Rainfall Influences Survival of *Culex pipiens* (Diptera: Culicidae) in a Residential Neighborhood in the Mid-Atlantic United States

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ABSTRACT Measurement of the survival and dispersal rates of mosquito vectors is an important step in designing and implementing control strategies. Vector survival plays a key role in determining the intensity of pathogen transmission, and vector movement determines the spatial scale on which control efforts must operate to be effective. We provide the first estimates of field survival and dispersal rates for *Culex pipiens* L. in North America, an important enzootic and bridge vector for West Nile virus (WNV). We conducted mark-release-recapture studies in a residential area near Washington, DC, in two consecutive years and fit nonlinear regression models to the recapture data that incorporate weather information into survival and recapture probabilities. We found that daily survival rates were not significantly different between the 2 yr but were negatively affected by rainfall. The daily survival rate was 0.904 ± 0.037 (SE), which implies an average longevity of 10.4 d. As with other vector-borne pathogens, the measured survival rate suggests that at our site the majority of WNV-infected *Cx. pipiens* mosquitoes may perish before becoming infectious (being able to transmit WNV to hosts). We found relatively little evidence of dispersal after the initial night after release. Our results suggest that transmission of WNV and other pathogens transmitted by *Cx. pipiens* may be highly local and they highlight the importance of factors that influence survival of mosquito vectors.

KEY WORDS *Culex pipiens*, dispersal, mosquito, survival, West Nile virus

Longevity of adult female mosquitoes is a key variable in the transmission of pathogens. After ingesting an infectious blood meal, a mosquito must survive the extrinsic incubation period of the pathogen before it can transmit it to a susceptible host (Davis 1932, Milby and Reisen 1989). In some cases, variation in mosquito survival may be the dominant factor regulating transmission intensity, and increasing mortality of infected females through adulticiding is one strategy used to control some vector-borne diseases. It follows that determining the survival rate of vectors can allow a better understanding of pathogen transmission, can aid in control efforts and, if the factors influencing survival can be identified, may help predict the occurrence of outbreaks.

At the same time, dispersal of adult mosquitoes from their larval habitats and mosquito movement between feeding and oviposition sites play key roles in the spatial scale of transmission of vector-borne pathogens. Thus, understanding mosquito movement is critical in determining effective control strategies because if mosquitoes move over large distances (e.g.,

several kilometers) then larviciding and adulticiding efforts must cover a large area to effectively decrease mosquito abundance and/or the intensity of a local epidemic. In contrast, if mosquitoes have low dispersal rates, and move little between feeding and oviposition sites, then if hosts are also sedentary transmission may be highly heterogeneous and very focal with transmission hotspots near key larval habitats or competent hosts.

The introduction of West Nile virus (WNV) to North America in 1999 brought renewed importance to understanding the vector ecology of North American mosquitoes (Lanciotti et al. 1999). WNV has since become the most important mosquito-borne disease in North America, with 35,231 reported cases, 12,852 cases of encephalitis, 1,308 deaths, and an estimated 360,000 illnesses from 1999 to 2010 in the United States and Canada (Centers for Disease Control and Prevention 2011, Health Canada 2011). WNV is a member of the Japanese encephalitis antigenic complex of the genus Flavivirus, family Flaviviridae and is transmitted worldwide primarily by *Culex* mosquitoes (Kramer et al. 2008, Kilpatrick 2011). In North America, the dominant enzootic and bridge vectors of WNV across many regions are *Cx. tarsalis* Coquillett, *Cx. quinquefasciatus* Say, and *Cx. pipiens* L. (Turell et al. 2002, Kilpatrick et al. 2005, Hamer et al. 2008) and *Cx. pipiens* also appears to be the predominant vector in urban epidemics of WNV in Romania, and southern Russia (Hubalek and Halouzka 1999). *Cx. tarsalis* and

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Cx. quinquefasciatus have been relatively well studied over the past 60 yr because of their important roles in the transmission of St. Louis Encephalitis virus (SLEV) and Western Equine Encephalitis virus (Reeves 1965; Reisen et al. 1991, 1992b, 1995, 2003). However, despite its global importance in transmission of WNV and other arboviruses (e.g., SLEV), the field survival rate and dispersal of *Cx. pipiens* have not been measured in North America.

Cx. pipiens mosquitoes are abundant in urban environments, using storm drains and other sources of organically rich, stagnant water for oviposition and larval development (Spielman and D'Antonio 2001, Andreadis et al. 2004). They often feed primarily on birds, which makes them an ideal vector for avian pathogens like WNV and SLEV (Kilpatrick et al. 2006a, Molaei et al. 2006, Hamer et al. 2009). However, they also feed on humans and other mammals, especially in the late summer, which results in their serving as an important bridge vector (Kilpatrick et al. 2005, 2006b; Hamer et al. 2008). Thus, measuring the dispersal and survival of this species could offer important insights into the transmission of WNV.

Measuring survival and dispersal rates of mosquitoes in the field is a logistically challenging task, and can be especially difficult in urban and residential areas where releasing thousands of laboratory-reared mosquitoes might have detrimental impacts on public health. However, previous work has shown that measurements of survival in a laboratory setting are frequently very different from those obtained in the field, making field studies necessary. For example, the life expectancy of *Cx. quinquefasciatus* in the lab at 25–28°C was estimated to be 74 d (Suleman and Reisen 1979), whereas a field study estimated longevity to be 6.25 d in a residential area of California when temperatures averaged 23.9°C (Reisen et al. 1991).

The purpose of our study was thus to determine the survival and dispersal rates of *Cx. pipiens* mosquitoes in a residential area where WNV has been actively transmitted yearly since at least 2003. We hypothesized that the feeding and larval habitat of *Cx. pipiens* would result in low dispersal rates because both avian hosts and larval habitat are locally available. As a result, mosquitoes need not fly long distances for either resource, especially in comparison with mosquito species whose vertebrate hosts and larval habitats may be separated by several kilometers (Walton et al. 1999).

Materials and Methods

We performed mark-release-recapture (MRR) studies at a residential site in Takoma Park, MD, during the summer in 2 yr, 2008 and 2009. The 2008 study was performed from 19 August until 2 September and the 2009 study was performed at the same site from 25 July until 8 August. The study site in Takoma Park, MD, ≈1.5 km northwest of Washington, DC (Latitude: 38.98° N, Longitude: 77.01° W) is in a residential neighborhood (Fig. 1). This site consists primarily of houses with yards and overhanging trees, and also includes a grassy park. The land use in a 500 m radius around the site is 26% impermeable surface and 28% forest cover, with the rest composed primarily of grass or lawns.

Egg Rafts. Egg rafts were collected for the two studies on 6 August 2008 and on 12 and 13 July 2009 by placing 10–15 navy blue, 5.7-liter plastic containers containing 2.5–5 cm organically enriched water (≈19 liters water mixed with 0.2–0.4 liters of rabbit chow in a plastic container and placed in the sun for >1 wk before use to stimulate bacterial growth). Tubs were covered with one-inch mesh chicken-wire screening to attract egg-laying *Cx. pipiens* and deter other species (Walther and Weber 1996). Egg rafts were collected daily and placed individually into 15 × 23 × 5 cm containers, inside a 0.23 m³ cage that was placed in a shaded location at the site. The cages had screen on all sides to allow airflow, and plastic covers over the top of the cage to protect mosquitoes from direct rainfall.

Rearing Mosquitoes. After 2–3 d, two larvae were removed from each container for species identification (Darsie and Ward 1981, Andreadis et al. 2005). Containers containing *Cx. pipiens* were retained and allowed to develop to adulthood, whereas containers containing larvae of other species were removed from the cage. Larvae were fed 0.5 g of fish food (Koi's premium choice fish food; Kaytee Inc., Chilton, WI) daily and adults were offered a 10% sucrose solution on cotton balls.

Spermathecal Dissections. After emergence, males and females were held in cages for 3 d to allow mating. On the third day, 10 females were removed from each cage and dissected to determine mating status by the presence or absence of sperm in spermathecae. Spermathecal dissections showed the presence of sperm in 10/10 (100%) of the reared mosquitoes from each year, suggesting that a large fraction of the marked and released mosquitoes had mated.

Marking Mosquitoes. We marked female mosquitoes on the day of release approximately an hour before dusk. Mosquitoes were removed from the cage using aspirators, counted in a clear plastic tube, and transported to 0.027 m³ cuboidal cages. Mosquitoes were dusted with Bioquip (Rancho Dominguez, CA) fluorescent powders dispensed from 4 oz handheld bulbs. In 2008, mosquitoes were released on a single night and dusted with red. In 2009, mosquitoes were released on two consecutive nights and were dusted with either yellow or blue to differentiate the two nights.

Releasing Mosquitoes. The marked mosquitoes were released at dusk at the approximate center of the study site and mosquito traps (Fig. 1). In 2008 we released 223 marked female mosquitoes on a single day (19 August, 2008), whereas in 2009, 500 marked female mosquitoes were released on each of two consecutive days (25 and 26 July, 2009).

Recapturing Mosquitoes. Twenty Centers for Disease Control and Prevention (CDC) light traps (baited with ≈1 kg of dry ice [solidified CO_2] in a 1.5-liter plastic thermos) and 4 (2008) or 10 (2009) gravid traps (baited with the organically enriched

Fig. 1. Map of the study area in Takoma Park, MD, with release site and trap locations, and number of mosquitoes caught in each trap in 2009. Numbers preceded by the letter "g" show CDC gravid trap locations (note: only g1–g4 were run during the 2008 study), and numbers not preceded by "g" refer to CDC light traps baited with dry ice (CO_2). The star shows the release site. (Online figure in color.)

water used in the ovitraps described above) were distributed throughout the site. Two CDC light traps were hung from parachute cord at 1.5m above the ground and the remainder were placed 2–10 m above the ground to attract mosquitoes feeding in the foliage and canopies of trees. Mosquitoes were removed from all traps every afternoon for 15 consecutive days. All trapped mosquitoes were examined for fluorescent dusts with ultraviolet (UV) light under a dissecting microscope. We obtained daily rainfall, temperature and wind speed and direction estimates for the duration of the study period from a nearby weather station ≈3 km away (http://www.wunderground.com/history/airport/KCGS/).

Statistical Analysis. We used nonlinear least squares regression to estimate survival rates (or more correctly, "retention rates" because mosquitoes that disperse outside the trapping area cannot be distinguished from death) and recapture probability by adapting a previous approach (Buonaccorsi et al. 2003). In the simplest model, we fit the number of marked female mosquitoes captured on each night j, C_j, to the following equation:

$$C_j = (N - \sum_{i=1}^{j-1} C_i)\theta\pi^{t_j} \qquad [1]$$

Here N is the number of mosquitoes of that color released, θ is the probability that a live marked mosquito is recaptured, π is the daily survival probability, j is the trapping occasion, and t_j is the number of days between release and trapping occasion j (in our case, $t_j = j$, because each trapping occasion was 1 d and mosquitoes were trapped every day). The summation of trapped mosquitoes from previous days ($\sum C_i$, $i = 1$

to j-1), removes mosquitoes from the marked population that were caught and removed in previous time steps (this was approximated by Buonaccorsi et al. as $(1-\theta)^{j-1}$ but equation 1 uses the exact number removed rather than an estimate).

We analyzed the influence of year and rain on recapture probability and survival using the equation:

$$C_j = (N - \sum_{i=1}^{j-1} C_i)((\theta + c_4 y)e^{-c_5 R_j})(\pi + c_3 y)^{t_j} e^{-c_6 \sum_{i=1}^{j} R_i}$$

[2]

Here c_5 measured the effect of rain on night j, R_j, on recapture probability, and c_6 measured the effect of rain on survival (note that the effects of previous rain, if any, must be compounded as indicated by the summation), y was a dummy variable (0 for 2008, and 1 for 2009), the coefficient c_3 measured the difference in survival between the years, and c_4 measured the difference in recapture probability between the 2 yr. It is important to note that this model assumes the impact of rain on survival is nonlinear and saturating. Comparisons between years were then made by determining whether the year coefficients (c_3 and c_4) were significantly different from 0. The nonlinear regression models were fit to the data using function nls in R (R Development Core Team 2011). The variance of the parameters in equation 2 is estimated from a linearized version of the model (Bates and Watts 1988). Finally, we calculated an estimate of the average longevity by inverting the daily mortality rate (average longevity = 1/(1-survival rate)).

Mosquito Dispersal. The average daily dispersal distance was estimated by calculating the effort-weighted average distance that marked individuals were trapped away from the release site. We estimated trapping effort by calculating the number of traps in a disc with the distance between outer and inner circles of 20 m and dividing by the area in this disc. For example, if there were three traps that were between 20 and 40 m from the release site, the trapping effort in this disc would be $3/(\pi(40^2-20^2))$. We then calculated the distance dispersed on day j, D_j, using the equation:

$$D_j = \sum_{i=1}^{n} \frac{E^i}{C_j^i} \cdot \sum_{i=1}^{n} \frac{\sum_{k=1}^{m} C_j^{i,k} d^k}{E^i}$$

[3]

Here $C_j^{i,k}$ is the number of mosquitoes trapped on day j in trap k that is within disc i ($i = 1$ to n, with $i = 1$ being a 20 m radius circle, $i = 2$, a disc with outer diameter 40 m and inner diameter 20 m, etc., and $i = n$ being the disc containing the traps furthest from the release site; $k = 1$ to m, where m is the number of traps within disk i), d^k is the distance between trap k and the release site, and E_i is the trapping effort in that disc, as described above. We estimated the dispersal rate by regressing the effort-weighted average distance that marked mosquitoes were caught each day against the number of days since the release, starting with day 1 postrelease (we did not include a distance of 0 on day 0). Thus, dispersal from the release location on the night of
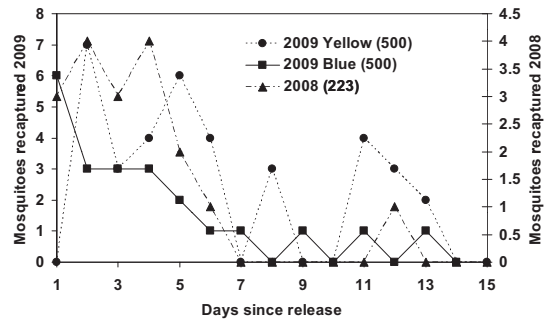

Fig. 2. Number of *Cx. pipiens* recaptured each day in 2008 and 2009. In 2009, 500 mosquitoes were marked and released on each of two consecutive days and were dusted with different colors (yellow and blue). In 2008, a single batch of 223 mosquitoes were released. Numbers recaptured in 2009 and 2008 are given on the left and right Y-axes, respectively, and the two Y-axes are scaled so the numbers recaptured are comparable.

release does not influence this calculation. We also performed a set of simulations of mosquitoes dispersing across our trapping grid to assess whether our relatively narrow-distance trapping grid could underestimate the rate of dispersal (Supp. Material [online only]).

The direction traveled by the mosquitoes was determined by averaging the direction (in degrees) of the release site for each site to a trap that captured a marked mosquito. A χ^2 test was used to determine if the mosquitoes dispersed in random directions or showed evidence of directional movement. We separated the site into six sectors, the largest number that could be used and still satisfy the assumptions of a χ^2 test. We used the following equation to calculate the χ^2 statistic:

$$\chi^2 = \sum_{i=1}^{q} \frac{(O_i - (Cx_i/n/q))^2}{(Cx_i/n/q)}$$

[4]

Here O is the observed number of marked mosquitoes trapped in the sector, and the term in parentheses is the expected number in sector i, which is the product of C, the total number of mosquitoes recaptured and x_i, the number of traps in a sector divided by n, the total number of traps at the site, and q the number of sectors. Numbers of recaptured mosquitoes were large enough to permit analysis for the study in 2009, but were too small for 2008.

Results

We captured a total of 1818 mosquitoes in 2008 and 5493 mosquitoes in 2009. Thus, the overall impact of our study on local mosquito populations was to reduce them at least five-fold relative to the 223 and 1,000 mosquitoes that were locally reared from egg rafts laid at the site. Marked female mosquitoes were captured throughout the study area with 38% of the traps recapturing at least one marked mosquito in 2008 and 73% in 2009 (Fig. 1). The fraction of female mosqui-
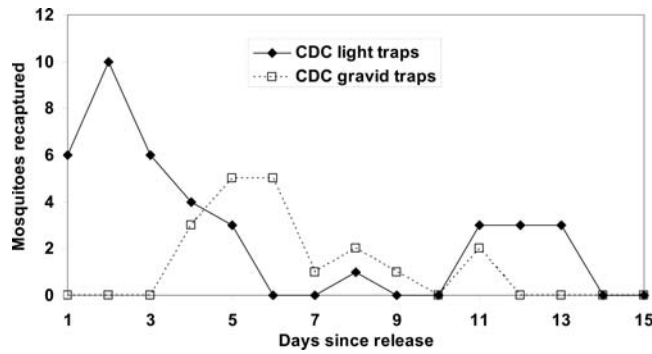
Fig. 3. Number of *Cx. pipiens* recaptured each day postrelease in CDC light traps baited with dry ice (CO_2) and CDC gravid traps in 2009.

toes recaptured was slightly higher in 2008 (8.1%, 18 of 223) than in 2009 (5.8%, or 58 of 1,000) but there was no evidence that survival or recapture probability differed between the 2 yr (survival: $c_3 = -0.0055 \pm 0.006$ (SE); $t = -0.88$; df = 1; $P = 0.38$; recapture probability: $c_4 = 0.060 \pm 0.078$; $t = 0.776$; df = 1; $P = 0.44$). The number of recaptured marked female mosquitoes was highest in the first few days following the release and declined thereafter, with mosquitoes being trapped through day 11 in 2008 and day 13 in 2009 (Figs. 2 and 3). The temporal pattern of recaptures in CDC light and CDC gravid traps in 2009 varied through time with no recaptures in gravid traps until day 4 postrelease and a second rise in recaptures in light traps on days 11–13 (Fig. 3). In both years more mosquitoes were recaptured by CO_2-baited CDC light traps than gravid traps possibly because of the larger number of CDC light traps than CDC gravid traps (2008: 20 light and four gravid traps; all 18 recaptures in light traps; $\chi^2 = 3.6$; df = 1; $P = 0.058$; 2009: 20 light vs. 10 gravid traps; 39 of 58 recaptures were in light traps; $\chi^2 = 0.01$; df = 1; $P > 0.95$) and because mosquitoes had to survive feeding and egg development before becoming gravid.

Rainfall occurred on several days during the study in both years (Fig. S3), and there was evidence that rain negatively affected mosquito survival (Table 1) but only weak and nonsignificant evidence that rain reduced the recapture probability ($c_5 = -5.42 \pm 3.25$; $t = -1.67$; df = 1; $P = 0.10$). The estimated coefficient for rain, -0.042, (Table 1) implies that a 1 cm rainstorm in 24 h would decrease daily survival by 34% from 0.904 to 0.594.

Dispersal rates (mean distance of marked mosquitoes recaptured each day, weighted by trapping ef-

fort) were estimated for both years (Fig. 4). For the 2008 study, there was marginal support for *Cx. pipiens* mosquitoes dispersing at a very low rate (Fig. 4; 8.8 $\pm$ 3.3 m/d). However, in 2009 there was no evidence for dispersal in that the distance of trapped mosquitoes from the release site did not increase with days since release (Fig. 4; -2.2 ± 2.5 m/d). These low estimates for dispersal rate do not appear to be an artifact of the small spatial extent of our trapping grid (Supp. Material [online only]). There was some evidence that the direction of dispersal of mosquitoes in 2009 was not random, with more mosquitoes being caught, after adjusting for trapping effort, in traps in a NNW direction, and fewer in the NNE direction from the release site ($\chi^2 = 12.8$; df = 5; $P = 0.025$). This is opposite the predominant wind direction during the study, which was southwest (Fig. S4). The number of recaptured mosquitoes was too low to determine if the direction of dispersal was different from random in 2008.

Discussion

Variation in the survival of *Cx. pipiens* mosquitoes could play an important role in the transmission of several arboviruses including WNV and SLEV. Our MRR study suggests that the daily survival rate for *Cx. pipiens* females in a suburban area in the mid-Atlantic was 90.4% with a 95% confidence interval (CI) of 83.1–97.9%. This is somewhat higher than survival estimates for other WNV vectors. For example, the 95% CI for *Cx. pipiens* from our study barely includes the estimate of 83.8% obtained for *Cx. quinquefasciatus* in Rossmoor, Orange County, CA (Milby and Reisen 1989), and the mean for *Cx. pipiens* is also substantially

Table 1. Daily survival and recapture probability (θ) for *Cx. pipiens* mosquitoes calculated using nonlinear least squares on data from both years combined

Parameter	Estimate	SE	t	P
Recapture probability, θ	0.013	0.002	6.48	8.8×10^{-08}
Survival, π	0.905	0.037	24.56	1.00×10^{-16}
Rain on survival, $c_2{}^a$	-0.042	0.015	-2.90	0.0068

There was no evidence for differences in survival or recapture probability between the 2 yr, 2008 and 2009; see text for further details.

^{a} Parameter c_2 indicates the effect of rainfall, R, in mm, on mosquito survival given by the expression survival = survival*$e^{c2 *R}$. See Methods and Materials for further explanation.
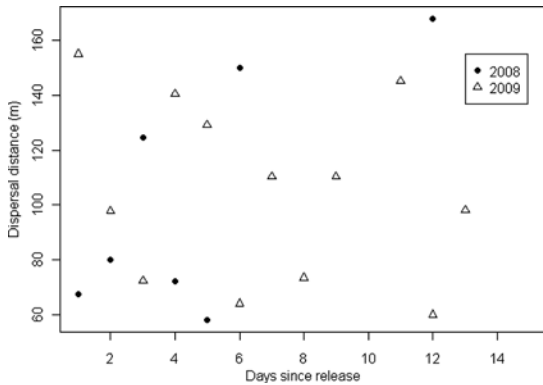
Fig. 4. Average distance of recaptured mosquitoes on each day postrelease, corrected for trapping effort. In 2008 mosquitoes dispersed ≈9 m per day (Distance from release site (m) = 61.3 + 8.8*Day; $n = 7$; $P = 0.06$). In 2009 there was little statistical evidence for positive dispersal (Distance from release site (m) = 119.4–2.1*Day; $n = 12$; $P = 0.10$).

higher than estimates from MRR studies of *Cx. tarsalis* (47–75%) in the Coachella Valley of California (Reisen and Lothrop 1995). However, estimates of daily survival of *Cx. tarsalis* at the same sites based on parity dissections, which are less biased by dispersal but require other assumptions, were much higher (80–92% in 4 of 5 mo). These latter estimates are similar to our estimate for *Cx. pipiens* and to those for *Cx. erythrothorax* across three months in southern California (84–89%) (Walton et al. 1999).

Trapping of mosquitoes with significant numbers of host seeking and gravid traps in 2009 allows a preliminary estimate of the lengths of the stages of a single gonotrophic cycle in the field including the period of host seeking, digestion, and egg laying (Fig. 3). All mosquitoes caught in the first 4 d were caught in host-seeking traps, suggesting that the released mosquitoes, which had already mated, may have taken up to 4 d to find and feed on a host. In the subsequent 4 d, recaptured mosquitoes were primarily captured in gravid traps suggesting they had successfully fed and were ready to lay eggs. Finally, a second "wave" of mosquitoes was caught in host-seeking traps between days 11 and 13. These data provide a crude estimate of 8–10 d for the length of the gonotrophic cycle over a 2 wk period when the average temperature was 25.2°C. This is longer than the 5 d estimated for *Cx. tarsalis* in May when temperatures were similar (Reisen and Lothrop 1995), but we acknowledge that our estimate is somewhat crude and based on limited sample sizes.

Mosquitoes appeared to disperse throughout the study areas in the initial night after the release but there was only weak evidence of very limited dispersal afterward. Although some mosquitoes likely moved beyond our furthest traps (200 m from the release site) on the first night and continued to disperse, the remaining mosquitoes showed little evidence of movement after the first night. Our simulations suggest that despite the limited spatial extent of our trapping grid, our data are inconsistent with significant mosquito

dispersal (Supp. Material [online only]). If our low estimates of dispersal after the release night are valid, they contrast markedly with mark-recapture studies of *Cx. tarsalis* in which mosquitoes appeared to be actively dispersing for at least 3 d and moved over one km during this time (Reisen and Lothrop 1995). In another study *Cx. tarsalis* moved ≈110 m/d and *Cx. quinquefasciatus* dispersed ≈180 m/d (Reisen et al. 1992a). The difference in dispersal rates may be because of differences in larval habitat and host preferences of the three species. In a residential area with an ample supply of larval habitats, and 15.3 birds/ha (Kilpatrick et al. 2006a) little movement would be required to find both hosts and larval habitat. Limited dispersal by *Cx. pipiens* would result in highly focal WNV transmission where this species the dominant vector.

Our estimate for the survival rate of *Cx. pipiens* suggests an interesting implication for WNV transmission that is likely common to many vector-borne pathogens: ≈2.3% of *Cx. pipiens* that feed on competent hosts (e.g., those with a viremia of 10^8 PFU/ml such as an American robin; Kilpatrick et al. 2007) on day 3 after adult emergence would survive and be able to transmit WNV 7 d later. This scenario is based on the fact that during the time of our study, the average temperature was 25.2°C, and the average longevity of *Cx. pipiens* mosquitoes was 10.5 d (assuming a constant daily survival rate, 0.905). Under this model of exponentially distributed longevity, only ≈49.7% of mosquitoes would survive 7 d, and other research suggests that at 25.2°C, ≈4.7% would likely transmit WNV on their second feeding on day 10 if they fed on an infected host in their first feeding on day 3 (Kilpatrick et al. 2008). Thus, only a small fraction of mosquitoes would be capable of transmitting WNV, and decreases in adult mosquito survival, such as a severe rainstorm (that may also reduce larval survival; Koenraadt and Harrington 2008), could decrease transmission in the short term. It remains to be determined whether survival of *Cx. pipiens* varies among sites, regionally or seasonally, and how factors like mosquito predators, adulticiding, temperature, and humidity might influence both mosquito survival and pathogen transmission.

Acknowledgments

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