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Accelerated phenology of blacklegged ticks under climate warming

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The phenology of tick emergence has important implications for the transmission of tick-borne pathogens. A long lag between the emergence of tick nymphs in spring and larvae in summer should increase transmission of persistent pathogens by allowing infected nymphs to inoculate the population of naive hosts that can subsequently transmit the pathogen to larvae to complete the transmission cycle. In contrast, greater synchrony between nymphs and larvae should facilitate transmission of pathogens that do not produce long-lasting infections in hosts. Here, we use 19 years of data on blacklegged ticks attached to small-mammal hosts to quantify the relationship between climate warming and tick phenology. Warmer years through May and August were associated with a nearly three-week advance in the phenology of nymphal and larval ticks relative to colder years, with little evidence of increased synchrony. Warmer Octobers were associated with fewer larvae feeding concurrently with nymphs during the following spring. Projected warming by the 2050s is expected to advance the timing of average nymph and larva activity by 8–11 and 10–14 days, respectively. If these trends continue, climate warming should maintain or increase transmission of persistent pathogens, while it might inhibit pathogens that do not produce long-lasting infections.

1. Introduction

In eastern North America, the life stages of the blacklegged tick, *Ixodes scapularis*, have asynchronous phenology. Asynchrony generates a lag between nymphal tick inoculation of wildlife hosts with zoonotic pathogens and larval acquisition of those pathogens from infected hosts. Climate warming can disrupt existing host–vector–pathogen dynamics such as this by shifting phenologies [1,2], just as warming affects interactions in plant–pollinator, predator–prey and herbivore–plant systems [3,4]. For blacklegged ticks, a longer lag (greater asynchrony) should increase transmission of persistent pathogens, such as the Lyme bacterium (*Borrelia burgdorferi*), by allowing nymphs to inoculate the vertebrate host population prior to larval feeding. In contrast, greater synchrony should facilitate transmission of pathogens that do not persist in hosts for long periods [2,5].

Ixodes scapularis ticks transmit bacterial, protozoan and viral pathogens that cause Lyme disease, anaplasmosis, babesiosis and Powassan encephalitis. Lyme disease, in particular, is a major public health problem in the Northeastern and Midwestern USA and is the most common vector-borne disease in North America. Powassan encephalitis is a currently rare but severe disease that causes mortality in approximately 10% of patients and persistent illness in at least 50% of survivors [6]. *I. scapularis* requires a single bloodmeal to transition between each of the larval, nymph and adult life stages. Nymphs infect vertebrate hosts that subsequently infect larvae to maintain the enzootic cycle. Adult ticks are generally not part of the transmission cycle, because adult males do not feed and adult females feed primarily on large mammals such as deer, which are not competent reservoir hosts for the strains or genospecies of these tick-borne pathogens that infect humans [7–9]. Transmission of pathogens to humans is predominantly by the nymphal life stage, because larvae are not yet

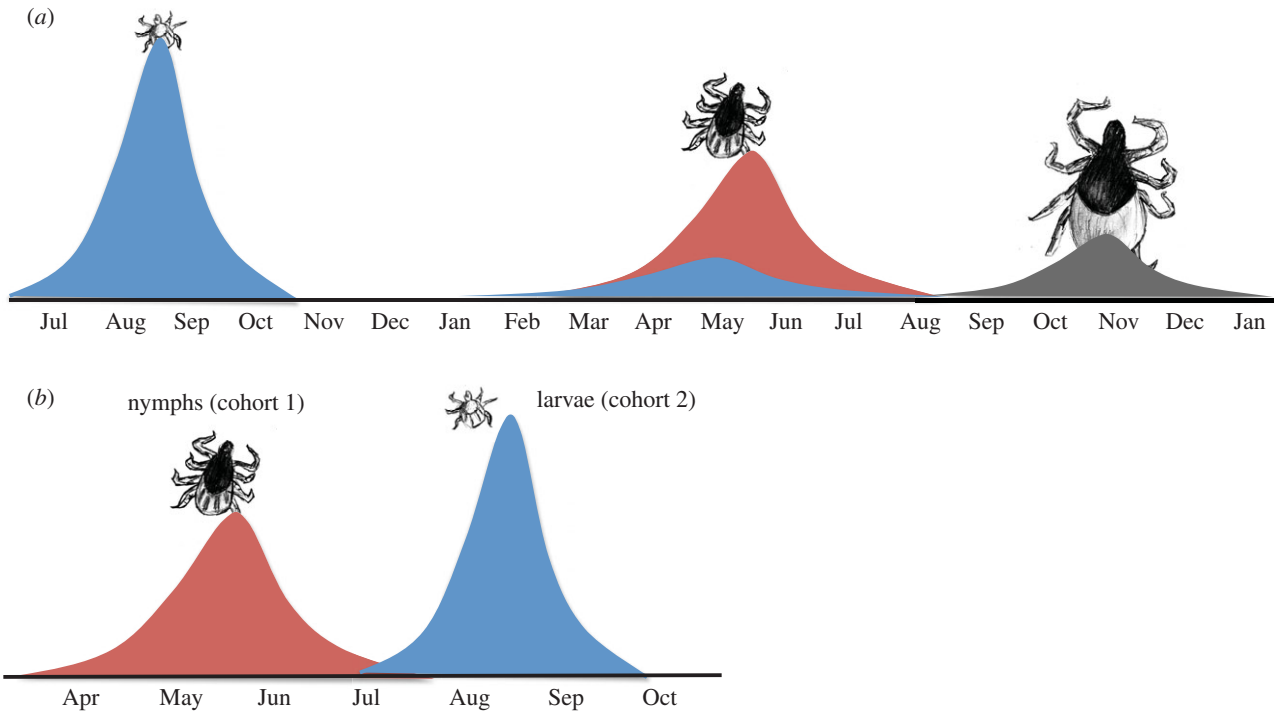

Figure 1. Conceptual diagram of the two pathways by which larval and nymphal ticks can interact through phenology. (*a*) A single cohort of ticks during its larval (blue), nymphal (red) and adult (grey) stages. Larvae can overwinter and feed simultaneously with nymphs in May–June. It is unknown whether larvae feeding during this early activity period overwinter to feed as nymphs during the following year or if these larvae are responsible for the small number of nymphs that we observe in late summer/early autumn feeding coincidentally with the next cohort of larvae. (*b*) Two cohorts of ticks at the nymphal (first cohort) and larval (second cohort) stages. Host-seeking behaviour of nymphs from one cohort occurs shortly before host-seeking behaviour of larvae from the next cohort. (Online version in colour.)

infected (transovarial transmission is rare or absent), adult ticks are large enough to be easily noted and removed before pathogen transmission, and nymphal activity in spring and early summer coincides with a major period of human outdoor activity [10].

The phenology of Ixodid tick life stages is variable regionally and between tick species, which influences the proportion of nymphs infected with each pathogen. In northeastern North America (New England and mid-Atlantic states), there is an extended delay between peak *I. scapularis* nymph activity in May and June and peak larval activity in August and September, although a fraction of larvae overwinter and feed concurrently with nymphs in the spring [11] (figure 1). In contrast, all life stages of *Ixodes ricinus* in Europe, and *Ixodes persulcatus* in Asia, can feed synchronously [2], with the degree of synchrony varying geographically and likely determined by climate [12]. Laboratory experiments have demonstrated that the progression of multiple tick life-history stages vary with incubation temperature, including larval moulting and survival, and time to larval eclosion [13]. This has led to mathematical models suggesting that climate change will cause *I. scapularis* larvae that are active earlier in the year to moult into nymphs that quest synchronously with larvae during the autumn of the same year [14], but this prediction has yet to be tested with long-term empirical data linking variation in larval and nymphal phenology to climate.

The degree of synchrony between larvae and nymphs is important for pathogen transmission. Asynchrony allows pathogens to disseminate within the vertebrate host population following inoculation by nymphs and prior to the emergence of larvae, which should increase transmission of pathogens that maintain prolonged infectivity in vertebrate hosts. For example, most strains of the Lyme disease bacterium, *Borrelia burgdorferi*, produce persistent infections in rodent hosts that are efficiently transmitted to larvae months after inoculation [15,16]. Low infection prevalence of *B. burgdorferi* in nymphal ticks in Europe and Asia, compared with eastern North America, is thought to arise in part from synchronous feeding of larvae and nymphs in the former [2]. In contrast, synchronous phenology in some parts of Europe is responsible for the maintenance of enzootic cycles of tick-borne encephalitis virus, because the pathogen is most effectively transmitted from infected nymphs to larvae feeding in close proximity on the same host (i.e. co-feeding transmission) [12]. The bacterial pathogen *Anaplasma phagocytophilum* also benefits from increased synchrony, because vertebrate hosts transmit the pathogen efficiently for less than two weeks after exposure [17]. Thus, increased phenological synchrony in North America is expected to reduce Lyme disease risk, but increase the risk of anaplasmosis and Powassan encephalitis. However, changes in temperature and relative humidity may also influence tick abundance and infection prevalence independent of tick phenology [2].

There are two mechanisms by which *I. scapularis* phenology might synchronize. First, the major activity peaks of nymphal and larval feeding could increasingly overlap if the peak of larval activity advances more than the peak of nymphal activity, which could occur if adult ticks produce eggs earlier in the year or if egg incubation time is shorter. Second, the fraction of larvae that overwinter and feed in the spring, when nymphs are active, could increase so that the currently minor peak in larval activity would become larger (figure 1). While the main larval peak occurs in late summer, a portion of each year's larval tick cohort overwinters and becomes active concurrently with the nymphal peak the following late spring [18]. This phenomenon may be driven by climate if rapid cooling in the autumn causes larvae to reduce questing activity or enter diapause early rather than continuing to seek a host [12,18].

In addition to the timing of the larval and nymphal peaks relative to each other, the absolute timing of the nymphal peak is important in influencing human exposure rates. In the northeastern United States, the late spring to early summer timing of peak nymphal activity coincides with human outdoor activity, which is thought to increase risk of human exposure [10]. Substantial changes in the timing of this peak could influence the coincidence of tick and human activity, affecting epidemiological patterns.

Here, we use 19 years (1994–2012) of small-mammal and tick data from six trapping grids at the Cary Institute of Ecosystem Studies in Millbrook, NY to quantify the relationship between climate warming and the phenology of larval and nymphal ticks (figure 1). These data represent 53 918 mouse and 12 087 chipmunk captures leading to combined counts of 403 266 larvae and 44 372 nymphs on the heads and ears of mice and chipmunks. We hypothesized that tick phenology would advance with climate warming, but did not have an *a priori* hypothesis as to whether the nymphal or larval peak would advance more. We additionally hypothesized that the number of larvae feeding in spring, where co-feeding transmission is more likely to occur, would be higher if more larvae entered diapause earlier and overwintered owing to colder weather near the end of larval activity in October. We additionally use our results to predict the timing of nymphal and larval activity in the future (2020s and 2050s) under projected levels of climate warming in southeastern New York.

2. Methods

We analysed 19 years of data from a small-mammal trapping programme at the Cary Institute of Ecosystem Studies in Millbrook, New York [19]. We used mark–recapture techniques on six permanent trapping grids placed within similar oak-dominated forest, each consisting of 242 of Sherman traps arranged in pairs in an 11-by-11 grid (10-by-12 grid in one case), with 15 m between trap stations, covering approximately 2.25 ha. Each grid was trapped for two consecutive nights (=one trapping session) every three to four weeks between April/May and October/November, depending upon the year, from 1994 to 2012. In 1994, we trapped on only two grids; the other four were added in 1995. Upon first capture, white-footed mice (*Peromyscus leucopus*) and Eastern chipmunks (*Tamias striatus*) were given numbered metal ear-tags for individual identification. On first capture in a trapping session, each animal was weighed, sexed and aged according to pelage (juvenile, subadult, adult; mice only). While holding the animals by the scruff of the neck, we counted the number of larval and nymphal *I. scapularis* on their heads (entire head including under the chin, cheeks and top of head) and ears. Adult ticks are almost never found on these rodents. To compare direct counts in the field with actual body burdens, immediately after field inspection, we transported a sample of mice ($N = 60$) and chipmunks ($N = 28$) to a holding facility at the Cary Institute. We placed mice and chipmunks individually in cages (20-by-10 by 9 cm) with wire mesh floors, which were positioned directly over water-filled pans to collect all ticks as they dropped off the host. Hosts were supplied with ad libitum food and water and held for between 72 and 96 h to allow for all attached immature ticks to drop into the pans. Host animals were then returned to their point of capture.

We have observed a strong relationship between field counts and whole-body burdens for mice ($n = 60$, $R^2 = 0.79$ for larvae, $R^2 = 0.19$ for nymphs, presumably owing to low counts) and for chipmunks ($n = 28$, $R^2 = 0.67$ for larvae and $R^2 = 0.87$ of nymphs) [20]. Because field counts of larvae and nymphs more closely resemble whole-body counts on mice and chipmunks, respectively, we identified the timing of the peak of larval and nymphal activity by fitting a generalized additive model (a non-parametric smoother) to larval body burdens on mice and nymphal body burdens on chipmunks. We pooled field counts of attached larvae and nymphs from all grids to define the timing of peak activity at a fine temporal resolution. We focused on the timing of the peak as our measure of phenology because it is a clearly definable, unambiguous parameter that is unlikely to be affected by the size of the questing tick population or the host population. The nymphal peak also represents the maximal risk of human exposure to tick-borne pathogens. Additionally, because it was not logistically feasible to gather reliable data at such a high temporal resolution throughout the entire questing period (particularly during early spring), our ability to estimate variance, especially symmetrically on both sides of the peak, is limited. Climate and tick phenology data are available in the electronic supplementary material.

We used linear regression to relate the timing of the larval peak (the dependent variable) to cumulative degree-days above zero Celsius by the end of August (i.e. from the first degree-days in spring to 31 August), and the nymphal peak to cumulative degree-days above zero Celsius by the end of May. We used cumulative degree-days by the end of May and the end of August, because nymphal and larval activity peak near the end of these months (figure 2). Daily temperature data were obtained from the Cary Institute Weather Station in Millbrook, NY, which is centrally located between the six trapping grids. We used linear regression to determine whether cumulative degree-days through May or through August correlate with the time between the nymphal and larval peaks. We also used a z-score test to directly compare the regression coefficients for the rate at which the time of the nymphal and larval peaks advance with increasing cumulative degree-days.

To test whether a colder October truncates larval feeding, thus causing a higher fraction to overwinter and feed in the spring concurrently with nymphs, we used linear regression to compare cumulative degree-days in the month of October during year t with (i) the mean number of larvae counted on mice during the spring of year $t + 1$, and with (ii) the overwintering rate. The overwintering rate was calculated as the mean larval body burden on mice in the spring (before day 180) in year $t + 1$ divided by the mean larval body burdens on mice during the previous summer in year t (after day 200), where day 1 corresponds to 1 January. The thresholds of 180 and 200 were chosen because these dates consistently fall on either side of the trough between spring and summer larval activity (figure 2). We also used multiple linear regression with both mouse density and October cumulative degree-days as predictors, because mean larval body burdens on mice may be influenced by both mouse and tick abundance. In particular, body burdens on mice are higher when mice are rare and lower when mice are abundant, because larvae that attach to one mouse are removed from the pool of questing larvae.

To predict the timing of the nymphal and larval peaks into the future under climate warming scenarios, we first related mean annual temperature to cumulative degree-days by the end of May and August using linear regression. We used the regression fit to extrapolate from the projected increase in mean annual temperature to the number of cumulative degree-days through May and August. We used the 25th and 75th percentiles of the mean annual temperature increase by the 2020s (1.11–1.67°C) and 2050s (2.22–3.06°C) projected by the 2013 New York City Panel on Climate Change, which compiled the results of 35 general circulation models [21]. We related the predicted cumulative degree-days through May and August in the 2020s and 2050s to the timing of the nymphal and larval peaks using the regression

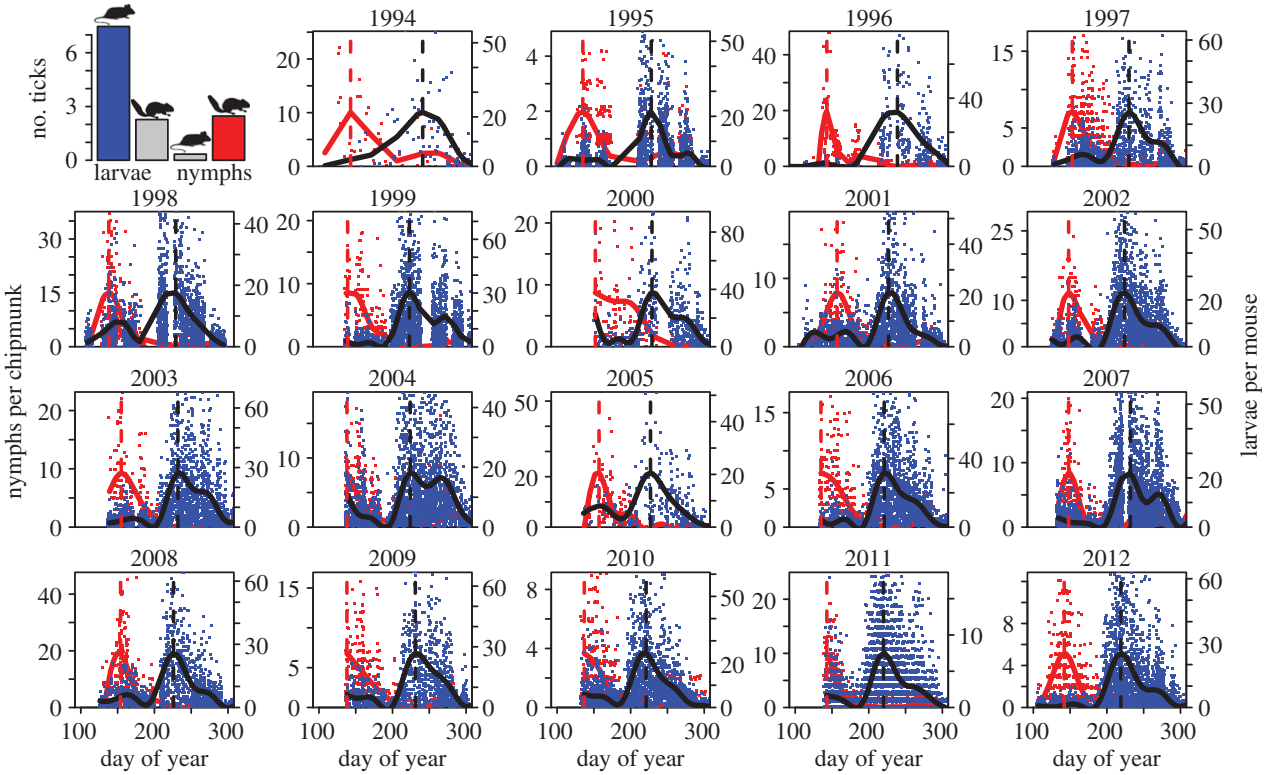

Figure 2. Body burdens counted on the head and ears of mice and chipmunks on six 2.25 ha trapping grids at the Cary Institute of Ecosystem Studies in Millbrook, NY. Larval body burdens were higher on mice than chipmunks (7.46 versus 2.26, *t*-test $p < 10^{-15}$); nymphal burdens were more than seven times higher on chipmunks than on mice (2.47 versus 0.34, *t*-test $p < 10^{-15}$). We thus used generalized additive models fit to larvae on mice (blue) and nymphs on chipmunks (red) to determine the timing of the nymphal and larval peaks from 1994 to 2012. Vertical red lines and vertical black lines correspond to the timing of the nymphal and larval peaks, respectively. (Online version in colour.)

results from our 19 years of data (see above). All data analyses and statistics were conducted in R v. 3.0.2 [22].

3. Results

Counted larval burdens were more than three times higher on mice than chipmunks (7.46 ± 13.4 versus 2.26 ± 6.1, *t*-test $p < 10^{-15}$); counted nymphal burdens were more than seven times higher on chipmunks than on mice (2.47 ± 5.4 versus 0.34 ± 1.0, *t*-test $p < 10^{-15}$). These results are consistent with prior data and probably reflect variation in host grooming efficiency and tick host preference [20,23] (figure 2). Approximately 34% of mice and 39% of chipmunks carried both larvae and nymphs during the spring. The proportion of individual animals that hosted both larvae and nymphs was 3.6 times higher for mice, and 2.2 times higher for chipmunks, during the spring nymphal season (before day 180) than during the summer larval season (after day 200).

We identified substantial climate warming at our field site between 1994 and 2012. Cumulative degree-days (sum of positive daily mean temperatures) by the end of May and August increased, respectively, by an average rate of 10.3 ± 3.96 and 13.5 ± 4.98 degree-days per year (May: $p = 0.018$, $R^2 = 0.29$; August: $p = 0.015$, $R^2 = 0.30$; figure 3*a*,*b*). The mean number of cumulative degree-days through May and through August was associated with a nymphal peak occurring on 24 May with a standard deviation of ± 6 days and a larval peak occurring on 15 August with a standard deviation of ± 8 days.

Climate warming through May and August was associated with advanced phenology of nymphs and larvae, respectively (figure 3*c*,*d*). The timing of the nymphal and larval peaks advanced 3.7 ± 1.5 and 3.0 ± 0.07 days, respectively, for every 100 cumulative degree-days by May (nymphs) or by August (larvae; nymph: $\beta = -0.037$, $p = 0.02$, $R^2 = 0.27$; larvae: $\beta = -0.030$, $p < 0.01$, $R^2 = 0.49$; figure 3*c*,*d*). There were five years in which the nymphal peak occurred at or near the onset of sampling. For these years, we were unable to definitively resolve the timing of the nymphal peak using generalized additive models (initial decline of the best-fit GAM; figures 1 and 3*b*). These years are clustered below the best-fit regression line and at higher than average warming, suggesting that our results may be conservative if the true nymphal peak was earlier than we measured (i.e. the best-fit regression would be steeper; figure 3*d*). The time between the nymphal and larval peaks did not vary as a function of cumulative degree-days through May or August (figure 4; May: $p = 0.83$, $R^2 = 0.00$; August: $p = 0.78$, $R^2 = 0.00$). Additionally, there was no significant relationship when directly comparing the effect sizes (i.e. slopes) for the effect of cumulative degree-days on the timing of the nymphal and larval peaks (*z*-score = 0.42, $p = 0.68$).

We observed no temporal trend towards more cumulative degree-days during the month of October (from 1 to 31 Oct; $p = 0.58$, $R^2 = 0.02$), but there was great interannual variation (mean: 321 cumulative degree-days, s.d.: 40 cumulative degree-days). Both the average number of spring-fed larvae and the ratio of spring-fed larvae from a given cohort (overwintering rate) declined as a function of cumulative degree-days during the previous October (figure 5; number: $p = 0.01$, $R^2 = 0.34$; ratio: $p < 0.04$, $R^2 = 0.26$). However, increased mouse population density is expected to reduce mean body burdens, because mice compete for the same larvae, each of which feeds only once. A multiple regression including predictors for both October cumulative degree-days and Jolly–Seber

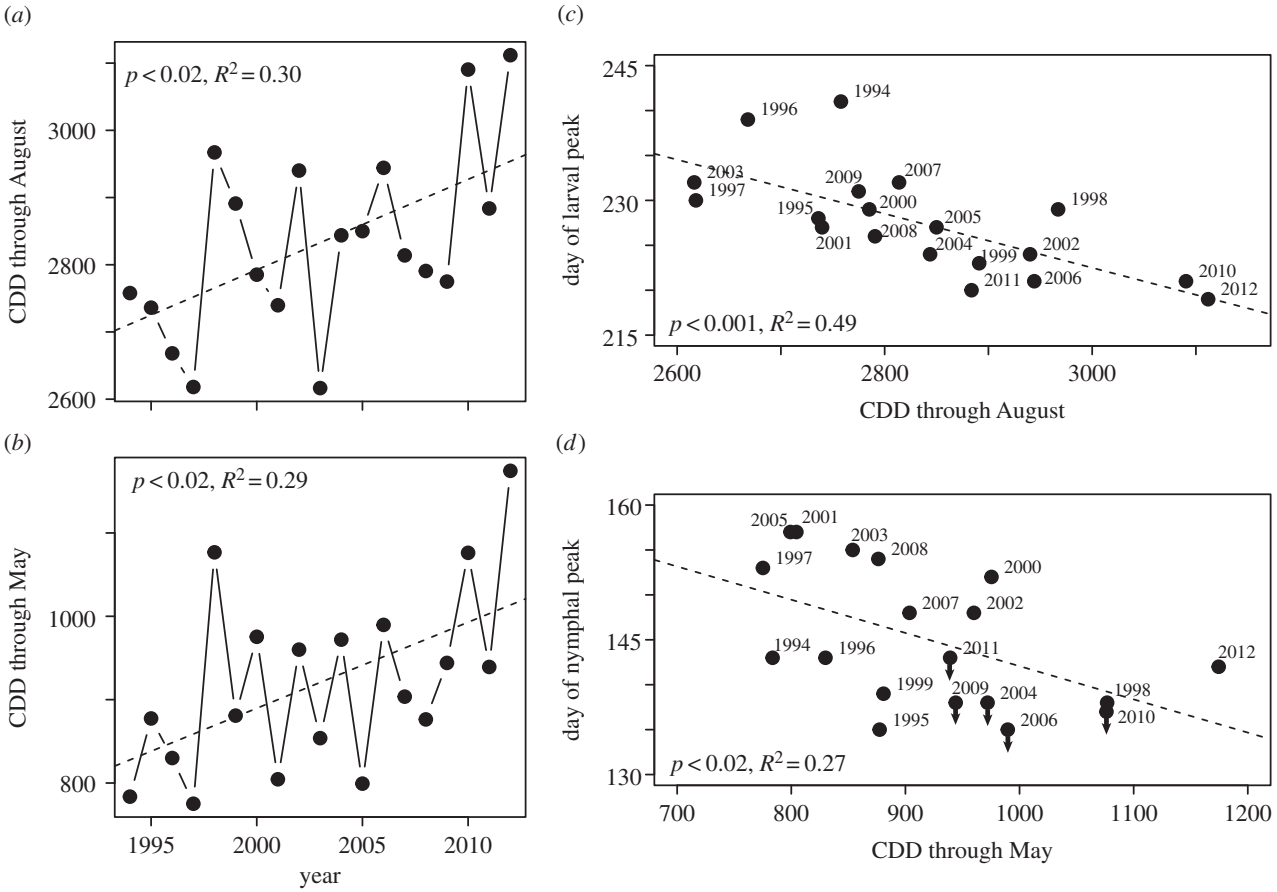

Figure 3. (*a*) Cumulative degree-days (CDD) measured as the sum of positive temperatures from the beginning of the year through the end of August and (*b*) the end of May from 1994 to 2012. All temperature measurements are taken directly from the Cary Institute of Ecosystem Studies Environmental Monitoring programme. Cumulative degree–days by (*c*) the end of August are correlated with advanced larval phenology and (*d*) by the end of May are correlated with advanced nymphal phenology. The timing of both life stages varies over nearly three weeks as a function of temperature. Downward-pointing arrows refer to years in which the true nymphal peak may have occurred earlier than we were able to definitively resolve. These points are clustered in warm years with earlier nymphal activity than predicted by the best-fit regression line. As a result, the true warming effect on nymphal phenology may be slightly stronger than projected here.

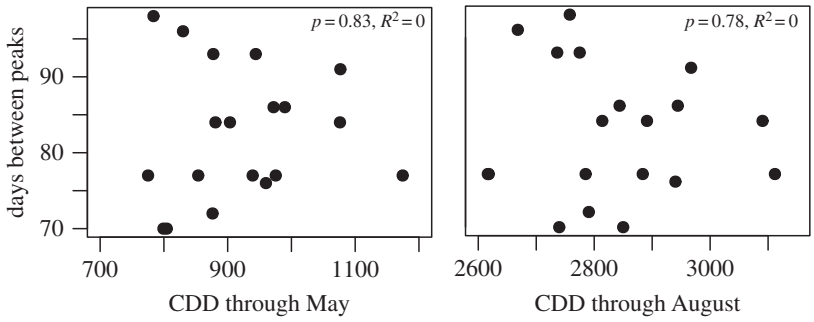

Figure 4. Number of days between the early nymphal peak and the later larval peak does not vary with cumulative degree–days (CDD) from the beginning of the year through the end of May ($p = 0.83$, $R^2 = 0.00$) or through the end of August ($p = 0.78$, $R^2 = 0.00$).

estimates of mouse population density [19] explained much more of the variance (number: $R^2 = 0.63$; ratio: $R^2 = 0.57$), and October cumulative degree-days achieved a higher level of statistical significance when controlling for mouse density (figure 5; number: $p < 0.01$; ratio: $p = 0.02$). We caution that 2008 was removed as an outlier (Cooks $D = 2.89$, standardized residual = 2.25) with a much higher proportion of spring-fed larvae than expected based on October cumulative degree-days. We speculate that this year may have been an outlier because of a 78% decline in mouse densities between 2007 and 2008, and a break in trapping during the larval peak of 2007 (figure 2) that led to underestimates of actual mean body burdens during summer 2007.

Every 1°C increase in the mean annual temperature was correlated with an additional 98 cumulative degree-days by the end of May ($\beta = 97.61 \pm 23.5$, $p < 0.0005$, $R^2 = 0.45$; figure 6) and 161 cumulative degree-days by the end of August ($\beta = 161.05 \pm 22.2$, $p < 10^{-6}$, $R^2 = 0.72$; figure 6). The projected 1.11–1.67°C increase in mean annual temperature by the 2020s is expected to increase the number of cumulative degree-days enough to advance the average nymphal peak by 4–6 days, and the mean larval peak by 5–8 days (figure 6). The projected 2.22–3.06°C increase in mean annual temperature by the 2050s is expected to advance the nymphal peak by 8–11 days, and the mean larval peak by 10–14 days (figure 6). By the 2050s, the average nymphal

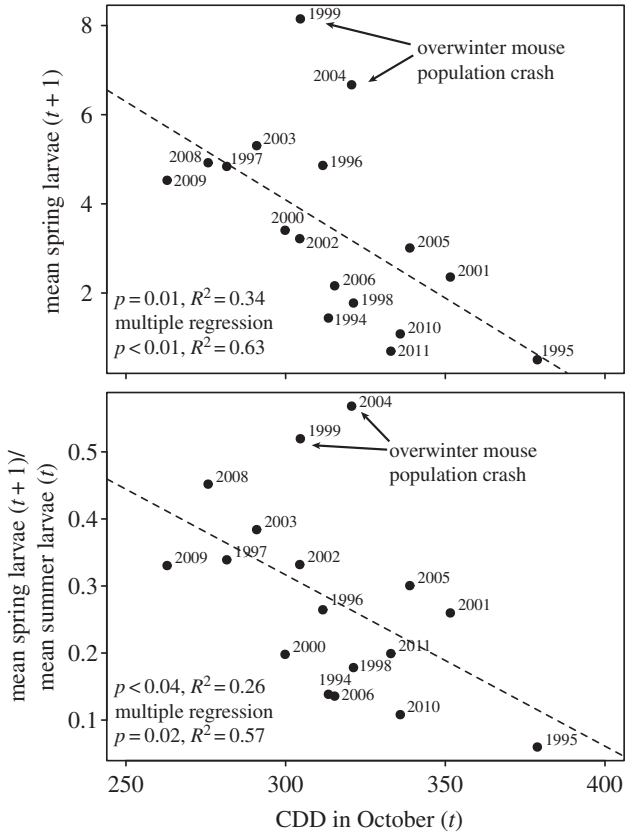

Figure 5. Larval ticks that do not find food in late summer can overwinter and quest in early summer synchronously with nymphs. A warmer October (cumulative degree-days, CDD) is correlated with reduced larval activity (average larvae per mouse) the following spring ($p = 0.01$, $R^2 = 0.34$), and a smaller proportion of the larval cohort feeding in spring relative to the previous summer ($p < 0.04$, $R^2 = 0.26$). Host abundance also influences the number of larvae per host, with larvae able to concentrate on fewer hosts when density declines. We controlled for the effect of mouse density in year *t* using multiple regression, which greatly increased the variance explained by the model and the level of statistical significance achieved by the October cumulative degree-days predictor (spring larvae regression: $p < 0.01$, $R^2 = 0.63$; ratio of spring larvae to previous summer larvae regression: $p = 0.02$, $R^2 = 0.57$).

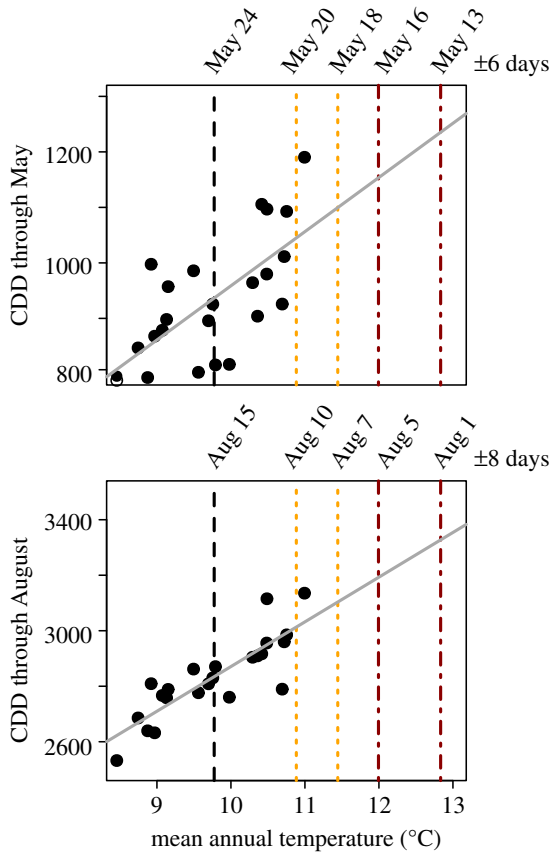

Figure 6. Projections for the timing of the nymphal and larval peaks with climate warming. Mean annual temperatures were highly correlated with both cumulative degree-days (CDD) through May and August. Projections of the mean annual temperature from the 2013 New York City Panel on Climate Change predict a temperature increase of 1.1–1.7°C (25th and 75th percentile) by the 2020s (orange dotted lines), and a 2.2–3.1°C increase by the 2050s (red dashed-dotted lines). The current baseline temperature at the Cary Institute (black dashed line) in Millbrook, NY, USA is associated with a mean nymphal peak occurring on 24 May and mean larval peak occurring on 15 August. One standard deviation in the observed mean annual temperatures was associated with a ±6 day change to the timing of the nymphal peak and a ±8 day change to the timing of the larval peak. The average nymphal and larval peaks are expected to advance to 18–20 May and 7–10 August, respectively, in the 2020s, and to 13–16 May and 1–5 August, respectively, in the 2050s. When accounting for the variance in temperatures, larvae are predicted to frequently peak in late July and nymphs in early May by the 2050s. (Online version in colour.)

peak is expected to advance from 24 May to 13–16 May, and the average larval peak is expected to advance from 15 August to 1–5 August. If the standard deviation of the timing of the nymphal and larval peaks remains ±6 and ±8 days, respectively, then by the 2050s, nymphal activity would be expected to peak as early as 7–10 May and larvae activity as early as 24–28 July approximately 16% of the time (i.e. more than 1 standard deviation below the mean) using the 75th percentile of projected temperature increase.

4. Discussion

Infectious diseases result from species interactions. Climate influences the behaviour, development, fecundity and mortality of species involved in these interactions, but the net result for disease risk can be difficult to predict [1]. Predicting how tick-borne disease risk will respond to climate change is particularly challenging owing to the complex interactions between host immune systems, pathogens, the abundance and phenology of ticks and multiple host species, and human behaviour. Our evidence over 19 years of monitoring tick abundance on thousands of small-mammal hosts indicated that seasonal activity peaks of both nymphs and larvae advanced by 3–4 days for every 100 cumulative degree-days before the end of May and August, respectively (figure 3). The evidence also supports the hypothesis that warmer autumns reduce the number of larvae that feed in the spring in synchrony with nymphs. If these trends continue as the climate warms, the asynchronous patterns of tick phenology in northeastern North America are likely to persist owing to the advance of both larval and nymphal phenology with climate warming. However, as predicted by mathematical models, it is possible that the larval peak will eventually advance early enough to cause larvae to moult into nymphs that are active in the autumn of the same year [14]. This seems plausible because, although data are limited, *I. scapularis* activity patterns appear to very different, both in timing and degree of synchrony, in the much warmer southern USA [24,25].

Our results have several implications for public health. First, earlier nymph activity shifts the period of greatest risk

earlier. If human outdoor activity in spring increases as temperatures warm, such phenological shifts might not drastically affect tick-borne disease risk because human and tick phenologies will remain synchronous. But if human outdoor activity is affected less by temperature and more by calendar date (e.g. peaking after the school year ends, typically in early–mid June), then earlier nymphal activity could reduce human exposure to tick-borne pathogens. In either event, people at risk and healthcare providers should be aware that risk of exposure is becoming substantially earlier in the spring as the climate warms.

We found little evidence that the primary larval and nymphal peaks are increasingly overlapping. Instead, we found evidence that, as autumn temperatures warm, a smaller number and fraction of larvae feed in the spring, when they are much more likely to feed shortly after host inoculation by nymphs or to co-feed with nymphs. This is consistent with previous research that surveyed ticks across space, rather than through time, and found increased phenological synchrony associated with rapid autumnal cooling [5]. Lower rates of larval and nymphal co-feeding are expected to reduce transmission rates of *A. phagocytophilum* and Powassan virus but could potentially increase transmission rates of *B. burgdorferi*. This prediction is supported by the observation that the relatively cold states of Minnesota and Wisconsin report much higher ratios of anaplasmosis and Powassan virus cases relative to Lyme disease cases compared with states in the northeastern USA [26,27]. Similarly, shorter-lived strains of *B. burgdorferi* are relatively common in the Upper Midwest, whereas longer-lived and more pathogenic strains are more common in the Northeast [5]. Our results suggest that substantial climate warming may reduce rates of anaplasmosis and the severe disease caused by Powassan virus, but that Lyme disease risk may increase, particularly in the Upper Midwest.

Climate warming by the 2050s is expected to substantially advance tick phenology in southeastern New York. Although 2012 was the warmest year during our study, it was the only year that crossed the 25th percentile of predicted warming during the 2020s. In other words, 2012 will be the new 'normal' in the near term, but will be substantially cooler than normal by the 2050s. By the 2050s, nymphal phenology is expected to advance from 24 May to 13–16 May, and larval phenology from 15 August to 1–5 August. This is a variable process with an expected standard deviation of 6 days for nymphs and 8 days for larvae. If we assume that the earliest plausible nymphal and larval peaks fall within 2 standard deviations of the mean (covering approx. 95% of the probability interval), then by the 2050s, the earliest nymphal peaks are predicted to occur near 1 May (using the 75th percentile of climate warming). Similarly, the earliest larval peaks are expected to occur near 16 July.

Phenological changes with climate warming constitute one of several mechanisms by which epidemiological patterns might change with climate in the coming decades. Human risk of exposure to tick-borne pathogens would also be affected if survival, moulting success, and therefore abundance of ticks are influenced by warming. Some evidence suggests that climate warming in eastern North America and northern Europe will increase overwinter survival, abundance and geographical ranges of ixodid tick vectors [28,29]. Future research should integrate the effects of climate change on phenology and population dynamics of ticks in order to more fully understand climate impacts on tick-borne disease.

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