ABSTRACT  Climate changes forecasted in the coming years are likely to result in substantial alterations to the distributions and populations of vectors of arthropod-borne pathogens. Characterization of the effect of temperature shifts on the life history traits of specific vectors is needed to more accurately define how such changes could impact the epidemiological patterns of vector-borne disease. Here, we determined the effect of temperatures including 16, 20, 24, 28, and 32°C on development time, immature survival, adult survival, mosquito size, blood feeding, and fecundity of both field and colonized populations of the *Culex* mosquitoes *Culex pipiens* L., *Culex quinquefasciatus* Say, and *Culex restuans* Theobald. Our results demonstrate that temperature significantly affects all of these traits, yet also that the extent of this effect is at times incongruent among temperatures, as well as being population and species-specific. Comparisons of colonized mosquitoes with field populations generally demonstrate decreased adult and immature survival, increased blood feeding and egg production, and significant variation in the effects of temperature, indicating that such colonies are not fully representative of natural populations. Results with field populations in general indicate that increases in temperature are likely to accelerate mosquito development, and that this effect is greater at temperatures below 24°C, but also that temperature significantly increases mortality. Among field populations, *Cx. restuans* were most affected by temperature increases, with decreased longevity relative to other species and significant increases in adult and immature mortality measured with each incremental temperature increase. Despite the unique climates characteristic of the geographic ranges of *Cx. quinquefasciatus* and *Cx. pipiens*, evidence of significant species-specific adaptation to temperature ranges was not seen. Taken together, these results indicate that geographic region, as well as species and population differences, must be considered when measuring the effect of temperature on vector populations.

KEY WORDS  temperature, *Culex*, life history traits
quitoes and other arthropods, as it directly affects mortality, life span, and development rates that can cause changes in morphology (Su and Mulla 2001, Deb et al. 2003, Gunay et al. 2011). The majority of insects function optimally within a narrow range of temperatures, and deviations from this range can cause stress during development, which may result in developmental inconsistencies (Mpho et al. 2002). In addition, there are often trade-offs between development time and both adult size and fitness, which can have significant downstream effects on survival, feeding behavior, and fecundity (Shelton 1973, Mohammed and Chadee 2011). Alterations to these life history traits can lead to substantial variations in vectorial capacity of mosquitoes that harbor and transmit pathogens (Dye 1992, Delatte et al. 2009).

It is now well-documented that colonized and field populations can differ significantly in genetic and phenotypic diversity, resulting in variability in larval and adult life-history traits (Mpho et al. 2002, Aguilar et al. 2005). While field conditions are highly dynamic and diverse, the homogeneous conditions common to laboratory colonies may result in the loss of allelic diversity and overall population fitness (Aguilar et al. 2005). Defining these differences is essential for interpreting studies of vector populations, which often rely on highly colonized populations to assess the effects of environmental conditions on vectorial capacity and fitness.

Here, we determined the effect of temperature on life history traits of Cx. pipiens, Cx. quinquefasciatus, and Cx. restuans mosquitoes. Specifically, we measured temperature-dependent variation in development time, immature survival, adult survival, mosquito size, blood-feeding, and fecundity both among species and between colonized and field-derived populations. Our results demonstrate the significant effects changing temperature has on these traits and identify critical population and species-specific differences, which have broad importance in contributing to our understanding of how changing climates will impact pathogen transmission.

Materials and Methods

Mosquitoes. All colonized Culex mosquitoes were maintained in 30.5-cm³ cages in an environmental chamber at 27 ± 2°C with a relative humidity of 45–65% and a photoperiod of 16:8 (L:D) h before the collection of experimental egg rafts. Cx. pipiens colony mosquitoes were originally collected in Pennsylvania in 2004 (courtesy of M. Hutchinson) and have been highly colonized at the Wadsworth Center Arbovirus laboratory. Cx. quinquefasciatus colony mosquitoes were derived from a laboratory colony provided by D. Fonseca (Rutgers University, New Brunswick, NJ) and initially derived from egg rafts from a highly colonized line from Benzon Research Inc. (Carlisle, PA). Cx. pipiens and Cx. restuans field egg rafts were collected in August, 2010 from Takoma Park, MD, near Washington, DC, and reared in an environmental chamber maintained at 25–27°C with a photoperiod of 16:8 (L:D) h for a single generation. Field Cx. quinquefasciatus egg rafts were collected in Orange County, CA (courtesy of R. Cummings). We confirmed species identifications and the absence of hybridization using morphological identification of larvae, and molecular identification using species-specific primers (Smith and Fonseca 2004, Bahnick and Fonseca 2006).

Mosquito Development. After hatching of individual groups, 400 larvae per population were counted and equally distributed into two transparent holding pans with 1 liter of filtered water each. Larvae were then placed in environmental chambers (Thera, San Jose, CA) and subjected to a photoperiod of 16:8 (L:D) h under five constant temperatures (16, 20, 24, 28, and 32 ± 1°C). Water dishes were placed inside the chambers to maintain humidity, and temperatures were monitored and recorded daily. Larvae were fed a 1:1:1 ratio of ground koi food, ground rabbit pellets, and bovine liver powder (MP Biomedicals, Solon, OH) in increasing quantities as follows: 60 mg—first instar, 100 mg—second instar, 120 mg—third instar, and 160 mg—fourth instar. Developing larvae were monitored daily for mortality, and dead larvae were counted, recorded, and discarded. Daily pupation also was recorded, and pupae were placed in distilled water in emergence jars (BioQuip Products Inc., Rancho Dominguez, CA) in preparation for eclosion.

Mosquito Survival, Feeding, and Fecundity. Newly emergent mosquitoes were sexed, counted, and housed at corresponding temperatures in 3.8-L mesh top paper cups provided with cotton pads soaked in 10% sucrose ad libitum. Survival of all groups was monitored and recorded daily. Dead adults were removed and frozen at −20°C. Wings from ∼20 adults per group per temperature were removed and placed on slides with double-sided tape and were subsequently measured from the alular notch to the distal margin, excluding the fringe using a Zeiss microscope, Axiocam camera, and Axiosvision software (Carl Zeiss Microscopy, Gottingen, Germany) to estimate mosquito size (Dodson et al. 2011). Adults were grouped and housed as they emerged in 3-d intervals and held for 5–7 d to allow for mating. Mosquitoes were starved overnight for 12–24 h and offered defibrinated goose blood (Hema Resources, Aurora, OR) with 2.5% sucrose for 1 h. Mosquitoes were then anesthetized using CO₂, and blood-fed females were sorted, counted, and separated for housing into individual holding cups. Unfed females were kept in the original cup with males, and offered a second bloodmeal 5–7 d later. Oviposition dishes were placed in holding cups containing blood-fed females and were checked daily for the presence of egg rafts. Statistical analyses were performed using GraphPad Prism 4.0 and Statsplus 9.0.

Results

Immature Development and Survival. We found significant differences in development time among species, population (field vs. colony), and temperature (Fig. 1). In general, increased temperatures accelerated development for all groups, yet this effect diminished with temperatures >24°C (Fig. 1;
Kruskall–Wallis test; \( P < 0.05 \). Specifically, the rate of development increased by an average of 2.9-fold with temperature increases from 16 to 24°C \( (P < 0.001) \) and an average of 2.3-fold with increases from 24 to 32°C \( (P < 0.001) \). When considered separately, development times of individual groups were significantly different when comparing rearing temperatures from 16 to 28°C (Dunn’s multiple comparison test; \( P < 0.05 \)). Increases from 28 to 32°C were also associated with decreased development times of colony-derived \( Cx. quinquefasciatus \) (Mann–Whitney test; \( P < 0.0001 \)), yet did not significantly alter development time of other groups. The largest effect of temperature on development time was measured for \( Cx. pipiens \) colony mosquitoes, for which mean time to emergence ranged from 29 d at 16°C to 9 d at 28°C, the temperature closest to colony rearing temperatures (26–28°C). Development times of field-derived \( Cx. pipiens \) were significantly shorter than colonized \( Cx. pipiens \) at 16°C (Mann–Whitney test; \( P < 0.0001 \)). Although differences between field and colony populations of \( Cx. quinquefasciatus \) were not as large as those measured at 16°C in \( Cx. pipiens \), significantly shorter development times were also measured in field-derived populations relative to colonized \( Cx. quinquefasciatus \) at 16, 20, and 25°C (Mann–Whitney test; \( P < 0.05 \)).

Species-specific differences in development time of field populations were also observed at all temperatures other than 28°C (Fig. 1). Specifically, \( Cx. quinquefasciatus \) and \( Cx. restuans \) emerged an average of 0.7 d later than \( Cx. pipiens \) at 32°C and 0.9 d earlier at 24°C (Kruskal–Wallis test; \( P < 0.0001 \)). Differences measured at lower temperatures were greater, with shorter development times measured in \( Cx. quinquefasciatus \) relative to \( Cx. pipiens \) at 16°C (5 d) and with \( Cx. restuans \) relative to both other species at 16 and 20°C. Although still significant (Kruskal–Wallis test; \( P < 0.0001 \)), the smallest range in development time was measured in \( Cx. restuans \), for which development time spanned from 18 d (16°C) to 8 d (32°C; Fig. 1).

Because proportions of larvae and pupae surviving were similar within groups, data were combined and depicted as proportions surviving to adult (Table 1; Fig. 2A). Temperature, population, and species were all associated with significant differences in immature survival, yet this trait overall varied less than both development time and adult survival. Immature survival was highest at 16°C for all groups, yet the degree to which increasing temperatures altered survival varied among species and populations (Table 1; Fig. 2A). Field populations of \( Cx. pipiens \) and \( Cx. quinquefasciatus \) were more robust than colonized mosquitoes, showing only modest fluctuations in immature survival resulting from temperature variation. Despite this, the proportion of field-derived \( Cx. quinquefasciatus \) surviving at 28°C (0.95) was significantly higher than field-derived \( Cx. pipiens \) (0.85; \( \chi^2 \) test; \( P = 0.009 \)). In contrast to the other groups, there was a significant negative correlation between temperature and immature survival for field-derived \( Cx. restuans \), as well as colony \( Cx. quinquefasciatus \), with <40% of immatures surviving at 32°C for both groups (linear regression analyses, \( r^2 = 0.85; \ P = 0.025 \); Fig. 2A). Colony \( Cx. pipiens \) again demonstrated adaptation to the temperature closest to that which they are reared (28°C), for which proportion surviving was significantly higher than both the 24 and 32°C groups (\( \chi^2 \) test; \( P < 0.01 \); Table 1). The low proportion of colony \( Cx. pipiens \) surviving at 24°C (0.61) can be attributed primarily to male death, as male/female ratio of emerged adults was significantly skewed toward females relative to other groups (\( \chi^2 \) test; \( P < 0.0001 \)). No other significant variations in sex ratios were observed among groups.

**Fig. 1.** Development time in mean days to emergence ± SEM of field (f) and colony (c) \( Cx. pipiens \) (CXP), \( Cx. quinquefasciatus \) (CQ), and \( Cx. restuans \) (CR) at various temperatures.

**Table 1.** Proportion of \( Culex \) (Cx) \( pipiens \) (P), \( quinquefasciatus \) (Q), and \( restuans \) (R) surviving immature stages of development at various temperatures.

<table>
<thead>
<tr>
<th>Group</th>
<th>CxP (pop)</th>
<th>CxQ (pop)</th>
<th>CxR (species)</th>
</tr>
</thead>
<tbody>
<tr>
<td>16°C</td>
<td>0.92</td>
<td>0.96</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Colony</td>
<td>0.57</td>
<td>0.81</td>
<td>0.012</td>
</tr>
<tr>
<td>20°C</td>
<td>0.57</td>
<td>0.0007</td>
<td>0.84</td>
</tr>
<tr>
<td>Colony</td>
<td>0.77</td>
<td>0.99</td>
<td>0.0099</td>
</tr>
<tr>
<td>24°C</td>
<td>0.57</td>
<td>&lt;0.0001</td>
<td>0.86</td>
</tr>
<tr>
<td>Colony</td>
<td>0.61</td>
<td>0.70</td>
<td>0.0090</td>
</tr>
<tr>
<td>28°C</td>
<td>0.52</td>
<td>0.7730</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Colony</td>
<td>0.53</td>
<td>0.53</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>32°C</td>
<td>0.53</td>
<td>&lt;0.0001</td>
<td>0.77</td>
</tr>
<tr>
<td>Colony</td>
<td>0.46</td>
<td>0.38</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>( P (temp)^a )</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
</tbody>
</table>

\( ^a \chi^2 \) test tests comparing immature survival of field and colony populations of the same species.

\( ^b \chi^2 \) test tests measuring the effect of species on immature survival for individual populations and temperatures.
sured, correlating with the increased development time in each group (Fig. 3; linear regression analyses; \( P < 0.001 \)). Although the size of colony Cx. pipiens was generally less affected by temperature than other groups, mean wing length of mosquitoes reared at 28°C was significantly larger than at all other temperatures (t-test; \( P < 0.001 \)). Field-derived Cx. pipiens wing lengths were significantly larger than Cx. quinquefasciatus and Cx. restuans at all temperatures and colony-derived Cx. pipiens at 16, 20, and 24°C (t-tests; \( P < 0.01 \)). No differences in wing length were identified between field and colony populations of Cx. quinquefasciatus.

Median female longevity decreased with temperature and differed between species and populations, with modest two- and three-way interactions among variables contributing significantly to the measured variation in longevity (three-factor analysis of variance [ANOVA]; \( P < 0.001 \)). Temperature alone accounted for 45.1% of the variation in longevity (\( F = 7328.1; P < 0.0001 \)), and the combined effect of all three factors accounted for 61.5% of the variation (\( F = 291.9; P < 0.0001 \)), indicating a significant effect of species and population but also variation in longevity among individuals independent of these factors. For all groups, there was a significant negative correlation between temperature and longevity (Fig. 2B; linear regression analysis; \( r^2 = 0.94; P = 0.006 \)) for which slopes (i.e., the effect of temperature) were not significantly different among groups (\( P = 4.9; P = 0.003 \)).

Fig. 2. Relationship between temperature and survival of field-derived (f) and colonized (c) Culex (Cx) mosquitoes, Cx. pipiens (P), Cx. quinquefasciatus (Q), and Cx. restuans (R). (A) Relationship between temperature and proportion of larvae surviving to adult. Statistically similar relationships are depicted by individual lines. A significant correlation was identified for Cx. restuans and colonized Cx. quinquefasciatus (solid line; linear regression analysis, \( r^2 = 0.85; P = 0.025; y = 139.5−3.01\times \), but not for Cx. pipiens or field-derived Cx. quinquefasciatus (dotted line; \( r^2 = 0.57; P = 0.139 \)). (B) Relationship between temperature and adult longevity. Slopes were statistically similar for all groups (linear regression analysis of mean, \( y = 151.6−4.57\times; r^2 = 0.94; P = 0.006 \), but intercepts were significantly different among groups (\( P = 4.9; P = 0.003 \)).

Fig. 3. Mean wing length (millimeters) of (A) field-derived and (B) colonized Culex (Cx) mosquitoes at various rearing temperatures. A negative correlation between temperature and winglength was measured in all groups with the exception of colony Cx. pipiens (linear regression analysis, \( P = 0.205 \)). Relationships were as follows: Cx. pipiens (P; field) \( y = 5.62−0.08\times; r^2 = 0.94; P = 0.0064 \); Cx. quinquefasciatus (Q; field) \( y = 4.37−0.04\times; r^2 = 0.99; P = 0.0006 \); Cx. restuans (R; field) \( y = 4.72−0.05\times; r^2 = 0.91; P = 0.016 \); Cx. quinqua (colony) \( y = 4.52−0.05\times; r^2 = 0.99; P = 0.0005 \).
tures, and survival of field-derived Cx. pipiens was greater than both other species at all temperatures but 16 and 24°C (Mantel–Cox test; \( P < 0.001 \)). With the exception of Cx. quinquefasciatus at 28 and 32°C, field populations generally outlived colony populations by highly significant margins (Gehan–Breslow–Wilcoxon test; \( P < 0.001 \)). The most significant of these differences was observed with Cx. pipiens at 20°C, for which median survival for the field-derived population was 112 d, as compared with just 44 d for the colony-derived population (Fig. 4).

**Blood Feeding and Fecundity.** Temperatures, population, and species significantly altered Culex blood feeding (Fig. 5). The colony populations had significantly higher proportion blood fed relative to field-derived populations at all temperatures for Cx. quinquefasciatus and all but 28 and 32°C for Cx. pipiens, for which field population feeding was significantly higher (\( \chi^2 \) test; \( P < 0.001 \)). In fact, individuals from field populations of Cx. quinquefasciatus fed only at 24 and 28°C (Fig. 5A). Species comparisons of colony-derived mosquitoes demonstrates significantly higher proportions of Cx. pipiens fed at the lowest temperature (16°C; Fig. 5A; \( \chi^2 \) test, \( P = 0.0021 \)), yet significantly higher proportions of Cx. quinquefasciatus fed at the two highest temperatures (28 and 32°C; Fig. 4A; \( \chi^2 \) test, \( P < 0.001 \)). Only a single Cx. restuans female fed during the study, emphasizing the difficulty of colonizing this species and the general reluctance of field-derived populations to feed from artificial systems.

Although the relatively small number of fed females in many groups made assessing fecundity differences difficult, some significant variation among groups was identified (Fig. 5B). Overall, egg raft production among blood-fed females was highest for both populations of Cx. pipiens at 20°C and both populations of Cx. quinquefasciatus at 24°C. In addition, with the exception of 24°C, for which proportions were statistically similar, a higher proportion of blood-fed field Cx. pipiens laid egg rafts than did colony Cx. pipiens at all temperatures. In contrast, blood-fed colony Cx. quinquefasciatus mosquitoes produced proportionally more egg rafts than field Cx. quinquefasciatus at all temperatures, and combined egg raft output was highest for this population (Fig. 5B; \( \chi^2 \) test, \( P < 0.001 \)).

**Discussion**

Although many studies have demonstrated a role for temperature in mosquito development and population dynamics of individual species (Lachmajer and Hien 1975, Rueda et al. 1990, Reisen 1995), quantifying the specific relationships between temperature and life history traits as well as direct comparison of the relative importance of temperature among medically important mosquito vectors is critical to our understanding of how climate shifts could ultimately alter vectorial capacities and patterns of disease transmission (Dye 1992; Rogers and Randolph 2000, 2006). Here, we provide a unique comparison of the effect of temperature on both field-derived and colonized Cx. pipiens and Cx. quinquefasciatus, as well as a field population of Cx. restuans. Our results demonstrate that temperature significantly affects rates of immature development, survival of immature stages, adult size, adult longevity, blood feeding, and fecundity of Culex mosquitoes, and that both species and colonization are additional factors significantly altering these life history traits and their susceptibility to temperature shifts.

![Fig. 4.](image1) Median longevity ± SEM of field (f) and colonized (c) Cx. pipiens (CxP), Cx. quinquefasciatus (CxQ), and Cx. restuans (CxR) at various temperatures.

![Fig. 5.](image2) (A) Proportion of blood-fed Culex mosquitoes at various temperatures. (B) Proportion of blood-fed Culex mosquitoes laying egg rafts at various temperatures.
In concordance with previous studies with other mosquito species, results here demonstrate a positive correlation between temperature and development rate (Lachmajer and Hien 1975, Rueda et al. 1990, Bayoh and Lindsay 2003), indicating that increasing temperatures could generally lead to a more rapid proliferation of *Culex* populations. Despite this, temperatures >24°C had more modest effects on development time than increases below this temperature, demonstrating that rising mean temperatures in milder regions may have lesser effects on the rate of *Culex* proliferation than would increases in regions where mean summer temperatures range from 16 to 24°C. In addition, the increased mortality observed at higher temperatures in all groups could result in an overall decline in the reproductive output of *Culex* mosquitoes despite modestly accelerated development. Indeed, only field *Cx. pipiens* produced egg rafts at 32°C. Similar effects of high temperature on adult longevity have been observed in other studies (Hawley 1985), including in *Cx. quinquefasciatus* (Rueda et al. 1990) and *Culex tarsalis* (Reisen 1995).

Although temperature was responsible for the majority of the variation in life history traits measured here and all groups were significantly affected by rearing temperatures, important species and population differences were also identified. Others have acknowledged differences in fitness of field and colonized mosquito populations (Tabachnick 2003), yet results here indicate that species and population differences likely require defining such differences for individual studies. Among the most distinct differences was the sensitivity of colonized larvae and pupae to variable temperatures, as opposed to the robustness of field *Cx. pipiens* and *Cx. quinquefasciatus*, for which little effect of temperature on immature survival was measured. The largest effect of temperature was observed with colonized *Cx. pipiens* mosquitoes, for which mean development time at 16°C was significantly higher than all other groups. Furthermore, colonized *Cx. pipiens* was the only group for which the shortest development time was measured at 28°C rather than 32°C. A lack of phenotypic variability was also observed with wing length of colony *Cx. pipiens*, where only modest variation in size was measured with variable temperatures, with 25°C producing the largest mosquitoes. For all other groups, a significant negative correlation was measured between size and temperature (i.e., development time) as has been shown in previous studies (Rueda et al. 1990, Chadee and Beier 1997, Gunay et al. 2011, Mohammed and Chadee 2011). In addition, survival of both immature stages and adults was significantly lower for colonized populations, and overall blood feeding and egg production were generally higher relative to field mosquitoes. These differences, which are consistent with previous studies investigating the effects of colonization (Aguilar et al. 2005, Vitek and Livdahl 2006), are likely a reflection of selection events resulting from long-term colonization and rearing at generally constant environmental conditions, indicating that the use of colonies to measure the effects of temperature or other environmental variables on life history traits may at times provide imprecise representations of natural populations.

Measurement of species-specific variation among field populations provided a direct assessment of the potential implications of natural temperature fluctuations among *Culex* mosquitoes. *Cx. restuans* were less sensitive to alterations in development time than *Cx. pipiens* or *Cx. quinquefasciatus*, yet had significantly shorter longevity than both other species at every temperature and were the only field population for which immature survival was significantly decreased at temperatures >24°C. These results suggest that *Cx. restuans*, which are important vectors of West Nile virus (Kilpatrick et al. 2005, Degroote and Sugumaran 2012) and more prevalent than *Cx. pipiens* in some rural areas of the eastern United States at certain times during the transmission season (Ebel et al. 2005, Diuk-Wasser et al. 2006), are likely to be the most susceptible of the studied species to population fluctuations as a result of increasing temperatures. Consistent with these findings, previous studies have indicated that *Cx. restuans* populations tend to peak in late spring and early summer, followed by a decline in the hotter summer months (Reiter 1988, Andreadis et al. 2001).

*Cx. quinquefasciatus* and *Cx. pipiens* are sibling species separated by a hybridization zone stretching from ~30°N and 40°N latitude in N. America (Kothera et al. 2009, Farajollahi et al. 2011, Huang et al. 2011), with pure *Cx. quinquefasciatus* to the south and *Cx. pipiens* to the north. This distribution would suggest that *Cx. quinquefasciatus* are more likely to be adapted to higher temperatures, yet only modest differences in life history traits were measured between the two species. Immature survival was significantly higher for *Cx. quinquefasciatus* at 25°C (but not 24 or 32°C), and development was slightly accelerated at 24°C, yet median longevity for *Cx. pipiens* was similar to *Cx. quinquefasciatus* at 24°C and in fact significantly higher than *Cx. quinquefasciatus* at both 28 and 32°C. This suggests that *Cx. quinquefasciatus*, as they currently reside in areas with mean summer temperatures generally between 24 and 25°C (www.noaa.gov), are likely to experience decreased survival as a result of rising temperatures. Because development rate is only modestly increased at temperatures >24°C, this increased mortality would decrease population size and, potentially, vectorial capacity of *Cx. quinquefasciatus*. *Cx. pipiens*, as they reside in areas with mean summer temperatures between 16 and 24°C, could also experience decreases in mean longevity with rising temperatures, but this negative effect on the population size could be compensated by the fact that greater increases in development rate occur with temperature increases within this range. Consistent with mortality results, field-derived *Cx. pipiens* blood feeding was also significantly greater than *Cx. quinquefasciatus* at temperatures >24°C, which could serve to further enhance differences in vectorial capacities. However, when considering the effect of temperature on vectorial capacity, the likelihood of increased pathogen proliferation at higher temperature, and therefore in-
increased vector competence, must also be considered (Dohn et al. 2002, Reisen et al. 2006, Kilpatrick et al. 2008). The fact that the field populations of Cx. pipiens were derived from the southern end of this species’ range (Washington DC area) may partially explain why decreased fitness at higher temperatures was not observed, and is consistent with the presence of significant population level variation. In support of this, colonized Cx. pipiens, originally derived from Pennsylvania, were indeed more susceptible to adult mortality and displayed decreased blood feeding at temperatures >24°C when compared with colonized Cx. quinquefasciatus, yet the potential effects of colonization make these differences difficult to interpret. Genetic diversity identified among populations and individuals of these species, particularly in the case of Cx. pipiens (Fonseca et al. 2004, Kilpatrick et al. 2007, Kothera et al. 2009, Huang et al. 2011), together with identification of substantial variation in vector competence for West Nile virus among Culex populations (Kilpatrick et al. 2010), support the idea of significant population-level phenotypic variation in life history traits and in susceptibility to environmental fluctuations, yet regardless of population variation, these results suggest that differences in mosquito fitness or in the capacity for adaptation to warmer temperatures cannot by itself explain the differences in geographic distributions of these sibling species. Because Cx. quinquefasciatus do not have the capacity to enter true diapause as Cx. pipiens do (Hayes 1975), the inability to successfully overwinter may explain why Cx. quinquefasciatus cannot establish themselves in the northern United States, yet the explanation for the lack of Cx. pipiens moving south requires further study.

A potentially important variable not considered in these studies is the fluctuating daily temperature experienced by natural Culex populations. Although constant temperatures may provide an accurate representation of the effects of daily mean temperature on mosquito development (Milby and Meyer 1986), some species and populations may be more likely to experience changes in life history traits as a result of diurnal fluctuations (Paijaimans et al. 2010, Lambrechts et al. 2011, Mohammed and Chadee 2011). Laboratory rearing containers are also poor representations of natural adult habitats, and differences in mating success, blood-feeding behavior, and overall reproduction output could differ significantly in natural settings. In addition, the largest effect of climate change on Culex populations could result from rising temperatures during breaks in transmission. Milder fall or winter months could serve to significantly alter the size and success of overwintering populations, and milder spring months may advance or accelerate the commencement of pathogen transmission (Gota et al. 2011). Despite these caveats, our results suggest life history traits of Culex mosquitoes are governed, to a large degree, by temperature and to a lesser extent by species and population differences and that these differences could have profound effects on the influence of climate change on the epidemiological patterns of vector-borne disease.

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