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Competitive interactions between larvae of the malaria mosquitoes *Anopheles arabiensis* and *Anopheles gambiae* under semi-field conditions in western Kenya

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ABSTRACT

The present paper reports the occurrence of competition between larvae of the malaria mosquito sibling species *Anopheles arabiensis* and *An. gambiae* under ambient conditions in western Kenya. Larvae of both species were reared at the same density and under the same food conditions outdoors in single-species and mixed-species populations (species ratio 1:1) in transparent cups that floated in small and large semi-natural pools, which experienced different diurnal variations in water temperature. In a second experiment, both species were reared at similar densities and under the same food conditions in trays in either single-species or mixed-species populations at different proportions (species ratio 1:1, 1:3 or 3:1). Competition affected the development rate of both species in an opposite way: the development time of larvae of *An. arabiensis* increased whereas the development time of larvae of *An. gambiae* decreased in the presence of its sibling species. In small pools larvae developing in mixed-species populations experienced a higher mortality than larvae reared in single-species populations, whereas no such effect was observed in the large pools. In both species the time to pupation was longer and emerging females were larger in the small pools. Larval mortality of *An. arabiensis* was lower in the small pools compared to the large pools, whereas *An. gambiae* showed the opposite trend. Overall *An. arabiensis* showed reduced development rates, higher mortality rates and emerged with a larger body size compared to *An. gambiae*. The implication of these competitive interactions between larvae of *An. arabiensis* and *An. gambiae* under semi-filed conditions needs to be considered in the design and implementation of programmes that aim to reduce malaria transmission as competition may alter the species composition in the field.

1. Introduction

The two sibling malaria mosquito species *Anopheles arabiensis* Patton and *An. gambiae* Giles sensu stricto (hereafter referred to as *An. gambiae*), both belonging to the *An. gambiae* sensu lato complex (hereafter referred to as *An. gambiae* s.l.), are widespread throughout sub-Saharan Africa. Although *An. gambiae* is usually the predominant species in environments with high humidity and *An. arabiensis* is more common in zones with less rainfall, both species occur sympatrically across a wide range of tropical Africa (Petrarca et al., 1998; Coetzee et al., 2000).

Their immature stages require an aquatic environment to develop and are found in transient, sunlit and small pools (Gillies and DeMeillon, 1968; Gimnig et al., 2001). A clear difference in breeding site preference of the two species has not been observed, but the requirements of both species for their larval habitats are subject of discussion. Several studies suggest these preferences are similar (Charlwood and Edoh, 1996; Gimnig et al., 2001), others think these are different but were unable to show that explicitly (Minakawa et al., 1999). As both species are often found to share larval habitats (Charlwood and Edoh, 1996; Minakawa et al., 1999; Gimnig et al., 2001; Edillo et al., 2002; Chen et al., 2006) and *An. gambiae* s.l. larvae tend to aggregate (Service, 1971; Koenraadt et al., 2004), there will be frequent contact between individuals. However, the effects of interspecific competition between larvae of *An. arabiensis* and *An. gambiae* have rarely been studied. Laboratory studies by Schneider et al. (2000) and Kirby and Lindsay (submitted) showed a competitive disadvantage of *An. arabiensis* over *An. gambiae*, which was expressed in a higher mortality rate in mixed-species populations. In a separate study, Koenraadt and Takken (2003) demonstrated the occurrence of intra- and interspecific competition within the *An. gambiae* s.l. complex, where older larvae preyed on younger ones.

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The existence of interspecific competition between immatures of certain culicine mosquito species (mainly *Aedes* species) has been well established and a wide range of effects has been observed. Interspecific competition may affect larval development rate (Ho et al., 1989; Barrera, 1996; Juliano et al., 2004), larval survivorship (Black et al., 1989; Barrera, 1996; Braks et al., 2004; Juliano et al., 2004), the resistance to larval starvation (Barrera, 1996), sex-ratios (Lowrie, 1973a,b) and adult mosquito size (Ho et al., 1989). Moreover, it may alter mosquito–virus interactions as shown by Alto et al. (2005) for *Aedes albopictus* Skuse and therefore affect pathogen transmission.

These studies further showed that the extent of interspecific competition may depend on a variety of factors, including temperature (Russell, 1986; Ho et al., 1989), larval densities (Lowrie, 1973a,b; Russell, 1986) and food quality and quantity (Russell, 1986; Novak et al., 1993; Barrera, 1996; Daugherty et al., 2000). Furthermore, interspecific differences in larval foraging behaviour may result in a difference in resource acquisition (Yee et al., 2004) and one species might obtain more energy from the substrate than the other (Barrera, 1996). This may be explained by morphological differences of the mouth brushes (Widahl, 1992), different speed of movement of the mouth brushes and therefore different food quantity consumed per unit time (Ho et al., 1989, 1992; Widahl, 1992), a difference in feeding activity (Grill and Juliano, 1996) or by a different efficiency of the digestive system (Ho et al., 1992).

Various mosquito control methods, such as the use of insecticide-treated bednets (ITNs) and the larvicide *Bacillus thuringiensis israeliensis* (*Bti*), are currently being applied and technologies like genetically modified mosquitoes and the sterile-male technique are under development. These methods may not only result in decreasing mosquito abundance but also in a shift in the local species composition. This has recently been shown in an ITN study by Lindblade et al. (2006), which overall reduced the number of vectors in the area, but also changed the *An. arabiensis* to *An. gambiae* ratio from 1:1 to proportionally more *An. arabiensis*.

As both species are frequently found to co-exist in the same larval habitats, a better understanding of the competitive interactions between *An. arabiensis* and *An. gambiae* is needed. These interactions may alter the distribution and abundance of adult mosquitoes and hence the risk of malaria. Therefore we studied whether competitive interactions occur between larvae of *An. arabiensis* and *An. gambiae* under ambient and semi-field conditions in western Kenya. In a first experiment we examined the effects of competition in habitats of different sizes, which experienced different diurnal temperature variations. In a second experiment the effect of various species ratios within a population was assessed. We analyzed the effect of competition and habitat temperature on the development time and mortality of the immature stages and on the adult sex-ratio and female wing length.

2. Materials and methods

2.1. Mosquitoes

Experiments were carried out at the Kenya Medical Research Institute (KEMRI) in Kisian, Western Kenya. We used larvae of *An. gambiae*, maintained at the Centre for Vector Biology and Control Research (CVBCR) at KEMRI and larvae of *An. arabiensis*. As there was no *An. arabiensis* available in culture, wild-caught gravid females were collected from houses near the Ahero rice fields, approximately 30 km from Kisumu, prior to each experimental series. These females were allowed to oviposit in the insectaries

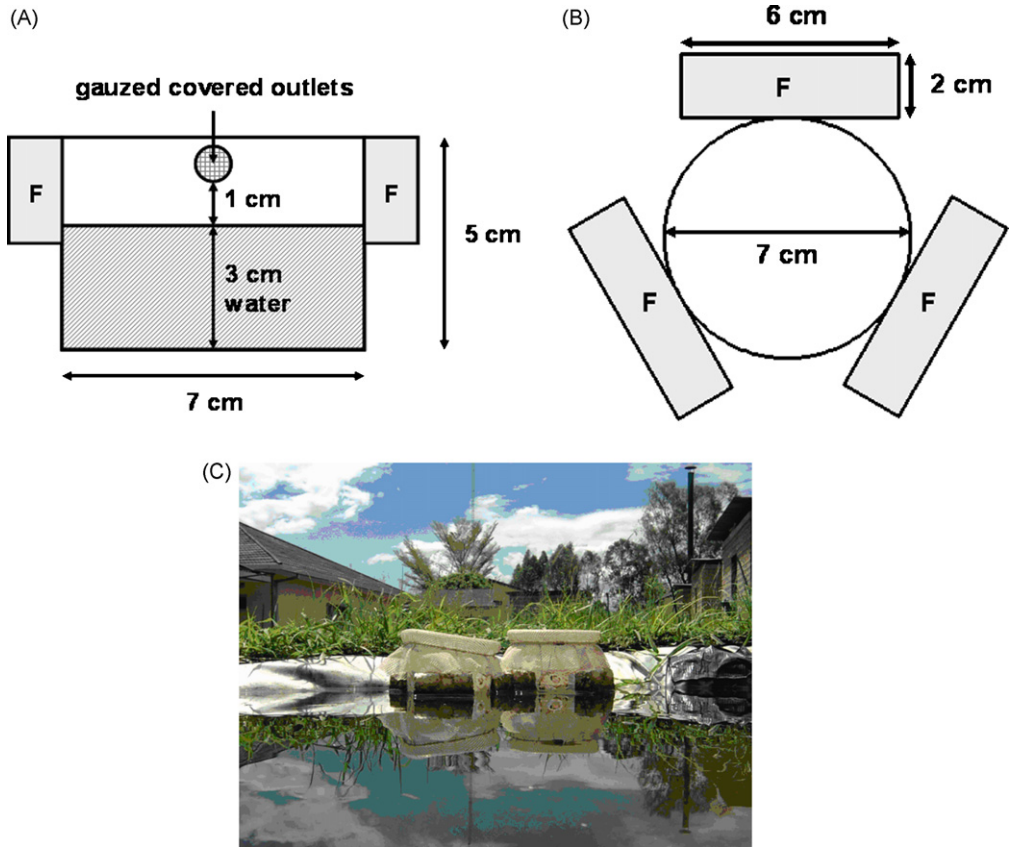

Fig. 1. (A) Schematic drawing of the side view of an experimental cup. F indicates a polystyrene float. (B) Schematic drawing of the top view of an experimental cup. F indicates a polystyrene float. (C) Experimental cups floating in a large-sized semi-natural pool.