

When is a parasite not a parasite? Effects of larval tick burdens on white-footed mouse survival

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Abstract. Many animal species can carry considerable burdens of ectoparasites or parasites living on the outside of a host's body. Ectoparasite infestation can decrease host survival, but the magnitude and even direction of survival effects can vary depending on the type of ectoparasite and the nature and duration of the association. When ectoparasites also serve as vectors of pathogens, the effects of ectoparasite infestation on host survival have the potential to alter disease dynamics by regulating host populations and stabilizing transmission. We quantified the impact of larval *Ixodes scapularis* tick burdens on both within-season and overwinter survival of white-footed mice (*Peromyscus leucopus*) using a hierarchical Bayesian capture-mark-recapture model. *I. scapularis* and *P. leucopus* are, respectively, vectors and competent reservoirs for the causative agents of Lyme disease, anaplasmosis, and babesiosis. Using a data set of 5587 individual mouse capture histories over sixteen years, we found little evidence for any effect of tick burdens on either within-season or overwinter mouse survival probabilities. In male mice, tick burdens were positively correlated with within-season survival probabilities. Mean maximum tick burdens were also positively correlated with population rates of change during the concurrent breeding season. The apparent indifference of mice to high tick burdens may contribute to their effectiveness as reservoir hosts for several human zoonotic pathogens.

Key words: Bayesian analysis; capture-mark-recapture model; ectoparasites; *Ixodes scapularis*; *Peromyscus leucopus*; state-space model; survival.

INTRODUCTION

Parasites, by definition, negatively impact hosts. The consequences of these negative impacts on host–parasite dynamics depend to a great extent on whether the cost to an individual host increases as the burden of parasites on that host increases. Macroparasites can regulate host populations in a density-dependent manner if hosts incur greater fitness costs as parasite burdens increase (Anderson and May 1978). This could lead to a negative feedback between host populations and parasite populations, particularly if overall parasite abundance increases with overall host abundance. In contrast, if the fitness effects of the parasite on the host are not correlated with parasite density, negative feedbacks would be less likely, and therefore, there would be less stability in the parasite–host relationship.

The effects of parasites on host fitness manifest themselves through their impacts on host health. We focused on ectoparasites, a taxonomically diverse group

of parasites that live exclusively on the outside of a host's body and that associate with their hosts for varying lengths of time. Some ectoparasites have been shown to affect host body condition and physiology (Hawlena et al. 2006b, Lourenco and Palmeirim 2007, Heylen and Matthysen 2008), reproduction (Moller 1993, Neuhaus 2003, Fitze et al. 2004a, b, Hillegass et al. 2010), and aspects of host behavior including grooming (Hillegass et al. 2010), dispersal (Brown and Brown 1992), and foraging (Raveh et al. 2011). Such impacts of ectoparasite infestation, both individually and in combination, could, in theory, influence host survival and population dynamics depending on the taxonomic identities of the host and parasite, along with the duration of the infestation.

Effects of ectoparasitism on animal survival are variable. In some cases, ectoparasites decrease survival at the scale of the whole population (Brown et al. 1995, Brown and Brown 2004, Krkosek et al. 2007, Devevey and Christe 2009), but effects are not uniform across individuals within a population. In several animal populations, including cliff swallows (Brown and Brown 2004), roseate terns (Monticelli et al. 2008), and gerbils (Hawlena et al. 2006a), negative effects on survival were more pronounced in juveniles than adults. Negative impacts of ectoparasites on nestling growth and survival

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have been observed in multiple bird species (Clayton and Tompkins 1995, Merino and Potti 1995, Ramos et al. 2001, Antoniazzi et al. 2011). Although an experimental study of tick infestation in birds found greater blood depletion in males than females (Heylen and Matthysen 2008), other avian studies have found no differences in parasite effects on survival between the sexes (Brown and Brown 2004). Environmental factors, such as water temperature with fish, can also alter the severity of any negative ectoparasite effects (Cardon et al. 2011) or the intensity of infection (Antoniazzi et al. 2011). Yet in some cases, organisms classified as ectoparasites have had no detectable influence (Lee and Clayton 1995, Gauthier-Clerc et al. 2003) or even a positive relationship with survival (Brown et al. 2006). This variation in the impact of ectoparasites on survival indicates that ectoparasites may not always have negative effects on all individuals in a population.

In addition, ectoparasite burdens can vary considerably between individuals, with high levels of aggregation at the individual level (Anderson and May 1978, Brunner and Ostfeld 2008, Devevey and Brisson 2012). This variation in ectoparasite loads could be the basis for differential effects on survival between individuals. Some patterns in variation among individuals can be due to individual characteristics or traits. For example, higher ectoparasite burdens in males are frequently documented (Perez-Orella and Schulte-Hostedde 2005, Gorrell and Schulte-Hostedde 2008, Devevey and Brisson 2012), but multiple exceptions to this general trend exist (Krasnov et al. 2005, Christe et al. 2007, Kiffner et al. 2011) or may be attributable to body size differences between the sexes (Harrison et al. 2010). Ectoparasite loads can vary with age (Cardon et al. 2011) or space use (Boyer et al. 2010, but see also Devevey and Brisson 2012). Individual differences in ectoparasite burdens may also be a function of chance alone, such as having a home range in a particularly ectoparasite-rich locality (Calabrese et al. 2011). Regardless of the mechanism driving variation in ectoparasite burdens, individual differences in loads could form the basis of differential effects on survival.

We examined the impacts of larval *Ixodes scapularis* (blacklegged) ticks on the survival of white-footed mice (*Peromyscus leucopus*). We focused on the effects of blacklegged tick parasitism on white-footed mouse survival because of the importance of this vector and host. Blacklegged ticks are generalist ectoparasites that serve as the vector of multiple disease agents in eastern and central North America, including the causal agents of Lyme disease (*Borrelia burgdorferi*), human granulocytic anaplasmosis (*Anaplasma phagocytophilum*), and human babesiosis (*Babesia microti*; LoGiudice et al. 2003, Hersh et al. 2012, Keesing et al. 2012). White-footed mice are one of the most competent reservoir hosts for all three of these pathogens (LoGiudice et al. 2003, Hersh et al. 2012, Keesing et al. 2012), and the abundance of *B. burgdorferi*-infected ticks is correlated

with abundance of mice (Ostfeld et al. 2006). These mice can carry large larval tick burdens (as many as 270 ticks/mouse in this study) and appear to be relatively tolerant of tick parasitism, allowing approximately half of the larval ticks they encounter to feed successfully (Keesing et al. 2009). Larval ticks are not infected with *B. burgdorferi*, *A. phagocytophilum*, or *B. microti*, as vertical transmission of these pathogens is nonexistent or rare (Civitello et al. 2010), so any negative effects of larval ticks on mice would likely be due to tick feeding alone rather than pathogen transmission. When an ectoparasite also acts as a vector and the host as a reservoir for a pathogen, ectoparasite-induced changes in host demography could translate into altered disease dynamics.

If blacklegged ticks have a strong negative impact on white-footed mouse health, then we expect to see a reduction in mouse survival probabilities as tick burdens increase. Such reduced survival should lead to negative correlations between mean tick burden and population rate of change. On the other hand, if ticks have little to no negative impact on host health, survival probabilities would be independent of variation in tick burden, heavily parasitized individuals would survive as long as unparasitized ones, and population rate of change should not decline with increasing tick burden. This has the potential to increase disease risk by increasing opportunities for ticks to feed on the hosts most permissive of feeding (Keesing et al. 2009), potentially resulting in higher overall tick densities.

To determine the effects of larval tick burden on survival of white-footed mice, we employed sixteen years of capture–mark–recapture data and tick counts at each capture of over 5500 individual mice. We investigated tick effects on both within-season and overwinter survival and considered potential sex differences given that male white-footed mice are known to have larger larval tick burdens than females (Brunner and Ostfeld 2008, Devevey and Brisson 2012). To determine if the effects of tick burdens were altered by stressors on resource availability, we ran the model on subsets of data representing variation in the effects of acorn production by the regionally dominant oaks (genus *Quercus*), given that overwinter survival and summer abundance of mice are correlated with acorn abundance the prior fall (Ostfeld et al. 1996, 2006, Jones et al. 1998), and mouse population density, as rodent survival rates are sometimes inversely correlated with population density (e.g., Turchin 2003). We predicted that if negative effects of larval burdens on survival did occur, they would be more pronounced during stressful periods of limited resource availability (e.g., due to low acorn availability or high mouse population density). We estimated survival probabilities using a state-space model implemented in a hierarchical Bayesian framework (Clark et al. 2005, Gimenez et al. 2007, Royle 2008), so that we could evaluate the effects of tick burden on survival, while accounting for both individual

and annual variation in mouse survival and allowing for observation error. We also examined the relationship between average tick burdens and population rates of change during the breeding season. Ultimately, our goal was to expand our understanding of the role of mice in the dynamics of tick-borne diseases via the effects of tick vectors on mouse survival.

MATERIALS AND METHODS

Field methods

Field data were collected from a long-term capture–mark–recapture study conducted from 1995 to 2011 on six 2.25-ha trapping plots in Millbrook, New York, USA (Ostfeld et al. 2006, Brunner and Ostfeld 2008). On each plot, an 11 × 11 point grid of Sherman live traps (H. B. Sherman Traps, Tallahassee, Florida, USA) was established, with 15 m between trap stations and two traps per station, for a total of 242 traps per grid. Trapping was conducted for two consecutive nights every three to four weeks, generally from May to November of each year. Traps were baited with crimped oats (sunflower seeds and cotton batting were added during cold weather), set at 16:00 and checked between 08:00 and about 12:00 the following morning. Small mammals were marked with individually numbered metal ear tags and released after handling at the point of capture. Data on age, sex, reproductive status, body mass, and trap station were recorded on each capture. Ectoparasite burden data was recorded on the first capture in each trapping session and consisted of carefully inspecting the head (including ear pinnae) and neck of each mouse while counting all attached ticks of each life stage. A strong relationship has been observed between these field counts and whole-body burdens and was determined by holding mice in wire-mesh cages over collecting pans for >3 d (the duration of larval feeding; $R^2 = 0.79$ [Brunner and Ostfeld 2008]). Protocols for animal handling were approved annually by an Institutional Animal Care and Use Committee. In six years (1995, 1997, 1998, 2008, 2009, and 2010), only data from three of six grids could be used given experimental manipulations on the other three grids, including acorn supplementation and mouse or chipmunk removal (Ostfeld 2011), that could affect estimates of survival. Summarized trapping data are included in Appendix A. Annual acorn production was measured using seed baskets as described in Ostfeld et al. (2006). White-footed mouse population density was estimated as the minimum number alive (MNA) or using a Jolly-Seber open population model (J-S) as described in Ostfeld et al. (2006).

Statistical modeling

White-footed mouse survival was estimated using a state-space formulation (Clark et al. 2005, Gimenez et al. 2007, Royle 2008) of the Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965), which estimates animal survival in an open population from capture–

mark–recapture data. This model was implemented in a hierarchical Bayesian framework and has two main components: a process model that describes the unobserved or partially observed process of interest, and an observation model that describes our ability to measure or sample this process. The data are a series of observations ($Y_1 \dots Y_T$) of whether or not animal i is captured (1, captured; 0, not captured) from times 1 through T . These observations are dependent on the actual state of the animal (1, alive; 0, dead) at each time step ($X_1 \dots X_T$), which we cannot directly observe for all individuals

$$Y_{i,t} | X_{i,t} \sim \text{Bernoulli}(X_{i,t}p) \quad (1)$$

$$X_{i,t+1} | X_{i,t} \sim \text{Bernoulli}(X_{i,t}\Phi_{i,t}). \quad (2)$$

Thus, we modeled both the observation (Eq. 1) and the process (Eq. 2) of survival, estimating the probability of observing an individual mouse (capture probability, p) in Eq. 1 and the probability that a given individual survives (survival probability, Φ) in Eq. 2.

Survival probability was modeled as a logistic generalized linear mixed model with a logit link

$$\text{logit } \Phi_{i,t} = \mu_t + \beta_t x_i + \alpha_{y(t)} + \gamma_i. \quad (3)$$

The process model includes parameter estimate values for the intercept (μ_t), the effect of tick burden (β_t), where x_i is the normalized maximum larval tick burden, and random effect estimates for each year ($\alpha_{y(t)}$) and individual (γ_i), modeled as a random effect with mean zero and variance σ_a^2 (α , year) and σ_g^2 (γ , individual), respectively. The individual random effects account for the nonindependent temporal structure of repeated measures for an individual. Subscript t indicates time steps (intervals between trapping sessions), while subscript $y(t)$ indicates trap sessions in each sampling year.

For each individual mouse, capture histories included five trapping sessions (encompassing four intervals). For this model, the first trapping session included for each individual (t_1) was by definition that which took place during the onset of larval peak determined for each year. Based on data from regular sampling conducted between 1992 and 1995 of immature (larval and nymphal) ticks seeking a host and attached to hosts, we observed that host-seeking and host-feeding activity of larvae were low until mid July, reached a peak between late July and late August, and declined to low levels by late September (see Brunner and Ostfeld 2008). Consequently, we defined larval peak as the two trapping sessions with highest mean tick burdens (late July–mid August), which typically began in week 31 or 32 of a calendar year. The first trapping session was followed by three additional sessions that year, approximately three weeks apart (t_{2-4}). The fifth trapping session (t_5) designates whether or not an individual was captured during the first trapping session of the following calendar year (interval occurring over the

winter). Of individuals that were captured in two consecutive years, 82.5% were captured during the first trapping session of the second calendar year (typically in April or May). Although trapping occurred prior to t_1 in all years, we only used samples during and after the larval peak in estimating survival to reduce the effects of mouse phenotype (e.g., home range size, behavior) during the pre-peak period on estimates of survival and capture probability.

We interpret the first three intervals as within-season survival or Φ_w and the final interval as overwinter survival or Φ_o . Eq. 3 was fit to both within-season and overwinter survival data, such that parameters for within-season (first three intervals, μ_w , α_w , and β_w) and overwinter (fourth interval, μ_o , α_o , and β_o) effects were estimated separately. Tick burdens (x_i) were defined as the maximum number of ticks counted from individual i on any single occasion during larval peak (either trapping sessions t_1 or t_2). Only individuals captured during larval peak were included in the model. If an individual was captured during larval peak in two consecutive years (0.03% of all individuals), only the first capture history was included in the model to maintain independence of individuals.

Capture probability, p , was assumed to be uniform across all time steps given the high capture probabilities of white-footed mice in this system (Ostfeld et al. 1997, Jones et al. 1998, Schmidt et al. 2001). We confirmed the validity of this simplifying assumption by directly estimating capture probability from a subset of individuals who survived one winter for the nine years in which more than 10 individuals survived the winter ($n = 305$ mice). Using strings of three consecutive trapping occasions, we identified individuals captured in the first and third trapping sessions and estimated capture probability based on the percentage of those individuals also captured in the middle session. The resulting mean capture probabilities were as follows (mean \pm SD): within-season trapping sessions t_2 , $p = 0.869 \pm 0.120$; t_3 , $p = 0.915 \pm 0.066$; and t_4 , $p = 0.755 \pm 0.115$; and overwinter trapping session t_5 , $p = 0.916 \pm 0.078$. Moreover, a review of variation on capture probabilities by Hammond and Anthony (2006) did not find support for temporal variability in white-footed mouse capture probabilities.

The model was implemented using the program WinBUGS version 1.4.3 via the R package R2WinBUGS (Sturtz et al. 2005) in the programming language R (R Core Development Team 2012). We used Uniform(0,1) prior distributions for logistic parameters μ_w , μ_o , and p , Normal(0,1000) prior distributions for β_w and β_o , and Uniform(0,5) distributions for precision parameters $\sigma_{a,w}^2$, $\sigma_{a,o}^2$, and σ_g^2 following Kery and Schaub (2012). Prior distributions for parameters were vague or diffuse in all cases. The model was run for 500 000 Gibbs steps, with the first 250 000 discarded as burn-in. Convergence was assessed using the Brooks-Gelman-Rubin criterion, Rhat (Brooks and Gelman

1998). If a model did not converge within 500 000 Gibbs steps (Rhat for any parameter ≥ 1.1), it was run for 1 000 000 Gibbs steps, with the first 500 000 discarded as burn-in. Only models for female mice, mice trapped in the three lowest acorn production years, and mice trapped in the three years following the three lowest acorn production years did not converge within 500 000 Gibbs steps.

We used a simulated data set with 4800 individuals over 16 years to confirm the ability of the model to identify the coefficients of the tick effect β_w and β_o . Posterior estimates for all other parameters from the model run for the full data set were used to generate simulated parameter values, excluding β_w and β_o . We then set β_w and β_o at all possible combinations of 0, 0.2, and -0.2 for nine total runs. In each iteration of the simulation, the model was run for 250 000 Gibbs steps, discarding the first 125 000 steps as burn-in. Prior distributions were vague or diffuse in all cases. In all nine runs, the 95% credible intervals of the posterior estimates captured the set values of β_w and β_o , indicating that the model is capable of accurately estimating these coefficients.

The model was run for all unique individuals ($n = 5587$ capture histories) over 16 years, and separately for all females ($n = 2573$) and all males ($n = 3014$). We also ran selected sets of three years as separate runs to estimate β_w and β_o under particular circumstances in which survival may have been affected by other factors. We performed these analyses to determine if the effects of tick burden on survival were affected by both extrinsic and intrinsic stressors related to resource availability. These included the three years in the data set with the highest acorn density (1998, 2006, and 2010; $n = 927$), the three years with the lowest acorn density (1999, 2004, and 2007; $n = 2197$), the three years following both high- (1995, 1999, and 2007; $n = 2015$) and low-acorn years (2000, 2005, and 2008; $n = 297$), the three years with the highest population density as measured using interpolated Jolly-Seber open population model estimates for 15 August (1995, 1999, and 2007; $n = 2015$; same as the three years following the highest acorn years), and the three years with the lowest population density (1996, 2000, and 2005; $n = 293$).

Finally, we quantified relationships among several population-level variables using regression-based methods. We examined the relationship between posterior survival estimates ($\Phi_{y,t}$) and interannual variation in acorn mast and population density using linear regression. In addition, we calculated population rate of change (λ) between the first trapping session of larval peak (t_1) and the last trapping session of the calendar year (t_4) using the population growth equation $N_t = N_0 \lambda^t$, where N_0 is the initial population size, N_t is the population size at the end of the sampling period, t is the number of time steps, and λ is the population rate of change. Population size at each sampling grid in this case was calculated using minimum number alive

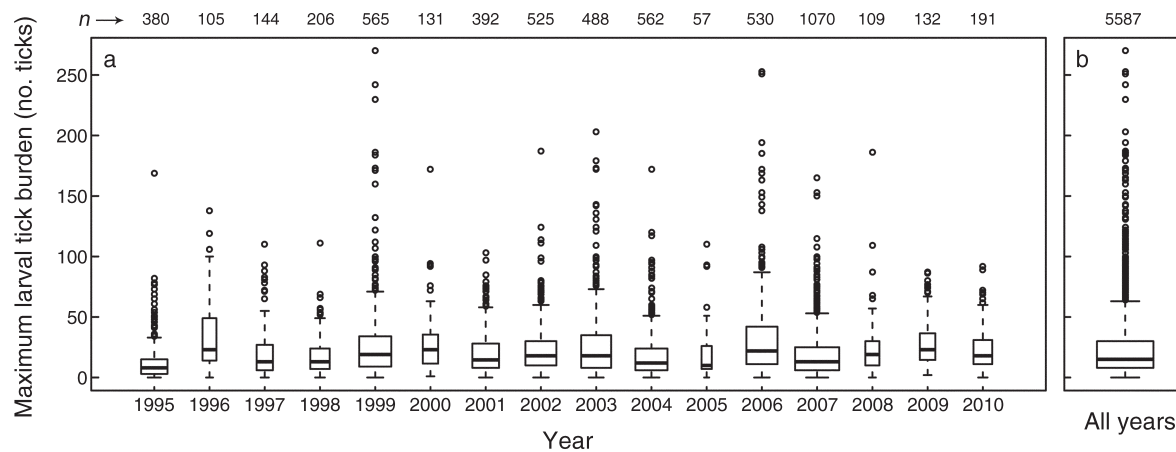


FIG. 1. Distribution of *Ixodes scapularis* larval tick burdens on white-footed mice (*Peromyscus leucopus*) (a) from 1995–2010 and (b) over the entire 16-year period. Horizontal lines are median tick burdens, and upper and lower edges of boxes are 25% and 75% quartiles, respectively. Boxes are scaled by mouse sample size, n . The upper whisker extends to the upper (75%) quartile plus 1.5 times the interquartile distance (the difference between the 75% and 25% quartiles). The lower vertical line extends to the lower (25%) quartile minus 1.5 times the interquartile distance. The circles represent outliers that are outside of the range of the whiskers.

(MNA), as referenced in the field methods. We then compared λ to mean maximum tick burdens and to the index of dispersion of maximum tick burdens (variance/mean ratio) accounting for grid identity, using analysis of covariance (ANCOVA). The negative correlation between mean maximum tick burdens and initial population size (ANCOVA; $F_{1,66} = 6.181$, $P = 0.0155$) prevented us from including initial population size in this analysis to avoid multicollinearity.

RESULTS

We incorporated 5587 white-footed mouse capture histories over 16 years into this analysis. The number of individual mice captured during larval peak varied annually, ranging from 57 in 2005 to 1070 in 2007 (Fig. 1). Maximum larval tick burdens (MLTB) during larval peak ranged from 0 to 270 ticks per mouse (Fig. 1, Appendix A). The overall MLTB was 22.7 ± 23.5 ticks/mouse (mean \pm SD) and ranged from 12.4 (1995) to 32.6 (1996). In general, distributions of tick burdens

were left skewed with a long tail (Appendix A) and the shapes of distributions varied among years (Fig. A2).

We found little evidence for an impact of larval tick burdens on white-footed mouse survival. In model runs including all individual mouse capture histories, the mean posterior estimates of β_w and β_o , the coefficient for tick effects on within-season and overwinter survival, respectively, were close to zero (Table 1) and credible intervals for posterior estimates of these parameters included zero (Table 1, Fig. 2). Similarly, there was not a significant tick effect for female within-season survival, female overwinter survival, or male overwinter survival (Table 2, Fig. 2). The mean posterior estimate of β_w was positive for male within-season survival, and the credible interval for β_w in males did not contain zero (Table 2, Fig. 2), suggesting a positive association between tick burden and within-season survival in male mice.

We did not find evidence for tick effects on survival when running subsets of the data incorporating particularly high and low values in acorn production and mouse population density (Fig. 3). Credible intervals for

TABLE 1. Estimates and credible intervals (CI) for the eight state-space model parameters for all individual white-footed mice (*Peromyscus leucopus*; $n = 5587$ mice) over 16 years.

Parameter	Mean	SD	2.5% CI	97.5% CI
μ_w	0.673	0.026	0.618	0.722
μ_o	0.100	0.043	0.039	0.205
$\sigma_{a,w}^2$	0.209	0.103	0.084	0.465
$\sigma_{a,o}^2$	3.053	1.714	1.123	7.413
β_w	0.009	0.027	-0.042	0.062
β_o	-0.030	0.086	-0.201	0.134
σ_g^2	0.558	0.146	0.280	0.859
p	0.860	0.005	0.850	0.870

Notes: Parameters are μ_w , intercept for within-season survival probability; μ_o , intercept for overwinter survival probability; $\sigma_{a,w}^2$, random year effects, within-season; $\sigma_{a,o}^2$, random year effects, overwinter; β_w , tick effect, within-season; β_o , tick effect, overwinter; σ_g^2 , individual random effects; p = capture probability. Parameters $\sigma_{a,w}^2$, $\sigma_{a,o}^2$, β_w , β_o , and σ_g^2 are on a logit scale.

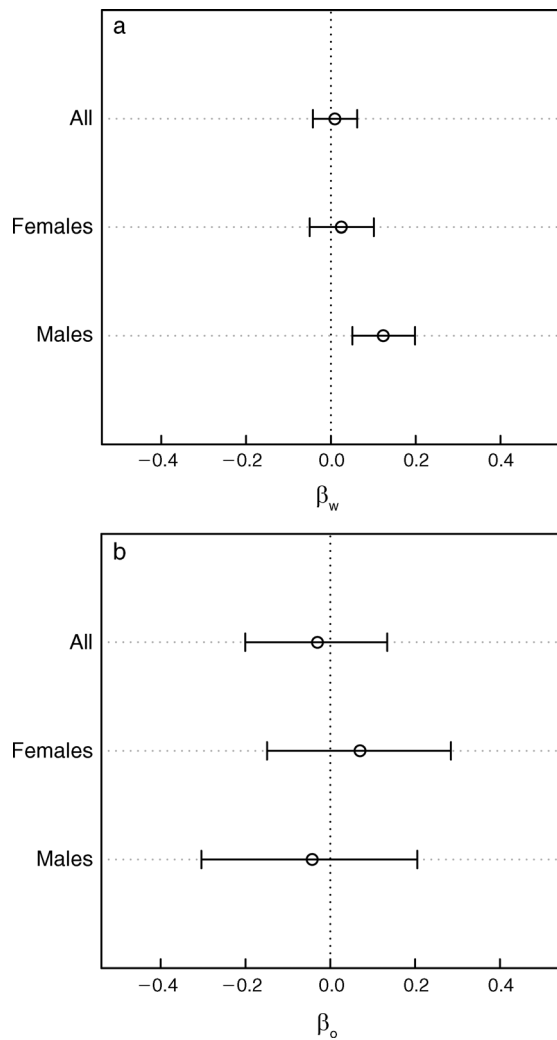


FIG. 2. Posterior estimates of (a) β_w and (b) β_o , regression coefficients for the effect of larval tick burdens on within-season and overwinter survival, respectively, of white-footed mice. Both parameters were estimated separately for all individuals, for females, and for males. Error bars are 95% credible intervals.

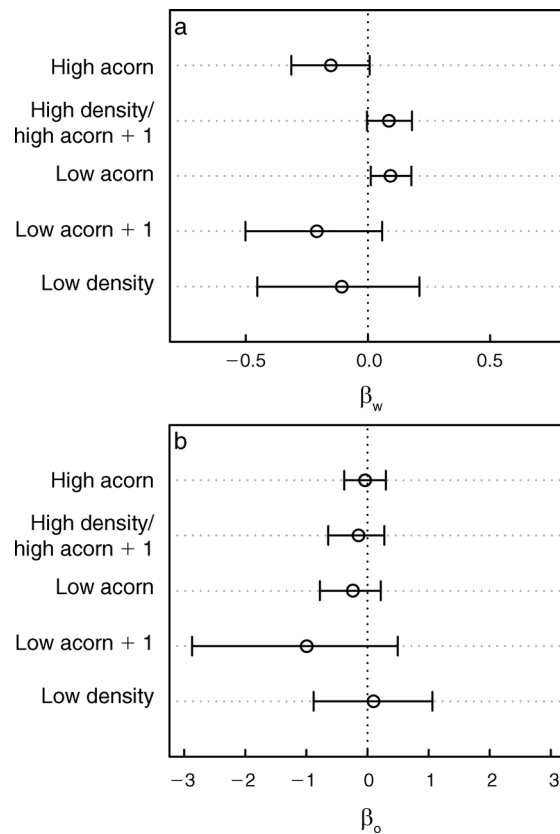


FIG. 3. Posterior estimates of (a) β_w and (b) β_o , regression coefficients for the effect of larval *Ixodes scapularis* tick burdens on within-season and overwinter survival probability, respectively, of white-footed mice. Parameters were estimated for the three highest acorn years (high acorn), the years immediately following the three highest acorn years (high acorn +1), the three highest density years (high density), and the lowest of all three scenarios. The three highest density years were also the three years following the three highest acorn years in this study. See Appendix B for all parameter estimates. Error bars are 95% credible intervals.

β_o contained zero in the three years with the highest and lowest acorn densities, and credible intervals for β_w contained zero in the three years following both the highest and lowest acorn densities (Fig. 3, Appendix B).

TABLE 2. Estimates and credible intervals for the eight model parameters for all male ($n = 3014$ mice) and female ($n = 2573$ mice) white-footed mice over 16 years.

Parameter	Females				Males			
	Mean	SD	2.5% CI	97.5%	Mean	SD	2.5% CI	97.5% CI
μ_w	0.734	0.026	0.678	0.783	0.627	0.026	0.574	0.674
μ_o	0.144	0.066	0.050	0.305	0.075	0.037	0.025	0.165
$\sigma_{a,w}^2$	0.249	0.128	0.097	0.571	0.157	0.089	0.051	0.388
$\sigma_{a,o}^2$	3.843	2.563	1.110	10.660	3.470	2.214	1.085	9.320
β_w	0.024	0.039	-0.050	0.101	0.124	0.038	0.051	0.198
β_o	0.070	0.111	-0.149	0.284	-0.043	0.130	-0.304	0.205
σ_g^2	0.199	0.175	0.004	0.629	0.696	0.194	0.347	1.099
p	0.861	0.007	0.847	0.875	0.859	0.008	0.843	0.873

Notes: Abbreviations for parameters follow Table 1. As above, parameters $\sigma_{a,w}^2$, $\sigma_{a,o}^2$, β_w , β_o , and σ_g^2 are on a logit scale.

Credible intervals for both β_w and β_o contained zero in the three years with the highest and lowest mouse population densities (Fig. 3, Appendix B).

Mean survival probability, including tick effects, yearly random effects, and individual random effects was 0.683 ± 0.006 (mean \pm SD) between trapping sessions within-season and 0.121 ± 0.009 over winter. Mean posterior variance estimates were greatest for the interannual random effects in overwinter survival ($\sigma_{a,o}^2$), although variance in within-season survival ($\sigma_{w,o}^2$) and individual random effects (σ_g^2) were also greater than zero (Tables 1, 2). We observed a positive correlation between mean annual posterior estimates of overwinter survival probability and log-transformed acorn density (same year; $F_{1,14} = 7.73$, adjusted $R^2 = 0.31$, $P = 0.0147$) but no analogous relationship between within-season survival and acorn density for the previous year ($F_{1,14} = 1.3$, adjusted $R^2 = 0.0194$, $P = 0.274$). There was no correlation between mean annual posterior estimates of overwinter survival and log-transformed mouse density ($F_{1,14} = 0.374$, adjusted $R^2 = 0.0435$, $P = 0.551$), but a positive relationship between density and within-season survival ($F_{1,14} = 5.46$, adjusted $R^2 = 0.229$, $P = 0.0348$).

Finally, population rate of change within a breeding season was not reduced by heavy tick burdens on mice (Fig. 4). Mean maximum tick burdens were positively correlated with the population rate of change (ANCOVA; $F_{1,66} = 8.663$, $P = 0.00448$; Fig. 4). The effect of individual trapping grids was not significant ($F_{5,66} = 0.341$, $P = 0.886$), nor was there an interaction between mean tick burdens and grid ($F_{5,66} = 1.638$, $P = 0.162$). The index of dispersion of maximum tick burdens (variance/mean ratio) was not correlated with the population rate of change (ANCOVA; $F_{1,66} = 3.100$, $P = 0.083$). In this analysis, the effect of individual trapping grids was also not significant ($F_{5,66} = 1.142$, $P = 0.347$), and again we did not find a significant interaction between mean tick burdens and grid ($F_{5,66} = 0.983$, $P = 0.435$).

DISCUSSION

We estimated the effects of larval tick burdens on within-season and overwinter mouse survival probabilities using 16 years of mark-recapture data for over 5500 individual mice. Although tick burdens sometimes reached over 200 ticks per host, we found that larval *Ixodes scapularis* ticks had few measurable effects on white-footed mouse survival probabilities and none that were negative. This lack of negative effects of heavy tick burdens on survival was contrary to our predictions. We would predict that high tick burdens have a negative effect on survival, given that ticks feed on mouse blood. The positive correlation between tick burdens and within-season survival probability in male mice was particularly unexpected. There are several reasons why we might not have observed the expected result.

First, heavy tick infestations in mice could be associated with behavioral patterns that may increase

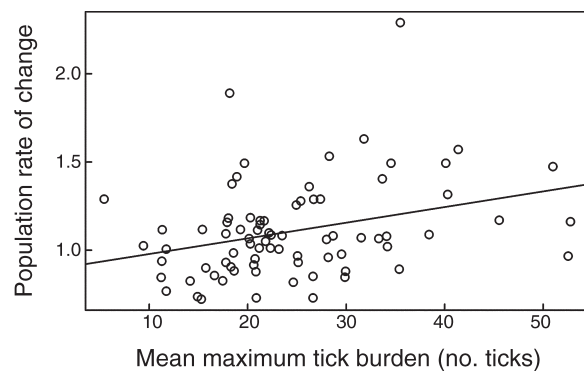


FIG. 4. Correlation between mean maximum tick burden and white-footed mouse population rate of change. Regression line is displayed as a simple linear model ($F_{1,76} = 8.675$, adjusted $R^2 = 0.09$, $P = 0.00428$), given that there was not a significant main effect of grid in this analysis.

survival and offset health costs of parasitism. Heavily infested mice may exhibit more risk-averse behavior in response to predation. For example, flea-infested gerbils had a stronger response to the threat of fox predation than uninfested gerbils, leaving food trays at higher giving-up densities and spending less time in food trays overall (Raveh et al. 2011). This kind of avoidance behavior lowers foraging success, but it also decreases predation risk. On the other hand, studies of endoparasite burdens have shown the opposite effect on tadpoles, where parasitized individuals became more susceptible to predation (Lefcort and Blaustein 1995).

Second, heavily tick-infested mice may occupy microhabitats more conducive to both tick and mouse survival. Other models of this system have shown that large tick aggregations on individual mice are due to the bad luck of occupying a tick-rich microhabitat rather than any individual predictor (Calabrese et al. 2011) and that individuals with high larval tick burdens also have high nymphal tick burdens (Brunner and Ostfeld 2008). Heavily infested individuals may reside in microhabitats with denser vegetation, which is more conducive to tick survival (Kiffner et al. 2011) but may also provide cover from predation for mice as well. Since predation is an important cause of mortality in small mammal populations (Meserve et al. 2003, Ekerholm et al. 2004, Previtali et al. 2009), behaviors associated with tick infestation that simultaneously decrease predation risk may balance out negative effects of tick feeding on mouse survival.

Potentially, several other individual-level traits might underlie both survival probability and the tendency of mice to accumulate ticks, disrupting a direct causal relationship. For instance, the biggest individuals in the population might simultaneously be most heavily parasitized and most likely to survive (Perkins et al. 2003, Devevey and Brisson 2012). Larger animals have been shown to have higher tick burdens in some systems (Kiffner et al. 2011) and the effect of body size has been

proposed to drive male-biased differences in tick burdens in other small mammal species (Harrison et al. 2010), but other studies have not found strong correlations between ectoparasite loads and body size (Perez-Orella and Schulte-Hostedde 2005). Previous work with an 11-year subset of the data in this study did not find sex, age, or body mass to explain aggregation patterns of tick burdens (Brunner and Ostfeld 2008). Another important trait could be home range size. Individuals with larger home ranges (such individuals may be dominant and thus more likely to survive) may simply encounter more ticks. Home range size was not found to be related to larval tick burdens in another population of *Peromyscus leucopus* (Devevey and Brisson 2012), but other studies have found increased tick burdens with higher space use or exploratory behavior in other small mammal species (Boyer et al. 2010). Finally, effects of tick burdens on survival may be nonlinear, perhaps due to the cost of resistance in individuals with low parasite loads (Stjernman et al. 2008). We note that larval and nymphal tick burdens are positively correlated in this system (Brunner and Ostfeld 2008). If nymphs or nymph-transmitted pathogens reduce mouse survival or population growth rates, then any correlated larval burden would also be associated with reduced mouse survival or population growth. Instead, the lack of negative effects of larval burdens suggests that effects of larvae are not masked by any potential negative effects of nymphs or nymph-transmitted pathogens.

In addition, there is a known trade-off between reproductive effort and survival in many animal species (Stearns 1992). It may be that any negative effects of ticks on mouse health are manifested in decreased reproductive effort, which can enhance survival. For instance, high bot fly parasitism was associated with reduced secondary reproductive success and increased survival in white-footed mice (Burns et al. 2005). Decreased reproductive success is a known consequence of ectoparasitism in some mammal systems (Neuhaus 2003, Hillegass et al. 2010) but not all (Gooderham and Schulte-Hostedde 2011). Measuring reproductive output was outside of the scope of this study; however, if heavy tick burdens reduce reproductive effort substantially without affecting survival, we would expect to find a negative correlation between maximum tick burdens and population rate of change. Our finding of a positive correlation between mean maximum tick burdens and population rate of change appears to reduce the likelihood that tick parasitism was reducing reproductive output in our populations.

Although mouse population density and acorn production can be correlated with survival probabilities, we did not find differences in the effect of ticks on survival in high-population vs. low-population years or in high-acorn vs. low-acorn years (Fig. 3). The weak (and occasionally positive, in the case of male mice) effects of ticks on mouse survival were robust over large

ranges of variation in extrinsic (food supply) and intrinsic (population density) factors. These observations contrasted with our expectation that, should a negative effect of ticks on mice occur, it would be stronger during stressful periods, such as years of high population density or low food supply.

The positive correlation between mean maximum tick burdens and λ (the population rate of change) and the lack of relationship between the variance/mean ratio of tick burdens and λ support the conclusion that high tick burdens have minimal to no cost to mice at the population level. Observed higher tick burdens when initial population size is low (see *Methods*), perhaps indicative of tick crowding on scarce hosts, could partially explain the positive correlation between λ and mean tick burden. In addition, this result suggests that high mean tick burdens are not increasing survival by reducing reproductive effort, because decreased reproductive effort should lower λ . The absence of a clear negative relationship between tick burdens and population rate of change suggests that mouse populations are unlikely to be regulated by these ectoparasites, though further study is needed.

Our observation that ticks do not decrease mouse survival probability or population growth rate has implications for the dynamics of blacklegged ticks and the pathogens they transmit. Prior research has demonstrated a strong, positive effect of mouse abundance on the subsequent abundance of tick nymphs (Ostfeld et al. 2001, 2006, Ostfeld 2011), the stage responsible for maintaining the enzootic cycle of tick-borne pathogens. In contrast to the role of mice in regulating tick abundance, we find no reciprocal regulatory effect of ticks on mice. The absence of this regulatory pathway increases the likelihood of destabilizing positive feedback loops. In theoretical models, this kind of mortality tolerance has positive effects on parasite fitness (Best et al. 2008). The apparent indifference of white-footed mice to variable tick burdens could contribute to their importance as reservoir hosts in the transmission of multiple tick-borne pathogens.

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SUPPLEMENTAL MATERIAL

Appendix A

Distributions of maximum *Ixodes scapularis* larval tick burdens on white-footed mice (*Peromyscus leucopus*) captured during larval peak from 1992–2010 for all years combined and each year separately ([Ecological Archives XXXXX](#)).

Appendix B

Parameter estimates for survival of white-footed mice in sets of three years representing particularly high or low levels of (1) acorn density in the current year, (2) acorn density in the previous year, and (3) mouse population density ([Ecological Archives XXXXX](#)).

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