

# Biotic and abiotic predictors of tick (*Dermacentor variabilis*) abundance and engorgement on free-ranging raccoons (*Procyon lotor*)

R. J. MONELLO\* and M. E. GOMPPER

Department of Fisheries and Wildlife Sciences, 302 Anheuser-Busch Natural Resources Building, University of Missouri, Columbia, MO 65211, USA

(Received 30 April 2007; revised 5 June and 25 June 2007; accepted 27 June 2007; first published online 23 August 2007)

## SUMMARY

We examined the relative importance of abiotic and biotic factors on the ability of adult *Dermacentor variabilis* ticks to attach and engorge with blood across 10 populations of free-ranging raccoons (*Procyon lotor*). We developed *a priori* models that represented explicit hypotheses based on the literature and tested the ability of these models to explain non-replete and replete (fully engorged with blood) tick infestation using generalized linear models and Akaike's Information Criterion. Abiotic models that included month and site of collection clearly provided a better fit for non-replete tick abundance data, while biotic models with host age and sex covariates best fit the replete tick data. Abiotic models of non-replete abundance were superior to biotic models because of large seasonal and site fluctuations in non-replete abundance that masked differences due to host characteristics. Conversely, best-fitting models of replete tick abundance included only age and sex and suggest that once a tick has reached a host, host-parasite interactions are the primary determinant of engorgement by female ticks. Host population structure may have a large influence on potential cohort size of ticks by reducing or increasing the total number and proportion that can become engorged and moult or lay eggs.

Key words: *Dermacentor variabilis*, *Procyon lotor*, model selection, tick, infestation.

## INTRODUCTION

The survival, population dynamics, and disease vector competency of ticks are a function of the ability of individuals to (1) survive while off the host until a host is found, and (2) once a host is found, to persist on the host for a sufficient period to gain a bloodmeal (Strickland *et al.* 1976; Allan, 2001). Factors that influence the ability of ticks to survive off-host and successfully infest and survive on a host are likely to be different. The former has been found to be a function of local site characteristics such as habitat and microclimate (Daniel, 1978; Lindström and Jaenson, 2003) or host diversity (LoGiudice *et al.* 2003). Thus, factors affecting the number of ticks that ultimately find a host are likely to be intrinsic to the local environment, with the host itself playing a secondary role. Once a host has been found, however, environmental effects may be of secondary importance relative to the density of ticks on a host (competition among ticks resulting in density dependency), and the host behavioural and physiological response to the attachment (factors intrinsic to the host). Together, these factors result in

characteristics of hosts being correlated with parasite prevalence and abundance.

Differences due to sex and weight are well documented in a diversity of mammalian host-parasite associations, including helminths (Poulin, 1996; Morales-Montor *et al.* 2004), arthropods (Schalk and Forbes, 1997), and unicellular parasites (Moore and Wilson, 2002). Male-biased rates of parasitism are primarily attributed to the immunosuppressive effects of male sex hormones (Zuk and McKean, 1996; Cox and John-Alder, 2007), larger body sizes that support more parasites (Folstad and Karter, 1992), or differences in grooming or movement patterns (Mooring *et al.* 1996; Zuk and McKean, 1996). While sex biases in host parasitism have been detected for ticks (Gallivan *et al.* 1995; Mooring *et al.* 1996; Gompper, 2004), few studies have examined patterns in the persistence of ticks once on a host, especially in free-ranging host populations. Yet such information is critical to understanding the likelihood of an individual tick obtaining a bloodmeal, and thereby surviving to reproduce (Wilson *et al.* 1990), as well as remaining on a host for sufficient time to act as a competent disease vector (Piesman *et al.* 1987).

In addition to general correlations with host sex and size, 3 contrasting relationships between host age and parasite abundance have been described: a continual increase over the life of the host; an initial

\* Corresponding author: Tel: +011 573 882 8099. Fax: +011 573 884 5070. E-mail: RyanMonello@mizzou.edu

increase until the number of parasites reaches an asymptote and levels off; and an initial increase and peak, followed by a decline in older animals due to host immune response, death of heavily parasitized animals, or other age-related factors (Hudson and Dobson, 1995). A continual increase or leveling off of parasite burden with age has been observed for a variety of helminth species in mammals (Halvorsen, 1986; Quinnell, 1992) and birds (Hudson, 1992), but few studies have documented an initial increase in young animals and subsequent decline in older animals (but see Gregory *et al.* 1992). Logistic difficulties associated with obtaining such data in the field may have contributed to the lack of such observations (Wilson *et al.* 2003).

Correlation of parasitism to local environmental factors and to host-intrinsic factors such as age or sex and weight suggest the need to study these factors in concert to gain a more precise understanding of the likelihood of ticks persisting on hosts long enough to obtain a bloodmeal and fully act as a disease vector. To gain insights into biotic and abiotic factors that may underlie the likelihood of ticks persisting on hosts to obtain bloodmeals, we examined data on parasitism by the tick *Dermacentor variabilis* from 10 host populations of raccoons (*Procyon lotor*). *Dermacentor variabilis* is the largest and most abundant ectoparasite of raccoons in the Midwest U.S. (Whitaker, 1982; Kollars *et al.* 2000). It is a 3-host tick that is only found on animals while feeding or mating. Once a bloodmeal is obtained, *D. variabilis* drop off the host, moult to the next stage or lay eggs and, if not an adult, seek another host. This life-history results in 2 distinct 'habitats' or 'environments' during each stage: free-living ticks that are seeking a host (questing) and ticks that have obtained a host and are attempting to mate or become fully engorged with blood (i.e. replete).

Our objective was to measure the relative influence of abiotic variables and host characteristics on 2 components of the tick population, male and non-replete female ticks (hereafter referred to as non-replete) and replete female ticks. Adult female *D. variabilis* must feed continuously for 7–10 days to become fully engorged and markedly distended (Atwood and Sonenshine, 1967). We hypothesized that different factors affect non-replete and replete female tick abundance on raccoons. Because free-living adult *D. variabilis* ticks are primarily influenced by local site conditions (Campbell and MacKay, 1979; Sonenshine, 1991) and time of collection (Kollars *et al.* 2000), we predicted that non-replete infestation will primarily be related to abiotic factors such as site or month of data collection that influence questing ticks. Conversely, we predicted that the ability of a female tick to remain on their host and become fully engorged is more likely to be influenced by host characteristics such as age or sex. Such effects are expected to be particularly

important if testosterone is suppressing the immune system, if acquired immunity is occurring, or if other age-related factors predict the extent of parasitism.

#### MATERIALS AND METHODS

##### *Host species and tick quantification*

Raccoons were sampled during summer 2005 and 2006 at 10 locations in central Missouri. All sites were located on state, federal, or university conservation or research areas within 60 km of Columbia, MO. Sites consisted of second growth oak (*Quercus* spp.) and hickory (*Carya* spp.) forest with a maple (*Acer* spp.) and cedar (*Juniperus virginiana*) understorey. All sites were >10 km apart, with the exception of 2 areas that had 2 sites each, that were 4 km apart. To reduce confounding effects of seasonal fluctuations in tick abundance, only animals captured between 20 May and 5 August were included in analyses. Our trapping extended beyond these dates, but tick infestations were not consistently observed across all study sites before mid-May or after early August in 2005 or 2006. This is consistent with other studies of raccoons and *D. variabilis* in Missouri (Kollars *et al.* 2000), and we assumed that all animals included in analyses were susceptible to infestation during this time period. Data from recaptured animals were not included in analyses. Research was carried out under Missouri Department of Conservation permit #12869 and University of Missouri Animal Care and Use Protocol #3927.

Trapping occurred at all 10 areas in 2005 but we only included data from 4 of the areas in 2006 because food supplementation treatments were initiated in the other 6 areas as part of a separate study. These areas were not included because raccoon behaviour and resource availability in these areas were altered, which may influence parasite prevalence and abundance (Wright and Gompper, 2005). Traps were baited with mackerel and checked daily. Raccoons were immobilized with an injection of ketamine hydrochloride and xylazine (Evans, 2002), marked with metal ear tags, weighed, sexed, and aged by body size, genital morphology, and tooth eruption and wear (Grau *et al.* 1970; Larson and Taber, 1980). Grau *et al.* (1970) provided tooth wear patterns for 5 age classes; I=0–14 months, II=15–38 months, III=39–57 months, IV=58–86 months, and V=over 86 months. We combined ages IV and V due to difficulty distinguishing between these groups (hereafter referred to as IV+), and included a cub category (0–5 months) based on date of capture, weight, and dental characteristics.

Adult *D. variabilis* ticks are distinct, relatively large (3–5 mm in length), and readily found and identified on animals in the field without magnification. We quantified adult *D. variabilis* by a

Table 1. *A priori* models used to estimate non-replete and replete *Dermacentor variabilis* tick abundance of raccoons in Missouri

( $\beta_0$  = intercept,  $\beta_i(X)$  are the parameters of independent variables.)

Hypothesis	Model	Model structure
<b>Host characteristics</b>		
Differences are due to host characteristics	Age + Sex + Weight	$\beta_0 + \beta_1(\text{Age}) + \beta_2(\text{Sex}) + \beta_3(\text{Weight})$
Differences are due to host age	Age	$\beta_0 + \beta_1(\text{Age})$
Differences are due to host sex	Sex	$\beta_0 + \beta_1(\text{Sex})$
Differences are due to host weight	Weight	$\beta_0 + \beta_1(\text{Weight})$
Differences are due to host age and sex	Age + Sex	$\beta_0 + \beta_1(\text{Age}) + \beta_2(\text{Sex})$
Age-related differences are related to host sex	Age * Sex	$\beta_0 + \beta_1(\text{Age}) + \beta_2(\text{Sex}) + \beta_3(\text{Age} * \text{Sex})$
Differences are due to host weight and sex	Weight + Sex	$\beta_0 + \beta_1(\text{Weight}) + \beta_2(\text{Sex})$
Weight-related differences are related to host sex	Weight * Sex	$\beta_0 + \beta_1(\text{Weight}) + \beta_2(\text{Sex}) + \beta_3(\text{Weight} * \text{Sex})$
<b>Abiotic factors</b>		
Differences are due to abiotic factors	Month + Site + Year	$\beta_0 + \beta_1(\text{Month}) + \beta_2(\text{Site}) + \beta_3(\text{Year})$
Differences are due to month and study site	Month + Site	$\beta_0 + \beta_1(\text{Month}) + \beta_2(\text{Site})$
Differences are due to month	Month	$\beta_0 + \beta_1(\text{Month})$
<b>Global</b>		
Differences are due to host characteristics and abiotic factors	Age + Sex + Weight + Month + Site + Year	$\beta_0 + \beta_1(\text{Age}) + \beta_2(\text{Sex}) + \beta_3(\text{Weight}) + \beta_4(\text{Month}) + \beta_5(\text{Site}) + \beta_6(\text{Year})$

thorough search of the entire body (Kollars *et al.* 2000; Kollars and Kengluetcha, 2001), and classified each tick as non-replete (i.e. not engorged with blood), replete (engorged), or semi-replete. We considered ticks to be non-replete if they were not discolored and similar in width (2–3 mm) to questing adult *D. variabilis* ticks found off host. We considered a tick to be replete when it was obviously engorged with blood,  $\geq 5$  mm width, and discolored. Ticks that were not clearly in either category were noted as semi-replete and not included in analyses.

Prevalence and abundance were estimated, respectively, as the number of animals infested by ticks divided by the total number of animals examined, and as the total number of ticks observed on each individual animal (Bush *et al.* 1997). We also calculated the ratio of replete:non-replete ticks for each individual host; this measure approximates a proportion of ticks that encounter a host that persist to the point of fully obtaining a bloodmeal. We used Mann-Whitney U tests to examine sex-related differences in tick abundance in each age category. Separate comparisons were conducted within age classes to ensure statistical differences due to sex would not be masked or biased by divergent patterns in older or younger individuals and reveal the nature of sex\*age interactions. Because there were 5 age-class analyses for each of non-replete tick abundance, replete tick abundance, and the ratio of replete to non-replete abundance, we used a Bonferroni correction ( $\alpha = 0.05/5 = 0.01$ ) to qualify statistically supported relationships. Thus, values of  $P \leq 0.01$

were deemed significant, and values of  $0.05 > P > 0.01$  were deemed weakly significant.

#### Model selection

We used information-theoretical model selection to test *a priori* models predicting non-replete tick abundance and replete tick abundance. Model selection refers to the process of using the observational data to evaluate a suite of models that represent hypotheses. Models are ranked and weighted to evaluate the probability that the model in question is the best fitting model. Although rarely applied in ecological parasitology, model selection has been increasingly used in the broader ecological literature over the last 20 years (Johnson and Omland, 2004), and can provide a powerful tool to identify the most relevant ecological factors influencing dependent variables such as parasite abundance.

We erect a series of explicit hypothesis-based models that relate abiotic and host characteristics to the abundance of parasitizing ticks (Table 1), and rank the fit of these models using an information-theoretical approach. Such an approach allows us to identify not only the support for an array of hypotheses, but also to rank the hypotheses and thereby discern the model with the greatest support in explaining parasitism by ticks. Model covariates included 3 abiotic (site, month, year of collection) and 3 biotic variables (sex, age, weight of host). The same set of models were used to predict non-replete and replete abundance to evaluate differences in

Table 2. Prevalence (%) of *Dermacentor variabilis* on raccoons

(Raccoon age class designations are cub = 0–5 months, I = 5–14 months, II = 15–38 months, III = 39–57 months, IV+ =  $\geq 58$  months. Sample sizes ( $n$ ) represent number of individual raccoons.)

Ticks	All	Males	Females	Cubs	I	II	III	IV+
Non-replete	92%	92%	92%	56%	95%	95%	97%	85%
Replete	64%	63%	65%	11%	38%	75%	78%	75%
$n$	177	75	102	9	37	79	32	20

predictive abilities across tick populations as a whole. The number of non-replete ticks was not included as an independent parameter in models of replete tick abundance as we were specifically interested in whether and how biotic and abiotic factors influence replete tick abundance, and including non-replete ticks as a parameter for replete tick models would likely confound the test of the hypothesis that temporal and spatial abiotic factors are important drivers of tick abundance (Burg, 2001; see below).

We tested whether non-replete and replete ticks differed from a negative binomial distribution using the maximum-likelihood method of Bliss and Fisher (1953) with the program Quantitative Parasitology 3.0 (Rozsa *et al.* 2000). We used generalized linear models with a negative binomial distribution for model selection. Tick abundance of individual raccoons was the sample unit and all covariates were fixed effects. We calculated Akaike's Information Criterion (corrected for small sample size;  $AIC_c$ ) to rank the models and calculated the difference between the best approximating model (i.e. the model with the lowest  $AIC_c$ ) and all other models ( $\Delta AIC_c$ ) in the candidate set. Only models with an  $AIC_c$  value within 2 points of the best-fitting model were considered to have substantial empirical support as a best-fitting model (Burnham and Anderson, 2002).

## RESULTS

### Quantitative patterns

We captured 177 individual raccoons, with an average of  $17.7 \pm 2.63$  (s.e.) animals caught per study area. Prevalence of non-replete ticks did not vary between males and females (92% for both) and, with the exception of cubs (56%), was  $\geq 85\%$  for all age classes. Prevalence of replete ticks was also similar among males (63%) and females (65%). Prevalence of replete ticks increased in older animals, ranging from 11 to 38% for cubs and age class I animals, and 75 to 78% for age class II and above (Table 2).

Tick distributions did not differ from a negative binomial distribution (non-replete  $\chi^2 = 21.67$ , D.F. = 22,  $P = 0.520$ ; replete  $\chi^2 = 10.09$ , D.F. = 13,  $P = 0.310$ ). The exponent of the negative binomial ( $k$ ) indicated that both non-replete ( $k = 0.890$ ) and

replete ( $k = 0.600$ ) ticks were highly aggregated on raccoons. Replete ticks displayed a greater degree of aggregation, with 10% ( $n = 18$ ) of hosts harbouring 51% of the replete *D. variabilis* (Fig. 1). Non-replete tick abundance across all sites combined ranged from 0 to 95 and averaged  $16.27 \pm 1.35$  (s.e.). Replete tick abundance ranged from 0 to 21 and averaged  $2.54 \pm 0.28$ . Across sites, the range of means for ticks per animal was 3.63 to 30.23 for non-replete and 0.42 to 3.69 for replete ticks. There were temporal differences in the mean abundance for non-replete and replete ticks; both peaked in July, but replete abundance displayed less variation than non-replete abundance (Fig. 2). The ratio of replete:non-replete did not differ by month (Kruskal-Wallis  $H' = 5.990$ , D.F. = 3,  $P = 0.112$ ).

Non-replete tick abundance increased with age, with the exception of females in age class IV+ (Fig. 3A). In age class II, males supported a greater number of non-replete ticks than females (Mann-Whitney U-test,  $P = 0.001$ ), and there was a weakly significant pattern ( $P = 0.037$ ) for age class IV+. No other sex-related differences were detected among non-replete ticks ( $P \geq 0.160$  for all other comparisons), although males consistently had higher tick burdens. Replete tick abundance displayed an increasing trend with age of host; however, both females and males in age class IV+ exhibited declines in replete tick abundance when compared to age class III (Fig. 3B). No sex-related differences were detected among replete tick abundance in any age class ( $P \geq 0.181$  for all comparisons), although as for non-replete ticks, males consistently had higher tick burdens (excepting cubs).

There was a significant difference among age classes in the ratio of replete to non-replete ticks (Kruskal Wallis  $H' = 18.54$ , D.F. = 4,  $P = 0.001$ ) (Fig. 3C). Post-hoc comparisons indicated significant differences between age classes I and II (Mann-Whitney U-test,  $P = 0.001$ ) and I and III ( $P = 0.001$ ), and weakly significant differences between age classes III and IV+ ( $P = 0.025$ ). Within each age class, no sex-related differences were detected for the ratio of replete to non-replete ticks (Mann-Whitney U-test,  $P \geq 0.054$  for age class II and  $P \geq 0.432$  for all other age classes).

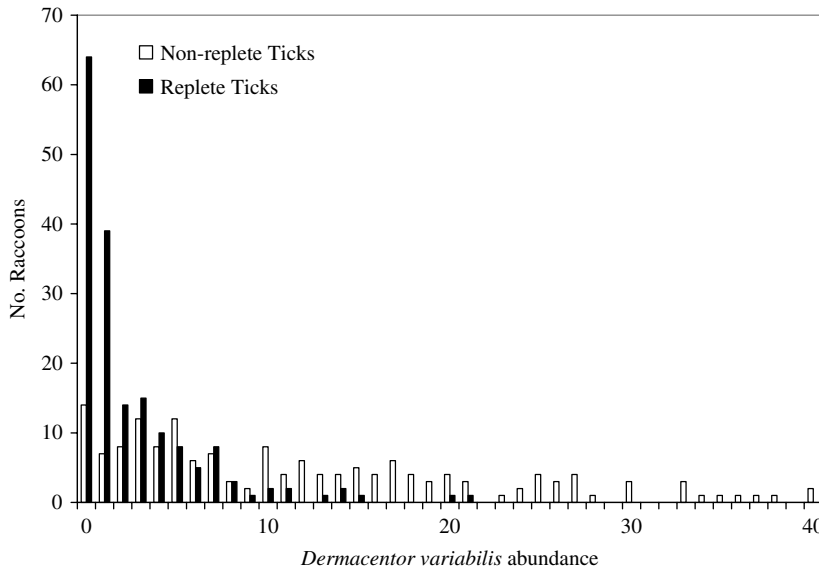


Fig. 1. Number of non-replete and replete *Dermacentor variabilis* adult ticks infesting raccoons in mid-Missouri. Note: 15 raccoons had >40 non-replete ticks (range=41 to 95). These data were removed for figure clarity.

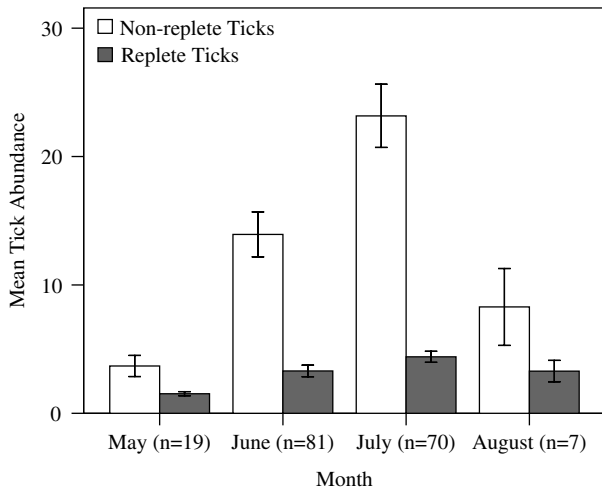


Fig. 2. Mean ( $\pm$  S.E.) seasonal abundance of *Dermacentor variabilis* adult ticks on raccoons in Missouri during 2005 and 2006. Sample sizes represent number of animals captured in each month.

Model selection

Non-replete tick abundance was best predicted by abiotic models (Table 3). The non-replete<sub>month+site</sub> model was the best fitting model of the data, with no other models falling within 2 AIC<sub>c</sub> units; thus this model represents the only model considered to have substantial empirical support as the best fitting model. The weight of evidence (i.e. probability) in favour of non-replete<sub>month+site</sub> being the best model was 0.66. The non-replete<sub>month+site+year</sub> model ranked second ( $\Delta$ AIC<sub>c</sub> = 2.21) and had a weight of 0.22. Global and host characteristic (biotic) models had little support as a best-fitting model (AIC<sub>c</sub> weight  $\leq$  0.04 in all cases; Table 3).

Conversely, biotic models provided a better fit for replete tick data. The top 5 models were based on factors intrinsic to the host, with replete<sub>age</sub> and replete<sub>age+sex</sub> both having substantial empirical support as the best fitting model (Table 4). The AIC<sub>c</sub> values for these models differed little and both had similar weight of evidence as the best fitting model (replete<sub>age</sub> AIC<sub>c</sub> weight = 0.45, replete<sub>age+sex</sub> AIC<sub>c</sub> weight = 0.36). The only other model with substantial support based on weight of evidence was replete<sub>age+sex+weight</sub> (AIC<sub>c</sub> weight = 0.11). None of the abiotic models had an AIC<sub>c</sub> weight > 0.01 (Table 4).

DISCUSSION

We observed clear differences in factors predicting the abundance of non-replete and replete *D. variabilis* on raccoons. Non-replete abundance was primarily a function of month and site of collection and, while a relationship between abundance and host age and sex was observed, these relationships were of secondary importance in predicting tick abundance on hosts. In contrast, replete tick abundance was best predicted by biotic covariates, in particular host age and sex. Such differences are surprising because age profiles of non-replete and replete abundance were similar, both displaying a positive relationship with age. However, seasonal fluctuations of non-replete abundance were >400% greater than replete abundance. This suggests that for non-replete ticks seasonal and site-specific effects overshadow age and sex-specific differences in susceptibility to tick attachment, but factors intrinsic to the host are more important for predicting the abundance of ticks that are able to both reach a host by questing and subsequently persist on the host long enough to become fully engorged.

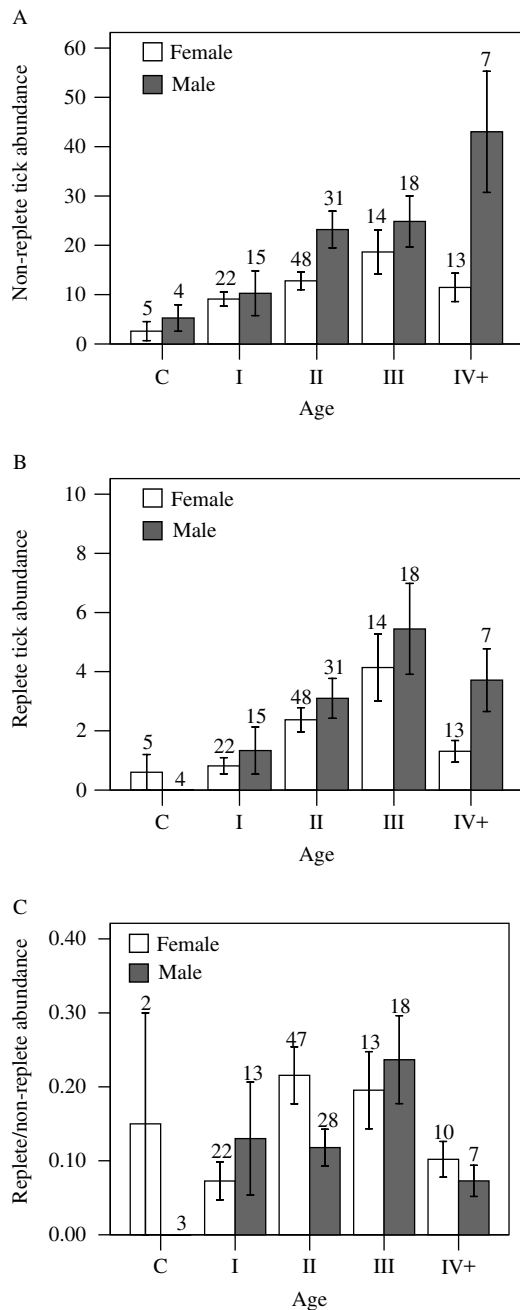


Fig. 3. Mean ( $\pm$  S.E.) abundance of non-replete (A) and replete (B) *Dermacentor variabilis* ticks; and the ratio ( $\pm$  S.E.; only animals with at least 1 non-replete tick are included) of replete to non-replete *Dermacentor variabilis* ticks (C) on raccoons. Raccoon age class designations are c = cub, I = 5–14 months, II = 15–38 months, III = 39–57 months, IV+ =  $\geq$  58 months. Sample sizes are shown above S.E. bars.

Previous research had found that host-seeking adult *D. variabilis* display large seasonal fluctuations in abundance and are aggregated in habitats and locations where the likelihood of survival and host attachment are best. Kollars *et al.* (2000) sampled free-living adult *D. variabilis* in Missouri and observed a peak in July with similar magnitudes of difference between months to that observed in this

Table 3. Ranking of *a priori* models estimating abundance of non-replete *Dermacentor variabilis* adult ticks on raccoons

(Rankings are based on Generalized Linear Models with a negative binomial distribution;  $n = 177$ .)

Model	$\log(l)^a$	$k^b$	$\Delta AIC_c^c$	$AIC_c$ weight
Month + Site	-657.09	14	0.00	0.66
Month + Site + Year	-657.01	15	2.21	0.22
Weight + Sex	-670.92	4	5.56	0.04
Month	-670.26	5	6.35	0.03
Weight	-672.52	3	6.69	0.02
Weight * Sex	-671.62	5	6.98	0.02
Age + Sex + Weight	-668.95	8	10.15	0.00

<sup>a</sup> Maximized log-likelihood value.

<sup>b</sup> The number of model parameters.

<sup>c</sup> The lowest  $AIC_c$  score was 1342.41.

Table 4. Ranking of *a priori* models estimating abundance of replete female *Dermacentor variabilis* adult ticks on raccoons

(Rankings are based on Generalized Linear Models with a negative binomial distribution;  $n = 177$ .)

Model	$\log(l)^a$	$k^b$	$\Delta AIC_c^c$	$AIC_c$ weight
Age	-413.86	6	0.00	0.45
Age + Sex	-413.18	7	0.48	0.36
Age + Sex + Weight	-413.16	8	2.91	0.11
Weight	-419.54	2	5.06	0.04
Weight + Sex	-419.35	4	6.77	0.02
Month	-418.47	5	7.08	0.01
Age * Sex	-412.16	7	7.56	0.01
Weight * Sex	-419.23	4	8.61	<0.01
Sex	-422.07	3	10.13	0.00

<sup>a</sup> Maximized log-likelihood value.

<sup>b</sup> The number of model parameters.

<sup>c</sup> The lowest  $AIC_c$  score was 838.08.

study. These patterns are also consistent with those observed in northeastern North America (Campbell, 1979; McEnroe, 1979; McEnroe and Specht, 1987). In contrast, adult *D. variabilis* in Southeast U.S. display bimodal or multimodal activity patterns due to the large numbers of adult ticks that successfully overwinter and attach to hosts in spring (Sonenshine and Stout, 1971; McEnroe, 1974; Sonenshine, 1979; Newhouse, 1983; Carroll and Nichols, 1986; McEnroe and Specht, 1987; Burg, 2001). Based on seasonal fluctuations in this study and that of Kollars *et al.* (2000), Missouri populations appear to primarily consist of overwintering larvae that result in summer cohorts of adults. Burg (2001) suggested that summer cohorts of *D. variabilis* may have greater energy reserves than overwintering adults. Future research should determine whether this

results in higher rates of host attachment, feeding success, or transovarial disease transmission via greater egg mass size and zoonotic amplification of tick-borne pathogens such as Rocky Mountain spotted fever (*Rickettsia* spp.).

Site and month of collection were the primary influence on non-replete tick abundance, but there were consistent increases in tick burden through age class III (declines in age class IV+ are discussed below). This suggests that there may be age-related behavioural or physiological factors that influence tick infestation (as there are with sex-related differences). The most likely explanation is that the youngest animals (age classes C and I) may receive the benefits of grooming from adult females that they den and travel with, while for older animals (age classes II–IV+) greater movements may increase susceptibility to infestation. Therefore, on a smaller scale (within a site *vs* between sites), age is of greater relative importance than sex when considering tick infestation in general. A variety of patterns have been described for helminths and mammals (e.g. Halvorsen, 1986; Gregory *et al.* 1992; Quinnell, 1992); however, we know of no studies that have examined the influence of age on tick acquisition in free-living mammals. Hudson (1992) found that tick intensity declined in red-grouse chicks after 2 weeks when Louping ill virus was present, but continually increased in the absence of this disease. Further investigation is needed to determine whether such relationships are common.

The finding that the best-fitting models of replete tick abundance included age and sex and no abiotic covariates suggests that once a tick has reached a host, host-parasite interactions are the primary determinant of full engorgement by female ticks, independent of where the host is found. This is also supported by the observations that replete tick abundance exhibited little difference between months, and a greater degree of aggregation than non-replete abundance. Several mechanisms may underlie the prominent role of host characteristics, including acquired immunity, tick-associated mortality of hosts, or the effect of density dependence on numbers of ticks on a host. Previous research has found a variety of mammals to acquire resistance to tick infestation (Wikel, 1996; Hughes and Randolph, 2001; Castagnoli *et al.* 2003), including *D. variabilis* (Trager, 1939; denHollander and Allen, 1985). Raccoons have been found to develop immunity to *Ixodes scapularis* (Craig *et al.* 1996), but this has not been examined for *Dermacentor* spp. Our results do not, however, support acquired immunity as underlying our models, for although we saw a decline in the absolute number and proportion of replete tick abundance in older age classes, acquired immunity is predicted to occur at a much earlier age. Craig *et al.* (1996) found a significant decline in the proportion of engorged *Ixodes scapularis* larvae within 2 months

of initial tick infestation, and antibody production displayed a 2 to 10-fold increase within weeks of infestation. Other studies also suggest that immunity to ticks develops in mammals and birds within weeks or months (Hudson, 1992; Hughes and Randolph, 2001; Castagnoli *et al.* 2003). Acquired immunity might be perceived as underlying the decline in the abundance of replete compared to non-replete ticks observed between months (excepting August for which sample sizes were small). However, these data disassociated the abundance of these 2 classes of ticks on individual hosts. When the ratio of replete:non-replete ticks on individual hosts is examined, there is no temporal decline in the likelihood of a female tick persisting to become engorged.

The decline of replete ticks in the oldest age class suggests that the most heavily infested older animals may die earlier, perhaps due to persistently high tick burdens or due to causes that correlate with, or result in, higher tick burdens. *Dermacentor* spp. are known to cause tissue damage, anaemia, and paralysis in domestic animals (Strickland *et al.* 1976; Allan, 2001). Hawlena *et al.* (2006) observed age-related differences in flea-induced mortality of rodents; thus while tick-driven effects have not been evaluated in natural hosts, older animals are likely to be more susceptible to such impacts. Alternatively, ticks may be more abundant on less healthy animals that have higher mortality rates. Ticks may also have indirect effects by transmitting diseases or creating sites suitable for bacterial infection. Problematically for the explanation that declines in replete tick abundances in older age classes may be a function of host mortality, however, is the finding that non-replete tick burdens also decline among the oldest females (but not males). Such a pattern seems unlikely to derive from host mortality.

Lack of variation in replete compared to non-replete abundance may be due to ticks reaching their carrying capacity and exhibiting density dependence due to limited host resources or intraspecific interactions. Competition between ectoparasites is not expected to have a significant influence on rates of infestation because many species spend long periods of time off the host, and thus it has received little research attention (Krasnov *et al.* 2005). Adult *Dermacentor* ticks exhibit high prevalence (Kollars *et al.* 2000; this study), however, and are located almost exclusively on the head of raccoons, primarily on the back of the neck and in and around the ears (R. Monello, unpublished observation). Raccoons can presumably self-groom all other locations and thus space may be limited for tick attachment sites. In addition, several studies have documented the effect of density dependence on numbers of ticks on hosts that can develop acquired immunity (Randolph, 1994) and competition for food between and within haematophagous flea species (Tripet and Richner, 1999; Krasnov *et al.* 2005).

Although differences in parasitism between male and female raccoons were not statistically significant within most age classes, the consistent trend of greater tick burdens in males was important in model formulation. The lack of large sex-related differences within age classes is not surprising as male raccoons in Missouri are only ~12% larger than females (Lotze and Anderson, 1979) and the degree of male-biased parasitism is often associated with sexual dimorphism (Moore and Wilson, 2002). In addition, *D. variabilis* parasitize raccoons pre- and post-parturition, and the immunosuppressive effects of hormones or energy required during pregnancy or lactation can increase rates of parasitism in females (Festa-Bianchet, 1989; Dobson and Meagher, 1996).

Factors that influence the ability of female ticks to feed to repletion may impact tick population and disease dynamics because female egg mass is related to the amount of blood ingested (Strickland *et al.* 1976; Allan, 2001), and transovarial pathogen maintenance of *Rickettsia* spp. (including *R. rickettsii*, i.e., Rocky Mountain spotted fever) and *Francisella tularensis* has been documented in *Dermacentor variabilis* (Macaluso *et al.* 2002; Goethert and Telford, 2005; Parola *et al.* 2005). Thus, while environmental factors are of importance during free-living stages, host population structure may have a large influence on potential cohort size of ticks by reducing or increasing the total number and proportion that can become engorged and moult or lay eggs. Such effects may be particularly important when the host is the primary feeding source for the tick and when individuals exhibit large differences in susceptibility or response to parasitism as a function of sex and age. Further research on host-tick interactions should focus on mechanisms underlying these patterns and the ability of ticks to become engorged.

This work was supported by an NSF grant (DEB-0347609) to M. Gompper. We thank J. Millspough for assistance with model analyses and B. Cook, T. Hamilton, K. McBride, T. McVicker, A. Wiewel, and J. Wisdom for assistance in the field.

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