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Water Surface Area and Depth Determine Oviposition Choice in *Aedes albopictus* (Diptera: Culicidae)

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ABSTRACT Oviposition choice is a well-studied aspect of the mosquito life cycle, and offers a potential avenue for species-specific surveillance and control. In container inhabiting mosquitoes, there has been a focus on how the components of the aquatic media determine choice, with little work on the physical characteristics of the containers themselves. We performed five experiments examining the effect of physical container parameters on oviposition choice by *Aedes albopictus*. We examined containers of three different surface areas (small, 496 cm^2; medium, 863 cm^2; and large, 1,938 cm^2) at the same water depth and the same or different heights in a series of binary choice assays. We also examined different depths with the same surface area in clear containers (where the depth may be perceived by the darkness of the water) and in opaque containers, which appear uniformly dark at different depths. We found a significant preference for medium containers over large containers, whether the containers were different or the same heights, and a trend toward a preference for small containers over medium containers. There was a preference for deeper water regardless of whether containers were clear or opaque. These behaviors suggest mosquitoes take into account physical aspects of their habitats and their oviposition choices are consistent with minimizing the risk of habitat drying.

KEY WORDS container, chikungunya, dengue, Asian tiger mosquito

Aedes albopictus (Skuse) (Diptera: Culicidae), the Asian tiger mosquito, is a worldwide vector of disease, now found in Europe, North and South America, and Africa from its native range in Asia (Hawley 1988, Lounibos 2002). A pernicious pest throughout its invasive range, *Ae. albopictus* also may affect the transmission of a number of pathogens. Long considered a secondary vector to *Aedes aegypti* L., recent epidemics of chikungunya, dengue, and dog heartworm carried by *Ae. albopictus* illustrate the potential for this species to alter disease transmission (Nayar and Knight 1999, Cancrini et al. 2003, Effler et al. 2005, Rezza et al. 2007, Lambrechts et al. 2010). Effective control of this mosquito, particularly during an outbreak of disease, can be achieved through different strategies targeting specific life-history stages.

The lifecycle of mosquitoes offers several critical junctures for control, including the juvenile stage, host, sugar, resting-site, or oviposition site-seeking females. Of these, attacking ovipositing female mosquitoes may maximize the disruption of disease transmission, while minimizing control effort (Le Menach et al. 2005, Gu et al. 2006). This approach has been used with mixed results by employing "lethal ovitraps" for container inhabiting *Aedes* mosquitoes in areas of disease transmission (Perich et al. 2003, Williams et al. 2007, Kittayapong et al. 2008). However, the effectiveness of this approach is dependent upon optimizing the attractiveness of containers to ovipositing mosquitoes, which is often species specific, in addition to having adequate density of traps (Allan and Kline 1995, Dhileepan 1997, Trexler et al. 1998, Reiskind et al. 2009).

The behavioral ecology of oviposition choice in container mosquitoes has been studied, particularly the effects of various biotic inputs into the aquatic media such as nutrients, conspecific larvae and eggs, or larval predators (Bentley and Day 1989). Less well studied have been the physical characteristics that dictate mosquito oviposition choice. Studies have examined color of container or media for mosquitoes in *Aedes, Anopheles,* and *Culex* (Bates 1940, Williams 1962, Yap 1975, Beehler et al. 1993, Dhileepan 1997); abundance of available oviposition habitat in an area for *Culex restuans* (Reiskind and Wilson 2004); and container size, e.g., depth or surface area, for some species of *Aedes* and *Culex* (Dhileepan 1997, Harrington et al. 2008).

The importance of size and shape of containers has received little systematic investigation for mosquitoes. Harrington et al. (2008) conducted a semifield experiment in Thailand that used linear regression of egg numbers on container diameter, volume, and surface area to conclude that *Ae. aegypti* deposited more eggs

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in larger containers in all three physical aspects. They also concluded these physical parameters significantly increased the probability of a container receiving any eggs. Others have suggested water depth might be an important factor for oviposition choice in *Culex* mosquitoes, although the importance of this factor appeared species specific within *Culex* (Dhileepan 1997). A number of studies have used the pattern of larvae and pupae found in containers in the field to suggest the importance of physical container characteristics in oviposition choice for a variety of mosquito species, but there are obvious problems of inference to actual oviposition choices (Sunahara et al. 2002, Lester and Pike 2003, Morrison et al. 2004, Derraik and Slaney 2005, Harlan and Paradise 2006, Wong et al. 2011). There has been no systematic work examining the importance of container size or shape for *Ae. albopictus* oviposition preferences. Several field studies have noted *Ae. albopictus* immatures were found more commonly in smaller containers relative to the distribution of containers available, although larvae and pupae are reported using a wide range of volumes from <100 ml to over 200 liters (Sunahara et al. 2002, Carrieri et al. 2003, Carvajal et al. 2009).

We tested the hypothesis that the physical characteristics of containers, in addition to chemical and biological factors, determine the oviposition choice of *Ae. albopictus.* We predict, based upon the results for the congener *Ae. aegypti*, that *Ae. albopictus* will choose larger containers in both depth of water and surface area. We also offer the alternative prediction that *Ae. albopictus* will select containers more likely to persist throughout the larval period, and thus prefer deep water over shallow water (more water) and small surface area over larger surface area (less evaporation) (Bartlett-Healy et al. 2011). To test these predictions, we performed five binary oviposition-choice experiments comparing oviposition habitats of the same depth but different surface areas, and oviposition habitats of the same surface area but different water depths.

Materials and Methods

Mosquitoes. All mosquitoes used in these experiments were F_4 (2010)or F_8 (2011) *Aedes albopictus* from a colony originally collected in Palm Beach County, FL, during the summer of 2009. We reared mosquitoes in conditions of low density ($\approx$100 larvae/liter infused with 4 g of dried live oak (*Quercus virginiana* Mill.) or Eastern red cedar (*Juniperus virginiana* L.) leaves and 0.15 g of 1:1 yeast:albumin) in 3 liters of infusion. We removed pupae from rearing pans and placed them in emergence cages with 20% sucrose solution, ad libitum. We maintained adults under conditions of high humidity (>95% rH) at 26°C with a photoperiod of 14:10 (L:D) h before use in each experiment. Adults were between 4 and 7 d old when we provided them the opportunity to blood feed on a fully-informed, consenting human volunteer for at least 15 min, 2 to 4 d before use (IRB exemption, 24 August 2008, OK State Institutional Review Board). Numbers of mosquitoes used for each experiment were limited by a variety of logistical considerations, and varied from 8 to 20. Consequently, all results are reported as number of eggs oviposited per female released.

Oviposition Media and Arena. Oviposition medium was prepared using 4-g dried live oak leaves per liter of tap water, infused for 24–48 h to assure attractiveness in the appropriate containers before the release of mosquitoes (Walker and Merritt 1988, Walker et al. 1991, Trexler et al. 1998, Trexler et al. 2003, Reiskind et al. 2009). Both experiments were performed in a pole barn with eight separate cages, with east and west sides of the arena open ($n = 8$). Each cage was 2.0 by 1.2 by 1.4 m (l $\times$ w $\times$ h) and oriented with the long sides east-west. Frames were made of 0.754-cm-diameter PVC, and covered with a commercially available mosquito bed net ("Double Wide Mosquito Net", Coughlan's Ltd, Winnipeg, Manitoba, Canada). The bottoms of the mosquito net were tucked underneath the frame, and packed with sand to seal the cages. Cages were arranged in two rows, on the east and west sides of the pole barn. The east side was more shaded by trees; the west side opened onto a grass field. At the end of each experiment, we brought the seed germination paper back to the laboratory, allowed it to dry, and counted all eggs.

Experiment 1. We tested whether mosquitoes prefer a large surface area to a small surface area of water. We used two different sized clear, hard plastic containers. Medium surface area containers were 41.9 by 29.2 by 15.9 cm (l $\times$ w $\times$ h) at the top, with slightly sloping sides, and a total internal volume of 11.4 liters (hereafter "medium," model 1843, Sterilite Inc., Townsend, MA). Larger surface area containers were 57.5 cm by 34.5 cm by 26 cm (l $\times$ w $\times$ h) at the top, again with slightly sloping sides, and a total internal volume of 47.3 liters (hereafter "large," model 3R41, Rubbermaid Inc., Huntsville, NC). These two containers fall within the range of the most productive containers for *Ae. albopictus* from a variety of studies, although are on the larger size of all occupied containers (Sunahara et al. 2002, Carrieri et al. 2003, Carvajal et al. 2009). Before use, all containers were rinsed with tap water at least five times. Both container sizes were filled to a depth of 4.5 cm at their centers. This required different volumes of water (9.0 liters for large containers and 3.6 liters for medium containers). The resulting surface areas for medium and large containers were 863 cm^2 and 1,938 cm^2, respectively, lined with seed germination papers (Seedburo Equipment Company, Des Plaines, IL) centered on the water line, cut into strips 7 cm wide to ensure they would still be at waterline after 7 d. We placed containers at either end of the release cages, and the placement with respect to direction was alternated between the two sizes of containers. We released eight gravid or blood-fed (by visual inspection before release) *Ae. albopictus* in each cage. After 7 d (22–29 June 2010), we collected all seed germination papers and aspirated the cages to recapture any volant females. We only caught one female in one cage of the 64 released.

Experiment 2. In this experiment, we repeated the set-up in experiment 1, with several important differences. First, we cut the large container to the same height as the medium container, such that the distance from the waterline to the top of the container is the same (11.4 cm). Second, all containers were painted flat black on the outside to make the containers opaque and avoid any differences in color perception by the mosquitoes. For this experiment, we released 16 gravid or blood-fed *Ae. albopictus* mosquitoes in each cage. Because of extreme heat and low humidity, we terminated this experiment after 6 d (24–30 June 2011). We did not recapture any female mosquitoes.

Experiment 3. Because the containers tested in experiments 1 and 2 were are the large end of containers in which *Ae. albopictus* are found, we examined oviposition preference between the medium (41.9 by 29.2 by 15.9 cm) and an even smaller containers (hereafter "small," 34.9 by 20.3 by 12.7 cm, internal volume: 5.7 liters, model 1851N, Sterilite Inc., Townsend, MA). Depth of water was 4.5 cm for both containers, resulting in a volume of 3.6 liters and 2.3 liters for the two containers and a surface area of 496 cm^2 for the small containers. The medium containers were cut to the same height as the small containers, such that the distance from waterline to the top of the containers was 8.2 cm. This experiment was conducted in the same manner as experiment 2, with 16 gravid females released, and terminated after 6 d (18 July-23, 2011). We did not recapture female mosquitoes.

Experiment 4. We tested whether mosquitoes prefer deep water to shallow water by using the medium, uncut containers from the previous experiment. We filled the shallow containers to a depth of 4.5 cm (3.55 liters of water) and the deeper containers to 9 cm (7.5 liters of water) at the center of the container, and lined the containers with seed germination papers centered on the water line, cut into strips 7 cm wide. We placed containers at either end of the release cages, and the placement with respect to direction was alternated between the two depths of containers. We released 20 gravid or blood-fed *Ae. albopictus* mosquitoes in each cage. After 6 d (21 August-26, 2010), we caspirated the cages to recapture any volant females of the released mosquitoes. We did not capture any mosquitoes.

Experiment 5. This experiment followed the same protocol as experiment 4, with several exceptions. First, to standardize the color of the water, the containers were painted black. Second, 16 gravid females were released. Finally, because of extremely hot and dry weather and to avoid drying out the shallow habitat, the experiment was run only for 5 d (8 July-13, 2011). On the third night of the experiment, strong winds blew down two cages, and these were removed from analysis.

Statistical Analysis. All analyses were done in SAS 9.2 (SAS Inc., Cary, NC). We examined oviposition data for normality. As all of the experiments yielded non-normal data, we initially analyzed them with a generalized linear mixed-model (PROC GLIMMIX) with a negative binomial error distribution and cage as a random effect. However, iterations of the equations estimating the optimal dispersion parameter, k, did not converge for the first experiment, so we used a nonparametric Mann–Whitney *U*-test to assess differences in median eggs oviposited between large and small surface area containers. For all other experiments, the equations did converge, and the ratio of χ^2 goodness-of-fit measurements to degrees of freedom was close to 1.00, suggesting a very good fit to the negative binomial error distribution. Mean or median eggs oviposited per female released for experiments 1, 2, and 3 are displayed in one graph (Fig. 1), and mean eggs oviposited per female released for experiments 4 and 5 in a second graph (Fig. 2).

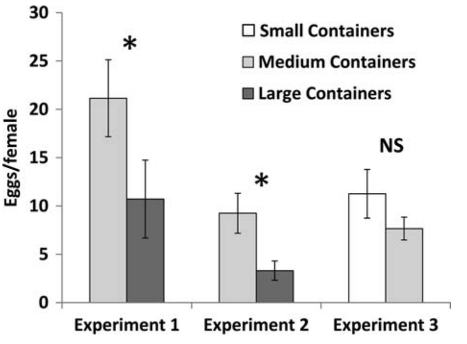

Fig. 1. Median eggs oviposited per female from experiment 1 (left-hand bars) and mean eggs oviposited per female for experiment 2 (middle bars) in middle (light gray) and large (dark gray) surface area containers and for experiment three (right-hand bars) in middle (light gray) and small (white) surface area containers. Error bars are 25–75% range for experiment 1 and ± 1 SEM for experiments 2 and 3. *$P <$ 0.05. N.S.: not significant.

Results

We observed about twice as many eggs in containers with medium surface area and identical depth than in containers with large surface areas in experiment 1 (Mann–Whitney U = 88.00, Z approximation = 2.0479, $P < 0.05$, Fig. 1). This result was confirmed in experiment 2 in which the distance from the waterline to the

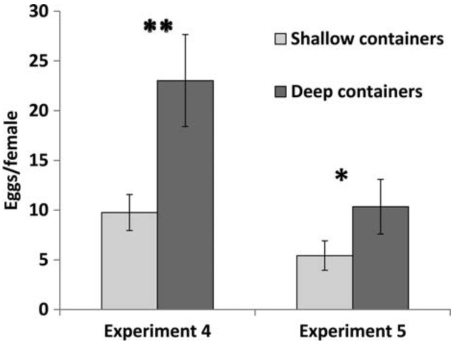

Fig. 2. Mean eggs oviposited per female from experiment 4 (left-hand bars) and 5 (right-hand bars) in shallow (light gray) and deep (dark gray) containers. Error bars are ± 1 SEM *$P < 0.05$. **$P < 0.01$.

top of the container was the same for both large and medium containers (Mixed model GLM: $F_{1,7}$ = 9.88, P = 0.0163, Fig. 1). In experiment 3, there was no significant difference between small and medium containers, although a trend toward preference for the small container (Mixed model GLM: $F_{1,7}$ = 4.76, P = 0.0654, Fig. 1) .

In the water depth experiments, we found more than twice as many eggs per female released in clear containers of greater depth than in shallower clear containers of nearly identical surface area (Mixed model GLM: $F_{1,7}$ = 19.7, P = 0.003, Fig. 2). There was a similar result when containers were painted black (Mixed model GLM: $F_{1,5}$ = 8.97, P = 0.0402, Fig. 2).

Discussion

We provide evidence that *Ae. albopictus* avoided containers with a large surface area and showed a similar trend in preferring small over medium surface area containers. In addition, we found that *Ae. albopictus* preferred containers with deeper water over containers with shallower water, regardless of the perceived color of the media. The surface area experiments used different manufacturers of clear plastic containers, which may offer an alternative explanation for the observed differences. However, the two containers were made with polypropylene plastic of the same grade (recyclable no. 5). All container sizes were rinsed thoroughly, and set with water and leaf material for the same amount of time before commencing the experiment. Therefore, we do not believe the difference in oviposition preference can be attributed to differences in plastic manufacture.

Another possible interpretation of the results from experiment 1 is that the mosquitoes are responding not to surface area, but to the distance of the waterline from the top of the container, which was larger in the large surface area containers. To rule out this possibility, we conducted experiment 2 with containers of the same height, and observed a similar qualitative response. It seems likely that the mosquitoes are responding to surface area alone and not some combination of surface area and potential container depth. Repeating this experiment with even smaller containers continued to show a trend toward preferring even smaller containers, but the lack of significant differences between medium and small containers suggests that either our experiment lacked sufficient statistical power to detect more subtle differences or we may be approaching the limits to *Ae. albopictus*' ability to discriminate on the basis of container surface area.

Experiment 4 demonstrated that *Ae. albopictus* females were choosing containers that held deeper water over containers with shallower water. Because the containers were clear, it is possible that the choice of deeper water represents a choice for darker media, which in turn may correlate with organic matter content. Consequently, we repeated this experiment (experiment 5), but with containers that were painted black, making the water appear uniformly dark. We documented a similar response, with deep-water containers preferred to shallow-water containers.

Experiments 2, 3, and 5 resulted in a much lower number of eggs per female than experiments 1 and 4. This may be because of differences in ambient conditions when experiments 2, 3, and 5 were conducted (in 2011), as the average daily temperature was 3.7–7.2°C higher and the average daily humidity 15.3–16.3% lower during 2011, taken from a weather station ≈250 m from the oviposition arena (www.mesonet.org) during the experiments. *Aedes albopictus* is tolerant of both high temperatures and low humidity, but do show shorter lifespans under these conditions (Hawley 1988, Reiskind and Lounibos 2009). In addition, it is possible there were other, unmeasured influences on the number of eggs per female released that were different in 2011 relative to 2010, including different laboratory generations (F4 versus F8) and different incubators used for rearing (although all controllable conditions were kept the same in 2011 as in 2010). The important result in these experiments is the choice of ovipositing females, not the total number of eggs laid.

Studies of the physical parameters that influence *Ae. albopictus* oviposition choice previously were restricted to examinations of container color (Yap 1975). A congener of *Ae. albopictus*, *Ae. aegypti,* has been noted to use larger containers, both in surface area and depth (Harrington et al. 2008). However, the experimental hut in which Harrington and her colleagues conducted their experiment was unreplicated and a very different setting from our replicated cage experiment, being a single experimental hut in a tropical climate with clay containers. Although there are few studies on the effect of the wider context within which oviposition choices are made (Reiskind and Wilson 2004), the experimental venue may explain the difference between their findings and our results. In addition, *Ae. albopictus* and *Ae. aegypti* have different oviposition behavior in certain contexts, in spite of considerable overlap in larval habitat use in the field (Hawley 1988, Allan and Kline 1995, O'Meara et al. 1995, Allan and Kline 1998). Therefore, the differences in this study on *Ae. albopictus* and previous work on container size in *Ae. aegypti* (Harrington et al. 2008) may be attributable to intrinsic differences in oviposition behavior between these two species. Habitat segregation between these mosquitoes has been noted at larger spatial scales, but whether oviposition choice contributes to these patterns is not known (Thavara et al. 2001, Braks et al. 2003).

Aedes albopictus may favor deeper water and smaller surface-area containers for several reasons. They may be assessing the likelihood of habitat drying, which would be more likely in shallower containers (lower initial volume) or those with large surface areas (higher evaporation) (Bartlett-Healy et al. 2011). Habitat drying has impacts on mosquito development that range from catastrophic, e.g., complete drying, to merely significant in terms of larval growth and survival (Juliano and Stoffregen 1994). Another possibility is that ovipositing females are determining the likelihood of colonization of a habitat by a larval predator. Larvae of *Ae. albopictus* are susceptible to predation by a variety of insect predators (Kesavaraju and Juliano 2004, Griswold and Lounibos 2006), larger containers are more likely to contain predators (Sunahara et al. 2002, Lester and Pike 2003, Banerjee et al. 2010), and some mosquitoes alter their oviposition behavior based upon the presence of a predator, although *Ae. albopictus* is not known to avoid predators in their oviposition behavior (Angelon and Petranka 2002, Kiflawi et al. 2003). However, we know of no studies that show ovipositing mosquitoes anticipate colonization by predators, and we did not examine the importance of predators in this study. Furthermore, there are correlations between depth and predator presence (Sunahara et al. 2002, Lester and Pike 2003, Banerjee et al. 2010), suggesting *Ae. albopictus* should avoid deep as well as large surface area containers to avoid predators, which they did not in this study. Finally, *Ae. albopictus* may be using physical characteristics of containers as cues for nutrient availability, a factor that has been important in numerous oviposition choice experiments (Bentley and Day 1989). However, the avoidance of large surface area containers, which by having larger volumes also contain more available nutrients, suggests they are not using physical parameters as cues of nutrient availability to make their choices. We conclude that the most likely explanation for their oviposition choices is the avoidance of containers that are likely to desiccate.

Our conclusions are based on controlled, two-choice experiments. This limits our ability to determine the shape of the response to container surface area or depth. It is possible that mosquitoes avoid very small containers, or very deep containers. Continued examination of aspects of container size could include a wider variety of sizes to determine the limits of choice.

Physical characteristics of oviposition containers remain an under-studied aspect of oviposition choice in mosquitoes. In particular, the mechanisms by which the mosquito assesses the physical qualities of the habitat deserve attention. Future studies should assess whether they use visual cues, flight times, or both to determine the surface area and whether they use physical, visual, or chemical cues to determine depth. Understanding the egg-laying behavior of these important vectors of disease can aid in surveillance and the development of effective control methodologies.

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