

## Short Communication

# *Aedes albopictus* Body Size Differs Across Neighborhoods With Varying Infrastructural Abandonment

Grace Katz,<sup>1</sup> Paul T. Leisnham,<sup>2,✉</sup> and Shannon L. LaDeau<sup>1,3,✉</sup><sup>1</sup>Cary Institute of Ecosystem Studies, PO Box AB, Millbrook, NY 12545, <sup>2</sup>Department of Environmental Science and Technology, University of Maryland, College Park, MD 20742, and <sup>3</sup>Corresponding author, e-mail: [ladeaus@caryinstitute.org](mailto:ladeaus@caryinstitute.org)

Subject Editor: Dina Fonseca

Received 19 June 2019; Editorial decision 29 August 2019

## Abstract

Mosquitoes pose an increasing risk in urban landscapes, where spatial heterogeneity in juvenile habitat can influence fine-scale differences in mosquito density and biting activity. We examine how differences in juvenile mosquito habitat along a spectrum of urban infrastructure abandonment can influence the adult body size of the invasive tiger mosquito, *Aedes albopictus* (Skuse) (Diptera: Culicidae). Adult *Ae. albopictus* were collected across 3 yr (2015–2017) from residential blocks in Baltimore, MD, that varied in abandonment level, defined by the proportion of houses with boarded-up doors. We show that female *Ae. albopictus* collected from sites with higher abandonment were significantly larger than those collected from higher income, low abandonment blocks. Heterogeneity in mosquito body size, including wing length, has been shown to reflect differences in important traits, including longevity and vector competence. The present work demonstrates that heterogeneity in female size may reflect juvenile habitat variability across the spatial scales most relevant to adult *Aedes* dispersal and human exposure risk in urban landscapes. Previous work has shown that failure to manage abandonment and waste issues in impoverished neighborhoods supports greater mosquito production, and this study suggests that mosquitoes in these same neighborhoods could live longer, produce more eggs, and have different vector potential.

**Key words:** development, life history, ecology and population dynamics, vector ecology

Mosquito vector competence is the probability that a vector can become infected and transmit infection to hosts (LaDeau et al. 2015). Fundamental to vector competence is the density and fitness of the biting vector population. Environmental heterogeneity that influences juvenile habitat can result in intraspecific differences in life-history traits that affect adult fitness (Armbruster & Hutchinson 2002, Delatte et al. 2009, Leisnham et al. 2009), biting behavior (Leisnham et al. 2008), and longevity (Leisnham et al. 2008, Reiskind and Lounibos 2009, Alto 2011, Westby and Juliano 2017), and these traits can then influence variation in vector competence (Nasci and Mitchell 1994; Alto et al. 2005, 2008a; Bevins 2008; Muturi and Alto 2011; Alto and Bettinardi 2013; Zirbel et al. 2018). However, few studies have examined trait differences in the field under natural environmental conditions (Schneider et al. 2004, Walsh et al. 2011, Juliano et al. 2014). Improved understanding of the causes and consequences of variability in life-history traits that influence vector competence is an important challenge for managing arboviral risk at scales relevant to human exposure.

Among the most widely measured life-history traits of adult mosquitoes is body size. Larger mosquito size has been related to survival (Ameneshewa and Service 1996; Briegel and Timmermann 2001; Alto 2011; Alto et al. 2012, 2015; Juliano et al. 2014) and

blood-feeding frequency (Takken et al. 1998, Leisnham et al. 2008, Xue et al. 2008, Farjana and Tuno 2013) in a number of species. Adult female survival is one of the most important parameters in many mathematical models of pathogen transmission (Hawley 1985, Smith et al. 2012, LaDeau et al. 2015). Field-based data on dengue virus infection in *Aedes (Stegomyia) aegypti* (L.) support a positive size effect (Juliano et al. 2014), although lab-based studies suggest both positive and negative associations between size and mosquito susceptibility to virus infection (Alto et al. 2005, 2008b; Bevins 2008). Body size is also positively associated with mosquito fecundity (Blackmore and Lord 2000, Armbruster and Hutchinson 2002, Leisnham et al. 2009), which is likely to indirectly lead to higher disease transmission by increasing population growth rate and the density of biting females (Livdahl and Sugihara 1984, Costanzo et al. 2018). One of the most widely used measures of body size is wing length since it is relatively easy to collect and highly correlated with other measures of body size, including body weight (Petersen et al. 2016) and adult reserves at emergence (Briegel et al. 2001). Wing length has been used as a critical metric in both ecological and human health studies (Hawley 1985, Nasci and Mitchell 1994, Zirbel et al. 2018).

The tiger mosquito, *Aedes albopictus* (Skuse), is a globally invasive mosquito species that was first introduced to the southern United States from Japan in the mid-1980s (Hawley et al. 1987). Since its introduction, the species has spread rapidly to become the dominant mosquito in many urban areas and a predominant human-biting species across much of its new temperate range (Lounibos 2002; Benedict et al. 2007; Paupy et al. 2009; Kraemer et al. 2015, 2019). Like other *Aedes* species, *Ae. albopictus* oviposits drought-resistant eggs that can remain viable for months, facilitating its spread into new ranges (Juliano and Lounibos 2005). Transmission of dengue and chikungunya viruses by *Ae. albopictus* has supported human epidemics in temperate regions of Europe (Chretien and Linthicum 2007, Rezza et al. 2007) and Asia (Tsuda et al. 2016, Quam et al. 2015) and the species is a competent vector for zoonotic arboviruses circulating in the United States, including West Nile virus (Turell et al. 2005). Even without the potential disease risk, *Ae. albopictus* is a significant nuisance for residents in cities where it has established due to its aggressive daytime biting (Worobey et al. 2013, Halasa et al. 2014, Bodner et al. 2016, Biehler et al. 2018, Goodman et al. 2018).

Adult *Ae. albopictus* population size is strongly associated with variation in the quantity and type of local juvenile habitat (Bartlett-Healy et al. 2012, Dowling et al. 2013, LaDeau et al. 2013, Little et al. 2017, Bodner et al. 2019). *Aedes albopictus* have limited dispersal and are most likely to be sampled within 100 m of their juvenile habitat (Niebylski and Craig 1994, Honório et al. 2003, Guerra et al. 2014). Greater numbers of discarded (unmanaged and abandoned) container habitat were predictive of host-seeking adult *Ae. albopictus* density at the scale of a city block in Baltimore, MD (Bodner et al. 2019) and adult and juvenile densities increased with the proportion of abandoned buildings on a block (Little et al. 2017). Given differences in the quantity and type of juvenile habitat observed in Baltimore (LaDeau et al. 2013, Little et al. 2017) and the strong spatial association between juvenile habitat and adult numbers (Bodner et al. 2019), we hypothesized that adult body size might also reflect block- and neighborhood-level differences in juvenile habitat. The present study examines body size of individual female *Ae. albopictus* collected over 3 yr from the same 13 blocks examined by Little et al. (2017).

## Materials and Methods

Adult mosquitoes were trapped using BG-Sentinel traps baited with CO<sub>2</sub> and a 2.0-ml Octenol Lure (a mammal-derived attractant) for 3 d every third week during June and July 2015–2017. Two traps were placed in two to three focal blocks in five neighborhoods in West Baltimore, MD (13 blocks total). The neighborhoods examined in this study were predominantly residential and spanned a range of socioeconomic status (SES)-related conditions, from blocks with a relatively high level of management and occupancy (high SES) to a low level of management and high infrastructure abandonment (low SES). Infrastructure abandonment was measured as the proportion of buildings that were uninhabitable with boarded-up doors. More details on study design can be found in Little et al. (2017). Two neighborhoods each were categorized as low and intermediate SES and one neighborhood was high SES. In 2017, focal blocks were revisited in only the four low and intermediate SES neighborhoods due to funding constraints. All neighborhoods were similarly distant from large water bodies and forested parks. To evaluate whether the differences in unmanaged and discarded container habitat across sites was associated with differences in adult body size, we examined

samples from across blocks with variable levels of abandoned infrastructure. Information about the number of abandoned buildings and vacant parcels was recorded for each focal block and proportion abandoned has been previously shown to be an important local predictor of juvenile habitat and larval mosquito abundance across these same neighborhoods (Little et al. 2017). For exploratory figures, abandonment levels were classified as low (0–5% buildings uninhabitable), intermediate (18–29%), or high (42–58%) based on observed occupancy and infrastructure condition of each block.

Mosquito collections were identified by species and labeled with the date, neighborhood and block number, species, and sex at the time of collection. Female mosquitoes were dried in microcentrifuge tubes with silicate beads. The right wing of each female was removed, photographed, and measured using Olympus cellSens digital imaging software. Wings were all measured from the jugal fold to the end of the Radius 1 (R1) vein in millimeters.

Wing lengths were transformed to log scale for all statistical analyses to meet parametric and homogeneity of variance assumptions. All graphs, figures, and analyses were completed using the R Statistical Software (R Core Team 2018). Differences in wing length among months, years, and abandonment categories were evaluated with analysis of variance and, when appropriate, Bonferroni-corrected pairwise *t*-tests. To assess the relationship between female wing length and block abandonment level, we then used mixed-effects models in the LME4 package, with month, year, and block all treated as random effects to account for repeated measures at each of these levels (Bates et al. 2015).

## Results

In total, 1,097 female *Ae. albopictus* wings were measured, with 341, 353, and 403 wings from 2015, 2016, and 2017, respectively. Wing sizes differed between months ( $F = 123.47$ ,  $df = 1$ ,  $P \leq 0.001$ ; Fig. 1), years ( $F = 16.40$ ,  $df = 2$ ,  $P < 0.001$ ), and grouped abandonment level ( $F = 9.51$ ,  $df = 2$ ,  $P < 0.001$ ). *Aedes albopictus* size did not differ between 2015 and 2016 (2.63 mm  $\pm$  0.51), but wing lengths were smaller on average for samples collected in 2017 (2.47 mm  $\pm$  0.30;  $t = -4.73$ ,  $df = 603.6$ ,  $P < 0.001$ ). Regardless of year, mosquitoes were generally smaller in July (2.46 mm  $\pm$  0.35) relative to June (2.69 mm  $\pm$  0.41;  $t = 10.35$ ,  $df = 1,021.8$ ,  $P < 0.001$ ). Likewise, wing lengths were on average smaller for *Ae. albopictus* collected from sites classified as low abandonment (2.47 mm  $\pm$  0.34) relative to high abandonment (2.58 mm  $\pm$  0.40;  $t = 3.16$ ,  $df = 624.7$ ,  $P = 0.002$ ).

The mixed-effects model testing the relationship between wing length and abandonment suggests that mosquito size is positively associated with the proportion abandoned infrastructure on a given block, after accounting for the sampling design (Fig. 2; coef = 0.08 [log scale],  $df = 13.39$ ,  $t = 2.27$ ,  $P = 0.041$ ).

## Discussion

We found that female *Ae. albopictus* mosquitoes collected from urban blocks with higher levels of infrastructure abandonment had larger wing sizes relative to females collected on blocks with little or no abandonment. This study demonstrates that fine-scale spatial variation in juvenile mosquito habitat can generate block and neighborhood-level heterogeneity in mosquito size. Although this study did not directly address potential mechanisms for observed size differences, the results are consistent with the conclusion that juvenile habitat associated with infrastructural abandonment supports the production of larger female *Ae. albopictus*. The study also

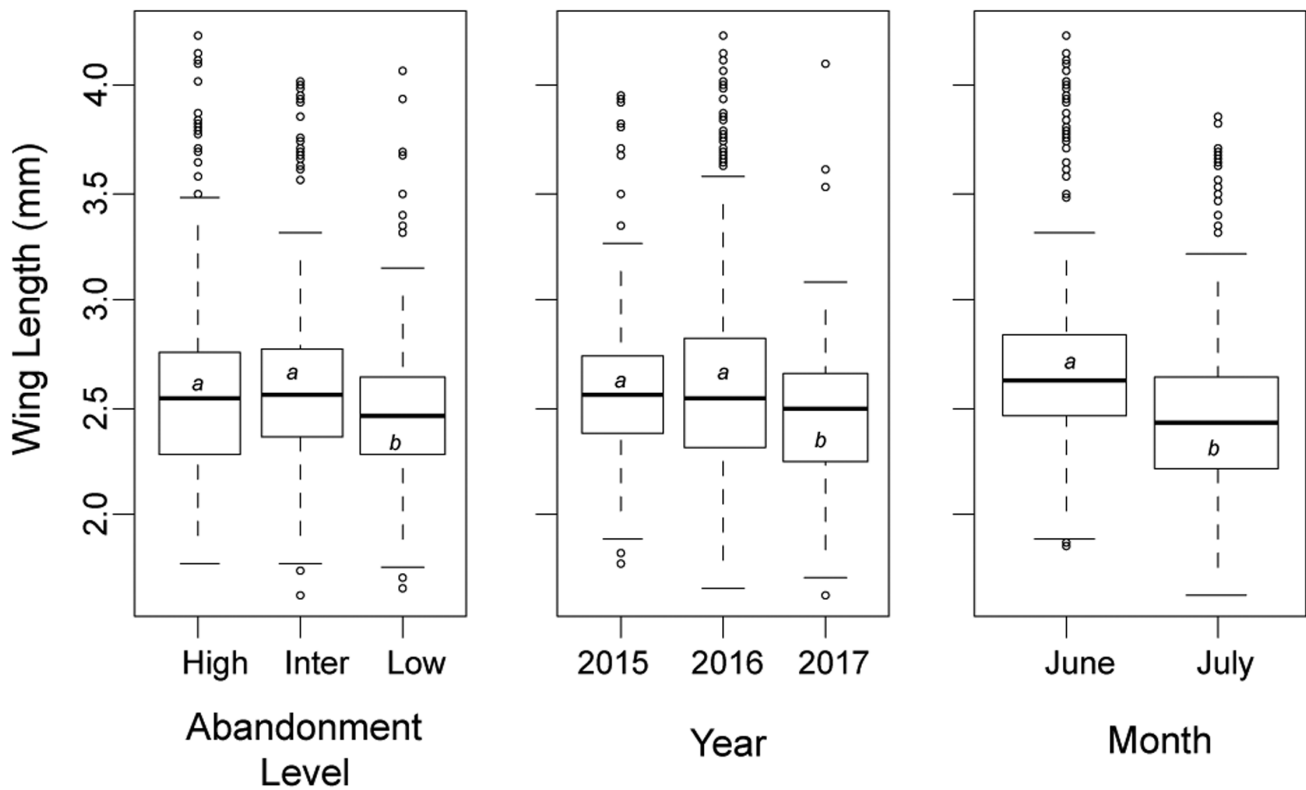


Fig. 1. Boxplots show quartiles and spread in wing measurement data. Heavy lines denote median values, and points are outliers. Letters denote significant differences given Bonferroni-corrected  $P$ -values  $< 0.05$ .

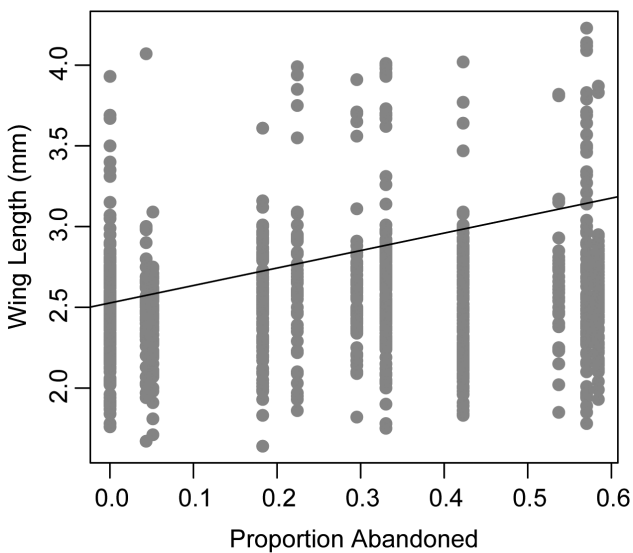


Fig. 2. There is a positive association between wing size and the proportion abandoned infrastructure on the block where individual was collected. Points represent individual mosquitoes; line shows fit from mixed-effects model.

collected larger wings in June relative to the warmer month of July, providing vital field data that is consistent with past studies showing the development of smaller bodied adult mosquitoes under warmer conditions (Armbruster and Conn 2006, Muturi and Alto 2011, Barreaux et al. 2018, Evans et al. 2018).

Research conducted across the same sites in Baltimore reported significantly higher densities of juvenile *Ae. albopictus* in lower

SES blocks where the majority of container habitats were unmanaged (i.e., discarded trash; Little et al. 2017). On average, lower SES blocks had about 400 habitats per km<sup>2</sup> with 80% positive for *Ae. albopictus* larvae compared with higher income blocks that had fewer than 50 containers per km<sup>2</sup> with less than 5% positive (Little et al. 2017). Bodner et al. (2019) further demonstrated that the amount of discarded container habitat with juvenile mosquito present on a block was a positive predictor of adult *Ae. albopictus* densities on that same block (Bodner et al. 2019). If *Ae. albopictus* from lower SES blocks are also larger, as suggested in the study reported here, variation in container habitat conditions experienced by juveniles may also be predictably influenced by neighborhood economics and infrastructural maintenance.

Numerous studies have shown sizes of adult *Aedes* mosquitoes to be positively related to available animal and plant detritus and associated microbial food resources (Nasci 1986, Teng and Apperson 2000, Costanzo et al. 2011, Walsh et al. 2011, Alto et al. 2012) and negatively related to temperature (Armbruster and Conn 2006, Muturi and Alto 2011, Evans et al. 2018). Among our study blocks, Little et al. (2017) showed that vegetation was positively associated with juvenile *Ae. albopictus* indices in lower SES blocks, suggesting that higher allochthonous litter inputs related to opportunistic or unmanaged vegetation might result in reduced density-dependent competition in these areas. On the other hand, temperature data collected from loggers positioned at adult trapping sites on each block showed that mean daily temperatures were greatest at both the highest (low abandonment) and lowest (high abandonment) SES blocks (unpublished data). These results suggest that food resources within container habitats may be the main factor causing differences in female *Ae. albopictus* sizes at this block scale. Nevertheless, temperature records at adult trap sites may not accurately reflect

container temperatures on the same block. Future studies should attempt to determine the relative roles of container resources and temperatures at influencing *Ae. albopictus* size in urban landscapes.

Studies consistently show that size of female *Aedes* is associated with differences in longevity, fecundity, and individual capacity for transmitting mosquito-borne viruses, although the magnitude and direction of these effects may be highly context dependent and nonlinear (Nasci and Mitchell 1994, Alto et al. 2005, Alto et al. 2008b, Bevins 2008, Muturi and Alto 2011, Buckner et al. 2016, Zirbel et al. 2018). Higher competition at larval stages has been associated with smaller adults and increased susceptibility to dengue virus infection (Alto et al. 2008a). However, the frequency of dengue virus infection was greater for larger, field-caught *Ae. aegypti* from Brazil, presumably due to greater longevity and biting frequency that offset decreases in viral susceptibility (Juliano et al. 2014). Although the present study does not measure vectorial capacity, previous studies have demonstrated that wing length differences less than 1 mm can affect important traits such as fecundity and longevity and may influence potential transmission risk (e.g., Juliano et al. 2014, Costanzo et al. 2018). The present work demonstrates that significant heterogeneity in body size is evident across fine spatial scales representative of adult *Aedes* dispersal and human exposure risk and highlights a need for vector competence studies across individuals at these same scales. Failure to manage abandonment and waste issues in impoverished neighborhoods supports greater mosquito production, and mosquitoes in these same neighborhoods may live longer, produce more eggs, and could have greater vector potential.

## Acknowledgments

Mosquito samples used for this study were collected with the financial support from the National Science Foundation - Coupled Natural Human Systems award (DEB 1211797) and the Baltimore Ecosystem Study (National Science Foundation - Long Term Ecological Research (DEB 1027188)). G.K. thanks Dr. Barbara Han, Heather Malcolm, and Nicholas Ristic for their assistance in the project and thanks to Spackenkill High School science research instructors, Mrs. Maloney, Mr. Latino, and Ms. Matts, for all of their dedicated support, guidance, and mentorship.

## References Cited

Alto, B. W. 2011. Interspecific larval competition between invasive *Aedes japonicus* and native *Aedes triseriatus* (Diptera: Culicidae) and adult longevity. *J. Med. Entomol.* 48: 232–242.

Alto, B. W., and D. Bettinardi. 2013. Temperature and dengue virus infection in mosquitoes: independent effects on the immature and adult stages. *Am. J. Trop. Med. Hyg.* 88: 497–505.

Alto, B. W., L. P. Lounibos, S. Higgs, and S. A. Juliano. 2005. Larval competition differentially affects arbovirus infection in *Aedes* mosquitoes. *Ecology* 86: 3279–3288.

Alto, B. W., L. P. Lounibos, C. N. Mores, and M. H. Reiskind. 2008a. Larval competition alters susceptibility of adult *Aedes* mosquitoes to dengue infection. *Proc. Biol. Sci.* 275: 463–471.

Alto, B. W., M. H. Reiskind, and L. P. Lounibos. 2008b. Size alters susceptibility of vectors to dengue virus infection and dissemination. *Am. J. Trop. Med. Hyg.* 79: 688–695.

Alto, B. W., E. J. Muturi, and R. L. Lampman. 2012. Effects of nutrition and density in *Culex pipiens*. *Med. Vet. Entomol.* 26: 396–406.

Alto, B. W., D. J. Bettinardi, and S. Ortiz. 2015. Interspecific larval competition differentially impacts adult survival in dengue vectors. *J. Med. Entomol.* 52: 163–170.

Ameneshewa, B., and M. W. Service. 1996. The relationship between female body size and survival rate of the malaria vector *Anopheles arabiensis* in Ethiopia. *Med. Vet. Entomol.* 10: 170–172.

Armbruster, P., and J. E. Conn. 2006. Geographic variation of larval growth in North American *Aedes albopictus* (Diptera: Culicidae). *Ann. Entomol. Soc. Am.* 99: 1234–1243.

Armbruster, P., and R. A. Hutchinson. 2002. Pupal mass and wing length as indicators of fecundity in *Aedes albopictus* and *Aedes geniculatus* (Diptera: Culicidae). *J. Med. Entomol.* 39: 699–704.

Barreaux, A. M. G., C. M. Stone, P. Barreaux, and J. C. Koella. 2018. The relationship between size and longevity of the malaria vector *Anopheles gambiae* (s.s.) depends on the larval environment. *Parasit. Vectors* 11: 485.

Bartlett-Healy, K., I. Unlu, P. Obenauer, T. Hughes, S. Healy, T. Crepeau, A. Farajollahi, B. Kesavaraju, D. Fonseca, G. Schoeler, et al. 2012. Larval mosquito habitat utilization and community dynamics of *Aedes albopictus* and *Aedes japonicus* (Diptera: Culicidae). *J. Med. Entomol.* 49: 813–824.

Bates, D., M. Machler, B. M. Bolker, and S. C. Walker. 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67: 1–48.

Benedict, M. Q., R. S. Levine, W. A. Hawley, and L. P. Lounibos. 2007. Spread of the tiger: global risk of invasion by the mosquito *Aedes albopictus*. *Vector Borne Zoonotic Dis.* 7: 76–85.

Bevins, S. N. 2008. Invasive mosquitoes, larval competition, and indirect effects on the vector competence of native mosquito species (Diptera: Culicidae). *Biol. Invasions* 10: 1109–1117.

Biehler, D., J. Baker, J. H. Pitas, Y. Bode-George, R. Jordan, A. Sorensen, H. Goodman, S. Wilson, M. Saunders, D. Bodner, P. Leisnham, and S. LaDeau. 2018. Beyond “the mosquito people”: the challenges of engaging community for environmental justice in infested urban spaces, pp. 295–318. *In R. Lave, C. Biermann, and S. N. Lane (eds.), The palgrave handbook of critical physical geography*. Palgrave Macmillan, Cham, Switzerland.

Blackmore, M. S., and C. C. Lord. 2000. The relationship between size and fecundity in *Aedes albopictus*. *J. Vector Ecol.* 25: 212–217.

Bodner, D., S. L. LaDeau, D. Biehler, N. Kirchoff, and P. T. Leisnham. 2016. Effectiveness of print education at reducing urban mosquito infestation through improved resident-based management. *PLoS One.* 11: e0155011.

Bodner, D., S. L. LaDeau, and P. T. Leisnham. 2019. Relationships among immature-stage metrics and adult abundances of mosquito populations in Baltimore, MD. *J. Med. Entomol.* 56: 192–198.

Briegel, H., and S. E. Timmermann. 2001. *Aedes albopictus* (Diptera: Culicidae): physiological aspects of development and reproduction. *J. Med. Entomol.* 38: 566–571.

Briegel, H., I. Knüsel, and S. E. Timmermann. 2001. *Aedes aegypti*: size, reserves, survival, and flight potential. *J. Vector Ecol.* 26: 21–31.

Buckner, E. A., B. W. Alto, and L. P. Lounibos. 2016. Larval temperature-food effects on adult mosquito infection and vertical transmission of Dengue-1 virus. *J. Med. Entomol.* 53: 91–98.

Chretien, J. P. and K. J. Linthicum. 2007. Chikungunya in Europe: what's next? *Lancet* 370: 1805–1806.

Costanzo, K. S., E. J. Muturi, R. L. Lampman, and B. W. Alto. 2011. The effects of resource type and ratio on competition with *Aedes albopictus* and *Culex pipiens* (Diptera: Culicidae). *J. Med. Entomol.* 48: 29–38.

Costanzo, K. S., K. M. Westby, and K. A. Medley. 2018. Genetic and environmental influences on the size-fecundity relationship in *Aedes albopictus* (Diptera: Culicidae): impacts on population growth estimates? *PLoS One* 13: e0201465.

Delatte, H., G. Gimonneau, A. Triboire, and D. Fontenille. 2009. Influence of temperature on immature development, survival, longevity, fecundity, and gonotrophic cycles of *Aedes albopictus*, vector of chikungunya and dengue in the Indian Ocean. *J. Med. Entomol.* 46: 33–41.

Dowling, Z., P. Armbruster, S. L. LaDeau, M. DeCotiis, J. Mottley, and P. T. Leisnham. 2013. Linking mosquito infestation to resident socioeconomic status, knowledge, and source reduction practices in suburban Washington, DC. *Ecohealth* 10: 36–47.

Evans, M. V., J. C. Shiau, N. Solano, M. A. Brindley, J. M. Drake, and C. C. Murdock. 2018. Carry-over effects of urban larval environments on the transmission potential of dengue-2 virus. *Parasit. Vectors* 11: 426.

Farjana, T., and N. Tuno. 2013. Multiple blood feeding and host-seeking behavior in *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae). *J. Med. Entomol.* 50: 838–846.

Goodman, H., A. Egizi, D. M. Fonseca, P. T. Leisnham, and S. L. LaDeau. 2018. Primary blood-hosts of mosquitoes are influenced by social and ecological conditions in a complex urban landscape. *Parasit. Vectors* 11: 218.

- Guerra, C. A., R. C. Reiner, Jr, T. A. Perkins, S. W. Lindsay, J. T. Midega, O. J. Brady, C. M. Barker, W. K. Reisen, L. C. Harrington, W. Takken, et al. 2014. A global assembly of adult female mosquito mark-release-recapture data to inform the control of mosquito-borne pathogens. *Parasit. Vectors* 7: 276.
- Halasa, Y. A., D. S. Shepard, D. M. Fonseca, A. Farajollahi, S. Healy, R. Gaugler, K. Bartlett-Healy, D. A. Strickman, and G. G. Clark. 2014. Quantifying the impact of mosquitoes on quality of life and enjoyment of yard and porch activities in New Jersey. *PLoS One* 9: e89221.
- Hawley, W. A. 1985. The effect of larval density on adult longevity of a mosquito, *Aedes sierrensis* epidemiological consequences. *J. Anim. Ecol.*, 54, 955–964.
- Hawley, W. A., P. Reiter, R. S. Copeland, C. B. Pumpuni, and G. B. Craig, Jr. 1987. *Aedes albopictus* in North America: probable introduction in used tires from northern Asia. *Science* 236: 1114–1116.
- Honório, N. A., W. d. a. C. Silva, P. J. Leite, J. M. Gonçalves, L. P. Lounibos, and R. Lourenço-de-Oliveira. 2003. Dispersal of *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae) in an urban endemic dengue area in the State of Rio de Janeiro, Brazil. *Mem. Inst. Oswaldo Cruz* 98: 191–198.
- Juliano, S. A., and L. P. Lounibos. 2005. Ecology of invasive mosquitoes: effects on resident species and on human health. *Ecol. Lett.* 8: 558–574.
- Juliano, S. A., G. S. Ribeiro, R. Maciel-de-Freitas, M. G. Castro, C. Codeço, R. Lourenço-de-Oliveira, and L. P. Lounibos. 2014. She's a femme fatale: low-density larval development produces good disease vectors. *Mem. Inst. Oswaldo Cruz* 109: 1070–1077.
- Kraemer, M. U., M. E. Sinka, K. A. Duda, A. Q. Mylne, F. M. Shearer, C. M. Barker, C. G. Moore, R. G. Carvalho, G. E. Coelho, W. Van Bortel, et al. 2015. The global distribution of the arbovirus vectors *Aedes aegypti* and *Ae. albopictus*. *eLife* 4: e08347.
- Kraemer, M. U. G., R. C. Reiner, Jr, O. J. Brady, J. P. Messina, M. Gilbert, D. M. Pigott, D. Yi, K. Johnson, L. Earl, L. B. Marczak, et al. 2019. Past and future spread of the arbovirus vectors *Aedes aegypti* and *Aedes albopictus*. *Nat. Microbiol.* 4: 854–863.
- LaDeau, S. L., P. T. Leisnham, D. Biehler, and D. Bodner. 2013. Higher mosquito production in low-income neighborhoods of Baltimore and Washington, DC: understanding ecological drivers and mosquito-borne disease risk in temperate cities. *Int. J. Environ. Res. Public Health* 10: 1505–1526.
- LaDeau, S. L., B. F. Allan, P. T. Leisnham, and M. Z. Levy. 2015. The ecological foundations of transmission potential and vector-borne disease in urban landscapes. *Funct. Ecol.* 29: 889–901.
- Leisnham, P. T., L. M. Sala, and S. A. Juliano. 2008. Geographic variation in adult survival and reproductive tactics of the mosquito *Aedes albopictus*. *J. Med. Entomol.* 45: 210–221.
- Leisnham, P. T., L. P. Lounibos, G. F. O'Meara, and S. A. Juliano. 2009. Interpopulation divergence in competitive interactions of the mosquito *Aedes albopictus*. *Ecology* 90: 2405–2413.
- Little, E., D. Biehler, P. T. Leisnham, R. Jordan, S. Wilson, and S. L. LaDeau. 2017. Socio-ecological mechanisms supporting high densities of *Aedes albopictus* (Diptera: Culicidae) in Baltimore, MD. *J. Med. Entomol.* 54: 1183–1192.
- Livdahl, T. P., and G. Sugihara. 1984. Non-linear interactions of populations and the importance of estimating per-capita rates of change. *J. Anim. Ecol.* 53, 573–580.
- Lounibos, L. P. 2002. Invasions by insect vectors of human disease. *Annu. Rev. Entomol.* 47: 233–266.
- Muturi, E. J., and B. W. Alto. 2011. Larval environmental temperature and insecticide exposure alter *Aedes aegypti* competence for arboviruses. *Vector Borne Zoonotic Dis.* 11: 1157–1163.
- Nasci, R. S. 1986. Relationship between adult mosquito (Diptera, Culicidae) body size and parity in field populations. *Environ. Entomol.* 15, 874–876.
- Nasci, R. S., and C. J. Mitchell. 1994. Larval diet, adult size, and susceptibility of *Aedes aegypti* (Diptera: Culicidae) to infection with Ross River virus. *J. Med. Entomol.* 31: 123–126.
- Niebylski, M. L., and G. B. Craig, Jr. 1994. Dispersal and survival of *Aedes albopictus* at a scrap tire yard in Missouri. *J. Am. Mosq. Control Assoc.* 10: 339–343.
- Paupy, C., H. Delatte, L. Bagny, V. Corbel, and D. Fontenille. 2009. *Aedes albopictus*, an arbovirus vector: from the darkness to the light. *Microbes Infect.* 11: 1177–1185.
- Petersen, V., M. J. Marchi, D. Natal, M. T. Marrelli, A. C. Barbosa, and L. Suesdek. 2016. Assessment of the correlation between wing size and body weight in captive *Culex quinquefasciatus*. *Rev. Soc. Bras. Med. Trop.* 49: 508–511.
- Quam, M. B., O. Sessions, U. S. Kamaraj, J. Rocklöv, and A. Wilder-Smith. 2015. Dissecting Japan's dengue outbreak in 2014. *AM. J. TROP. MED. HYG.* 94:409–412.
- R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <http://www.R-project.org/>.
- Reiskind, M. H., and L. P. Lounibos. 2009. Effects of intraspecific larval competition on adult longevity in the mosquitoes *Aedes aegypti* and *Aedes albopictus*. *Med. Vet. Entomol.* 23: 62–68.
- Rezza, G., L. Nicoletti, R. Angelini, R. Romi, A. C. Finarelli, M. Panning, P. Cordioli, C. Fortuna, S. Boros, F. Magurano, G. Silvi, P. Angelini, M. Dottori, M. G. Ciufolini, G. C. Majori, A. Cassone, and C. S. Grp. 2007. Infection with chikungunya virus in Italy: an outbreak in a temperate region. *Lancet* 370: 1840–1846.
- Schneider, J. R., A. C. Morrison, H. Astete, T. W. Scott, and M. L. Wilson. 2004. Adult size and distribution of *Aedes aegypti* (Diptera: Culicidae) associated with larval habitats in Iquitos, Peru. *J. Med. Entomol.* 41: 634–642.
- Smith, D. L., K. E. Battle, S. I. Hay, C. M. Barker, T. W. Scott, and F. E. McKenzie. 2012. Ross, Macdonald, and a theory for the dynamics and control of mosquito-transmitted pathogens. *PLoS Pathog.* 8: e1002588.
- Takken, W., M. J. Klowden, and G. M. Chambers. 1998. Effect of body size on host seeking and blood meal utilization in *Anopheles gambiae* sensu stricto (Diptera: Culicidae): the disadvantage of being small. *J. Med. Entomol.* 35: 639–645.
- Teng, H. J., and C. S. Apperson. 2000. Development and survival of immature *Aedes albopictus* and *Aedes triseriatus* (Diptera: Culicidae) in the laboratory: effects of density, food, and competition on response to temperature. *J. Med. Entomol.* 37: 40–52.
- Tsuda, Y., Y. Maekawa, K. Ogawa, K. Itokawa, O. Komagata, T. Sasaki, H. Isawa, T. Tomita, and K. Sawabe, 2016. Biting density and distribution of *Aedes albopictus* during the September 2014 outbreak of dengue fever in Yoyogi Park and the Vicinity of Tokyo Metropolis, Japan. *Jpn. J. Infect. Dis.* 69: 1–5.
- Turell, M. J., D. J. Dohm, M. R. Sardelis, M. L. Oguinn, T. G. Andreadis, and J. A. Blow. 2005. An update on the potential of north American mosquitoes (Diptera: Culicidae) to transmit West Nile virus. *J. Med. Entomol.* 42: 57–62.
- Walsh, R. K., L. Facchinelli, J. M. Ramsey, J. G. Bond, and F. Gould. 2011. Assessing the impact of density dependence in field populations of *Aedes aegypti*. *J. Vector Ecol.* 36: 300–307.
- Westby, K. M., and S. A. Juliano. 2017. The roles of history: age and prior exploitation in aquatic container habitats have immediate and carry-over effects on mosquito life history. *Ecol. Entomol.* 42: 704–711.
- Worobey, J., D. M. Fonseca, C. Espinosa, S. Healy, and R. Gaugler. 2013. Child outdoor physical activity is reduced by prevalence of the Asian tiger mosquito, *Aedes albopictus*. *J. Am. Mosq. Control Assoc.* 29: 78–80.
- Xue, R. D., A. Ali, and D. R. Barnard. 2008. Host species diversity and post-blood feeding carbohydrate availability enhance survival of females and fecundity in *Aedes albopictus* (Diptera: Culicidae). *Exp. Parasitol.* 119: 225–228.
- Zirbel, K., B. Eastmond, and B. W. Alto. 2018. Parental and offspring larval diets interact to influence life-history traits and infection with dengue virus in *Aedes aegypti*. *R. Soc. Open Sci.* 5: 180539.