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Clash of mosquito wings: Larval interspecific competition among the mosquitoes, *Culex pipiens*, *Aedes albopictus* and *Aedes aegypti* reveals complex population dynamics in shared habitats

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Abstract

Globalisation, climate change and international trade are the factors contributing to the spread of *Aedes albopictus* (Diptera: Culicidae) and *Ae. aegypti* into new areas. In newly invaded habitats, these non-native species can serve as arbovirus disease vectors or increase the risk of disease spill over. These mosquitoes continue to emerge in new areas where they have or will have overlapping ranges with other resident mosquito species. The study investigates how invasive *Aedes* mosquitoes compete with the native *Culex pipiens* in Türkiye, which might affect the overall mosquito population dynamics and disease transmission risks. Both *Aedes* species exhibited contrasting responses to interspecific competition with *Cx. pipiens*. While *Ae. albopictus* suffers reduced emergence primarily in larger containers with abundant food, *Ae. aegypti* surprisingly thrives in mixed cultures under all food conditions. Adult *Cx. pipiens* emergence drops by half against *Ae. albopictus* and under specific conditions with *Ae. aegypti*. Competition influences mosquito size differently across species and life stages. *Culex pipiens* females grow larger when competing with *Ae. aegypti*, potentially indicating resource advantage or compensatory strategies. However, *Ae. albopictus* size shows more nuanced responses, suggesting complex interactions at play. Understanding how invasive and native mosquitoes interact with each other can provide insights into how they adapt and coexist in shared habitats. This knowledge can inform effective control strategies. The study highlights the differential responses of invasive *Aedes* species and the potential for managing populations based on their competitive interactions with the native *Cx. pipiens*. It can contribute to improved monitoring and prediction systems for the spread of invasive mosquitoes and the associated disease risks.

KEYWORDS

Aedes, competition, *Culex*, interspecific interactions

INTRODUCTION

Mosquitoes are important cosmopolitan insects in the Culicidae family. Over the years, several non-native mosquito species have increasingly spread into new areas because of globalisation, land-use change and international trade. An increase in global temperature and unexpected changes in rainfall because of climate change are creating new sites for mosquitoes to spread and breed. This results in significant increases in mosquito populations. These non-native species can serve as vectors for disease transmission of arboviruses including West Nile, yellow fever, Dengue and Zika viruses in human communities or increase the risk of disease spill over in their newly invaded and established areas (Deblauwe et al., 2022; Juliano & Lounibos, 2005; Smitz et al., 2021).

Aedes albopictus and *Ae. aegypti* are invasive *Aedes* species that are being introduced to several countries outside their native range during the international transport of goods, especially used tyres or ornamental plants. These species were geographically restricted to humid climates in East Asia and Africa (Caminade et al., 2012, 2019; Nie & Feng, 2023), but their strong ecological and phenotypic plasticity has facilitated a dramatic global expansion which is a major concern as their presence in new areas constitutes a threat to human and animal health (Kampen et al., 2017; Medlock et al., 2015, 2017). *Aedes aegypti* has been detected in a limited range in Russia, Georgia and eastern Türkiye, whereas *Ae. albopictus*, which is more invasive and produces eggs more tolerant to temperate winters, has more successfully adapted to temperate climates and has established in countries like Switzerland, Germany, France, Croatia, the Netherlands, Spain, Luxembourg, Cyprus, Türkiye, etc. (Kraemer et al., 2015; Vasquez et al., 2023). In Türkiye, *Ae. albopictus* was first identified in coastal areas near ports within Thrace, and ever since, it has been reported in numerous locations across the Black Sea, Marmara and Aegean regions (Akiner et al., 2016, 2019; Demirci et al., 2021). In contrast, *Ae. aegypti* appears to be restricted to northeastern region of the country (Demirci et al., 2021). There has been a surge in arbovirus cases globally in recent years. This includes an increase in the number of autochthonous cases of dengue fever and chikungunya in some countries across Europe (Deblauwe et al., 2022; Juliano & Lounibos, 2005; Touray et al., 2023). Additionally, a rise in West Nile virus (WNV) cases has been observed, with 40 cases reported between 2017 and 2019 in Türkiye (Bursali & Simsek, 2024). Studies have also shown WNV is also circulating in *Aedes* mosquitoes established in Türkiye, as well as native *Culex* spp. (Ergunay et al., 2013; Gunay et al., 2015).

Aedes albopictus and *Ae. aegypti* breed in natural and artificial containers like man-made containers, tree holes, flowerpots, discarded tyres, etc. These habitats might range in size and nutrient availability, influencing the interactions between immature mosquitoes and other organisms. Here, they compete for limited nutritional resources, produce toxins and waste products, interfere with mating or are aggressive towards other less effective competing resident mosquito species (Alto et al., 2015; Bara et al., 2015; Juliano, 2009; Juliano & Lounibos, 2005; Marini et al., 2017). It is known that interspecies competition, as well as other parameters such as larval diet, density, presence of certain mosquito microbiota and temperature during larval development, can, directly and indirectly, impact many aspects of adult mosquito traits such as size, fecundity and lifespan (Price et al., 1980; Romoli et al., 2021; Sasmita et al., 2019). Studies on how *Aedes* spp. compete with other mosquito species have determined that interactions are mostly asymmetrical with negative impacts on the development time, survival, adult body size, blood feeding rates vectorial competence and capacity of less competitive container-dwelling mosquitoes (Black et al., 1989; Bursalı, 2024; Lizuain et al., 2022; Parker et al., 2019). Giatropoulos et al. (2022) assessed the competition between *Ae. albopictus* and *Ae. cretinus* larvae and showed that *Ae. albopictus* larvae outcompeted and developed faster than larvae of *Ae. cretinus* especially when the food amount was low.

This study focuses on the interspecific interactions between *Ae. albopictus* and *Ae. aegypti*, which have invaded provinces with ports or close to the coast in Türkiye (Akiner et al., 2016, 2019; Demirci et al., 2021), and Turkish *Culex pipiens* based on larval competition experiments. These vectors continue to invade and emerge in other provinces where they have overlapping ranges with 62 other resident mosquito species. Some of these resident mosquitoes are active in the same period and breed in similar habitats with standing water often found near human settlements or farms (Touray et al., 2023). In the larval co-breeding studies, we assessed the impact of container size, food ration and their interactions on the mosquito emergence and adult body size of *Ae. aegypti*, *Cx. pipiens* and *Ae. albopictus* mosquitoes.

MATERIALS AND METHODS

Maintenance of mosquito colonies

Aedes albopictus was collected from Guzelcamli, Aydin, *Ae. aegypti* was collected from the Black Sea region and *Cx. pipiens* were collected from Soke, Aydin. Collected larvae were brought to the Vector Control laboratory of the Biology Department at Aydın Adnan Menderes University, and emerged species was confirmed using morphological identification keys (Rueda, 2004; Schaffner et al., 2001). Laboratory colonies of adult mosquitoes were maintained in insect cages (40 × 40 × 40 cm) in an insectary at 27 ± 1°C, a 12 h light: 12 h dark photoperiod and 60 ± 5% relative humidity (RH), with ad libitum access to 10% sugary water. Every 2–3 days, females were provided with a blood meal using de-fibrinated sheep blood through a membrane, and eggs laid on filter papers in water-filled cups were hatched in tap water and emerged larvae were provided with crushed fish food and maintained at 24 ± 1°C (Bursali & Simsek, 2023). For the experiments, sufficient eggs hatched synchronously.

Larva experiments

Experiments were established to assess the effects of three treatments (container size, food ration or larval ratio) on mosquito interaction. Containers of 10.7 cm length × 10.1 cm width × 5.5 cm depth filled with 250 mL water were considered as small size; 18 cm length × 11 cm width × 6 cm depth with 500 mL water as medium size and 22 cm height × 15.5 cm width × 8 cm depth with 750 mL water as large size. The ratio of the one-by-one interaction of the mosquitoes used (*Cx. pipiens* vs. *Ae. albopictus* and for *Cx. pipiens* vs. *Ae. aegypti*) were 100:0, 50:50, 0:100, and food ration was 0.1 g or 0.15 g of ground Tetramin

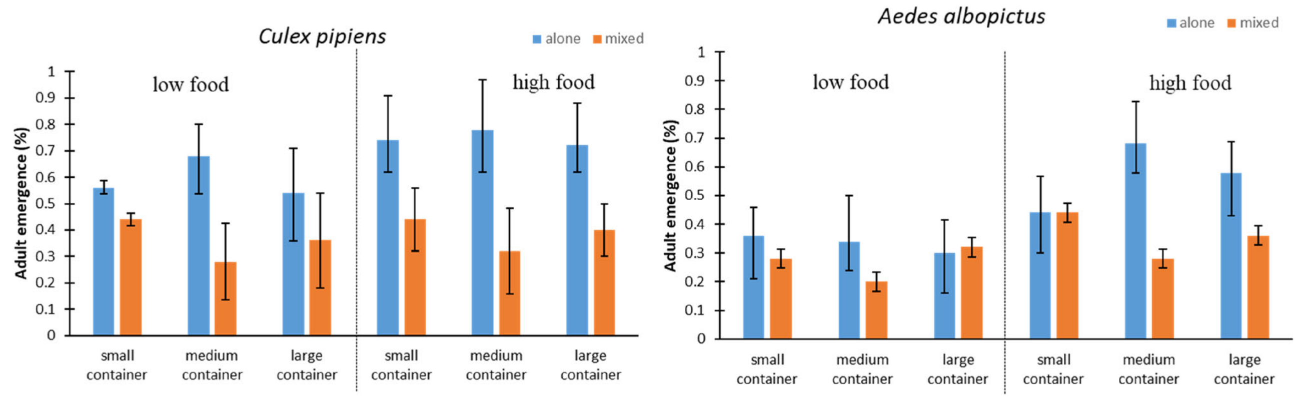

FIGURE 1 Adult emergence after larval competitions between *Aedes albopictus* against *Culex pipiens*.

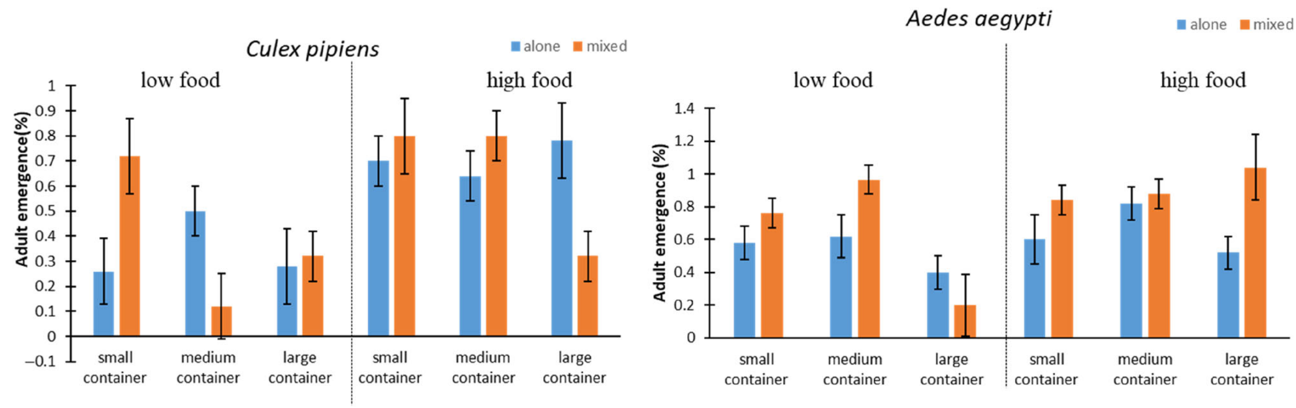

FIGURE 2 Adult emergence after larval competitions between *Aedes aegypti* against *Culex pipiens*.

fish food added to these containers . This resulted in 18 treatment combinations with 2 replicates for a total of 36 containers. Initial food was added to containers after the first instar larvae were introduced and another 5 days later. All containers were maintained at 27 ± 1°C, 70% RH and a 12 h dark photoperiod in a cage until eclosion. The developmental rate (ratio of individuals developing into adults), developmental time (period from addition to eclosion) and species of newly eclosed adults were recorded and used as measures of competitive outcome. Newly emerged adults were held for another 24 h at 27 ± 1°C and 60 ± 5% RH, with access to sugary water until full expansion and sclerotisation of the cuticle before measurement of wing span/length, which is a proxy for body size of a mosquito (Nasci, 1990; Petersen et al., 2016; Yeap et al., 2013). The adults were freeze-killed, wings were detached and wing lengths (axial incision to apical margin, excluding the fringe) of 20 randomly selected females from each group were measured under a microscope equipped with an ocular micrometre (precision ±0.03 mm) (Nasci, 1990).

Statistics

Data on the emergence ratio and adult body size based on the wing length of the mosquitoes were analysed using the Shapiro–Wilk normality test and homogeneity of variance to address normal distribution. Differences in adult emergence and adult body size were determined using generalised linear models with container size, amount of food, competition and their interactions as the main factors taken into consideration ($p<0.05$).

RESULTS

The results of interspecific and intraspecific competition between invasive species *Aedes aegypti*, *Ae. albopictus* against *Cx. pipiens* are summarised in Figures 1–4 and Table 1. Interspecific competition significantly influenced mosquito emergence and adult size, depending on species and amount of food.

Competition between *Cx. pipiens* and *Ae. albopictus* had a statistically significant impact on adult emergence with fewer mosquitoes collected from containers with mixed species compared with monospecific cultures (*Cx. pipiens* df = 1; $F = 96.587$; $p < 0.001$; *Ae. albopictus* df = 1; $F = 13.62$; $p = 0.001$) (Figure 1). The negative effect of interspecific competition was stronger in all containers with the percentage emergence nearly halved as compared with single cultures for *Cx. pipiens*. For *Ae. albopictus*, the effect of interspecific competition was stronger in medium and large containers when the food supply was high (Figure 1). In the case of mosquito size, container type had no impact on adult size for both mosquitoes, but all other factors and their interaction were statistically significant ($p < 0.05$; Table 1). The male size was only different in small containers at high food, and for females in small and medium containers at high food supply for *Cx. pipiens*. Larger *Ae. albopictus* female mosquitoes were obtained from small containers with monospecific cultures at high food supply and for males in small containers at high food and from medium-sized containers at low food supply with interspecific competition.

Similarly, adult emergence during the interaction between *Ae. aegypti* and *Cx. pipiens* varied. Regardless of the amount of food provided, more adults emerged in mixed cultures for *Ae. aegypti* as compared with monospecific cultures. When food was in limited supply, statistically more *Cx. pipiens* adults emerged in small and large containers with *Ae. aegypti* species but fewer adults were obtained in medium containers (df = 1; $F = 105.769$; $p < 0.001$) (Figure 2). For *Ae. aegypti*, mixed containers had more adult emergence (*Ae. aegypti* df = 1; $F = 29.83$; $p < 0.001$). Analysis of variance showed that the amount of food (df = 1; 68.21; $p < 0.001$) and container type (df = 2; $F = 36.008$; $p < 0.001$) and their interaction (df = 2; $F = 120.851$; $p < 0.001$) affected the outcome of the competition. In the case of the wing lengths,

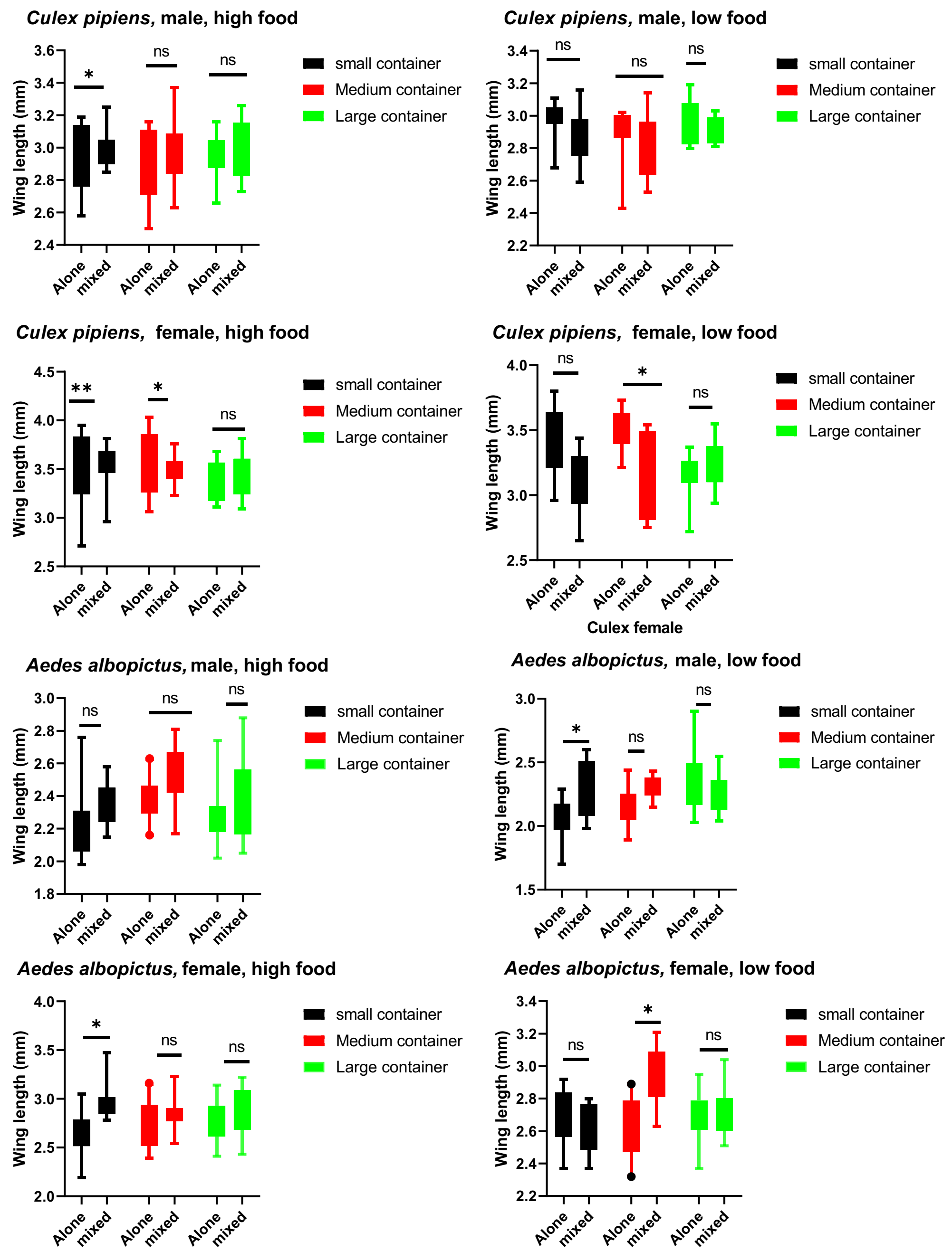

FIGURE 3 Wing length of *Aedes albopictus* and *Culex pipiens* after intraspecific and interspecific competitions. Statistical significances determined by Tukey's test (*$p \leq 0.05$, **$p \leq 0.01$; ***$p < 0.001$).

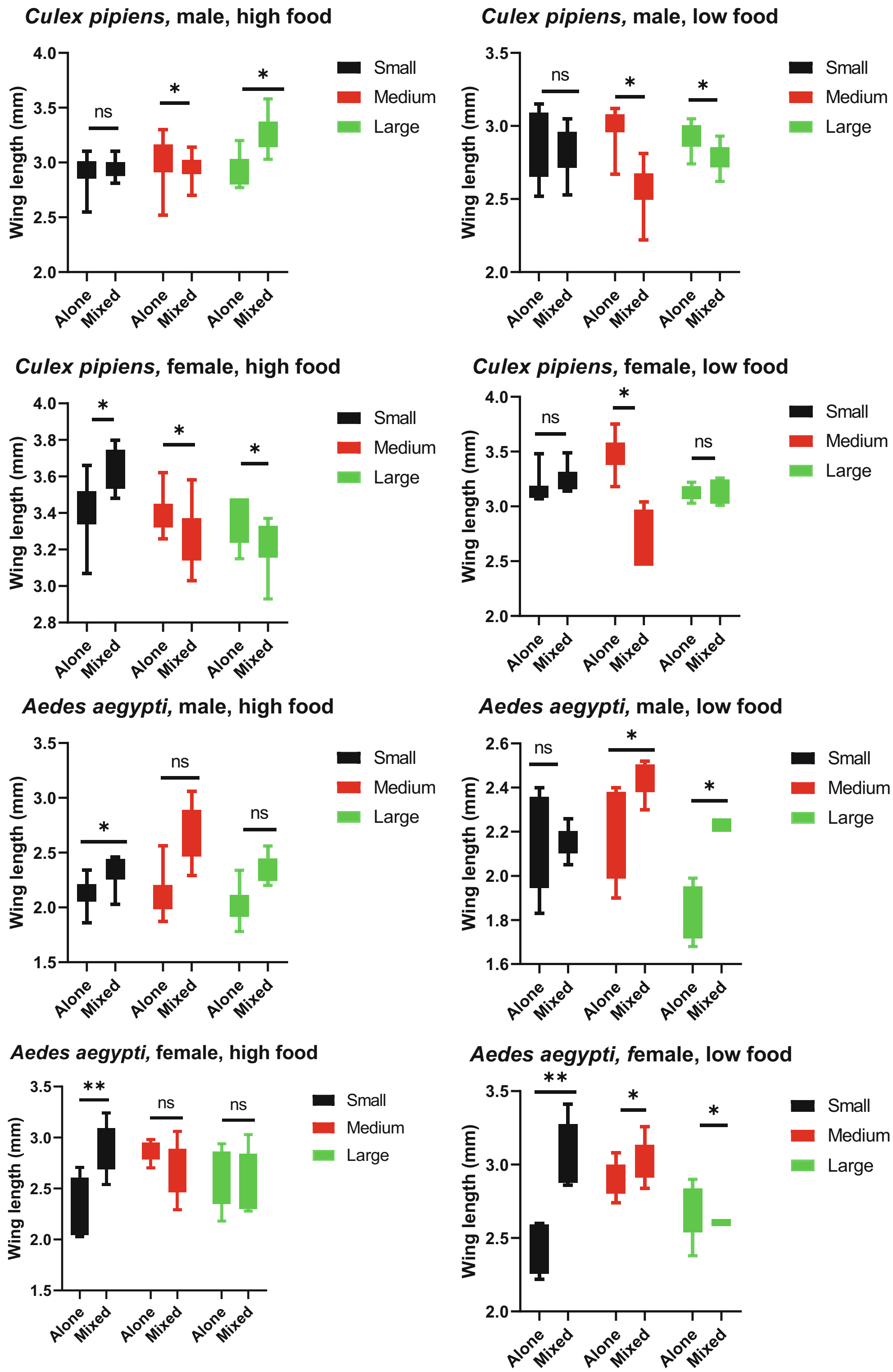

FIGURE 4 Wing length of *Aedes aegypti* and *Culex pipiens* after intra- and interspecific competitions. Statistical significances determined by Tukey's test (*$p \leq 0.05$, **$p \leq 0.01$; ***$p < 0.001$).

ANOVA shows that the various parameters (competition, amount of food, container type) when considered simultaneously influence each other and that significant differences occur both in the female ($p < 0.001$) and in the male ($p < 0.001$) for both species between controls and mixed treatments (Table 1). Competition caused a demonstrable increase in the mosquito size of *Cx. pipiens* mosquitoes during interspecific competition with *Ae. aegypti*.

TABLE 1 Results for three-factorial significance tests (df, degree of freedom) with the independent factors competition (alone, mixed), food regime (0.1 and 0.15 g) and container size (small, medium and large).

	Culex pipiens								*Aedes albopictus*							
	Female				Male				Female				Male			
Cx. pipiens* versus *Ae. aegypti	Df	Mean square	*F*	*p*	Df	Mean square	*F*	*p*	Df	Mean square	*F*	*p*	Df	Mean square	*F*	*p*
Competition	1	0.502	10.307	0.002	1	0.064	2.559	0.112	1	0.189	6.466	0.012	1	0.207	5.692	0.019
Ration	1	2.601	53.426	<0.001	1	0.305	12.275	0.001	1	0.489	16.702	<0.001	1	0.301	8.276	0.005
Container	2	0.072	1.484	0.231	2	0.06	2.412	0.094	2	0.037	1.023	0.363	2	0.092	3.145	0.047
Ration × competition	1	0.055	1.129	0.29	1	0.14	5.624	0.019	1	0.28	7.691	0.006	1	0.025	0.858	0.356
Ration × container	2	0.245	5.04	0.008	2	0.025	1.014	0.366	2	0.002	0.053	0.949	2	0.136	4.639	0.011
Container × competition	2	0.251	5.163	0.007	2	0.054	2.185	0.117	2	0.011	0.305	0.738	2	0.015	0.525	0.593
Ration × container × competition	2	0.078	1.602	0.206	2	0.123	4.95	0.009	2	0.093	2.546	0.083	2	0.005	0.166	0.847
	Culex pipiens								*Aedes aegypti*							
Cx. pipiens* versus *Ae. albopictus	df	Mean square	*F*	*p*	df	Mean square	*F*	Sig.	df	Mean square	*F*	*p*	df	Mean square	*F*	*p*
Competition	1	0.424	21.942	<0.001	1	0.365	15.867	<0.001	1	1.074	26.466	<0.001	1	1.337	66.795	<0.001
Ration	1	1.747	90.471	<0.001	1	0.385	16.735	<0.001	1	0.44	10.853	0.001	1	0.011	0.553	0.459
Container	2	0.331	17.156	<0.001	2	0	0.005	0.995	2	0.91	22.417	<0.001	2	0.133	6.644	0.002
Ration × competition	2	0.046	2.389	0.097	2	0.065	2.85	0.062	2	0.36	8.871	0	2	0.257	12.854	0
Ration × container	1	0.182	7.918	0.006	1	0.036	0.886	0.349	1	0.009	0.474	0.493	2	1.018	52.715	<0.001
Container × competition	2	0.2	8.684	<0.001	2	0.608	14.984	<0.001	2	0.183	9.143	<0.001	2	0.183	9.143	0
Ration × container × competition	2	0.39	20.179	<0.001	2	0.088	3.811	0.025	2	0.178	4.38	0.015	2	0.072	3.613	0.03

Note: Differences in wing length were tested with a general linear model (ANOVA, *F* and *p* values).

DISCUSSION

This study investigated the interspecific competition between the invasive mosquito species *Ae. albopictus* and *Ae. aegypti* against the native *Cx. pipiens*. Our findings demonstrate that competition significantly influences mosquito emergence and adult body size, with the effects varying depending on the mosquito species involved, container size and food availability. Interspecific competition significantly reduced the emergence of both *Cx. pipiens* and *Ae. albopictus* compared with their respective monocultures. *Aedes albopictus* emergence was more susceptible to competition especially in medium and large containers with high food availability. *Aedes aegypti* emerged successfully in mixed cultures regardless of food availability, suggesting a potential competitive advantage. Conversely, *Cx. pipiens* emergence was hindered when competing other species, particularly in medium containers with limited food.

These findings align with previous studies on the larval competition between these *Aedes* spp. with other mosquito species such as *Ae. triseriatus* (Livdahl & Willey, 1991; Novak et al., 1993) and *Ae. japonicus* (Armistead et al., 2012) and European *Cx. pipiens* s.l. (Carrieri et al., 2003; Costanzo et al., 2011 and Costanzo et al., 2011). Interspecific interactions are mostly asymmetrical with negative impacts on the development time, survival, adult body size, vectorial competence and capacity of less competitive container-dwelling mosquitoes (Black et al., 1989; Lizuain et al., 2022; Parker et al., 2019). We observed a significant reduction in *Ae. albopictus* emergence, particularly in larger containers with abundant food resources. Noden et al. (2016) measured the impact of interspecific and intraspecific larval competition on *Ae. aegypti* and *Ae. albopictus* adult mosquito traits and found that competitive treatments affected hatch-to-adult survivorship and development time to adulthood of females for both species. They observed that competition only affected the median wing length of *Ae. albopictus* adults. Giatropoulos et al. (2022) assessed the competition between *Ae. albopictus* and *Ae. cretinus* larvae and showed that *Ae. albopictus* larvae outcompeted and developed faster than larvae of *Ae. cretinus* especially when food amount was low.

Given the diverse range of mosquito breeding sites and the potential for overlap between *Ae. aegypti*, *Ae. albopictus* and *Cx. pipiens* (Carrieri et al., 2003; Vezzani, 2007), understanding how these species interact in shared habitats is crucial. These mosquitoes can co-occur in a variety of aquatic environments, including natural and artificial containers such as tree holes, bamboo internodes, fruit shells and husks, snail shells and plastic container (Vezzani, 2007; Carrieri et al., 2003). These habitats offer diverse sizes and organic content, influencing the mosquito species composition and potential for competition (Carvajal-Lago et al., 2021; Souza et al., 2019). These species may compete and coexist even if this coexistence has detrimental effects on each other (Price et al., 1980; Romoli et al., 2021; Sasmita et al., 2019). They possess unique adaptations that influence their competitive abilities. For example, *Ae. aegypti* thrives in various habitats and outcompetes rivals in resource-rich environments, whereas *Ae. albopictus* tolerates diverse temperatures but requires ample food (Hawley, 1988; Heath et al., 2020; Vinogradova, 2012; Yee, 2016; Yee et al., 2004). *Culex pipiens*, larger and a more efficient resource utilizer, thrives in diverse habitats, typically larger than those preferred by *Ae. albopictus* and *Ae. aegypti*. However, it lays fewer eggs and feeds less efficiently on blood (Vinogradova, 2012).

Factors like food availability, water chemistry, predators, competitors and even gut bacteria can all influence the outcome of interspecific competition (Souza et al., 2019), as highlighted in our study. Larval diet is an important factor for mosquito growth and development. It has been determined that larval density and food limitation can lead to nutritional asymmetry/imbalance and may impact mosquito development (Carvajal-Lago et al., 2021; Jannat & Roitberg, 2013; Lang et al., 2018; Souza et al., 2019; Yoshioka et al., 2012). Container size plays a crucial role. In our study, container size did not significantly affect adult body size for either mosquito species, but it interacts with food availability and competition to influence emergence success. Competition, food availability and their interactions all had a significant impact on adult wing length (proxy for body size). Larger containers, while offering more space, can dilute available nutrients, forcing larvae to expend more energy foraging (Leisnham et al., 2021; Parker et al., 2019). This, coupled with competition from other mosquito species, can significantly hinder emergence success. For instance, *Ae. albopictus* emergence was significantly reduced, particularly in larger containers with abundant food resources, whereas *Cx. pipiens* emergence even showed some increase particularly in large containers with limited food. Competition with *Ae. albopictus* and *Ae. aegypti* seemed to increase *Cx. pipiens* size. Impact on adult size in *Aedes* mosquitoes varied depending on the mosquito species, food availability and container size. For instance, larger *Ae. albopictus* females emerged from small containers with high food (single-species) and from small and medium containers with competition (depending on food). Male size varied depending on container size and food availability. Likewise, Müller et al. (2018) observed that *Cx. pipiens* biotype *molestus* is superior to *Ae. albopictus; during* larval competition, temperature, and food treatment had little impact on their interactions. The effects of competition can extend beyond larval development. While Noden et al. (2016) observed no significant impact on blood feeding or reproduction in *Ae. aegypti* and *Ae. albopictus* adults emerged from competitive environments, they did report a decrease in *Ae. albopictus* female wing length. This suggests potential fitness consequences for this species. Interestingly, Steinwascher (2020) found that *Ae. aegypti* competition can be sex-based, with females and males competing more intensely with their own sex. Additionally, larval nutrition levels can differentially affect female mosquito life history trait, that is, adult size, survival and fecundity (Yan et al., 2021).

The recent expansion of *Ae. albopictus* and *Ae. aegypti* raises concerns about the potential for increased arbovirus transmission in Europe. These mosquito species have been steadily establishing in various countries (Brem et al., 2023; Oliveira et al., 2021). Understanding how these invasives interact with native mosquitoes can provide insights into how they adapt and coexist in shared habitats. For example, the differential competitive abilities observed here suggest that *Ae. albopictus* might be particularly susceptible to competition in resource-limited environments, potentially hindering its ability to establish in certain areas. However, *Ae. albopictus* is more widespread than *Ae. aegypti* in Türkiye, despite *Ae. aegypti*'s apparent competitive advantage under some conditions. *Aedes albopictus* tolerates a wider range of temperatures than *Ae. aegypti* and is more adaptive to urban environments (Reinhold et al., 2018). Colder winters in some parts of Türkiye might limit *Ae. aegypti*'s establishment and spread and While both can utilise artificial containers, *Ae. albopictus* might be more opportunistic in utilising various breeding sites.

The study can contribute to improved monitoring and prediction systems for the spread of invasive mosquitoes and the associated disease risks. Our study just explores the one-on-one species interaction of these mosquito species. In natural settings, competition might involve multiple mosquito species, and the outcome could be different. As a laboratory study, findings offer valuable insights into competition, but they might not fully represent the complex interactions in natural environments. Field studies are needed to understand how factors like temperature, habitat availability and human behaviour interact and influence the distribution of these mosquito species in Türkiye.

AUTHOR CONTRIBUTIONS

Fatma Bursali: Conceptualization; investigation; writing – original draft; methodology. **Derya Ulug:** Conceptualization; writing – original draft; methodology. **Mustapha Touray:** Conceptualization; writing – original draft; methodology; writing – review and editing; formal analysis.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

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