Molting Success of *Ixodes scapularis* Varies Among Individual Blood Meal Hosts and Species

JESSE L. BRUNNER,[1,2] LAURA CHENEY,[3] FELICIA KEESING,[3] MARY KILLILEA,[4] KATHLEEN LOGIUDICE,[5] ANDREA PREVITALI,[2] AND RICHARD S. OSTFELD[2]

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ABSTRACT The blacklegged tick (*Ixodes scapularis*) is an important vector of emerging human pathogens. It has three blood-feeding stages, as follows: larva, nymph, and adult. Owing to inefficient transovarial transmission, at least for the Lyme disease agent (*Borrelia burgdorferi*), larval ticks rarely hatch infected, but they can acquire infection during their larval blood meal. Nymphal ticks are primarily responsible for transmitting pathogens to hosts, including humans. The transition from uninfected host-seeking larva to infectious host-seeking nymph is therefore a key aspect of human risk of infection. It can be divided into a series of steps, as follows: finding a host, taking a blood meal, becoming infected, molting, and overwintering. The chance of succeeding in each of these steps may depend on the species identity of the blood meal host. We used a Bayesian method to estimate the molting success of larval *I. scapularis* collected from four commonly parasitized species of birds and eight commonly parasitized small and mid-sized mammals found in the forests of Dutchess County, New York. We show that molting success varies substantially among host species; white-footed mice, veeries, and gray catbirds support particularly high molting success, whereas ticks feeding on short-tailed shrews, robins, and wood thrushes were less successful. We also show that larval molting success varies substantially between individual blood meal hosts, and that this intraspecific variability is much higher in some species than in others. The causes of both inter- and intraspecific variation in molting success remain to be determined.

KEY WORDS molting success, *Ixodes scapularis*, blood meal host, intraspecific variation, interspecific variation

The transmission of most vector-borne diseases requires that a vector find and successfully feed upon a host, is infected by that host, and then survives long enough to infect another host. It is becoming increasingly clear that each of these steps may be influenced by the species identity of the host. Consider the blacklegged tick, *Ixodes scapularis*, which is the vector of the agents of Lyme disease, human granulocytic anaplasmosis, babesiosis, and other important emerging pathogens such as Powassan virus (Burgdorfer et al. 1982, Spielman et al. 1985, Costero and Grayson 1996, Telford et al. 1996). Whereas *I. scapularis* have been found on over 125 vertebrate host species (Keirans et al. 1996), they seem to prefer some host species over others (James and Oliver 1990, Schmidt et al. 1999, Shaw et al. 2003). Once on a host, the chances that a larval tick successfully feeds and acquires the pathogen during the blood meal vary a great deal depending on the species identity of that host (Levin et al. 2002, LoGiudice et al. 2003, Ginsberg et al. 2005, Brunner et al. 2008, Keesing et al. 2009).

To propagate the infection, these newly fed and infected larvae must first molt into nymphs and overwinter. Although it is commonly thought that a fed tick's chances of molting and surviving the winter are determined primarily by environmental factors such as temperature and humidity (Lindsay et al. 1998, Estrada-Peña 2002, Ginsberg et al. 2004), Ostfeld et al. (2006) found that the best predictor of the abundance of nymphs in a given year was the density of mouse or chipmunk hosts rather than environmental factors, emphasizing the importance of the host community. LoGiudice et al. (2003) observed that the molting success of larval blacklegged ticks depends on the species identity of the blood meal host. LoGiudice et al. (2003), however, had small samples of some hosts, particularly songbirds and sciurid rodents, and did not statistically assess differences among or within host species.

In this study, we substantially broaden and improve estimates of the molting success of fed larval black-

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[1] Corresponding author: School of Biological Sciences, Washington State University, PO Box 644236, Pullman, WA 99164-4236 (e-mail: jesse.brunner@wsu.edu).

[2] Cary Institute of Ecosystem Studies, Millbrook, NY 12545.

[3] Department of Biology, Bard College, Annandale-on-Hudson, NY 12504.

[4] Department of Biology, New York University, New York, NY 10003.

[5] Department of Biological Sciences, Union College, Schenectady, NY 12308.

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legged ticks collected from four commonly parasitized species of birds and eight common small and mid-sized mammal species found in the forests of Dutchess County, New York. These forests are representative of the Lyme disease endemic zone of the northeastern United States. In addition, we hypothesized that individual blood meal hosts of a given species might vary in their quality to ticks because of, for instance, differences in nutritional status or levels of prior exposure to ticks, and hence, levels of immune responses to the ticks. We used a Bayesian model that could accommodate this individual-to-individual variation and allowed us to compare the degree of intraspecific variation between these 12 host species.

This study is part of a broad effort to understand how tick demography and infection prevalence vary as a function of the species identity of the host, and therefore, how host community composition affects the abundance of infected ticks. A better understanding of the factors that influence the abundance of infected ticks, as well as those that increase human exposure to ticks, is critical for predicting risk to humans in the acquisition of tick-borne pathogens.

Materials and Methods

We trapped mammals and mist-netted birds from mid-July through October 2009 on oak- and maple-dominated forests and lowland areas on the property of the Cary Institute of Ecosystem Studies (Millbrook, NY) following the methods of Keesing et al. (2009). White-footed mice (*Peromyscus leucopus*) and eastern chipmunks (*Tamias striatus*) were captured in Sherman traps (7.6 × 8.9 × 30 cm) baited with crimped oats. We caught northern short-tailed shrews (*Blarina brevicauda*) in these traps as well as in smaller (7.6 × 8.9 × 23 cm) Sherman and Longworth traps (13.8 × 6.4 × 8.4 cm). Gray squirrels (*Sciurus carolinensis*) were captured in small Tomahawk traps (15 × 15 × 48 cm) baited with peanut-flavored suet and apple slices, whereas southern flying squirrels (*Glaucomys volans*) were targeted by securing small Tomahawk traps with a similar bait to the sides of trees on or near hillsides or ravines, often in pine- and hemlock-dominated stands. Virginia opossums (*Didelphis virginiana*), striped skunks (*Mephitis mephitis*), and raccoons (*Procyon lotor*) were captured in medium-sized (25 × 30 × 81 cm) and large-sized (106 × 30 × 30 cm) Tomahawk traps baited with canned cat food and barbeque sauce. All traps were covered with plywood boards for protection from sun and rain. Traps for squirrels were checked twice per day, in the morning between 0600 and 0800 h and in the afternoon between 1500 and 1700 h. Traps for shrews were set after 1700 h on misty and rainy nights and checked every 1–2 h until closed. All other traps were set between 1600 and 1800 h and checked the following morning between 0800 and 1200 h. All captured animals were weighed, sexed, assessed for reproductive status, and tagged. Pregnant and lactating females were released at the site of capture, as were recaptured individuals. Captured animals were transported in their traps to the Rearing Facility at the Cary Institute of Ecosystem Studies, an approved animal-holding facility, and provided immediately with appropriate food, as follows: earth worms and mealworms for shrews; rodent blocks and apple slices for mice and chipmunks; rodent blocks, apple slices, and whole walnuts for squirrels; and dog kibble and hard-boiled eggs for opossums, skunks, and raccoons.

Veeries (*Catharus fuscescens*), gray catbirds (*Dumetella carolinensis*), American robins (*Turdus migratorius*), and wood thrushes (*Hylocichla mustelina*) were captured in mist nets that were erected each morning immediately after dawn and checked every 30 min until 1100 h. Nontarget species and fledgling birds were released. Target birds were placed in commercial birdcages covered with burlap, provided with mealworms and honeysuckle (*Lonicera mackii*) berries, and transported to the Rearing Facility.

At the Rearing Facility, animals were housed in appropriately sized wire cages (shrews, mice, and chipmunks in cages constructed of one-fourth-inch mesh galvanized hardware cloth; squirrels in commercial flying squirrel cages; opossums in dog crates; skunks in medium-sized Havahart traps (91 × 25 × 30 cm); raccoons in large dog cages; and birds in bird cages), and supplied with food and water ad lib. Squirrels, opossums, skunks, and raccoons were also provided with a bottomless wooden nest box. The cages were each suspended over a pan containing a moistened paper towel and bordered with either double-sided tape or Vaseline to prevent ticks from climbing out of the pan (Sonenshine 1993). The pans and paper towel were checked exhaustively for ticks every day for 3 d, after which the animals were released at the site of capture. Ticks collected from the few animals that died during this holding period were excluded from analyses. Some animals that dropped <10 ticks were held for an additional day in an attempt to achieve at least 10 fed larvae per host.

Fed larvae found on a pan were collected with a small paintbrush and placed in an autoclaved glass scintillation vial with moistened plaster of Paris in the bottom. When ticks were soiled with feces or food debris, they were first rinsed with distilled water. Only *I. scapularis* were included in this study. Up to 10 fed larvae were placed into a vial before a new vial was started for an individual. As a result of space limitations, ticks from animals with >100 fed larvae (e.g., opossums and raccoons) were stored in larger groups of 20 or 50 fed larvae per vial. There is no evidence that these inconsistencies in the number of larvae per vial affected molting success (data not shown). The plaster in the vials was kept moist with distilled water. Vials were checked at least once per week for newly molted nymphs or mortality. Dead ticks were recorded and removed from the vial. If mold was observed growing in the vial, the ticks were transferred with a brush to a new vial. Vials were checked for molted nymphs through January 2010.

Analyses. We estimated the probability that an engorged larva molted (P_{molt}) after successfully feeding on each of the 12 species by fitting two models to the

data for each species individually. In the first model, this binomial probability is simply a species-specific constant—all individual hosts have the same P_{molt}. Given that individual blood meal hosts may vary in their quality to ticks, in the second model we allowed the binomial probability, P_{molt}, to vary from individual to individual as random draws from a beta distribution with shape parameters α and β and an expected (i.e., mean) value of $E(P_{molt}) = \alpha/(\alpha + \beta)$. The beta distribution is a very flexible distribution bounded between 0 and 1. It can be U shaped, flat, or have a peak anywhere along its range, so it can accommodate a range of forms that might describe the variability in P_{molt}.

We excluded from the analyses vials of ticks that had mold, regardless of whether mortality was noted. The proportion of vials that developed mold varied among species, as follows: ~40% of those from short-tailed shrews and Virginia opossums, but none of the 13 vials from flying squirrels. In general, the engorged larvae in these moldy vials were less likely to molt, but there is little reason to think that the occurrence of mold and its impact on the ticks represent anything other than an artifact of our methods of collecting ticks and separating them from the feces, urine, and food waste of the host (and perhaps that the feces and urine of opossums and shrews are quite toxic). We did, however, also fit to the full data set a version of the second model in which P_{molt} was reduced by a factor, m, when the vial had mold detected (data not shown). The estimates of P_{molt} in this more complex model did not differ qualitatively or substantially from the simpler model with a variable P_{molt} fit to nonmolded vials.

To accommodate host-to-host variability and to provide clear metrics of the uncertainty in the estimated parameters, we used a Bayesian approach implemented in WinBUGS 1.4.3 (Lunn et al. 2000) using the R2WinBUGS package in R 2.10.1 (Sibylle et al. 2005, R Development Core Team 2009). See the Appendix for the syntax of the models and prior distributions. We used the difference in deviance information criteria (DIC; Spiegelhalter et al. 2002) to compare the short-term predictive ability of the two models for each species. DIC is a Bayesian measure of model fit (deviance calculated at the posterior mean) penalized by model complexity (twice the effective number of model parameters). As with Akaike's Information Criteria, lower values indicate a better model, but it is the difference in DIC that is useful for comparing models. Models with a DIC difference >10 need not be considered (Spiegelhalter et al. 2002).

Results

Excluding those from molded vials, we collected 6,507 engorged larvae from a total of 214 individuals of eight mammalian and four avian species, 5,253 (80.7%) of which successfully molted (Table 1). In most cases, we were able to collect ticks from ≥15 individuals, but in the case of flying squirrels and skunks we had only a few individuals (Table 1). Even in these cases, however, we recovered a large number of engorged larvae

Table 1. The number of individual hosts of each species; the mean (and SD) number of engorged larvae observed for molting; the mean (SD) number of molted nymphs recovered; and the mean (and 95% credible interval) of parameter estimates from two Bayesian models

Species	N	Fed larvae per host[a] Mean (SD)	Molted nymphs per host Mean (SD)	P_{molt} of constant model Mean (95% CI)	Mean P_{molt} from variable model Mean (95% CI)	α Mean (95% CI)	β Mean (95% CI)
Northern short-tailed shrew (*Blarina brevicauda*)	23	13.1 (10.9)	10.2 (11.1)	0.78 (0.73–0.82)	0.68 (0.55–0.78)	1.82 (0.71–3.86)	0.82 (0.37–1.68)
White-footed mouse (*Peromyscus leucopus*)	16	17.9 (18)	16.4 (16.5)	0.91 (0.88–0.94)	0.9 (0.83–0.95)	13.83 (2.3–38.63)	1.41 (0.29–3.9)
Eastern chipmunk (*Tamias striatus*)	23	18.1 (21.2)	13.7 (16.2)	0.75 (0.71–0.8)	0.77 (0.68–0.85)	7.64 (2.62–17.22)	2.22 (0.75–5.36)
Eastern gray squirrel (*Sciurus carolinensis*)	27	23.9 (46.2)	18.2 (36.5)	0.67 (0.58–0.74)	0.7 (0.51–0.87)	8.07 (1.54–21.95)	3.35 (0.6–9.24)
Southern flying squirrel (*Glaucomys volans*)	4	31.5 (23.6)	21 (14.7)	0.76 (0.73–0.79)	0.77 (0.69–0.85)	5.13 (1.98–10.55)	1.47 (0.6–3.08)
Virginia opossum (*Didelphis virginiana*)	18	53 (67.4)	45.4 (63.6)	0.86 (0.84–0.88)	0.82 (0.73–0.89)	5.65 (2.31–11.21)	1.2 (0.53–2.22)
Striped skunk (*Mephitis mephitis*)	2	115.5 (37.5)	79 (NA)	0.68 (0.62–0.74)	0.71 (0.5–0.88)	8.56 (1.27–22.3)	3.41 (0.59–10.01)
Raccoon (*Procyon lotor*)	15	82.1 (59.2)	66.3 (55.4)	0.81 (0.78–0.83)	0.78 (0.68–0.86)	4.07 (1.6–7.69)	1.1 (0.54–1.91)
American robin (*Turdus migratorius*)	15	23.3 (20.2)	18.3 (20.8)	0.78 (0.74–0.82)	0.65 (0.5–0.79)	1.45 (0.5–3.1)	0.72 (0.33–1.42)
Gray catbird (*Dumetella carolinensis*)	21	16.5 (18.2)	15 (17.6)	0.9 (0.87–0.93)	0.89 (0.83–0.94)	11.78 (3.36–27.35)	1.38 (0.43–3.14)
Veery (*Catharus fuscescens*)	17	36.8 (30.8)	33.6 (29)	0.91 (0.89–0.93)	0.9 (0.86–0.94)	22.54 (8.29–47.68)	2.35 (0.92–4.87)
Wood thrush (*Hylocichla mustelina*)	32	30.3 (20.6)	22.4 (17.6)	0.74 (0.71–0.77)	0.72 (0.65–0.79)	3.75 (1.85–6.93)	1.4 (0.71–2.46)

In the constant model, the probability of molting (P_{molt}) is a species-specific constant; in the variable model, P_{molt} can vary among individuals according to a beta distribution with parameters α and β. For this second model, the expected value ($E[P_{molt}] = \alpha/[\alpha + \beta]$) of P_{molt} is reported.

[a] These numbers represent only the numbers of fed larvae that were placed in vials for this study. They do not represent accurate estimates of body burden.

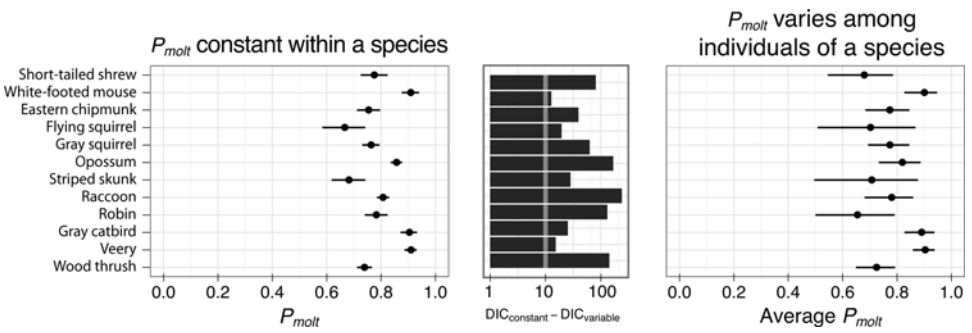

Fig. 1. The mean (●) and 95% credible interval (lines) of the estimates of the species-specific constant P_{molt} (left) and the average value of P_{molt} when individuals of a species were allowed to vary in their quality as hosts (right). The middle panel shows the difference in DIC between the models, with larger values favoring the variable host model. The vertical line at Δ DIC = 10 shows the cutoff for beyond which the simple model with a constant P_{molt} need not be considered (Spiegelhalter et al. 2002). In every case, the DIC values favored the model incorporating variation among individuals within a species.

with which to estimate the probability that an engorged larva molts after successfully feeding.

For every species, the model in which P_{molt} could vary from individual to individual was strongly favored over the model with a constant P_{molt}—differences in DIC were always >10 and in many cases much more than 10 (Fig. 1). This provides strong support for the hypothesis that individual hosts within a species can vary, sometimes substantially, in their quality as blood meal hosts (Fig. 2B).

It is important to note that support for the model with a beta-distributed P_{molt} does not imply that a species-specific P_{molt} could not be resolved because of a lack of data (which would have resulted in a wide posterior distribution of P_{molt} in the simpler model instead of the peaks shown by the dotted lines in Fig. 2A). Rather, this strongly suggests that molting success varies substantially from individual host to individual host. Using the robust data for short-tailed shrews, for instance, we can clearly resolve the parameters of the beta distribution of individual molting probabilities, and the distribution is estimated to be very broad, which matches fairly well the highly variable observations of the proportion of larvae that molted after feeding on different individuals (Fig. 2B).

Allowing for this individual-to-individual variation in P_{molt}, there is still a great deal of variability in the mean or expected value of P_{molt} from species to species (Figs. 1 and 2A). Mice, veeries, and gray catbirds are very good hosts for larval blacklegged ticks—nine of 10 larvae that engorged on one of these hosts can be expected to molt—whereas on average approximately seven of 10 fed larvae will molt after feeding on shrews, robins, and wood thrushes (Table 1, Fig. 1). Given the broad credible intervals for some of the less well-represented species, however, it is difficult to state with certainty that these species vary from one another.

Among those species for which we obtained a good sample size, we found that the amount of individual variation present varied among species. Short-tailed shrews, gray squirrels, and robins, for instance, have large individual variation in their quality as hosts, whereas ticks that fed on mice, veeries, and gray catbirds had consistently high molting success regardless of the individual upon which they fed (Fig. 2B).

Discussion

It is clear from our data that the probability of a larval *I. scapularis* tick successfully molting can vary a great deal depending on the individual blood meal host upon which it fed. Similar host-to-host variability has been observed in deer mice (*Peromyscus maniculatus*) and white-footed mice (Hazler and Ostfeld 1995), although the underlying causes of this variability are unclear. Ross and Levin (2004) demonstrated that certain strains of *Anaplasma phagocytophilium* can reduce the molting success of ticks feeding on infected hosts. The infection status of hosts might therefore explain some of the host-to-host variability in molting success that we observed, although it is worth noting that Ross and Levin (2004) observed similar host-to-host variability even after accounting for infection status. Another explanation is that hosts differ in their immune response to ticks, either because of differences in prior exposure to *I. scapularis* or because of differences in the number of ticks infesting a host. Randolph (1994), for instance, found that molting success of *I. trianguliceps* fed on bank voles (*Myodes glareolus*) decreased with the number of ticks that had previously fed on a host, although a similar effect was not seen with wood mice (*Apodemus sylvaticus*). Similarly, Hazler and Ostfeld (1995) found a large, but nonsignificant decrease in the molting success of larvae fed on previously exposed white-footed mice as compared with naive mice. However, they also found that molting success increased with the density of ticks feeding on individual deer mice such that higher densities of cofeeding ticks facilitated feeding and molting success, although the same effect was not found with ticks fed on white-footed mice. In general, prior exposure to ticks and high tick densities seems to affect feeding success much more than molting success. Davidar et al. (1989), for instance, found that whereas larvae that had fed on previously infested

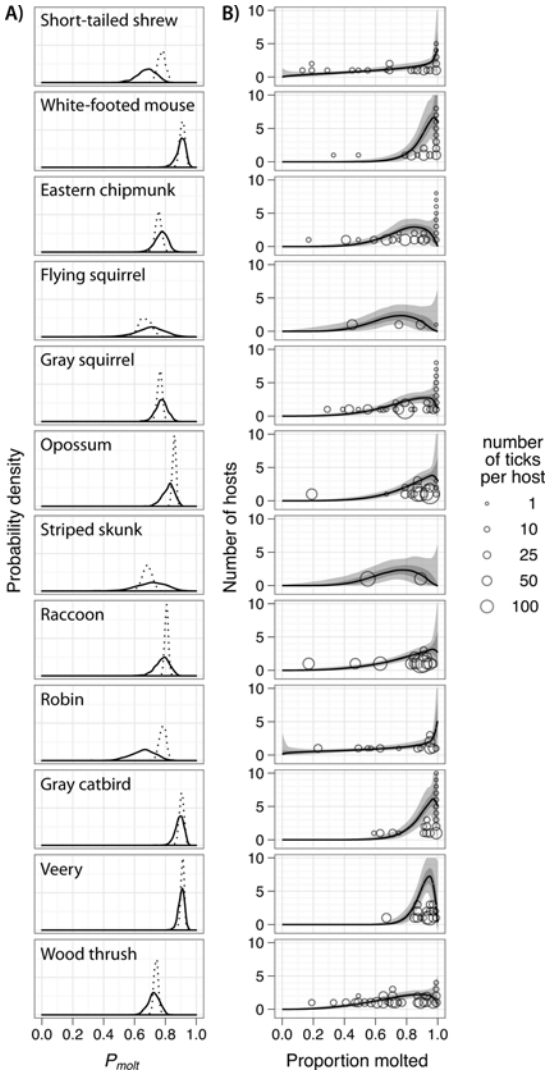

Fig. 2. (A) The posterior distributions of P_{molt} when P_{molt} is a species-specific constant (dotted lines) and expected values of P_{molt} when individuals of a species vary in their quality as hosts (solid line). (B) Circle-size histograms of the proportion of engorged larvae that molted for each blood meal host species. Each circle represents an individual host; its size is proportional to the number of engorged larvae collected from it. The solid lines on the panels are the beta distributions of values of P_{molt} at the median posterior values of α and β. The gray envelopes are the central 50% (dark gray) and 90% (light gray) most probable values of P_{molt} derived from the posterior distributions of α and β.

meadow voles (*Microtus pennsylvanicus*), white-footed mice, and guinea pigs (*Cavia porcellus*) were less likely to successfully feed and were slightly smaller than when fed on naive hosts, the proportion of ticks that successfully molted did not vary accordingly. Our results do not suggest a general trend among species for either higher or lower molting success with increasing numbers of engorged larvae (Fig. 2B).

Whatever the cause, it is clear that the degree of host-to-host variation depends on the species in question. Some species, such as white-footed mice, veeries, and gray catbirds, are consistently very permissive hosts—larvae that fed on almost any individual of one of these host species were very likely to molt. For most of the other host species, interindividual variability was high, such that differences among host species are difficult to discern. It is also worth noting that even among related species—the squirrels and chipmunks (family Sciuridae) and the robins, veeries, and wood thrushes (family Turdidae)—there was substantial variation in molting success. Quality as a blood meal host does not appear to follow these broad taxonomic groups.

Our estimates of molting success were much higher than those presented by LoGiudice et al. (2003). Our lowest estimate of molting success (0.65 for robins) was higher than the highest estimate (0.64 for skunks) in LoGiudice et al. (2003). This discrepancy is most likely a result of improved methods for collecting and molting fed larvae. What is more difficult to explain is the fact that our two sets of estimates are not positively correlated. In fact, there is a slight negative correlation (rho = −0.38). It is possible that different species vary in their quality to ticks from year to year, perhaps depending on nutrition or on prior exposure to ticks. A more straightforward, if not entirely satisfactory, explanation is sampling error. Given the large differences in molting success among ticks feeding on different individual hosts, a few poor quality hosts could drive down the estimates of molting success. This issue would be exacerbated by the method of averaging used in their paper. Given the high rates of molting in the current study, reasonably large sample sizes, and more thorough statistical analysis, we feel that the results presented in this study represent the best host-specific estimates of molting success of larval *I. scapularis* to date.

Prior research has demonstrated that vertebrate hosts for ticks vary strongly in the efficiency by which they transmit tick-borne pathogens to feeding larval *I. scapularis* ticks (e.g., Anderson and Magnarelli 1980, Mather et al. 1989). Recent studies by our group also have shown that host species differ in their likelihood of grooming off and killing ticks, and conversely, in their propensity to support larval feeding (Keesing et al. 2009). In this study, we show that the probability of molting from replete larva to nymph can depend on the host species and host individual from which the blood meal was taken. For some host species, quality as a pathogen reservoir and as a host for vector feeding and molting is strongly correlated. For example, white-footed mice are highly competent reservoirs for pathogens and support highly successful feeding by larvae and high molting success to the nymphal stage (LoGiudice et al. 2003, Keesing et al. 2009, current study). Other hosts, however, can have less consistent impacts on the larva-to-infected-nymph transition. For example, Virginia opossums are incompetent reservoirs for *Borrelia burgdorferi* and kill a high percentage of

larvae during feeding attempts, but are intermediate in their ability to support successful molting. Veeries are relatively poor reservoirs, but strongly support larval feeding and molting success (LoGiudice et al. 2003, Keesing et al. 2009, current study). Future research will need to integrate the variable roles played by host species in affecting tick feeding, infection, and molting success, as well as substantial intraspecific variability, to predict how changes in host community composition will affect the abundance of infected nymphs, and hence, risk of exposure to tick-borne pathogens.

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References Cited

Anderson, J. F., and L. A. Magnarelli. 1980. Vertebrate host relationships and distribution of ixodid ticks (Acari: Ixodidae) in Connecticut, USA. J. Med. Entomol. 17: 314–323.

Brunner, J. L., K. LoGiudice, and R. S. Ostfeld. 2008. Estimating reservoir competence of *Borrelia burgdorferi* hosts: prevalence and infectivity, sensitivity and specificity. J. Med. Entomol. 45: 139–147.

Burgdorfer, W., A. G. Barbour, S. F. Hayes, J. L. Benach, E. Grunwaldt, and J. P. Davis. 1982. Lyme disease: a tick-borne spirochetosis. Science 216: 1317–1319.

Costero, A., and M. A. Grayson. 1996. Experimental transmission of Powassan virus (Flaviviridae) by *Ixodes scapularis* ticks (Acari: Ixodidae). Am. J. Trop. Med. Hyg. 55: 536–546.

Davidar, P., M. Wilson, and J.M.C. Ribeiro. 1989. Differential distribution of immature *Ixodes dammini* (Acari: Ixodidae) on rodent hosts. J. Parasitol. 75: 898–904.

Estrada-Peña, A. 2002. Increasing habitat suitability in the United States for the tick that transmits Lyme disease: a remote sensing approach. Environ. Health Perspect. 110: 635–640.

Ginsberg, H. S., E. Zhioua, S. Mitra, J. Fischer, P. A. Buckley, F. Verret, H. B. Underwood, and F. G. Buckley. 2004. Woodland type and spatial distribution of nymphal *Ixodes scapularis* (Acari: Ixodidae). Environ. Entomol. 33: 1266–1273.

Ginsberg, H. S., P. A. Buckley, M. G. Balmforth, E. Zhioua, S. Mitra, and F. G. Buckley. 2005. Reservoir competence of native north American birds for the Lyme disease spirochete, *Borrelia burgdorferi.* J. Med. Entomol. 42: 445–449.

Hazler, K. R., and R. S. Ostfeld. 1995. Larval density and feeding success of *Ixodes scapularis* on two species of *Peromyscus.* J. Parasitol. 81: 870–875.

James, A. M., and J. H. Oliver. 1990. Feeding and host preference of immature *Ixodes dammini*, *I. scapularis*, and *I. pacificus* (Acari: Ixodidae). J. Med. Entomol. 27: 324–330.

Keesing, F., J. L. Brunner, S. T. Duerr, M. E. Killilea, K. LoGiudice, K. A. Schmidt, H. Vuong, and R. Ostfeld. 2009. Hosts as ecological traps for the vector of Lyme disease. Proc. R. Soc. B. 276: 3911–3919.

Keirans, J. E., H. J. Hutcheson, L. A. Durden, and J.S.H. Klompen. 1996. *Ixodes* (Ixodes) *scapularis* (Acari: Ixodidae): redescription of all active stages, distribution, hosts, geographical variation, and medical and veterinary importance. J. Med. Entomol. 33: 297–318.

Levin, M. L., W. L. Nicholson, R. F. Massung, J. W. Sumner, and D. Fish. 2002. Comparison of the reservoir competence of medium-sized mammals and *Peromyscus leucopus* for *Anaplasma phagocytophilum* in Connecticut. Vector Borne Zoonotic Dis. 2: 125–136.

Lindsay, L. R., I. K. Barker, G. A. Surgeoner, S. A. McEwen, T. J. Gillespie, and E. M. Addison. 1998. Survival and development of the different life stages of *Ixodes scapularis* (Acari: Ixodidae) held within four habitats on Long Point, Ontario, Canada. J. Med. Entomol. 35: 189–199.

LoGiudice, K., R. S. Ostfeld, K. A. Schmidt, and F. Keesing. 2003. The ecology of infectious disease: effects of host diversity and community composition on Lyme disease risk. Proc. Natl. Acad. Sci. USA 100: 567–571.

Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS: a Bayesian modelling framework: concepts, structure, and extensibility. Stat. Comput. 10: 325–337.

Mather, T. N., M. L. Wilson, S. I. Moore, J.M.C. Ribeiro, and A. Spielman. 1989. Comparing the relative potential of rodents as reservoirs of the Lyme disease spirochete (*Borrelia burgdorferi*). Am. J. Epidemiol. 130: 143–150.

Ostfeld, R. S., C. D. Canham, K. Oggenfuss, R. J. Winchcombe, and F. Keesing. 2006. Climate, deer, rodents, and acorns as determinants of variation in Lyme-disease risk. PLoS Biol. 4: e145.

R Development Core Team. 2009. R: a language and environment for statistical computing, 2.10.1 ed. R Foundation for Statistical Computing, Vienna, Austria.

Randolph, S. E. 1994. Density-dependent acquired resistance to ticks in natural hosts, independent of concurrent infection with *Babesia microti.* Parasitology 108: 413–419.

Ross, D. E., and M. L. Levin. 2004. Effects of *Anaplasma phagocytophilum* infection on the molting success of *Ixodes scapularis* (Acari: Ixodidae) larvae. J. Med. Entomol. 41: 476–483.

Schmidt, K. A., R. S. Ostfeld, and E. M. Schauber. 1999. Infestation of *Peromyscus leucopus* and *Tamias striatus* by *Ixodes scapularis* (Acari: Ixodidae) in relation to the abundance of hosts and parasites. J. Med. Entomol. 36: 749–757.

Shaw, M. T., F. Keesing, R. McGrail, and R. S. Ostfeld. 2003. Factors influencing the distribution of larval blacklegged ticks on rodent hosts. Am. J. Trop. Med. Hyg. 68: 447–452.

Sibylle, S., L. Uwe, and G. Andrew. 2005. R2WinBUGS: a package for running WinBUGS from R. J. Stat. Softw. 12: 1–16.

Sonenshine, D. E. 1993. The Biology of Ticks. Oxford University Press, New York, NY.

Spiegelhalter, D. J., N. G. Best, B. P. Carlin, and A. van der Linde. 2002. Bayesian measures of model complexity and fit. J. R. Stat. Soc. Ser. B Stat. Methodol. 64: 583–639.

Spielman, A., M. L. Wilson, J. F. Levine, and J. Piesman. 1985. Ecology of *Ixodes dammini*-borne human babesiosis and Lyme disease. Annu. Rev. Entomol. 30: 439–460.

Telford, S. R., J. E. Dawson, P. Katavolos, C. K. Warner, C. P. Kolbert, and D. H. Persing. 1996. Perpetuation of the agent of human granulocytic ehrlichiosis in a deer tick-rodent cycle. Proc. Natl. Acad. Sci. USA 93: 6209.

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Appendix

WinBUGS Models.

The first model of molting success assuming that the probability of molting, P_{molt}, is constant for a species was as follows:

```
model
  {
    for (i in 1:N) molted[i] ~ dbin(Pmolt, total[i])
  }
  Pmolt ~ dbeta(1.01, 1.01)
}
```

where N is the number of hosts, total is the number of engorged larvae in all vials that were collected from a host, and molted is the number of those engorged larvae that successfully molted. The prior distribution of P_{molt} was assumed to be a very flat beta distribution, although the posterior distribution was not sensitive to other realistic versions of the prior with a positive skew, nor to informative priors estimated from the summary statistics presented in LoGiudice et al. (2003) using the method of moments.

The second model that allowed P_{molt} to vary from host to host was:

```
model
  for (i in 1:NumVials){
    molted[i] ~ dbin(Pmolt[hostNum(i)], total[i])
  }
  for (j in 1:NumHosts){
    Pmolt[j] ~ dbeta(A, B)
  }
  A ~ dgamma(1, 0.1)
  B ~ dgamma(1, 0.1)
  mean <- A/(A + B)
}
```

where P_{molt} takes on different values for each of the j = 1, 2,., NumHosts individual hosts. In this model, each vial from a given host is treated separately. The prior distributions of the shape (A = α) and rate (B = β) parameters of the beta distribution are distributed as flat gamma distributions. Without further data on the distribution of P_{molt} from host to host, it was not feasible to use more informative priors.