Temporal and Spatial Synchrony of *Culex territans* (Diptera: Culicidae) with Their Amphibian Hosts

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ABSTRACT *Culex territans* Walker (Diptera: Culicidae) larvae share nonpolluted freshwater habitats with amphibians, which are bloodmeal hosts of their adults. To examine synchrony of *Cx. territans* with amphibian species, 10 larval habitat sites were sampled weekly from March to November of 2004. *Cx. territans* larvae were temporally and spatially associated with the green frog, *Rana clamitans* Latrielle. We predicted that if the preferred hosts were abundant at low temperatures, *Cx. territans* might be able to digest bloodmeals at those same temperatures. Using the thermal heat summation model, 192.3 d above 3.9°C were needed to complete the gonotrophic cycle. This is the lowest thermal minimum reported for a Nearctic species of mosquito. Using this model, we calculated that the first larvae of *Cx. territans* field collected on 6 May 2004 were the progeny of females that bloodfed during the last week of March or first week of April. We conclude that *Cx. territans* has physiological mechanisms that allow them to take advantage of early season bloodmeal sources.

KEY WORDS amphibians, gonotrophic cycle, temperature, thermal heat summation model

Culex territans Walker (Diptera: Culicidae), a widely distributed mosquito species, is found throughout most of the Northern hemisphere (Knight and Stone 1977). *Cx. territans* females in Tennessee have a preference for amphibian bloodmeals (63%) and also feed on Reptilia, Aves, and Mammalia (Savage et al. 2007). In New Jersey, *Cx. territans* occasionally feed on reptile and avian sources but prefer amphibians (88.5%) (Crans 1970). *Cx. territans* females harbor several parasites and pathogens that may be transmitted to amphibians, including *Foleyella flexicauda* Schacher and Crans (Benach and Crans 1973), frog erythrocytic virus (Gruia-Gray and Desser 1992), and *Hepatozoon clamatae* Stebbins (Kim et al. 1998). *Cx. territans* has also tested positive for West Nile virus in the United States (CDC 2005).

Culex territans adult females have been collected overwintering in New York (Nasci et al. 2001) and New Jersey (Farajollahi 2005). Collections of larvae in the spring (Smith 1903) are consistent with the report that females exit diapause in New Jersey in March (W. Crans, personal communication). At this time, females will seek a bloodmeal and oviposit their first batch of eggs. Eggs are generally laid above the water line on emergent vegetation (McIver 1969). Reproduction continues throughout the growing seasons, with the greatest numbers of this species occurring before the first frost in the fall.

Culex territans are often collected in nonpolluted water including permanent swamps, marshes, ponds, streams, containers, and large wetland pools (Joy and Clay 2002) and share habitats with amphibian species (Benach 1971). Amphibians are good indicators of water quality (Boyer and Grue 1995), because they are sensitive to toxicants and acidic conditions (Freda and Taylor 1992). Therefore, amphibians are restricted to habitats that are nonpolluted. Some species of mosquito that share larval habitats with amphibians may compete with tadpoles for limited resources (Mokany and Shine 2003).

Many amphibian species in New Jersey exit diapause throughout March (Gessner and Stiles 2001). At this time, adult female *Cx. territans* have been collected in traps as part of the New Jersey State Surveillance and Vector Surveillance projects (Reed et al. 2008). Monthly mean temperatures in northern New Jersey in March are ≈3°C (New Jersey Weather and Climate Network, Office of the NJ State Climatologist). Rates of bloodmeal digestion and ovarian development are temperature dependent (Vinogradova 2000). *Culiseta melanura* Coquillett is a common mosquito species in New Jersey, which can only complete a gonotrophic cycle at temperatures >6.4°C (Mahmood and Crans 1997). *Culex pipiens pipiens* L., which overwinters as an adult female, requires temperatures >9.6 (Madder et al. 1983) or 10°C (Vinogradova 2000) to complete a cycle. If *Cx. territans* coordinates its life cycle to that of its amphibian host, it might be able to complete a gonotrophic cycle at temperatures around 3°C, when its hosts are exiting diapause.

Our goal was to determine which factors contribute to the temporal and spatial synchrony of *Cx. territans*

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larvae with their amphibian hosts and to use these factors to predict the presence of *Cx. territans* larvae. Our hypothesis was that *Cx. territans* synchronize their life cycle to match their amphibian hosts. Because amphibian hosts exist in aquatic habitats, we predicted that the presence of amphibians might coincide with the temporal and spatial distribution of *Cx. territans* larvae. We also predicted that if *Cx. territans* females co-occur temporally with their amphibian hosts, females might be capable of digesting bloodmeals at those temperatures.

Materials and Methods

Field Study Sites. Field study sites ($N = 11$) were located in a 47-km^2 area of Stokes Forest and High Point State Park in northwestern New Jersey. Sites were 1–2 km apart and were examined the summer before field experiments to identify the presence or absence of mosquito larvae and amphibians, vegetation type, and flooding regimen. The 11 sites were classified according to the Cowardin classification system (Cowardin et al. 1979) and consisted of five seasonally flooded forested wetlands and five permanently flooded habitats with emergent vegetation. One permanent pond acted as a comparison site, whose depth and lack of vegetation was suitable for amphibians, but not for *Cx. territans* larvae. Global positioning system (GPS) coordinates were recorded for each site and analyzed using ArcView 3.1 software (ESRI, Redlands, CA). GPS site locations were overlaid onto Geographic information system (GIS) maps to determine soil type, soil acidity, percent organic matter, slope, drainage, elevation, wetland type, and wetland size. Additional information was collected weekly at each site, including current weather conditions (raining, overcast, sunny, snowing, and foggy), absence of water, and habitat disturbance. Weekly temperature, precipitation, barometric pressure, water table depth, and wind speed records were downloaded from the High Point and Sussex County weather stations (New Jersey Weather and Climate Network, Office of the New Jersey State Climatologist). The High Point station was chosen because it is located within our 47-km^2 study area. The Sussex County station is located 11.8 km away from the High Point station and was used to fill in any gaps in the weather data.

Field Collections. Collections were made weekly from 14 March to 10 November 2004. Road closings during the first week limited access to four sites within hiking distance. Sampling was conducted in 20-min periods to allow equal access to all 11 sites during daylight hours. During the first 15 min, all aquatic organisms were sampled using a standard mosquito dipper at different depths in the water column. Each site was sampled by skimming the surface, scanning below the surface, dipping into aquatic vegetation, and dipping into small areas and cavities. Mosquito larvae were placed in 2-liter coolers and transported to the laboratory for species and instar identification. When other invertebrates were collected while sampling, they were identified to family and immediately released.

Amphibians were also collected with the mosquito dipper or by hand. The final 5 min of each sampling period was used to sample additional amphibians and organisms using an aquatic net. All amphibians were identified on site by stage and species and released.

Laboratory Colony Maintenance. *Culex territans* were colonized from field-collected larvae and adults from Sussex County based on techniques described by Benach (1970). Cultures were maintained at 23.8 ± 0.3°C and a 16:8 (L:D) cycle. Field-collected larvae were held in shallow pans of tap water and fed ground rat chow daily (Purina Mills, St. Louis, MO). Water was changed daily, and pupae were removed and placed in glass bowls, which were transferred to 61-cm^3 cages for emergence. Adults were provided a continuous supply of 10% sucrose, on cotton wicks, which was removed 24 h before experiments to increase blood-feeding frequency.

Laboratory Studies. The effect of temperature on the length of the gonotrophic cycle was examined in nulliparous females (F_1 and F_2 generations), 6–9 d old. During each experiment, an unrestrained bullfrog was placed into a cage containing ≈100 female *Cx. territans.* Mosquitoes were given 4 h to blood feed, and a fully engorged female was removed and placed in a separate 30.5-cm ^{3} cage with a continuous supply of 10% sucrose. Cages were immediately placed in an incubator with a 16:8 (L:D) cycle. Blood feeding was repeated until 10 females were available for each temperature.

Ten individual females were held at each of 11 temperatures: 3.5, 6.7, 9.0, 13.7, 16.8, 23.8, 24.5, 25.6, 26.0, 27.3, and 28°C, for a total of 110 females. Each cage contained one fully engorged female, a white enamel pan with an octagonal brick on which females oviposited, and 10% sucrose. Cages were covered with wet towels and placed under plastic to increase humidity. Females were examined daily to record egg rafts and mortality. The mean duration from blood feeding to oviposition (g_c) was determined for each temperature.

The number of days from egg to adult at temperatures 23.8, 26.0, and 27.3°C were recorded for 15 egg rafts (5 per temperature), for a total of 1,662 mosquitoes examined. Each egg raft was placed in a separate white enamel pan with ground rat chow. Water was changed daily. Pupae were placed in glass bowls, and emerging adults were added to an existing colony. The three temperatures were chosen to simulate the peak monthly temperatures for High Point weather station (New Jersey Weather and Climate Network, Office of the New Jersey State Climatologist) for June (23.5°C), July (26.1°C), and August (25.2°C).

Statistical Analysis. Data were analyzed using SPSS software (SPSS 2005). The database consisted of 10 sample sites examined weekly over a 35-wk period. To determine which factors correlated spatially with *Cx. territans* larvae, a single week was chosen from the dataset to compare the 10 sites. A Pearson correlation analysis was performed, where the dependent vari-

able, presence of *Cx. territans* larvae at a given site, was correlated to soil pH, drainage, organic matter, elevation, slope, and the presence/absence of amphibians within the same sites. The analysis was repeated three times (a total of 4 wk) with randomly selected weeks. Variables with correlations >0.5 for 2 or more of the wk were added to a logistics regression model to predict the presence of *Cx. territans* larvae. For the logistics regression model, a single week was randomly selected for the months of June, July, August, and September (total of 4 wk). Variables not significant at 0.05 were removed from the model, until an appropriate model was determined. A model was determined satisfactory when all predictors in the model were significant and the accuracy of predicting *Cx. territans* larvae was >80%.

To analyze the temporal distribution of *Cx. territans* larvae an autoregressive integrated moving average (ARIMA) time series analysis was performed using density (number of sites containing *Cx. territans* larvae) as the dependent variable. This was analyzed against water table depth, daylength, temperature, precipitation, relative humidity, wind, barometric pressure, *R. catesbeiana, R. clamitans, Pseudacris crucifer* Wied-Neuwied (spring peeper), invertebrate predators, salamanders, water presence, and other mosquito species. Normality of the data was assessed using Q-Q plots, and data were transformed according to results. The best ARIMA model was chosen based on the highest stationary R^2 values and the lowest root mean square error (RMSE) values. Variables that were determined to be predictors of *Cx. territans* larvae using the ARIMA model were further analyzed using a cross-correlation analysis to find significant relationships between the data and weekly lags. Significant lags were determined by Box-Ljung Q-statistic <0.05.

Thermal Heat Summation Model. The thermal heat summation model (Mahmood and Reisen 1981) was used to predict the temporal distribution of *Cx. territans* larvae based on temperature and degree-days. This model $[V = (t - t_0)/k]$ was used to determine the thermal minimum (t_o) in which females are capable of digesting bloodmeals and the number of degree-days above this thermal minimum (k) to complete one gonotrophic cycle. The time in days to complete one gonotrophic cycle (g_c) for *Cx. territans* was calculated for increasing temperatures, where g_c = mean number of days from eggs in stage I (Christophers 1911) to oviposition. The rate of ovarian development (V), was calculated as $V = 1/g_c$. By plotting rate of ovarian development (V) over increasing temperatures, a linear regression $(V = a + bt)$ was created. The thermal minimum (t_o) was calculated using the regression as $(-a/b)$. The number of degree-days above thermal minimum (k) was calculated as $(1/b)$ using this regression.

To estimate the days since blood feeding (D) for field-collected larvae, a new model was created using the thermal minimum t_0 and the thermal constant k. In this model $D = k - \Sigma n_i(t_i - t_0)$, where n_i = the number of days occurring at the mean temperature t_i. This model was used to determine the date when *Cx. territans* females took their first bloodmeal based on the first field collections of larvae. To test our model, we used the formula $g_c = k/\sum(t - t_0)$ to predict the first occurrence of *Cx. territans* larvae based on mean daily temperatures at the Sussex County weather station. We calculated the total degree-days for temperatures above the thermal minimum (t_0), starting with the first day in which the mean was above t_0. From these data, we could estimate the date on which degree-days approached the thermal constant (k). If our model is accurate, this date should accurately predict the date of our first collection of *Cx. territans* larvae.

Results

Field Studies. *Culex territans* larvae were present in 71 of the 350 collection attempts and were present at least once in 7 of the 10 collection sites. Two of the sites that did not hold larvae were small temporary pools that briefly held water. The third site that did not contain larvae was the lake that served as our control. Of the total collections, 58% of amphibians were collected in permanent water and 42% in seasonally flooded habitats. *Cx. territans* larvae showed a similar trend toward permanent water (77%), as opposed to seasonally flooded habitats (23%).

Culex territans larvae were present earlier than other adult overwintering species. In 2004, *Cx. territans* larvae in northern New Jersey were first detected on 6 May. In contrast, *Anopheles quadrimaculatus* Say larvae first appeared on 28 May and *Uraenotania sapphirina* (Osten Sacken) on 7 June.

Culex territans were collected with other species of mosquito larvae, including *Ur. sapphirina, An. quadrimaculatus, Aedes canadensis canadensis* (Theobald), *Psorophora* sp., and *Ae. trivittatus* (Coquillett). Sampling sites were rich in invertebrate fauna, including Dysticidae, Notonectidae, Chaoboridae, Lestidae, Aeshnidae, and Amphipoda. *Cx. territans* larvae were collected (89%) in habitats with invertebrate predators.

Of the 71 collections of *Cx. territans* larvae, the following amphibians occurred concurrently: *R. clamitans* (56), *R. catesbeiana* (20) *P. crucifer* (10), *Ambystoma sp.* (9), *R. palustris* (5), *R. sylvatica* (3), and *H. versicolor* (2). Pearson correlations were conducted for week 23 of sampling, and although they were not significant, the presence of *Cx. territans* larvae showed the strongest correlations with the presence of *Rana clamitans* ($r = 0.56$, $P = 0.074$) and number of weeks with continuous water in habitat ($r = 0.56$, $P = 0.074$). The presence of *Cx. territans* larvae did not correlate with soil pH, drainage, elevation, slope, other amphibian species, or wetland size. Results did not differ when we reran the analysis using weeks 21 or 27. Both presence of *R. clamitans* and water were added to the logistics regression analysis to predict *Cx. territans* larvae. In this analysis, the presence of water was not significant and could not predict the presence of mosquito larvae. Water was removed from the logistics regression analysis, and the presence

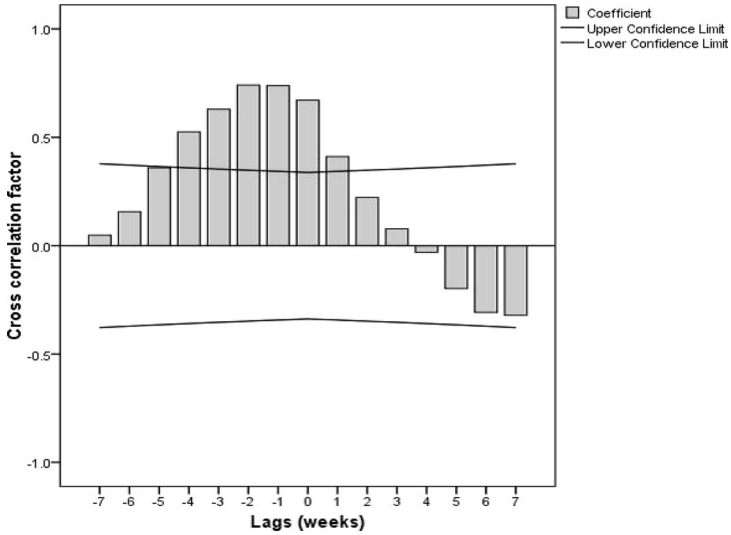

Fig. 1. Cross-correlation functions (CCFs) between the presence of *Cx. territans* and the presence of *R. clamitans*. Lag periods are in weeks. Upper and lower confidence intervals are indicated by the two horizontal lines. Coefficients must cross the confidence interval to be statistically significant. The greater the CCF value, the stronger the correlation.

of *R. clamitans* was significant ($P = 0.05$) and alone could predict *Cx. territans* larvae (88.9%) using this model.

Time series analysis produced two separate models to predict the temporal distribution of *Cx. territans* larvae. The first ARIMA model (0,1,0) predicted *Cx. territans* larvae based on its own temporal distribution ($R^2 = 0.531$, RMSE = 0.104). The second ARIMA model (0,1,0) showed the presence of *R. clamitans* was the best fitting model to temporally predict the presence of *Cx. territans* larvae ($R^2 = 0.794$, RMSE = 0.107). Cross-correlation analysis (Fig. 1) showed *Cx. territans* larvae correlated temporally with the presence of *R. clamitans* during the same week ($R^2 = 0.672$, $P = 0.004$) and when *R. clamitans* occurred 2 wk before ($R^2 = 0.742$, $P < 0.001$). Precipitation, water table depth, barometric pressure, standing water presence, invertebrates, or other amphibian species did not correlate with the temporal distribution of *Cx. territans* larvae using either of these analyses.

On average, *Cx. territans* larvae appeared in sites 2.36 ± 0.67 (SE) wk after the first appearance of *R. clamitans* within the same site. This trend was seen in permanent water habitats (4 ± 1.5 wk), vernal pools (1.67 ± 1.2 wk), and autumn pools (1.8 ± 0.92 wk). Of the 71 collections of *Cx. territans* larvae, 15 did not occur concurrently with *R. clamitans.* All collections of *Cx. territans* larvae occurred in a site that either currently or had previously contained *R. clamitans.*

Laboratory Studies. The average number of days from egg to adult [$D_a = 62.7 - 1.8(t\ °C)$] for *Cx. territans* was 15.7 ± 0.76 d and decreased as the temperature increased. Developmental time from egg to adult was 13.8 ± 0.37 d at 27.3°C and 13.8 ± 0.2 d at 26.8°C but was longer (19.6 ± 0.6 d) for 23.9°C ($F = 62.3$; df = 2,12; $R^2 = 0.87$; $P < 0.001$).

As temperature increased, the number of days needed from blood feeding to oviposition decreased ($y = -0.998x + 34.75$; $R^2 = 0.96$, $F = 1{,}003$, $P < 0.001$). The average length of the gonotrophic cycle ranged from 6 to 26 d depending on temperature (Fig. 2), differing significantly every 2–3°C ($F = 1{,}886$; df = 8,81; $P < 0.001$). The regression of ovarian development rate against temperature was used to calculate the thermal minimum and length of gonotrophic cycle (Fig. 3). The slope and intercept were used to determine the thermal minimum of the gonotrophic cycle and the number of degree-days needed for oviposition. To complete one gonotrophic cycle, 192.3 DD (k) above the thermal minimum (t_0) 3.9°C are needed. Therefore, the rate of ovarian development can be calculated as $V = (t - 3.9)/192.3$. *Cx. territans* did not oviposit at temperatures of 3.2 and 6.5°C, despite a mean longevity for females of 31 d.

Using the thermal heat summation model, the number of degree-days and days to complete the gonotrophic cycle can be determined using the average temperatures (Fig. 4). Based on these data, the date of blood feeding can be extrapolated from field-collected larvae. The first larval collections of *Cx. territans* occurred on 6 May 2004. The mean monthly temperatures during March, April, and May were 3, 9.5, and 17.6°C, respectively. *Cx. territans* requires 192.3 DD to complete its gonotrophic cycle. By adding mean monthly temperatures to the formula for D, the first larvae collected were derived from a female that blood fed 33 d prior. This indicates that *Cx. territans* took its first bloodmeal the last week of March or the first week of April, corresponding to initial collections of amphibians in the same area.

To test our model, we applied mean daily temperatures to $\Sigma(t - 3.9) = 192.3$ for all days >3.9°C. The first date >3.9°C was 29 March 2004. Based on our model, the first oviposition should have occurred in nature on 4 May 2004, which corresponds to our first collection of *Cx. territans* larvae on 6 May 2004.

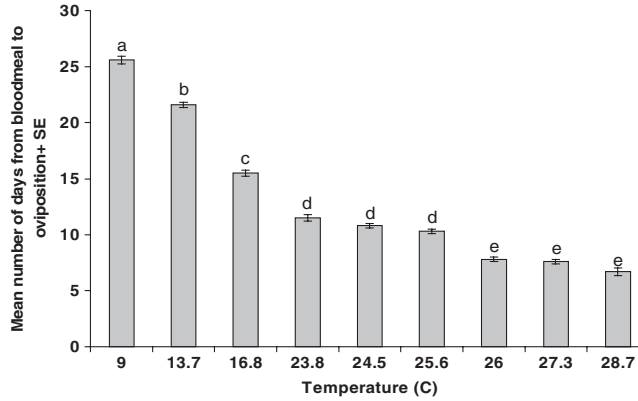

Fig. 2. Length of gonotrophic cycle (d) at increasing temperatures (°C) for *Cx. territans*. Temperatures were compared using an analysis of variance. Bars followed by the same letter are not statistically significant ($P = 0.05$) based on Tukey's post hoc test.

Discussion

The presence of *R. clamitans* was the only variable that could spatially predict the presence of *Cx. territans* larvae. Crans (1970) found *Cx. territans* readily blood feeding on *R. clamitans* in nature. If *Cx. territans* are obtaining bloodmeals from *R. clamitans*, they are ovipositing in sites containing their preferred hosts. The advantage of ovipositing where there are *R. clamitans* is that, as adult mosquitoes emerge, females will be close to bloodmeals. *R. clamitans* prefer to remain in the same habitat throughout the course of the summer (Breder et al. 1927). Therefore, by ovipositing where hosts will be available, female *Cx. territans* aid in the survival of their offspring.

Occasionally, *R. clamitans* will move outside of its home range during precipitation, breeding activities, and overwintering (Martof 1953). This behavior allows *R. clamitans* to forage for prey, build lipid reserves for overwintering, and establish new breeding and overwintering sites (Lamoureux et al. 2002). This foraging behavior occurs in the late summer and fall (Lamoureux et al. 2002) when vernal pools begin to hold water for extended periods. Vernal pools by definition are wetlands that are temporarily flooded during the winter and spring and dry throughout the summer (Mitsch and Gosselink 2000), but can retain water during periods of heavy rain. As trees begin to lose foliage and water demand is reduced, rainfall persists in pools for longer durations. The autumn pools at our study sites held water for 10.5 ± 1.6 wk from September to November. In weeks where pools became reflooded, amphibians were found in all pools immediately after rainfall. As *R. clamitans* colonized new habitats, *Cx. territans* larvae appeared in the same sites 2 wk later. Use of the pools by *Cx. territans* always occurred after amphibians were already present. Therefore, both amphibians and mosquito larvae were taking advantage of new habitats as they became available.

Our study showed that *Cx. territans* females oviposit in permanent and vernal habitats. Early populations of *Cx. territans* are found in permanent water habitats, where subsequent populations of *Cx. territans* use permanent water and late summer temporary pools. Vernal pools were not used in the spring because they were almost dry when *Cx. territans* females initiated oviposition. *Cx. territans* larvae require at least 2 wk (15.7 ± 0.8 d) to complete development from egg to

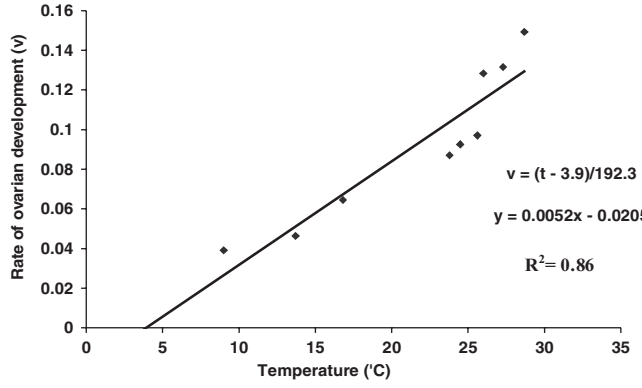

Fig. 3. Rate of ovarian development [$V = (t - t_0)/k$] for *Cx. territans*, correlated with increasing temperatures (°C).

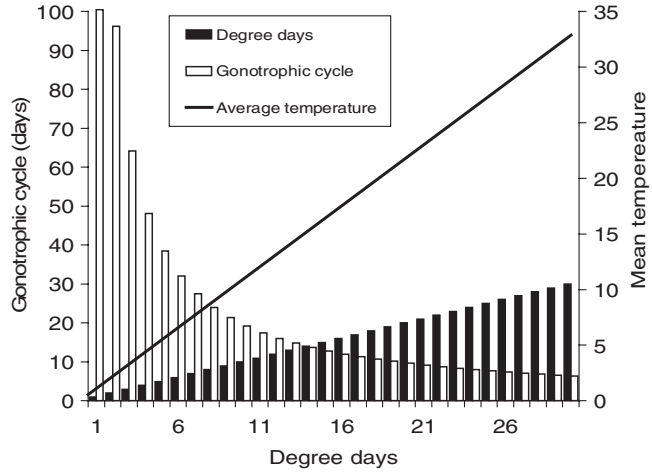

Fig. 4. Relationship among degree-days, gonotrophic cycle, and mean temperature for *Cx. territans*. The black line indicates the mean temperature. The white bar indicates how many days a female would take to complete one gonotrophic cycle at that mean temperature. The black bar indicates the number of degree-days that accumulates at the mean temperature.

adult. The earliest frogs collected on 14 March, *R. sylvatica*, occurred in vernal pool habitats. If *Cx. territans* were using *R. sylvatica* for bloodmeals, they would have needed to migrate after the bloodmeal to find a permanent water site for oviposition. *Cx. territans* has been observed bloodfeeding from *P. crucifer* (Crans 1970), which uses both permanent and vernal pool habitats and may provide the first bloodmeals of the season.

The spatial distribution of *Cx. territans* larvae did not correlate with soil characteristics. *Cx. territans* larvae occurred in sites with a range of pH values, slopes, elevations, soil types, and wetland characteristics. Udevitz et al. (1987) showed that *Cx. territans* larvae occurred in water with a wide range of water chemistry profiles, such as pH and other ion concentrations. This lack of preference may explain why *Cx. territans* larvae have been reported from many types of habitats including permanent water, containers, ditches, marshes, ponds, streams, and tires (Joy and Clay 2002).

Low temperatures may impose the greatest physical barrier to *Cx. territans* existing temporally with their amphibian hosts. Near freezing temperatures can cause reduced oxygen consumption and increased risk of desiccation in terrestrial arthropods (Soemme 1999). If *Cx. territans* are using early amphibians as a bloodmeal source, they would need to be able to digest bloodmeals <5°C, when amphibians are exiting diapause in New Jersey. *Cx. territans* has a thermal minimum of 3.9°C, in which females can digest a bloodmeal. This value is lower than for *Cu. melanura* (Coquillett) (Mahmood and Crans 1997), *An. culicifacies* Giles (12.6°C) (Mahmood and Reisen 1981), and *An. stephensi* Liston (8.9°C) (Mahmood and Reisen 1981). These data indicate that *Cx. territans* has a threshold lower than other species of mosquitoes and likely has thermoregulation mechanisms that allow them to function at lower temperatures. In northern New Jersey, the first amphibians begin to appear in March and April. At that time, the mean daily temperature is rising from 2.9 to 8.8°C. *Cx. territans* females have been collected in resting boxes as early as late March in northern New Jersey as part of the New Jersey State Surveillance and Vector Surveillance programs. The mean monthly temperatures in northern New Jersey for the month of March average around 3.5°C, with an average of 4.2°C in the past decade (New Jersey Weather and Climate Network, Office of the New Jersey State Climatologist). If females are exiting diapause at this time, they may be able to take advantage of early season bloodmeals. Our data support that females would have taken their first bloodmeal around the last week of March, when temperatures were ≈3°C. *Cx. pipiens* with a thermal minimum of 10°C would not be able to digest bloodmeals until late April or early May. Lobkova (1980) found that female *Cx. p. pipiens* left hibernacula when the temperatures were 10–16°C, corresponding to the temperatures in which they are capable of undergoing a gonotrophic cycle. Therefore, it would be a disadvantage to exit diapause early if they are not capable of digesting bloodmeals.

Temporal distribution did not overlap with precipitation events, number of wet sites, or fluctuations in water table. Because they use available sites of varying types, their distribution would not be affected by precipitation events. However, based on climatological data from New Jersey, 2004 was neither an unusually wet or dry year. Habitat quantity can affect the oviposition behavior of mosquitoes (Reiskind and Wilson 2004), suggesting that extreme drought or rainfall could alter the oviposition behavior of *Cx. territans.*

Many parasites synchronize their life cycle to maximize the opportunity of finding a suitable host, which can be highly dependent on both biotic and abiotic factors (Cattadori et al. 2005). Temperature and weather conditions greatly affect populations of *R. clamitans* (Martof 1956). If *Cx. territans* are synchro-

nizing their life cycle to match that of *R. clamitans*, their distribution should also correlate with temperature and weather. However, the first amphibians to exit diapause include *R. sylvatica* and *P. crucifer*, both of which have freeze tolerance mechanisms (Schmid 1982). To synchronize its life cycle to its amphibian hosts, *Cx. territans* adapted by completing its first gonotrophic cycle of the season at near freezing temperatures. However, by ovipositing in sites that contain hosts, females maximize their offspring's potential to locate a host after emergence. Our results support the hypothesis that *Cx. territans* coordinate their life cycle events with their amphibian hosts, specifically to *R. clamitans.* By temporally and spatially co-occurring with their amphibian hosts, they are more likely to find bloodmeals, eliminating the need to travel long distances in search of a host. However, to coexist with their potential hosts, *Cx. territans* have adapted to lower temperatures by being able to undergo a gonotrophic cycle at near freezing temperatures.

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References Cited

Benach, J. L. 1970. Observations of a colony of *Culex territans* Walker. Proc. NJ Mosq. Ext. Assoc. 57: 70–76.

Benach, J. L. 1971. Studies on amphibian filariasis: relationships of *Foleyella sp.* (Filarioidea: Nematoda) from the bullfrog, *Rana catesbeiana,* and *Culex territans* (Culicidae: Diptera). PhD thesis, Rutgers University, the State University of New Jersey, New Brunswick, NJ.

Benach, J. L., and W. J. Crans. 1973. Larval development and transmission of *Foleyella flexicauda* Schacher and Crans, 1973 (Nematoda: Filarioidea) in *Culex territans.* J. Parasitol. 59: 797–800.

Boyer, R., and C. E. Grue. 1995. The need for water quality criteria for frogs. Environ. Health Persp. 103: 352–357.

Breder, C. M., R. B. Breder, and A. C. Redmond. 1927. Frog tagging: a method of studying anuran life habits. Zoologica 9: 201–229.

Cattadori, I. M., D. T. Haydon, and P. J. Hudson. 2005. Parasites and climate synchronize red grouse populations. Nature (Lond.) 433: 737–740.

[CDC] Centers for Disease Control and Prevention. 2005. CDC West Nile virus home page. (http://www.cdc.gov/ncidod/dvbid/westnile/mosquitoSpecies.htm).

Christophers, S. R. 1911. The development of the egg follicle in Anophelines. Paludism 2: 73–87.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Department of the Interior, Fish and Wildlife Service, Washington, DC.

Crans, W. J. 1970. The blood feeding habits of *Culex territans* Walker. Mosq. News. 30: 445–447.

Farajollahi, A. 2005. Seasonal dynamics of *Culex pipiens pipiens* L. (Diptera: Culicidae) in New Jersey and examination of its role as an overwintering reservoir for West Nile virus. MS thesis, Rutgers University, New Brunswick, NJ.

Freda, J., and D. H. Taylor. 1992. Behavioral response of amphibian larvae to acidic water. J. Herpetol. 26: 429–433.

Gessner, J., and E. Stiles. 2001. Field guide to reptiles and amphibians of New Jersey. Endangered and Non-game Species Program, New Jersey Department of Environmental Protection, Division of Fish and Wildlife, Trenton, NJ.

Gruia-Gray, J., and S. S. Desser. 1992. Cytopathological observations and epizootiology of frog erythrocytic virus in bullfrogs (*Rana catesbeiana*). J. Wildl. Dis. 28: 34–41.

Joy, J. E., and J. T. Clay. 2002. Habitat use by larval mosquitoes in West Virginia. Am. Midl. Nat. 148: 363–375.

Kim, B., T. G. Smith, and S. S. Desser. 1998. The life history and host specificity of *Hepatozoon clamatae* (Apicomplexa: Adeleorina) and ITS-1 nucleotide sequence variation of Hepatozoon species of frogs and mosquitoes from Ontario. J. Parasitol. 84: 789–797.

Knight, K. L., and A. Stone. 1977. A catalog of the mosquitoes of the World. Thomas Say Foundation, College Park, MD.

Lamoureux, V. S., J. C. Maerz, and D. M. Madison. 2002. Premigratory autumn foraging forays in the green frog, *Rana clamitans.* J. Herpetol. 36:245–254.

Lobkova, M. K. 1980. Ecology and biology of *Culex pipiens pipiens* in Karelia, pp. 80–95. *In* Blood-sucking arthropods of the European north. Petrozavodsk, Karelia.

Madder, D. J., G. A Surgeoner, and B. V. Helson. 1983. Number of generations, egg production, and development time of *Culex pipiens* and *Culex restuans* (Diptera: Culicidae) in southern Ontario. J. Med. Entomol. 20: 275–287.

Mahmood, F., and W. K. Reisen. 1981. Duration of the gonotrophic cycles of *Anopheles culicifacies* Giles and *Anopheles stephensi* Liston, with observations on reproductive activity and survivorship during winter in Punjab province, Pakistan. Mosq. News 41: 41–50.

Mahmood, F., and W. Crans. 1997. A thermal heat summation model to predict the duration of the gonotrophic cycle of *Culiseta melanura* in nature. J. Am. Mosq. Control Assoc. 13: 92–94.

Martof, B. 1953. Home range and movements of the green frog, *Rana clamitans.* Ecology 34: 529–543.

Martof, B. 1956. Factors influencing size and composition of populations of *Rana clamitans.* Am. Midl. Nat. 56: 224–245.

McIver, S. B. 1969. Notes on the biology of *Culex territans* Walker. Mosq. News 29: 135–136.

Mitsch, W. J., and J. G. Gosselink. 2000. Wetlands, 3rd ed. Wiley, New York.

Mokany, A., and R. Shine. 2003. Competition between tadpoles and mosquito larvae. Oecologia (Berl.) 135: 615-620.

Nasci, R. S., H. M. Savage, D. J. White, J. R. Miller, B. C. Cropp, M. S. Godsey, A. J. Kerst, P. Bennett, K. Gottfried, and R. S. Lanciotti. 2001. West Nile virus in overwintering *Culex* mosquitoes, New York City, 2000. Emerg. Infect. Dis. 7: 742–744.

Reed, L. M., S. Crans, and D. Fonseca. 2008. The surveillance of vector-borne arboviruses. (http://vectorbio.rutgers.edu/surveillance.php).

Reiskind, M. H., and M. L. Wilson. 2004. *Culex restuans* (Diptera: Culicidae) oviposition behavior determined by larval habitat quality and quantity in Southeastern Michigan. J. Med. Entomol. 41: 179–186.

Savage, H. M., D. Aggarwal, C. S. Apperson, C. R. Katholi, E. Gordon, H. K. Hassan, M. Anderson, D. Charnetzky, L. McMillen, E. A. Unnasch, and T. R. Unnasch. 2007. Host choice and West Nile virus infection rates in blood-fed mosquitoes, including members of the *Culex* pipiens complex, from Memphis and Shelby County, Tennessee, 2002–2003. Vector Borne Zoonotic Dis. 7: 365–386.

Schmid, W. D. 1982. Survival of frogs in low temperature. Science 215: 697–698.

Smith, J. B. 1903. The effect of low temperatures on mosquito larvae. Science 17: 244.

Soemme, L. 1999. The physiology of cold hardiness in terrestrial arthropods. Eur. J. Entomol. 96: 1–10.

SPSS. 2005. SPSS base 14.0 for Windows user's guide. SPSS, Chicago, IL,

Udevitz, M. S., P. Bloomfield, and C. S. Apperson. 1987. Prediction of the occurrence of four species of mosquito larvae with logistic regression on water-chemistry variables. Environ. Entomol. 16: 281–285.

Vinogradova, E. B. 2000. *Culex pipiens pipiens* mosquitoes: taxonomy, distribution, ecology, physiology, genetics, applied importance and control. Pensoft Publishers, Moscow, Russia.

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