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USE OF *ANOPHELES*-SPECIFIC PREY-CAPTURE BEHAVIOR BY THE SMALL JUVENILES OF *EVARCHA CULICIVORA*, A MOSQUITO-EATING JUMPING SPIDER

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ABSTRACT. The prey-capture behavior of the juveniles of *Evarcha culicivora*, an East African mosquito-eating jumping spider, was investigated in the laboratory using living prey and using dead, motionless lures made from two mosquito species, *Anopheles gambiae sensu stricto* and *Culex quinquefasciatus*. Having tested individuals of *E. culicivora* that had no prior experience with mosquitoes (rearing diet: only chaoborid and chironomid midges), our findings imply that the small, but not the large, individuals of *E. culicivora* have an innate predisposition to adopt *Anopheles*-specific prey-capture behavior. Findings from lure tests implicate posture as a primary cue by which the small juveniles of *E. culicivora* identify *Anopheles*. Each individual of *E. culicivora* was presented with lures, that were either in the posture typical of *Anopheles* or in the posture typical of *Culex*. Small, but not large, juveniles of *E. culicivora* often responded to *Anopheles* mounted in the *Anopheles* posture and *Culex* mounted in the *Anopheles* posture by taking an indirect route or a detour to the prey which enabled the salticid to approach the lure from behind. However, detours were not routine for small or for large individuals of *E. culicivora* when the lure, whether made from *Anopheles* or *Culex*, was in the *Culex* posture. When tested with live mosquitoes, small juveniles of *E. culicivora* were more effective at capturing *Anopheles* than *Culex*. Large juveniles were more effective than small *E. culicivora* juveniles at capturing *Culex*, but large and small juveniles had similar success at capturing *Anopheles*.

Keywords: Salticidae, mosquitoes, malaria vectors, predation, detours, predatory versatility

Distinctive prey-specific capture behavior has evolved in at least two groups of jumping spiders (Salticidae), the araneophagic species (i.e. species that prey especially on other spiders) and the myrmecophagic species (i.e. species that prey especially on ants). Sometimes araneophagic and myrmecophagic salticids use specialized tactics to target remarkably specific prey. For example, *Portia fimbriata* (Doleschall 1859) from Queensland (Australia) adopts tactics that are specific to a particular prey species, *Euryattus* sp., a common salticid in the same habitat (Jackson & Wilcox 1990, 1993a). *Euryattus* females are unusual among salticids because they make a nest by suspending a dead rolled-up leaf by silk lines from the vegetation. *Portia fimbriata* captures *Euryattus* females by mimicking the vibratory courtship displays of *Euryattus* males, luring the females out of their leaf nests.

Here we consider another example of remarkable predatory specificity. In this instance, the predator is *Evarcha culicivora* Wesolowska & Jackson 2003, a salticid that feeds especially often on female mosquitoes in the field (Wesolowska & Jackson 2003). Here we consider the specificity of the salticid's predatory behavior for a particular mosquito genus, *Anopheles*. *Evarcha culicivora* is known only from the vicinity of Lake Victoria in Kenya and Uganda. Its typical habitat is tree trunks and walls of buildings. When quiescent, it hides in the grass or in other vegetation close to the ground, but feeding individuals venture into more exposed locations, such as the inside walls of mosquito-infested houses.

In preliminary observations, we noticed that the small juveniles, but not the large individuals, of *Evarcha culicivora* appeared to

be influenced by the mosquito's posture. In particular, *Anopheles* is a mosquito genus known for its distinctive resting posture (Clements 1999): hind legs raised; abdomen angled up at about 45° from the surface on which the mosquito is standing; abdomen and proboscis form a straight line. This posture contrasts with the posture seen in other mosquito species. For example, in *Culex* spp., the abdomen is held parallel to the substrate and the head is tilted ventrally.

Larger individuals of *Evarcha culicivora* typically oriented towards the mosquito, regardless of its posture, and then adopted the type of prey-capture sequence that is typical of many salticid species (see Forster 1977, 1982; Richman & Jackson 1992), making a slow, direct approach, with its body lowered, pausing when close, fastening a dragline and then leaping onto the mosquito. However, when the salticid was a small juvenile of *E. culicivora* and the mosquito was an individual of *Anopheles*, approach was often by way of a detour that ended with the salticid moving in from behind, walking beneath the mosquito's elevated abdomen, and attacking from underneath.

If small juveniles of *Evarcha culicivora* grabbed hold of the dorsal thorax of *Culex*, and the attacked mosquito often flew away, then when the *Culex* took flight, the small juvenile would often lose its grip and fall off. However, when the small juvenile grabbed hold of *Anopheles*' ventral thorax, it generally would hold on when the mosquito took flight, with the mosquito soon succumbing and dropping to the ground, with the salticid on board (Fig. 1).

Here we investigate three hypotheses suggested by these preliminary observations: (1) the small juveniles, but not the larger individuals, of *Evarcha culicivora* adopt an innate *Anopheles*-specific capture tactic; (2) small juveniles use the characteristic rest posture of *Anopheles* as a primary *Anopheles*-identification cue; (3) their *Anopheles*-specific tactic enables the small *E. culicivora* juveniles to be especially effective at capturing *Anopheles*.

METHODS

General.—All testing was carried out between 0700 and1900 h (laboratory photoperiod 12L:12D, lights on at 0700) at the Thomas Odhiambo Campus (Mbita Point) of the

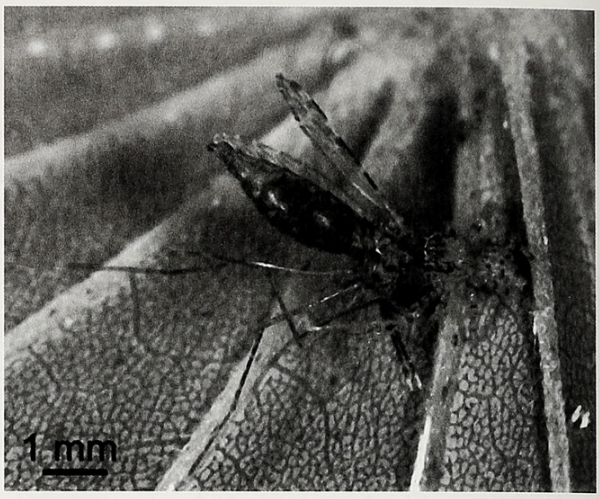

Figure 1.—Small juvenile of *Evarcha culicivora* feeding on female mosquito (*Anopheles gambiae*). After attacking by grabbing hold of mosquito's posterior ventral thorax from underneath, the salticid has now shifted to feeding from the side of mosquito's thorax.

International Centre of Insect Physiology and Ecology (ICIPE) in Kenya. The elevation of the campus at Mbita Point is 1200 m above sea level (0°25′S–0°30′S by 34°10′E–35°15′E), with 900 mm of rainfall per annum and mean annual temperature of 27 °C. The salticids came from laboratory cultures (for standard salticid-laboratory procedures see Jackson & Hallas 1986). The salticids' rearing environments were 'enriched' (spacious cages, meshworks of twigs within each cage) in a manner comparable to that described by Carducci & Jakob (2000). Maintenance diet consisted of letting each salticid feed to satiation three times per week (Monday, Wednesday, Friday) on midges (Chaoboridae & Chironomidae) collected locally at Mbita Point as needed (i.e. the salticids had no prior experience with mosquitoes of any kind).

For testing, we used adult females of two mosquito species, *Culex quinquefasciatus* Say 1823 and *Anopheles gambiae sensu stricto* Giles 1902. Body length of all mosquitoes used for testing (measured from the head's anterior end to the abdomen's posterior end, ignoring proboscis and ovipositor) was 4.5 mm (matched to the nearest 0.5 mm). Procedures for culturing *A. gambiae* were as described elsewhere (Gougana et al. 2004), and the cultures that we used were initiated from specimens collected at Mbita Point. Specimens of *C. quinquefasciatus* were collected as larvae

at Mbita Point and maintained in buckets filled with lake water in the laboratory until the adults emerged.

Two size classes (matched to the nearest 0.5 mm) of *Evarcha culicivora* juveniles were used: 'small' (body length 1.5 mm) and 'large' (body length 3.5 mm). The small juveniles were individuals that had emerged from their brood sacs 5 days before testing and had not been fed. The large juveniles were kept without prey for 7 days before testing. The 5-day pre-test period was adopted with small juveniles because preliminary trials showed that recent hatchlings became noticeably weak after more than 6 days without food. The 7-day pre-test period was adopted for large juveniles because preliminary trials showed that most individuals respond to live prey and to lures after a fast of this length. No individual of *E. culicivora* and no individual lure was used in more than one test.

Data were analyzed using chi-square tests of independence, with Bonferroni adjustments when multiple comparisons were made (Sokal & Rohlf 1995). Voucher specimens of *Evarcha culicivora* have been deposited at the Museum of Natural History (Wroclaw University, Poland), the National Museums of Kenya (Nairobi) and the Florida State Collection of Arthropods (Gainesville, Florida). Voucher specimens of insects have been deposited at the ICIPE Taxonomy Laboratory and at the Florida State Collection of Arthropods.

Testing whether posture of the prey influenced the decision by *Evarcha* to adopt *Anopheles*-specific capture behavior.—Four lure types were made, two from using each of the two mosquito species, with each species being in one of two postures (the resting posture typical of *Culex* or the resting posture typical of *Anopheles*). Each lure was made by immobilizing a mosquito with CO_2 and then placing it in 80% EtOH for 60 min. The mosquito was then mounted on the center of one side of a disc-shaped piece of cork (diameter 1.25 X the body length of the mosquito; thickness 2 mm). For preservation, the lure and the cork were next sprayed with a transparent aerosol plastic adhesive and left to air out for at least 24 h before being used.

All mosquitoes had been given blood 4–5 h before being immobilized and used for making lures. Previous work (unpubl. data) with *E. culicivora* has shown that all instars of these salticids choose blood-fed mosquitoes when the alternative is mosquitoes that have not fed on blood. Each individual of *E. culicivora* used for testing was assigned at random to one of four groups defined by mosquito species and posture, with the proviso that the number for each group was the same (n = 50).

Apparatus and testing procedures were similar to those detailed elsewhere (Li et al. 1996; Harland & Jackson 2000) except for modifications that facilitated testing small juvenile salticids. The apparatus was a wooden ramp (15 mm thick, 40 mm wide, 140 mm long) that, with the support of a wooden dowel (15 mm thick), angled up at 20°. The ramp and supporting dowel were on a wooden base (50 mm wide, 150 mm long, 15 mm thick). A lure was positioned at the top of the ramp, in front of a wall which served as a background against which salticids could see the lure. The wall was a piece of brown wood (55 mm high, 40 mm wide, 15 mm thick) glued perpendicular to the top end of the ramp. The lure was centered on the ramp 15 mm from the base of the wall, leaving 10 mm between the wall and the top edge of the cork disc. The lure was positioned so that it faced 45° away from forward (i.e. for *E. culicivora* walking directly up the ramp, the lure was facing 45° to the left or the right). For each lure, whether it was faced left or right was decided a random.

Before testing began, the salticid was kept in a covered pit (diameter 30 mm, depth 10 mm) drilled into the top surface of the ramp (equidistant from left and right side of ramp). The center of the pit was 50 mm from the bottom edge of the ramp (i.e. the lure was positioned 40 mm from the top end of the pit). Tests were allowed to start by removing a transparent glass plate used as a cover. After uncovering the pit, tests were aborted if the salticid failed to come out within 30 min or came out, but then moved off the ramp without first moving toward the lure. In successful tests, the salticid came out of the pit within 30 min after the cover was removed, walked up the ramp and, before 30 min elapsed after leaving the pit, contacted the cork disc or the mosquito, or both. The data we recorded were the salticid's horizontal orientation to the lure and the path it took to reach the lure.

Horizontal orientation of the salticid when approaching the lure was defined as follows:

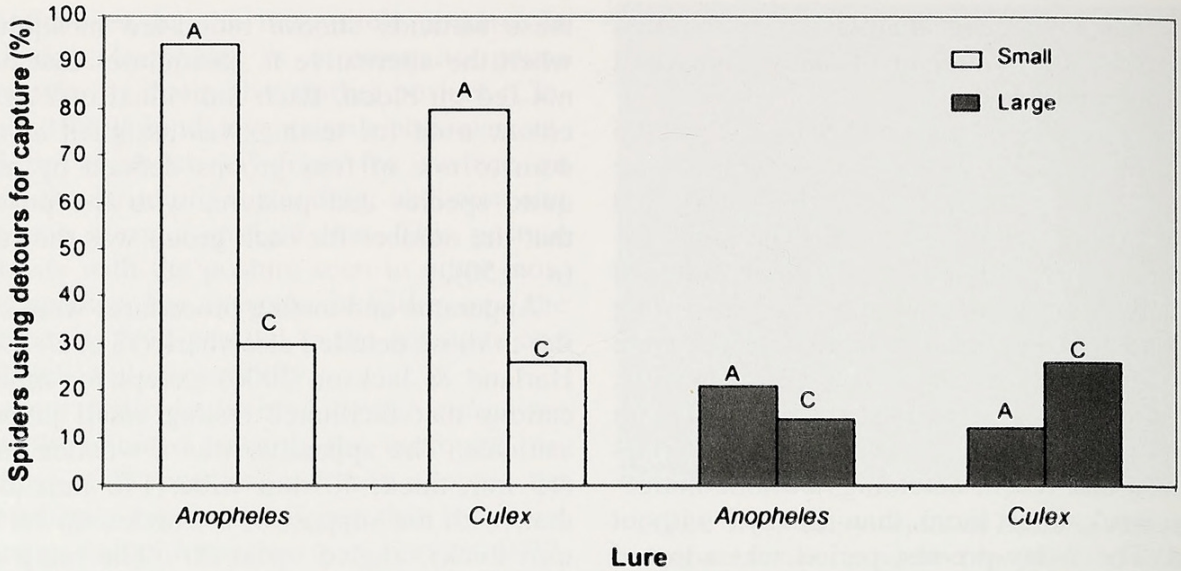

Figure 2.—Percentage of test spiders (juveniles of *E. culicivora*) that made detours when approaching lure (dead mosquito female mounted on cork disc). Two size classes of *E. culicivrora* were used: small (body length 1.5 mm) and large (3.5 mm). Four groups of spiders tested, each group defined by mosquito species and posture used for lures: *Anopheles gambiae* in *Anopheles* posture (A), *A. gambiae* in *Culex* posture (C), *Culex quinquefasciatus* in *Anopheles* posture (A) and *C. quinquefasciatus* in *Culex* posture (C). For each bar, n = 50 (no individual of *E. culicivora* and no individual lure used more than once).

front (no more than 45° to the left or the right of the anterior end of the sagittal plane of the mosquito's head); rear (no more than 45° to the left or the right of the posterior end of the sagittal plane of the mosquito's abdomen); side (between front and rear). "Detours" were defined as instances of salticids approaching the lure from the rear or else approaching the lure from the side in the first instance and then moving around to the rear. "Did not detour" was defined as instances of salticids approaching the lure from the front or approaching from the side without shifting to the rear.

Testing for prey-capture success.—Large and small juveniles of *Evarcha culicivora* were tested. In each test, one *E. culicivora* juvenile was put inside a clear Plexiglas box (300 mm X 300 mm X 300 mm) with one mosquito (one *Anopheles* or one *Culex* that had had a blood meal 4–5 h earlier). Observations were terminated after the salticid captured the mosquito or 30 min after the test elapsed without the salticid capturing the mosquito.

RESULTS

Testing whether posture of the prey influenced the decision by *Evarcha* to adopt *Anopheles*-specific capture behavior.—When the lures were made from *Anopheles*, significantly more small juveniles (χ^2 = 43.46, P < 0.001, df = 1, n = 100), but not large juveniles (χ^2 = 0.64, P = 0.42, df = 1, n = 100), of *Evarcha culicivora* made detours when the lure was in the *Anopheles* resting posture rather than in the *Culex* resting posture (Fig. 2). Likewise, when the lures were made from *Culex*, significantly more small juveniles (χ^2 = 29.27, P < 0.001, df =1, n = 100), but not large juveniles (χ^2 = 0.09, P = 0.77, df =1, n = 100), of *E. culicivora* made detours when the lure was in the *Anopheles* resting posture rather than in the *Culex* resting posture.

Small juveniles significantly more (Fig. 2) often than large juveniles of *Evarcha culicivora* made detours when approaching *Anopheles* that were in the *Anopheles* resting posture (χ^2 = 55.85, P < 0.001, n = 100) and *Culex* that were in the *Anopheles* posture (χ^2 = 46.54, P < 0.001, n = 100). However, the numbers of small and large juveniles of *E. culicivora* that made detours when approaching *Anopheles* in the *Culex* posture (χ^2 = 3.73, P = 0.05, n = 100) (Fig. 2) and *Culex* in the *Culex* posture (χ^2 = 2.25, P = 0.13, n = 100) were not significantly different.

Prey-capture success.—Large and small juveniles of *Evarcha culicivora* had greater

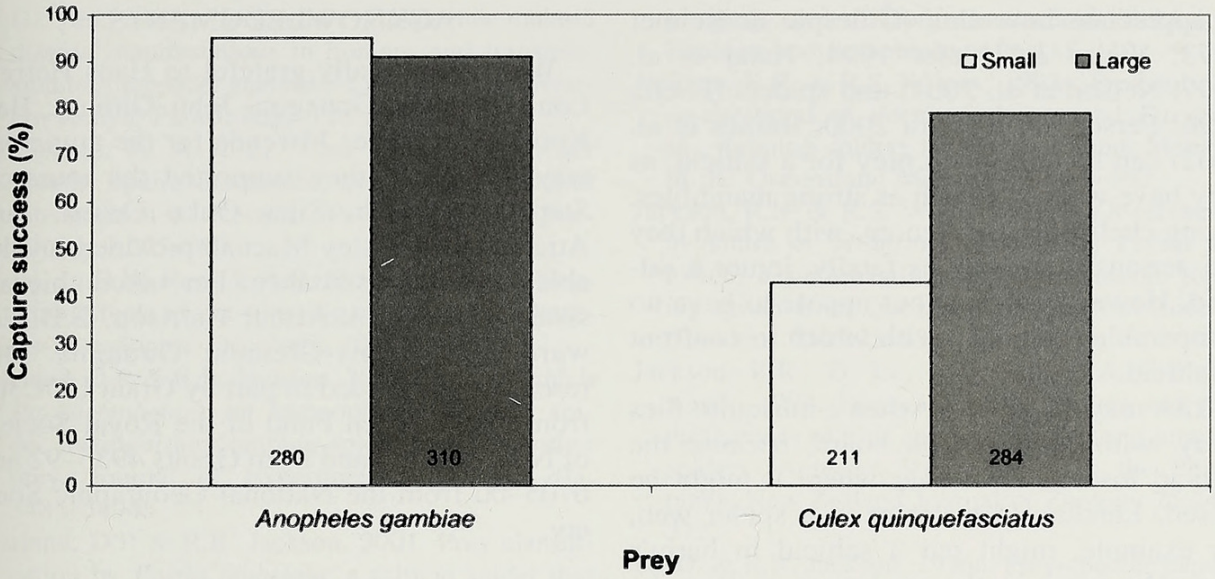

Figure 3.—Percentage of test spiders (juveniles of *Evarcha culicivora*) that captured *Anopheles gambiae* and *Culex quinquefasciatus* in 30 min test (one spider and one mosquito put together in plexiglas box). N is indicated with each bar (no individual of *E. culicivora* and no individual mosquito used more than once). Two size classes of *E. culicivrora*: small (body length 1.5 mm) and large (3.5 mm) (assigned at random to test with one or the other mosquito species).

success at capturing *Anopheles* than *Culex* (small, $\chi^2 = 163.16$, $P < 0.001$, $n = 491$; large, $\chi^2 = 17.78$, $P < 0.001$, $n = 594$) (Fig. 3). Small juveniles were less successful than large juveniles at capturing *Culex* ($\chi^2 = 63.94$, $P < 0.001$, $n = 495$), but large and small juveniles had similar success at capturing *Anopheles* ($\chi^2 = 4.13$, NS with Bonferroni adjustment, df = 1, $n = 590$).

DISCUSSION

The distinctive resting posture of *Anopheles* appears to increase the vulnerability of these mosquitoes to predation by the small juveniles of *E. culicivora*. As shown by their response to our experiments with lures and despite their minute eyes, these small salticids can apparently identify the stationary mosquito's posture by sight alone. Having identified the mosquito's posture, a small *E. culicivora* juvenile usually makes a detour that enables it to move under *Anopheles*' raised abdomen from behind. The posture of *Culex* does not afford the small juvenile with comparable easy access to the underside of the mosquito and, upon seeing a mosquito in the *Culex* posture, small *E. culicivora* juveniles usually do not make detours. Evidently, small *E. culicivora* juveniles have evolved fine-tuned innate tactics for predation on *Anopheles*.

That *Anopheles* is generally an easier mosquito than *Culex* for *Evarcha culicivora* to overpower is suggested by how both the large and the small juveniles of *E. culicivora* had greater success capturing *Anopheles* than *Culex*. Furthermore, the limited strength of small juveniles is suggested by the finding that small juveniles were considerably less successful at capturing *Culex* than large juveniles, yet they were not less successful at capturing *Anopheles*. Evidently, the *Anopheles*-specific tactic of small juveniles compensates for these spiders' small size, enabling them to be as effective as the larger juveniles when the prey is *Anopheles*. Large juveniles, being more capable of overpowering the mosquito, usually take direct routes. This way they can quickly attack the mosquito, foregoing the lengthier detours adopted by small juveniles.

Although *Evarcha culicivora* appears to be, along with examples from the myrmecophagic (Jackson & van Olphen 1991, 1992; Jackson & Wilcox 1993b; Jackson et al. 1998; Li & Jackson 1996a; Li et al. 1996; Li et al. 1999; Jackson & Li 2001) and the araneophagic salticids (Li & Jackson 1996b; Li et al. 1997; Jackson & Li 1998; Jackson 2000; Harland & Jackson 2001; Cerveira et al. 2003), a species that adopts distinctive prey-specific prey-capture behavior, *E. culicivora* seems to target a considerably different kind of prey. It is easy

to appreciate how ants (Gillespie & Reimer 1993; Vieira & Hoefer 1994; Halaj et al. 1997; Nelson et al. 2004) and spiders (Foelix 1996; Persons & Rypstra 2000; Barnes et al. 2002) can be dangerous prey for a salticid, as they have weapons, such as strong mandibles, strong chelicerae and venom, with which they can seriously, sometimes fatally, injure a salticid. However, mosquitoes appear to have no comparable weaponry with which to confront a salticid.

Risk may be relevant when a mosquito flies away, with a salticid on board, because the salticid loses control over where it might be tossed. Landing in water or in a spider web, for example, might put a salticid in harm's way. However, in the evolution of *Evarcha culicivora*'s prey-specific behavior, the risk of losing a meal may have outweighed these potential risks to life and limb. By attacking from underneath, the small juveniles of *E. culicivora* appear to minimize this risk of being thrown off by the mosquito in flight because they can hold on especially well after an attack from underneath. Another way in which *Anopheles*' posture may be important is by affording small juveniles of *E. culicivora* with the means of getting close without alerting a mosquito (i.e. it would be difficult for *E. culicivora* to move under *Culex* without first bumping into one of the mosquito's legs).

Although it is known that spiders rely to a considerable extent on learned behavior (e.g., Grunbaum 1927; Bays 1962; Edwards & Jackson 1994; Punzo 2004), our methods ruled out prior experience with mosquitoes (i.e. the individuals used in this study had either not been fed at all, or fed on midges alone before testing). Evidently, an innate *Anopheles*-specific tactic (taking a detour and attacking the mosquito from behind and underneath) is triggered when *E. culicivora* sees a mosquito in the *Anopheles* posture. This innate tactic appears to be specific to a remarkably precise prey category, female mosquitoes from one particular genus.

This study demonstrates another unusual example of prey-specific behavior in a salticid. Unlike the better-known examples of pronounced prey-specific prey-capture behavior in myrmecophagic and araneophagic salticids, *E. culicivora*'s *Anopheles*-specific tactic appears to be expressed by only the smaller juveniles.

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