COLONIZATION OF ROCK HOLES BY AEDES ALBOPICTUS IN THE SOUTHEASTERN UNITED STATES

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ABSTRACT. Aedes albopictus was collected from water-holding rock holes along 3 streams in Georgia and 1 in South Carolina. To compare the occurrence of Ae. albopictus and Aedes atropalpus, rock holes were sampled for immature Aedes at 2 sites where there were numerous rock holes harboring mosquitoes. At 1 of these sites, tree holes and various types of artificial containers were also sampled for immature Aedes. At both sites, immature Ae. albopictus occurred in rock holes much less frequently than the rock-pool specialist, Aedes atro-palpus. Moreover, the distribution of Ae. albopictus was limited to rock holes in less flood prone locations, whereas Ae. atropalpus was often a common mosquito even in rock holes that were among the most susceptible to flooding by rising stream levels. By contrast, Ae. albopictus was frequently found in the samples from tree holes and artificial containers. Thus, it appears that riverine rock holes that are flooded frequently may be, at best, marginal habitats for Ae. albopictus.

INTRODUCTION

In recent years, Aedes albopictus (Skuse) has become a very common mosquito in artificial containers in the southeastern part of the continental United States (Moore et al. 1988, 1990; Francy et al. 1990; O'Meara et al. 1993). Throughout this region, major declines in Aedes aegypti (Linn.) abundance have been associated with the spread and expansion of Ae. albopictus populations (Nasci et al. 1989, Hobbs et al. 1991, O'Meara et al. 1995a). Most of the surveys, which have been conducted to monitor the spread of Ae. albopictus, have focused on mosquitoes inhabiting scrap tires and other types of artificial containers (O'Meara et al. 1992, 1993; Womack 1993); whereas relatively few studies have examined the prevalence of Ae. albopictus in natural containers (O'Meara et al. 1995b).

Water-filled rock holes provide suitable aquatic habitats for immature Ae. albopictus in some regions, but little is known about the occurrence of the Asian tiger mosquito in North American rock pools (McClelland et al. 1973, Hawley 1988, Shroyer, personal communication). Aedes albopictus is a very common mosquito in artificial containers throughout the piedmont region of the southeastern United States (Richardson et al. 1995, Womack et al. 1995). Many of the streams that traverse this region have scoured pot and bore holes in the rocky substrate. Prior to the arrival of Ae. albopictus, the dominant Aedes mosquito in these types of rock holes was typically Aedes atropalpus (Coquillett). In the present study, riverine rock holes in Georgia and South Carolina were sampled for immature mosquitoes to determine the extent to which Ae. albopictus has invaded these microhabitats and to ascertain if Ae. atropalpus was still the dominant mosquito in rock holes, particularly those in flood-prone locations.

MATERIALS AND METHODS

Study sites: Rock holes in stream beds were sampled for immature Aedes mosquitoes at the 4 locations shown in Fig. 1. At Tallulah Gorge State Park in northeastern Georgia, collections were taken around the Bridal Veil Falls near the base of the South Wallenda Trail, approximately 700 ft. below the rim of the gorge. Along the Catawba River in South Carolina, sampling was conducted in rock holes, tree holes, scrap tires, and other types of artificial containers just south of the Fishing Creek Reservoir. This site was near the intersection of State Route 97 and U.S. Route 21. Water volumes flowing through the Tallulah Gorge and Fishing Creek sites have been greatly reduced since upstream hydroelectric projects began diverting much of the total stream flow around the natural river bed at these sites. Yet, when the reservoirs associated with these dammed riverine systems fill beyond storage capacity, the excess water is released down the old river beds.

A concrete diversion wall (ca. 15 ft. tall) placed across the Catawba River a few hundred yards south of the Fishing Creek Dam isolates the old river bed from a man-made channel that now directs most of the river flow into the Great Falls Reservoir. Under normal operating conditions, the water level is maintained at or near the top of the diversion wall with a very small percentage of the stream flow entering the old river bed. Most of the rock holes sampled at this site were below the diversion wall in the old river bed; however, a few were at less flood prone locations on the shore of the river between the dam and the diversion wall. Similarly, most of the rock holes harboring immature mosquitoes at the Tallulah Gorge site were in extremely flood-prone locations just a few centimeters above stream level during nonflood periods, but we were able to find 2 rock holes at a slightly higher elevation on the top of a large boulder. Rock holes were much less common, generally smaller, and in very flood prone locations at the Rocky Creek (Hard Labor Creek State Park, GA) and Ce-

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Fig. 1. Locations in Georgia (GA) and South Carolina (SC) where rock holes were sampled for immature mosquitoes.

leoth Creek (Talbot County, GA, just south of the bridge crossing this stream on State Route 36) sites.

Sampling procedures: Field trips to study sites were scheduled when regional weather patterns indicated that conditions were favorable for collecting immature Aedes from rock pools. In particular, we tried to avoid sampling at a site either during or for several weeks following a major flooding episode. Regional precipitation amounts and patterns were monitored from various internet sources. Moreover, Duke Power Company provided extremely valuable information on water level trends in reservoirs immediately upstream from the Fishing Creek site and on the frequency and severity of excess water spillage over the diversion wall. Estimates of flooding episodes at the Tallulah Gorge site were derived from data obtained from the Tallulah Gorge State Park.

Both the Tallulah Gorge and the Fishing Creek sites were sampled on 2 occasions, whereas rock holes at the Hard Labor Creek State Park and Celeoth Creek sites were sampled only once. Mosquito larvae and pupae were extracted from rock holes by bailing the water out with a plastic cup or tray and by sucking the larvae and pupae out with a meat baster. The water column in most rock pools was very clear, and under these conditions, a quick visual inspection was used to detect immature Ae-

des mosquitoes. Large rock holes (i.e., those holding more than 50 liters of water) were not sampled unless a quick visual inspection indicated the presence of Aedes larvae or pupae. For smaller holes, especially where debris, shade, or other features decreased visibility, sampling was conducted even when the initial visual inspection was negative for mosquitoes. Sampling effort varied with the size of the rock pool because more water was extracted from larger holes than from smaller ones. However, because the total amount of water taken from any rock pool never exceeded 25 liters, there was a greater chance of collecting nearly all the mosquitoes in small rock pools than in large rock pools. Similar sampling procedures were used to collect mosquitoes from water accumulations in tree holes, scrap tires, and other types of artificial containers; for each of these non-rock hole habitats, the entire aquatic contents were removed in an effort to collect immature mosquitoes. Collections from each rock hole or other type of container habitat were placed in separate plastic bottles and returned to the laboratory where the mosquito larvae and pupae were sorted and identified.

RESULTS AND DISCUSSION

On September 18, 1995 the river beds of several small streams in Hard Labor Creek State Park were

Site	Date	No. Aedes-positive rock holes	No. rock holes with	
			Ae. atropalpus	Ae. albopictus
Tallulah Gorge	Sept. 19, 1995	7	5	2
	June 13, 1996	12	12	1
Fishing Creek	June 11–12, 1996	34	32	3
	Oct. 2, 1996	27	26	2

 Table 1. The occurrence of immature Aedes atropalpus and Aedes albopictus in samples from water-holding rock holes at the Tallulah Gorge and Fishing Creek Dam sites.

examined for rock-pool mosquitoes. Only 1 Aedespositive rock hole was found, and it contained only Ae. albopictus larvae (n = 6). Four days later at the Celeoth Creek site, 2 rock holes were found harboring immature Ae. altopalpus, and 2 newly emerged adult Ae. albopictus were observed on the water surface of 1 of these rock holes. On these collection dates, water levels in the streams were extremely low (e.g., by walking on rock outcroppings it was possible to cross the streams without stepping into the water). Yet, just a modest rise in the water level (ca. 10–20 cm) would have inundated and flushed the Aedes-positive rock holes at both the Hard Labor Creek State Park and the Celeoth Creek sites.

At the Tallulah Gorge and the Fishing Creek sites, immature Ae. atropalpus were found in nearly all of the samples from rock holes, whereas very few of these samples had immature Ae. albopictus (Table 1). The only samples with Ae. albopictus at these sites came from rock holes that were in locations that were less likely to be flooded by rising water levels in the stream. At Tallulah Gorge on each collection date, all samples, with 2 exceptions were taken from rock holes that were in very flood prone positions just a few centimeters above the water level in the stream. The exceptions were 2 small man-made drill holes located more than a meter above the stream on the top of a large boulder, and these were the only rock holes at this site that were found to contain immature Ae. albopictus. At the Fishing Creek site in June 1996, collections were taken from 34 Aedes-positive rock holes. Aedes albopictus was not collected from rock holes below the diversion wall (0/29), but it was found in some of those above this wall (3/5) on the shore of the river just below the dam. Similar results were obtained when this site was sampled in October 1996. Once again, none of samples from below the diversion wall contained Ae. albopictus (0/25), but this mosquito species was present in rock holes above the wall (2/2).

Along the banks of the Catawba River at the Fishing Creek site, *Ae. albopictus* is a common mosquito in several other types of container habitats, such as tree holes, scrap tires, bottles, and cans. For example, on the June 1996 collection date, 3 scrap tires and 2 tree holes were sampled for mosquitoes and *Ae. albopictus* was collected in

each of these samples. On the October 1996 collection date, samples from 3 of 4 tree holes and 2 of 2 artificial containers were positive for *Ae. albopictus*, and in 5 *Aedes*-positive containers in a nearby cemetery (Elmwood Cemetery, Fort Lawn, SC), the Asian tiger mosquito was the only mosquito species collected.

The artificially maintained high water levels in the channel diverting the Catawba River into Great Falls Reservoir and the difference in elevation between rock holes below versus those above the diversion wall undoubtedly would make rock holes below the diversion wall susceptible to more frequent and more severe flooding than those above this wall. When a rock hole is inundated by stream flow, larvae, pupae, and eggs of Ae. albopictus probably would be swept away down the stream. Opportunities for Ae. albopictus to recolonize rock holes would seem to depend upon the availability of other types of container habitats and the amount of time between flooding episodes. Alternative microhabitats for Ae. albopictus in the form of tree holes and artificial containers were readily available around the Fishing Creek site, and a similar situation probably existed at our other study sites. By using these other aquatic habitats, populations of Ae. albopictus persist in spite of the temporary loss of the rock hole habitats.

On the basis of a review of the records of the Operations Division, Duke Power Company, there appear to have been 3 major flooding episodes during 1996 at the Fishing Creek dam site (Manuel, personal communication). On January 28, 1996, and again on February 3, 1996, the flow water over the diversion wall into the old river channel exceeded 2,000 CFS (60 CMS). On July 24, 1996, the area below the diversion wall was flooded all day at the rate of about 1,000 CFS (30 CMS). From January through September 1996, smaller flooding events with spillage of excess water over the diversion wall occured on 1 or more occasions in every month except August.

Just above the Bridal Veil Falls where the rock holes were sampled for mosquitoes, the floor of Tallulah Gorge is quite narrow (<50 m across), whereas at the top the gorge, the distance from 1 side to the other is several times greater. Bridal Veil Falls is about 0.5 km downstream from the Tallulah Dam. Hence, the rock pools at this site may be flooded either by the release of excess water from Tallulah Falls Lake or by moderate to heavy rainfall events (>1.5 cm/day) that cause water to cascade down the sides of the gorge. Permits are required for all persons accessing the gorge floor. No permits are issued on days when there is a good possibility of a flooding event. From August 3, 1995 through June 1996, the trail to the floor of the gorge was closed because of water releases from the dam or because of rainy weather or the threat of rainfall on 36 days, with 1 or more of these events occurring in every month during this period.

It is difficult to compare the results of the present study with many previous reports on the occurrence of Ae. albopictus in rock holes because some of these studies dealt with nonriverine rock holes (Halcrow 1955, McClelland et al. 1973) and others did not describe the specific type of rock holes harboring immature Ae. albopictus (Robertson and Hu 1935, Causey 1937, Bonnet 1947, Macdonald and Traub 1960). However, in mosquito surveys conducted on the islands of the Seychelles (Lambrecht 1971) and on Koh Samui Island in the Gulf of Thailand (Gould et al. 1968), the distribution of Ae. albopictus in rock holes occurred in patterns similar to that found in the present study. Although Ae. albopictus was collected very frequently from artificial containers in the Seychelles, only 2 of 19 pools along streams and 11 of 47 other types of rock pools were positive for Ae. albopictus. By contrast, Ae. albopictus was the only mosquito species found in a special type of nonriverine rock hole formed in honeycombed coral subsoil. Lambrecht (1971) attributed the absence of various mosquito species in pools along steep mountain streams to frequent flooding events during the rainy season. On Koh Samui Island, Ae. albopictus larvae were collected from both coastal and inland (near waterfall) rock holes but were collected less frequently than the rock-pool specialist, Aedes vittatus (Bigot) (Gould et al. 1968).

If the frequency of flooding events is indeed the major factor limiting the occurrence of Ae. albopictus in rock holes, then shouldn't this factor have a similar impact on the occurrence of immature Ae. atropalpus? Unless Ae. atropalpus possesses some special adaptations for dealing with a riverine environment, it would be more susceptible to local extinction than would Ae. albopictus because Ae. atropalpus generally inhabits a much narrower range of aquatic habitats, at least in this region. Among the non-rock hole samples taken at the Fishing Creek site, only (a scrap tire) contained immature Ae. atropalpus. On the other hand, immature Ae. atropalpus were present in many highly flood prone rock holes, often in large numbers (mean \pm SE/rock hole = 33.1 \pm 7.4, n = 17, range 2–124 for the Tallulah Gorge site; mean \pm SE/rock hole = 34.7 ± 5.2 , n = 58, range 1-190 for the Fishing Creek site). These values underestimate the number of immature mosquitoes per rock hole because in many cases only a small portion of the rock hole was sampled.

Seasonal variation in ovipositional behavior, the deposition of different types of eggs and possibly variable delays before hatching may be important factors enabling Ae. atropalpus to survive and to thrive in an environment frequently subjected to flooding. According to Means (1979), overwintering eggs of Ae. atropalpus are attached very firmly to the rock substrate, whereas those deposited in the spring and summer are often laid directly on the water surface. There are distinctive morphological differences between the overwinter and nonoverwinter eggs (Linley and Craig 1994). Eggs securely anchored to the rock substrate may be able to survive severe floods, like those associated with spring snow melt. If these eggs varied in the duration of their dormancy (e.g., displayed some type of installment hatching), some eggs might survive a flooding episode at any time of the year. Eggs deposited on the water surface would normally hatch in a few days, thereby enabling Ae. atropalpus to avoid delays in the life cycle during periods when water levels in rock holes were receding. Some rock holes at the Tallulah Gorge and Fishing Creek sites are deep (>0.5 m) and could provide suitable aquatic habitats for mosquitoes even during periods of extended drought. Shortly after emergence, nearly all Ae. atropalpus females produce a large egg clutch without the need for either a blood or a sugar meal (O'Meara and Krasnick 1970). This capacity (called autogeny) would facilitate the rapid recolonization of rock holes by Ae. atropalpus.

To assess accurately the impact of flooding on populations of *Ae. albopictus* and *Ae. atropalpus* in rock-hole habitats will require a more extensive monitoring effort than was done in the present study. Nevertheless, our preliminary findings suggest that such a follow up study could provide valuable information on how 2 species of containerdwelling mosquitoes (a generalist and the other primarily a specialist) cope with the environmental uncertainty associated with lotic ecosystems.

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