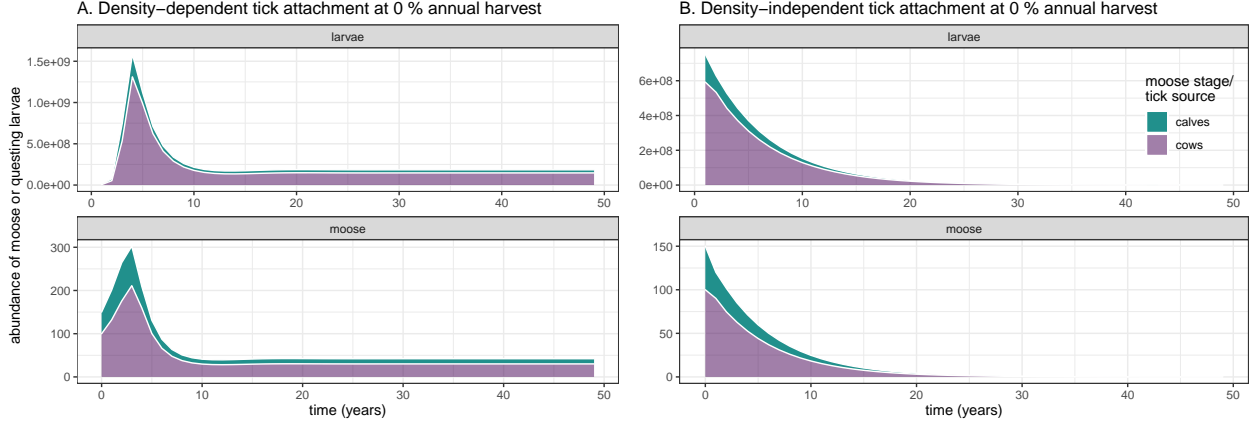


Fig. 3. Comparison of density-dependent and density-independent tick attachment.

Long term density-dependent projections result in a low moose populations which is regulated by tick parasitism. This is contrasted with density-independent projections which predict extirpation of both moose and ticks. Density-independent tick attachment was implicitly assumed in a previous model (Jones 2016). This is an issue because density-independent tick attachment cannot result in threshold for tick persistence because there is no feedback between moose population size and tick population growth (see Fig. 3-6 and 4-1 in Jones 2016). This is why the projections in Fig. 3B above and in Fig. 3-6 in Jones (2016) exhibit exponential declines to extirpation instead of a low and stable moose population (Fig. 3A). This issue could be circumvented by including moose population thresholds as a model assumption (Fig. 4-1 in Jones 2016). However, directly assuming that moose population thresholds exist precludes us from estimating the threshold and asking questions about what factors affect the value of thresholds. For this reason, the rest of the model projections in this document are for the density-dependent attachment case.

Note that the transient “spikes” in both tick and moose abundance at the start of simulations are artifacts caused by the assumption of density-independent moose population growth. This is because at the beginning of the simulation, there are too few ticks to regulate moose so they grow exponentially until tick burdens become heavy enough to regulate moose population growth. This should disappear if moose fecundity was density-dependent.

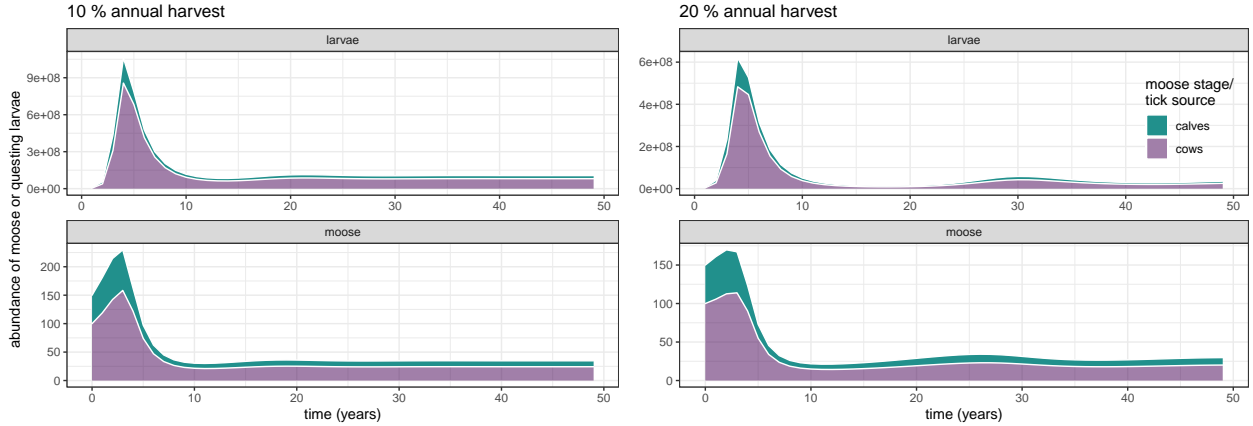


Fig. 4. Moose and questing tick population dynamics under low to moderate harvesting.

At low levels of harvest ($0 < \text{harvest} \leq 0.2$) the results are similar to the no harvest strategy. The main difference is that moose and ticks coexist at lower abundances than the unharvested case. These low levels of harvest also produced damped oscillations in moose and tick abundances which indicates that harvesting is destabilizing.

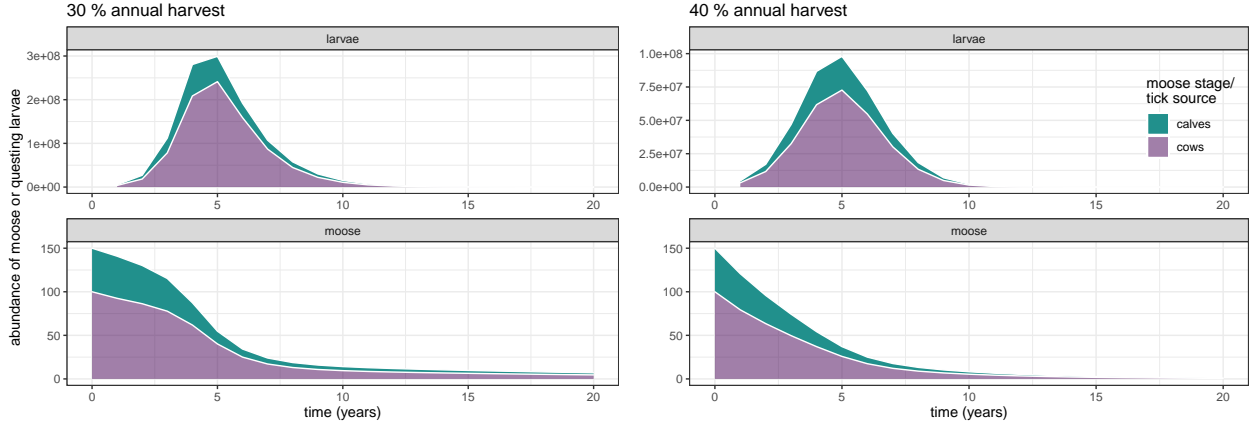


Fig. 5. Moose and questing tick population dynamics under heavy harvesting.

At higher levels of harvest ($0.3 \leq \text{harvest} \leq 1$) both moose and ticks populations decline to zero. But, notice that for intermediate harvesting intensities (0.4 and 0.5) ticks died out sooner than the moose. This indicates that harvesting can theoretically be used to control winter ticks. This result emerges from the feedback between moose population size and tick recruitment. Since constant harvesting strategies caused extirpation of both moose and ticks, it would be useful to model harvesting strategies that varied with time or were dependent on moose population size.

Using time- or state-dependent harvesting was proposed by Samuel (2004) to control tick outbreaks by dynamically regulating moose populations below levels which allow for tick outbreaks. However, the success of this approach depends on knowing the critical thresholds where tick outbreaks can occur so that moose populations can be managed below it. By parameterizing the burden-structured models I developed here with empirical data, we estimate the critical moose population thresholds for winter tick outbreaks from calculation of R_0 in a way similar to how herd-immunity thresholds are estimated for vaccine-preventable human diseases.

Overall, this approach will allow us to simultaneously account for the impact of tick-burdens on moose vital rates and the joint impact of moose population size and tick-burden distribution on tick recruitment. We find theoretical evidence that moose population thresholds for tick persistence exist and that harvesting may be a feasible strategy for controlling winter ticks epizootics. The flexibility of structured population models also will allow us (given adequate data) to included factors like moose population density and weather variables on moose and tick parameters. Furthermore, the output and structure of burden-structured models should be straight-forward to interpret for moose biologists and managers since burden-structured models share the ideas underlying the matrix population models commonly used in moose population assessment.

Appendix

$$n_{t+1} = PRSHA(q_t)n_t \quad (1)$$

$$q_{t+1} = Ln_t \quad (2)$$

Where:

$$\bullet \quad n_t = \begin{bmatrix} n_{c1} \\ n_{c2} \\ \vdots \\ n_{cb} \\ n_{a1} \\ n_{a2} \\ \vdots \\ n_{ab} \end{bmatrix} \text{ is a population vector where each element is the number of calves } (n_{ci}) \text{ or cow moose } (n_{ai})$$

in the $i = 1, \dots, b$ burden

- q_t is the number of total winter tick larvae questing for moose each fall. L is a diagonal matrix which contains the expected number of questing larvae recruited from each moose in each burden class. The determination of these values is as described in the main text.
- $A(q_t) = \text{diag}[p_{c1} \ p_{c2} \ \cdots \ p_{cb} \ p_{a1} \ p_{a2} \ \cdots \ p_{ab}]$ where p_{ci} and p_{ai} is the expected proportion of calves and cows that would acquire a number of ticks within the i^{th} burden class given that the burden distribution follows a negative binomial distribution where the mean of the negative binomial is an increasing and saturating function of q_t . In this document, it is assumed that $p_{ci} = p_{ai}$ for all $i = 1, \dots, b$.
- $H = (1-h)I_{2b \times 2b}$ is a matrix that reduces the population by the annual proportion of moose harvested h .
- $S = \text{diag}[s_{c1} \ s_{c2} \ \cdots \ s_{cb} \ s_{a1} \ s_{a2} \ \cdots \ s_{ab}]$ is the survival matrix which contains the probability of survival for calves and cows in each burden class. The probabilities are calculated from a logistic regression model of survival probability as a function of moose stage and burden level. Here, these data were simulated.
- $R = \begin{bmatrix} 0_{b \times b} & G_{b \times b} \\ I_{b \times b} & 0_{b \times b} \end{bmatrix}$ describes the number of calves born to cows in each burden class where G is a matrix that has a first row that contains the expected number of calves for cows in each burden class and 0 elsewhere. Here, the expected number of calves is predicted from a multinomial regression model fit to simulated data.
- $P = \begin{bmatrix} J_{b \times b} & 0_{b \times b} \\ 0_{b \times b} & J_{b \times b} \end{bmatrix}$ where J is a matrix that has 1s in the first row and zeros elsewhere. This matrix pools all moose back into the appropriate zero burden class since all ticks detach in the spring.

References

- Addison, Edward M., and Robert F. McLaughlin. 1988. "Growth and Development of Winter Tick, *Dermacentor Albipictus*, on Moose, *Alces Alces*." *The Journal of Parasitology* 74 (4): 670–78. doi:10.2307/3282188.
- Allen, Linda J. S., and P. van den Driessche. 2008. "The Basic Reproduction Number in Some Discrete-Time Epidemic Models." *Journal of Difference Equations and Applications* 14 (10-11): 1127–47. doi:10.1080/10236190802332308.
- Ball, Kyle. 2017. "Moose Density, Habitat, and Winter Tick Epizootics in a Changing Climate." Master's thesis, University of New Hampshire. <https://scholars.unh.edu/thesis/1104>.
- Bergeron, Daniel H., and Peter J. Pekins. 2014. "EVALUATING THE USEFULNESS OF THREE INDICES FOR ASSESSING WINTER TICK ABUNDANCE IN NORTHERN NEW HAMPSHIRE." *Alces: A Journal Devoted to the Biology and Management of Moose* 50 (0): 1–15. <http://alcesjournal.org/index.php/alces/article/view/114>.
- Campbell, Tyler, Scott Henke, and Alan Fedynich. 2007. "Wildlife Disease Management: An Insurmountable Challenge?" In *Wildlife Science*, edited by David Hewitt and Timothy Fulbright, 279–94. CRC Press. doi:10.1201/9781420007619.ch16.
- Drummond, R. O., T. M. Whetstone, S. E. Ernst, and W. J. Gladney. 1969. "Biology and Colonization of the Winter Tick in the Laboratory." *Journal of Economic Entomology* 62 (1): 235–38. doi:10.1093/jee/62.1.235.
- Fine, Paul, Ken Eames, and David L. Heymann. 2011. "'Herd Immunity': A Rough Guide." *Clinical Infectious Diseases* 52 (7): 911–16. doi:10.1093/cid/cir007.
- Ghosh, Souparno, Alan E. Gelfand, and James S. Clark. 2012. "Inference for Size Demography from Point Pattern Data Using Integral Projection Models." *Journal of Agricultural, Biological, and Environmental Statistics* 17 (4): 641–77. doi:10.1007/s13253-012-0123-9.
- González, Edgar J., Carlos Martorell, and Benjamin M. Bolker. 2016. "Inverse Estimation of Integral Projection Model Parameters Using Time Series of Population-Level Data." *Methods in Ecology and Evolution* 7 (2): 147–56. doi:10.1111/2041-210X.12519.
- Healy, Christine, Peter J. Pekins, Shady Atallah, and Russell G. Congalton. 2020. "Using Agent-Based Models to Inform the Dynamics of Winter Tick Parasitism of Moose." *Ecological Complexity* 41 (January): 100813. doi:10.1016/j.ecocom.2020.100813.
- Hobbs, N.T., and M.B. Hooten. 2015. *Bayesian Models: A Statistical Primer for Ecologists*. Princeton University Press. <https://books.google.com/books?id=mmmYDwAAQBAJ>.
- Jones. 2016. "Assessment of Health, Mortality, and Population Dynamics of Moose in Northern New Hampshire During Successive Years of Winter Tick Epizootics." Master's thesis, University of New Hampshire.
- Jones, P. Pekins, L. Kantar, I. Sidor, D. Ellingwood, A. Lichtenwalner, and M. O'Neal. 2018. "Mortality Assessment of Moose (*Alces Alces*) Calves During Successive Years of Winter Tick (*Dermacentor Albipictus*) Epizootics in New Hampshire and Maine (USA)." *Canadian Journal of Zoology* 97 (1): 22–30. doi:10.1139/cjz-2018-0140.
- Jones, Peter J. Pekins, Lee E. Kantar, Matt O'Neil, and Daniel Ellingwood. 2017. "FECUNDITY AND SUMMER CALF SURVIVAL OF MOOSE DURING 3 SUCCESSIVE YEARS OF WINTER TICK EPIZOOTICS." *Alces: A Journal Devoted to the Biology and Management of Moose* 53 (0): 85–98. <http://alcesjournal.org/index.php/alces/article/view/224>.
- Klepac, Petra, and Hal Caswell. 2011. "The Stage-Structured Epidemic: Linking Disease and Demography with a Multi-State Matrix Approach Model." *Theoretical Ecology* 4 (3): 301–19. doi:10.1007/s12080-010-0079-8.
- Lloyd-Smith, James O., Paul C. Cross, Cheryl J. Briggs, Matt Daugherty, Wayne M. Getz, John Latto, Maria S. Sanchez, Adam B. Smith, and Andrea Swei. 2005. "Should We Expect Population Thresholds for

- Wildlife Disease?” *Trends in Ecology & Evolution* 20 (9): 511–19. doi:10.1016/j.tree.2005.07.004.
- McCallum, Hamish. 2016. “Models for Managing Wildlife Disease.” *Parasitology* 143 (7): 805–20. doi:10.1017/S0031182015000980.
- Musante, Anthony R., Peter J. Pekins, and David L. Scarpitti. 2010. “Characteristics and Dynamics of a Regional Moose Alces Alces Population in the Northeastern United States.” *Wildlife Biology* 16 (2): 185–204. doi:10.2981/09-014.
- Samuel. 2004. *White as a Ghost: Winter Ticks & Moose*. Natural History Series. Federation of Alberta Naturalists. <https://books.google.com/books?id=h1T2zh3K-sMC>.
- . 2007. “FACTORS AFFECTING EPIZOOTICS OF WINTER TICKS AND MORTALITY OF MOOSE.” *Alces: A Journal Devoted to the Biology and Management of Moose* 43: 11.
- Shaw, D. J., and A. P. Dobson. 1995. “Patterns of Macroparasite Abundance and Aggregation in Wildlife Populations: A Quantitative Review.” *Parasitology* 111 (S1): S111–S133. doi:10.1017/S0031182000075855.