

Modeling the influence of *Peromyscus leucopus* body mass, sex, and habitat on immature *Dermacentor variabilis* burden

Tad A. Dallas¹, Stephanie A. Foré¹✉, and Hyun-Joo Kim²

¹Department of Biology, Truman State University, Kirksville, MO 63501, U.S.A, sfore@truman.edu

²Department of Mathematics and Computer Science, Truman State University, Kirksville, MO 63501, U.S.A.

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ABSTRACT: Immature (larvae and nymph) tick burden on rodents is an important determinant of adult tick population size and understanding infectious disease dynamics. The objective of this research was to build a descriptive model for immature *Dermacentor variabilis* burden on *Peromyscus leucopus*. Mice were live-trapped on two permanent grids in an old field and an early successional forest every other month between April and October, 2006-2009. Negative binomial regression was used to examine the association between immature *D. variabilis* burden and the host related variables of host habitat, body mass, and/or sex. The model containing all three variables had the lowest Akaike's Information Criterion (AIC), corrected AIC (AICc), and greatest AICc weight. Immature *D. variabilis* burden was positively associated with mice with higher body mass, male mice, and those captured in the field habitat. These data are consistent with studies from other tick-rodent systems and suggest that single factor models do not describe host burden. Variables other than those that are related to the host may also be important in describing the tick burden on rodents. The next step is to examine variables that affect tick development rate and questing behavior. *Journal of Vector Ecology* 37 (2): 338-341. 2012.

Keyword Index: *Dermacentor variabilis*, *Peromyscus leucopus*, modeling, negative binomial regression.

INTRODUCTION

Rodents are key hosts to the immature stages of many hard ticks. Immature burden on rodents is an important determinant of adult tick population size (Smart and Caccamise 1988). Therefore, identifying factors that affect individual mouse burden contributes to our understanding of infectious disease systems. Distribution of immature ticks on hosts has been observed to be clustered with a small portion of the host population carrying much of the burden (Kitron et al. 1991, Brunner and Ostfeld 2008, Kiffner et al. 2011). Host burden has been associated with a number of biotic and abiotic factors.

Tick burden in field populations has been observed to be disproportionately higher in male than female rodents (Laurance and Coan 1987, Brunner and Ostfeld 2008, Harrison et al. 2010). However, one report indicates that burden differs between sexes in *Tamias sibiricus* between years (Boyer et al. 2010). Manipulative laboratory experiments with rodents have found that males treated with testosterone had significantly more ticks, suggesting that testosterone affects the immune function (Hughes and Randolph 2001). Other studies have indicated that female hormones are associated with the reduced burden (Ali and Sweatman 1966, Rechav 1970).

Tick burden in field studies has been positively (Brunner and Ostfeld 2008, Harrison et al. 2010, Kiffner et al. 2011) and negatively associated (Brunner and Ostfeld 2008) with rodent body mass. Body mass is positively associated with gender in sexually dimorphic species and is a proposed explanation of sex-biased parasitism (Harrison et al. 2010). Host age is associated with body mass differences

and immature rodents have been reported to have higher tick burdens (Ali and Sweatman 1966, Rechav 1970, Boyer et al. 2010, Kiffner et al. 2011).

Higher tick burden has been associated with some habitat types (Sonenshine et al. 1966, Campbell and MacKay 1979, Laurance and Coan 1987, Boyer et al. 2010, Kiffner et al. 2011). Habitat type could influence the probability of encounter between hosts and ticks by influencing the abundance of hosts or immature ticks (Laurance and Coan 1987, Mannelli et al. 1994, Adler et al. 1992, Lindsay et al. 1999) or host movement within the habitat (Sonenshine and Stout 1968, Boyer et al. 2010).

The objective of this study was to build a model that describes immature (larval and nymphal) *Dermacentor variabilis* burden on *Peromyscus leucopus*, the primary host in northeast Missouri. Adult *D. variabilis* typically parasitize larger mammal hosts (Kollars 1996) and were not observed on *P. leucopus* in this study. As *D. variabilis* is heavily dependent on *P. leucopus* for feeding the early lifestages, the burden on this host will be important for the population dynamics of the tick and potential spread of *Rickettsia rickettsii*, the causative agent of Rocky Mountain spotted fever. This study is the first to model burden in the *D. variabilis*-*P. leucopus* system. Tick burden has been modeled in six other tick-rodent systems (Brunner and Ostfeld 2008, Kiffner et al. 2011). These models suggest that there may not be a specific set of variables that predict burden in all tick-rodent systems. Our model will be based on the host variables body mass, sex, and habitat as there is a large body of field and experimental data suggesting that these are important determinants of host burden in rodents.

MATERIALS AND METHODS

Small mammal sampling was performed in two habitat types, an early successional forest and an old field dominated by non-native grasses, approximately 300 m apart in Adair County, MO. In each site, a 70 m x 120 m grid with 104 sampling points 10 m apart was established. A Sherman live trap (H. B. Sherman, Tallahassee, FL, U.S.A.) baited with a mixture of peanut butter and rolled oats was set at each sampling point. Trapping was performed concurrently on both grids in three or four night sessions in April, June, August, and October for three years (2006-2009) for a total of 298 *P. leucopus* captures. Ticks were observed on mice in all months examined in this study. Host body mass, sex, tail, and right hind foot length were recorded for all captures. Animals were marked via toe clipping to identify individuals and assure only first captures were considered in the present study. All animals were handled according to the Animal Care Guidelines of the American Society of Mammalogists (American Society of Mammalogists 1998). Ticks were removed and stored in ethanol for later identification to life stage and species.

The response variable, immature *D. variabilis* burden, was count data and strongly right-skewed (Figure 1). The current data suggest significant overdispersion (variance is much greater than the mean) based on the likelihood ratio test ($F = 1782, p < 0.0001$). In addition, the variation inflation factor (\hat{c}) (Burnham and Anderson 1998) was 10.76 fitting Poisson and 3.46 fitting negative binomial regression. This suggests that negative binomial regression ($\hat{c} = 1$ means no overdispersion present) with some degree of overdispersion is an appropriate model without fitting more complicated models (Crofton 1971).

Seven candidate binomial regression models were compared, including all possible combinations of host body mass, sex, and habitat of the host. In *P. leucopus*, sex and body mass are assumed to be independent variables as sexual size dimorphism is not expressed in the species (Dewsbury et al. 1980). Akaike's information criteria (AIC) (Akaike 1974) and corrected AIC (AICc) (Hurvich and Simonoff 1998) were calculated for each model. However, only corrected AIC values are reported as AIC converges to AICc with larger sample sizes. Smaller AICc values are considered closer to the "true" model. Δ AICc and AICc weights (Stauffer 2007) were also calculated for each candidate model to find the difference between AICc value and minimum AICc value and the probabilistic weight of each model relative to the true model given the model set and available data (Link and Barker 2006, Anderson 2008).

Models were validated with test data gathered in 2010 from the same field site using the same methodology ($n = 69$). For the seven candidate negative binomial regression models, mean squared error (MSE) values were calculated using

$$\text{MSE} = (Y_i - \hat{Y}_i)^2/n$$

where Y_i is an observed and \hat{Y}_i is an expected value calculated from each candidate model of the response variable. MSE

values were used to access the fit of each candidate model to the test data. The model corresponding to the lowest MSE value for the test data (data not used to build the negative binomial regression models) corresponds to the "best" fit model.

RESULTS

The full parameter model containing host body mass, sex, and habitat has the lowest values of AICc (Table 1) indicating that this is the closest model to the "true" model. Akaike weight, representing the strength of evidence for a particular model, was 0.73 for the full parameter model. The model with host body mass and sex has the second largest AICc weight of 0.261. All other models have AICc weights of less than 0.05. The fitted negative binomial regression model with host body mass (X_1), host sex (X_2) (1=male; 0=female), and habitat (X_3) (1=field; 0=forest) can be written as

$$\ln[\hat{\lambda}(X_i)] = -0.694 + 0.067X_1 + 0.469X_2 + 0.294X_3 \quad (1)$$

where $\hat{\lambda}(X_i)$ is the estimated conditional expectation of the response variable given the independent variables.

The expected log count *D. variabilis* for a one-unit increase in host body mass increased by 0.067, meaning that an increase of one gram of host body mass would cause the expected immature *D. variabilis* burden to increase by a factor of $e^{0.067} = 1.07$ for the same host sex in the same habitat. Likewise, male hosts will have 1.6 more *D. variabilis* on the average for the same host body mass in the same habitat. Mice in the field habitat will have 1.34 more *D. variabilis* than forest habitat host on the average for the same host body mass and the same host sex.

MSE values of each candidate model for the test data are given in Table 2. The model containing host body mass, sex, and habitat (given in Equation 1) has the smallest MSE value, implying the lowest degree of error, thus "best" fit model. This heuristic, combined with the smallest AICc values, provide evidence that the model containing host body mass, sex, and habitat is the closest to the "true" model given the model set and available data.

DISCUSSION

The dynamics of tick populations are dependent on many variables affecting individual ticks on and off the host. *D. variabilis* is heavily dependent on *P. leucopus* in northeast Missouri to feed the immature lifestages. The host variables of body mass, sex, and habitat are important in describing immature *D. variabilis* burden on *P. leucopus*. These findings are consistent with observations of other rodent-tick systems in which a disproportionate number of ticks are observed on male mice (Laurance and Coan 1987, Brunner and Ostfeld 1991, Boyer et al. 2010, Harrison et al. 2010), larger mice (Brunner and Ostfeld 2008, Harrison et al. 2010, Kiffner et al. 2011), and mice in different habitats (Sonenshine et al. 1966, Laurance and Coan 1987, Boyer et al. 2010, Kiffner et al. 2011).

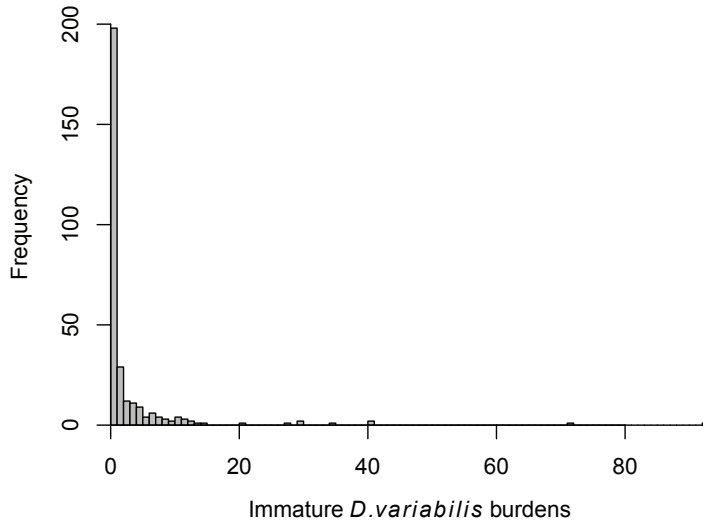


Figure 1. Frequency histogram depicting the distribution of immature *D. variabilis* on *P. leucopus* hosts.

Table 1. Negative binomial regression models examining the association between immature *D. variabilis* burdens and all possible combinations of *P. leucopus* body mass (Mass), sex (Sex), and habitat (Habitat). Model selection is based on AICc and AICc weights (w_i). Δ AICc is the difference between a given model and the model with the lowest AICc value.

Variables	AICc	Δ AICc	w_i
Mass Sex Habitat	1302.51	0.00	0.730
Mass Sex	1304.55	2.04	0.261
Mass Habitat	1310.95	8.44	0.011
Mass	1313.44	10.93	0.003
Habitat Sex	1323.23	20.72	0.000
Sex	1326.00	23.49	0.000
Habitat	1341.88	39.37	0.000

P. leucopus is typically found in wooded areas and ecotones between woods and fields (Brown 1964). As the preferred habitat of *D. variabilis* is old field or wood/field ecotones (Campbell and MacKay 1979), mice crossing the wood/field ecotone with greater frequency are more likely to encounter ticks. Home range size of *Peromyscus* differs among individuals (Metzgar 1971) is generally larger in males (Sonenshine and Stout 1968) and varies temporally (Stickel 1960). Differences in the portion of the habitat used by individual mice and the size of the home ranges likely

impact the likelihood of encounter with ticks. In addition to males having a greater probability of encountering ticks due to home range size differences, laboratory studies (Hughes and Randolph 2001) suggest they are more susceptible to tick infestation.

Although host-related variables are important in describing tick burden, the burden of immature *D. variabilis* on *P. leucopus* is likely influenced by additional biotic and abiotic variables. Models of other tick-rodent systems (Brunner and Ostfeld 2008, Kiffner et al. 2011) demonstrated that multiple variables predict tick burdens on rodents and suggest that each tick-rodent system may have a different suite of predictive variables. The next step in the *D. variabilis*-*P. leucopus* system is to develop a model that considers variables that influence development rate and questing behavior of immature ticks, including environmental and seasonal factors. In addition, other statistical models can be considered to improve model fit.

Table 2. Mean Squared Error values for each candidate negative binomial regression model.

Model	MSE
Mass Sex Habitat	39.49
Mass Sex	39.81
Mass Habitat	40.00
Mass	40.25
Habitat Sex	51.95
Sex	53.96
Habitat	58.29

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