A spider that feeds indirectly on vertebrate blood by choosing female mosquitoes as prey

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Spiders do not feed directly on vertebrate blood, but a small East African jumping spider (Salticidae), *Evarcha culicivora*, feeds indirectly on vertebrate blood by choosing as preferred prey female mosquitoes that have had recent blood meals. Experiments show that this spider can identify its preferred prey by sight alone and by odor alone. When presented with two types of size-matched motionless lures, *E. culicivora* consistently chose blood-fed female mosquitoes in preference to nonmosquito prey, male mosquitoes, and sugar-fed female mosquitoes (i.e., females that had not been feeding on blood). When the choice was between mosquitoes of different sizes (both blood- or both sugar-fed), small juveniles chose the smaller prey, whereas adults and larger juveniles chose the larger prey. However, preference for blood took precedence over preference for size (i.e., to get a blood meal, small individuals took prey that were larger than the preferred size, and larger individuals took prey that were smaller than the preferred size). When presented with odor from two prey types, *E. culicivora* approached the odor from blood-fed female mosquitoes significantly more often the odor of the prey that were not carrying blood.

predation | Salticidae | prey choice | behavior

No spiders are known to feed directly on vertebrate blood, but *Evarcha culicivora*, a jumping spider (Salticidae) from East Africa, preys frequently on blood-carrying mosquitoes in the field (1). That blood is ingested is evident when viewing the spider feeding under a microscope. Here we investigate a hypothesis suggested by field data and feeding observations: that *E. culicivora* has innate prey-choice behavior that enables it to feed on blood indirectly. Female mosquitoes, like sand flies, black flies, tsetse flies, and ticks, use specialized mouth parts for piercing vertebrate skin and ingesting blood (2), but spider mouth parts are not designed for this direct style of hematophagy (3). Our hypothesis is that *E. culicivora* lets the female mosquito extract the blood from the vertebrate and, by consistently choosing as prey mosquitoes that are carrying blood, gets blood meals without having to attack the vertebrate animal from which the blood originates.

For this hypothesis, distinguishing clearly between diet, choice, and preference (4, 5) is important, these being distinctions that are often blurred in the ecological literature (6, 7). "Preference" refers to the predator's attitude toward different types of prey (i.e., how it is motivated when the prey is encountered), and "choice" refers to a specific type of behavior that is driven by preference. Although diet (i.e., what the predator actually eats in nature) may suggest hypotheses about preference and choice, testing these hypotheses depends on experimental data.

Having a predator that makes vision-based decisions is convenient for experimental testing of prey-choice hypotheses, but most spiders have only poorly developed eyesight (8, 9). Salticids are a distinctive exception, because they have unique complex eyes (10–12) that support spatial resolution ($\approx$0.04°) without parallel in other animals of comparable size (13). For example, the highest acuity known for insects (14) is $\approx$0.4°, and the acuity

of the human eye (15) (0.007°) is only about five times better than that of a salticid.

Although there are well known examples of vision-based prey choice by salticids that feed on other spiders and salticids that feed on ants (16–18), the present study of *E. culicivora* documents strikingly more refined preference based on both vision and olfaction. The salticid genus *Evarcha* Simon 1902 is widespread in the Holarctic, Afrotropical, and Oriental Regions and includes >50 described species (19, 20), but *E. culicivora* is known only from the vicinity of Lake Victoria in Kenya and Uganda, where its typical habitat is tree trunks and the 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, including the inside walls of mosquito-infested houses. However, the most abundant mosquito-size insects by far in these habitats are nonbiting midges (Chironomidae and Chaoboridae) (21), known locally as "lake flies." Here we demonstrate that *E. culicivora* chooses specifically female mosquitoes that have recently fed on blood when the alternatives are lake flies, other arthropod species that do not carry blood, male mosquitoes, which never feed on blood, and female mosquitoes that have been feeding on sugar alone instead of blood.

Materials and Methods

General. The field site and laboratory were at the Thomas Odhiambo Campus (Mbita Point, western Kenya) of the International Centre of Insect Physiology and Ecology. All testing was carried out between 0800 h and 1100 h (laboratory photoperiod 12 light:12 dark, lights on at 0700). For *E. culicivora*, standard spider-laboratory procedures were adopted (22, 23).

The laboratory-rearing environment for *E. culicivora* was "enriched" (spacious cages, mesh works of twigs within each cage) (24) and during maintenance each salticid was allowed to feed to satiation on blood-fed female mosquitoes (*Anopheles gambiae*) and on lake flies three times per week (Monday, Wednesday, and Friday). All individuals tested were from the second or third generation reared under this regime. Each individual used in any one experiment always had a different combination of parents (i.e., each belonged to a different sibship).

Procedures for culturing *A. gambiae* were as described elsewhere (25), and the cultures that we used were initiated from specimens collected at Mbita Point. The other mosquito species were collected as larvae at Mbita Point and maintained in buckets filled with lake water in the laboratory until the adults emerged. Other prey (arthropods that do not feed on blood) were collected from the field as needed (Table 1).

Each adult mosquito was from one of two groups, "blood fed" or "sugar fed," both of which were maintained on glucose (6% solution, provided on filter-paper wicks), but blood-fed mosquitoes were also fed human blood three times per week. All blood-fed mosquitoes received blood 4–5 h before becoming

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Table 1. Arthropods used in laboratory experiments

Order	Family	Species	Body lengths of individuals used, mm
Diptera	Culicidae	*Aedes aegypti*	5.0
		Anopheles gambiae	4.5 and 5.5
		Anopheles funestus	3.5
		Culex quinquefasciatus	4.5
	Chaoboridae	*Chaoborus* sp.	4.5
	Chironomidae	*Ablabesmyia nilotica*	4.5
		Chironomus imicola	4.5
		Clinotanypus claripennis	6.0
		Conochironomus acutistilus	6.0
		Nilodorum brevibucca	4.5
	Tephritidae	*Ceratitis capitata*	4.5
Lepidoptera	Pyralidae	*Chilo partellus*	5.0
Homoptera	Aphididae	*Brevicoryne brassicae*	2.0
Araneae	Oecobiidae	*Oecobius amboseli*	2.0
	Tetragnathidae	*Nephilengys* sp.	4.5

prey during rearing, before being used for making lures, and before being used as odor sources in olfactometer tests.

Tests were carried out by using discrete size classes (body length measured with an ocular micrometer accurate to the nearest 0.5 mm) (1.5, 2.5, 3.5, 4.5, 5.5, 6.5 and 7.5 mm) of the adults (adult males, 3.5–5.5 mm; adult females, 4.5–7.5 mm) and the juveniles (juveniles, 1.5–5.5 mm) of *E. culicivora*.

Preliminary Testing. Although three different testing protocols (alternate day, simultaneous presentation, and alternative prey), based on using lures (dead prey mounted in life-like posture on cork disks) as well as on using living prey have been adopted in previous preference studies of araneophagic (spider-eating) and myrmecophagic (ant-eating) salticids (4, 26), the findings we present here are from only simultaneous-presentation testing (each individual salticid given access to two types of prey at the same time) and from using only lures. In earlier studies on araneophagic and myrmecophagic salticids, findings based on all of these testing methods, regardless of whether living prey or lures were used, have been consistent (26). However, in our preliminary studies, we also carried out live-prey simultaneous-presentation testing using each of the combinations of prey for which we also did lure testing, and the findings were all significant at $P < 0.05$ and consistent with the findings we present here from simultaneous-presentation lure testing.

In previous studies, simultaneous-presentation lure testing was carried out by using a two-arm (Y-shaped) wooden ramp (26). Each of the two ramp arms (ends of the Y) ended at a perpendicular pale-brown wooden wall, and there was a lure in front of each wall (a different lure type at the end of each fork of the Y; salticid chose one of the two lures by stalking until close enough to attack). A persistent problem with this procedure has been that the salticid sometimes leaves the ramp before making a choice. Here, instead of using the Y-shaped ramp, we use a more efficient experimental design (see below). However, in preliminary testing of *E. culicivora* using the Y-shaped ramp, findings were consistent with the findings we present here and always significant ($P < 0.05$).

Vision-Based Prey Choice. Each lure was made by immobilizing an arthropod with CO_2 and then placing it in 80% EtOH. One day later, the arthropod was mounted in a life-like posture on the center of one side of a disk-shaped piece of cork (diameter $1.25 \times$ the body length of the arthropod; thickness ≈ 2 mm). For preservation, the lure and the cork were next sprayed with a transparent plastic adhesive (26). No individual of *E. culicivora* and no individual lure were used more than once.

The testing apparatus (Fig. 1) was a square transparent glass box with four vials fitted into holes that were spaced around the four sides. There was a lure on each side of each vial (i.e., a total of eight lures surrounded the box). Each lure sat on the wooden platform and faced directly toward the side of the box. Two lure types were present during each test. One type was placed on the opposing sides (positions A), and the other type was placed on the other opposing sides (positions B). Which of the two lure types was placed in positions A was decided at random.

The box was mounted on a wooden platform (170×170 mm) and surrounded by a 40-mm-high pale-brown wooden fence. The fence served as a background against which *E. culicivora* saw the
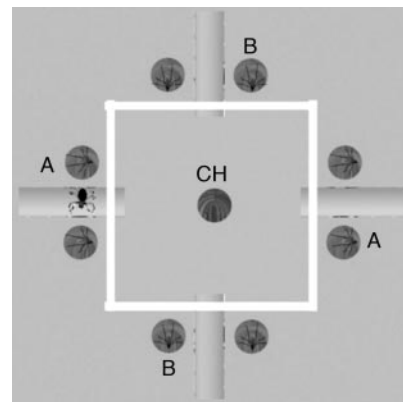

Fig. 1. Apparatus used for testing vision-based prey choice (not drawn to scale). The apparatus consisted of a glass arena (square box, 100×100 mm, walls 35-mm high, 5-mm thick), with a removable glass lid (100×100 mm). CH, hole in center of lid (diameter, 16 mm). The lid was held in place by a 5-mm-wide rim (5 mm from edge of box). A hole (diameter, 16 mm) was centered on each of four sides of the box (i.e., the center of hole was equidistant from the top and bottom of arena and also equidistant from the left and right sides of the wall). A transparent glass vial (diameter, 15 mm; 50-mm long) was positioned in each of these four holes (inner end open and flush with inner side of arena wall). The vial extended 45 mm out from the outer side of the arena wall. Lures were mounted on cork discs and positioned one on each side of each vial. The type of lure at A was different from the type at B. The center of the cork disk was 20 mm from the side of the arena and 10 mm from the side of the vial. Testing began by introducing the test spider through CH. Testing ended when the test spider entered a vial and remained there for >30 s.
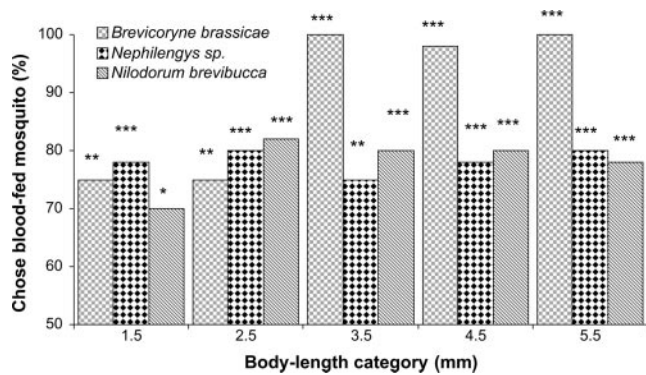
Fig. 2. Percentage (y axis) of test spiders (juveniles from different body-length categories) that chose lures (see Fig. 1) made from blood-fed female mosquitoes (*A. gambiae*) (body length, 4.5 mm) instead of alternative prey (indicated by bar stippling) (see Table 1 for body lengths). $n = 40$ for each bar. χ^2 tests of goodness of fit (null hypothesis: choose each prey type equally often). ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.

lures. The entire apparatus was lit by a 200-W incandescent lamp, positioned ≈400 mm overhead. Fluorescent ceiling lamps provided ambient lighting.

With our objective being to ascertain whether *E. culicivora* made the prey-choice decisions that gave it access to blood, we minimized the influence of prey-size preference as a potentially confounding variable during the majority of tests by ensuring that the body lengths of all mosquito lures were matched to the nearest 0.5 mm. However, in another test series, we first determined the prey-size preferences of *E. culicivora* when the presence or absence of blood in the prey was held constant and then, having ascertained prey-size preference, we next determined whether preference for blood took precedence over preference for particular prey sizes.

After introducing the test spider into the box and then plugging the hole in the lid with a rubber stopper, tests lasted 30 min or until the test spider made a choice. When the spider entered and then stayed inside any one of the four vials for 30 s, this was recorded as its choice. The rationale for the 30-s criterion was that, in preliminary trials, although individuals of *E. culicivora* often entered a vial for a few seconds and then left, all individuals that stayed in a vial for 30 s then remained in this
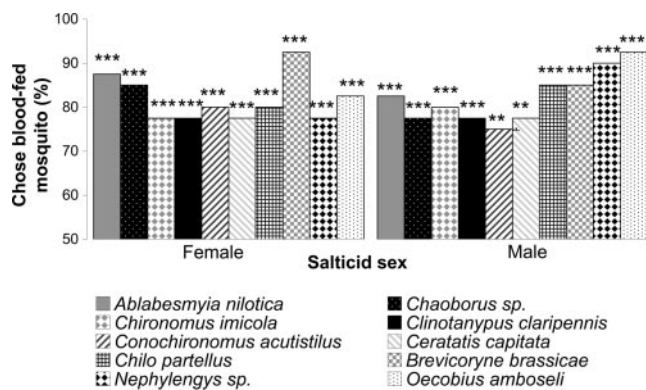
vial for at least 5 min longer, and any that subsequently left this vial never entered and remained in another vial for as long as 30 s.

A short pretest fast (7 days) was adopted, as in earlier studies (26), the rationale for this being to ensure that the test spiders would be motivated to feed during testing. Between tests, the box, the stopper, and all vials were washed with 80% EtOH followed by distilled water and then allowed to dry.

Olfaction-Based Prey Choice. *E. culicivora*'s response to specific odors was assessed by using a Y-shaped olfactometer similar to that used in previous studies (27), with airflow adjusted to 1,500 ml/min (Matheson FM-1000 flowmeter) and the odor source hidden from the test spider's view. There was no evidence that this airflow setting impaired locomotion or had any adverse effects on *E. culicivora*'s behavior. Air was pushed by a pump from a tap through two separate flowmeters into two stimulus chambers and from each stimulus chamber to a different choice arm. Air from the two choice arms then converged and moved into the test arm (i.e., the stem of the Y).

An odor source (10 prey of the same type) was placed in each stimulus chamber 30 min before each test. A test spider was placed in a holding chamber connected to the test arm 2 min before testing began, a removable metal grill (positioned in a slit in the glass) blocking the spider's access to the test arm. The grill was removed to start testing.
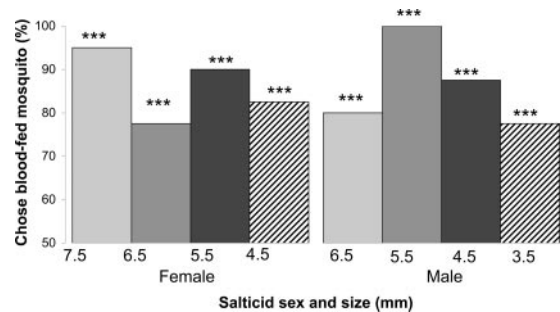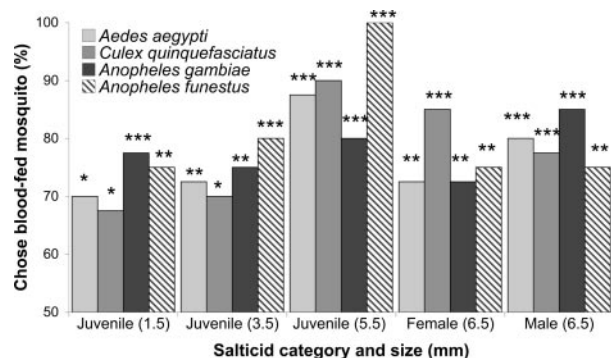

Fig. 4. Percentage (y axis) of test spiders (adult males and females from different body-length categories) that chose lures (see Fig. 1) made from blood-fed female mosquitoes (*A. gambiae*) (body length, 4.5 mm) instead of *Nilodorum brevibucca* (4.5 mm). $n = 40$ for each bar. χ^2 tests of goodness of fit (null hypothesis: choose each prey type equally often). ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.

Fig. 3. Percentage (y axis) of test spiders (adult males and females; body length, 6.5 mm) that chose lures (see Fig. 1) made from blood-fed female mosquitoes (*A. gambiae*) (body length, 4.5 mm) instead of alternative prey (indicated by bar stippling) (see Table 1 for body lengths). Except for *Brevicoryne brassicae*, *Clinotanypus claripennis*, *Conochironomus acutistilus*, and *Oecobius* sp., the body length of alternative prey matched that of the mosquito. $n = 40$ for each bar. χ^2 tests of goodness of fit (null hypothesis, choose each prey type equally often). ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.
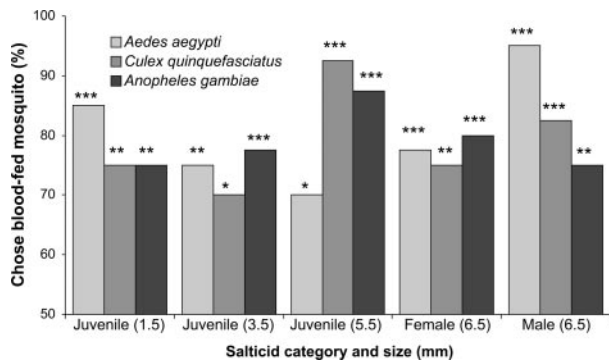

Fig. 5. Percentage (y axis) of test spiders (adult males, adult females, and juveniles; see x axis) that chose lures (see Fig. 1) made from blood-fed female mosquitoes (for body lengths, see Table 1; all *A. gambiae* 4.5 mm) instead of conspecific male mosquitoes (same body length as female). Bar stippling indicates mosquito species. $n = 40$ for each bar. Size on x axis, body length of test spider in mm. χ^2 tests of goodness of fit (null hypothesis, choose each prey type equally often). ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.

Fig. 6. Percentage (*y* axis) of test spiders (adult males, adult females, and juveniles; see *x* axis) that chose lures (see Fig. 1) made from blood-fed female mosquitoes (for body lengths, see Table 1; all *A. gambiae* 4.5 mm) instead of conspecific sugar-fed female mosquitoes (same body length as blood-fed females). Bar stippling indicates mosquito species. *n* = 40 for each bar. Size on *x* axis: body length of test spider in mm). χ^2 tests of goodness of fit (null hypothesis: choose each prey type equally often). ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.

Fig. 8. Percentage (*y* axis) of test spiders (adult males, adult females, and juveniles; see *x* axis) that chose the odor of blood-fed female (*A. gambiae*) instead of that of alternative prey (indicated by bar stippling). *n* = 40 for each bar. Odor source: hidden but not immobilized insects at the ends of a Y-shaped olfactometer. χ^2 tests of goodness of fit (null hypothesis, choose each prey type equally often). ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.

after which the stimulus chamber was connected again to the rest of the olfactometer and the pump was switched on again.

Once the grill was removed, the test spider had 30 min in which to make a choice (definition: entered a choice arm and remained there for 30 s). Earlier olfactometer studies (27, 28) have shown that this 30-s rule is reliable for other salticid species, and our preliminary testing confirmed that it was reliable for *E. culicivora*. After each test, the olfactometer was dismantled and washed with 80% EtOH followed by distilled water and then allowed to dry. No test spider and no odor source were used more than once.

That differences in prey activity influenced the choices made by *E. culicivora* appears unlikely because, on the whole, the arthropods used as odor sources were not especially active during the tests. However, in another test series, we controlled for prey activity by immobilizing all prey with CO_2 gas before they were put into the stimulus chamber. If prey began to show signs of activity at any time during the pretest or the test period, the pump was switched off, the stimulus chamber was disconnected from the rest of the olfactometer, and CO_2 gas was introduced into the stimulus chamber, rendering the prey quiescent again,
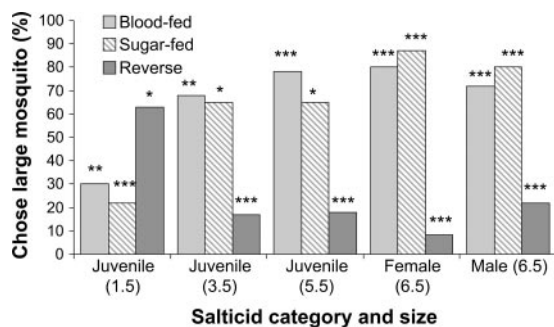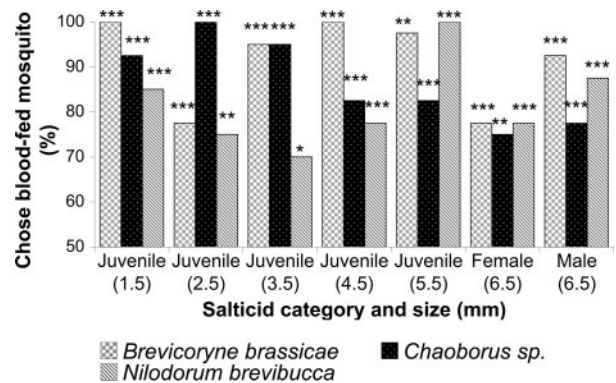
Data Analysis. For this study, all data were analyzed by using χ^2 tests for goodness of fit (null hypothesis: the two choices are made equally often) (29). Instances in which individuals failed to make a choice in the allotted test period were rare (never >5% for any prey combination in vision- or olfaction-based testing).

Results

Vision-Based Prey Choice When Body Lengths of the Two Prey Types Match. When the alternative was an arthropod other than a mosquito, the juveniles (Fig. 2) and both sexes of the adults (Fig. 3) of *E. culicivora*, regardless of size class (Fig. 4), chose blood-fed female mosquitoes significantly more often than they chose any alternative prey (Table 1). Pooling all data from these tests, 1,423 (83%) of the spiders chose the blood-fed mosquito, whereas only 297 (17%) of the spiders chose the alternative prey.

When the alternative was a conspecific male mosquito, *E. culicivora* chose blood-fed female mosquitoes significantly more often than they chose conspecific male mosquitoes. This trend held regardless of the mosquito species and regardless of the sex–age–size category of the individual of *E. culicivora* being tested (Fig. 5). Pooling all data from these tests, 627 (78%) of the
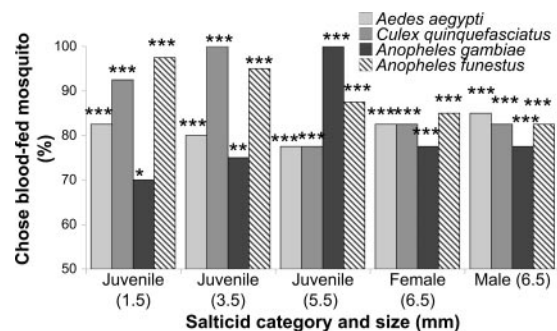

Fig. 7. Percentage (*y* axis) of test spiders (adult males, adult females, and juveniles; see *x* axis) that chose lures (see Fig. 1) made from large (*A. gambiae*, body length 5.5 mm) instead of small female mosquitoes (*A. gambiae*, body length 4.5 mm). Three types of testing (blood-fed, sugar-fed, and reverse) are indicated by bar stippling. Blood-fed, tested with large and small blood-fed female mosquitoes; sugar-fed, tested with large and small sugar-fed female mosquitoes; reverse, 1.5-mm juveniles of *E. culicivora* tested with large blood-fed female mosquitoes and small sugar-fed female mosquitoes; adult females, adult males, and juveniles >1.5 mm in body length tested with small blood-fed female mosquitoes and large sugar-fed female mosquitoes. *n* = 60 for each bar. χ^2 tests of goodness of fit (null hypothesis: choose each prey type equally often). ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.

Fig. 9. Percentage (*y* axis) of test spiders (adult males, adult females, and juveniles; see *x* axis) that chose the odor of blood-fed female. *A. gambiae* instead of that of conspecific male mosquitoes. *n* = 40 for each bar. Size on *x* axis, body length of test spider in mm. Odor source, hidden but not immobilized insects at the ends of a Y-shaped olfactometer. χ^2 tests of goodness of fit (null hypothesis: choose each prey type equally often). ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.
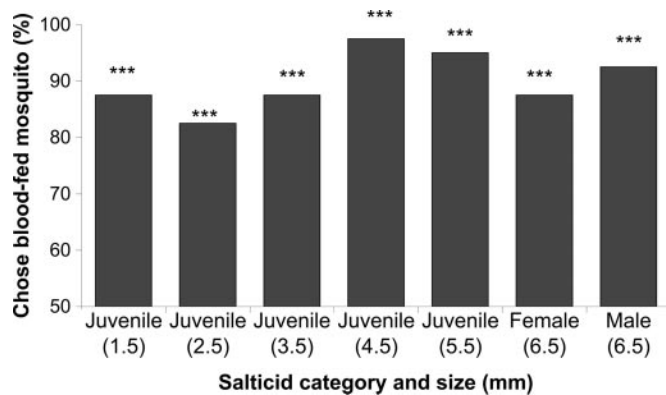
Fig. 10. Percentage (y axis) of test spiders (adult males, adult females, and juveniles; see x axis) that chose the odor of blood-fed female *A. gambiae* instead of that of conspecific sugar-fed females. $n = 40$ for each bar. Size on x axis, body length of test spider in mm. Odor source, hidden but not immobilized insects at the ends of a Y-shaped olfactometer. χ^2 tests of goodness of fit (null hypothesis: choose each prey type equally often). ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.

spiders chose the blood-fed female mosquito, whereas only 173 (22%) of the spiders chose the male mosquito.

When the alternative was a conspecific female mosquito that had been feeding on sugar only, individuals of *E. culicivora* chose blood-fed female mosquitoes significantly more often than they chose the sugar-fed female mosquitoes (Fig. 6). Pooling all data from these tests, 477 (79%) of the spiders chose the blood-fed female mosquito, whereas only 127 (21%) chose the sugar-fed female mosquito.

Vision-Based Prey Choice When Body Lengths of the Two Prey Types Differ. When the alternatives were a large and a small blood-fed or sugar-fed female mosquito, 1.5-mm juveniles of *E. culicivora* chose the small blood- or sugar-fed female mosquitoes, respectively. The larger juveniles and both sexes of the adults of *E. culicivora*, however, chose the large blood- and sugar-fed female mosquitoes (Fig. 7).

When the large female mosquito had been feeding on blood, and the small female mosquito had been feeding on sugar, 1.5-mm juveniles of *E. culicivora* reversed their prey-size pref-
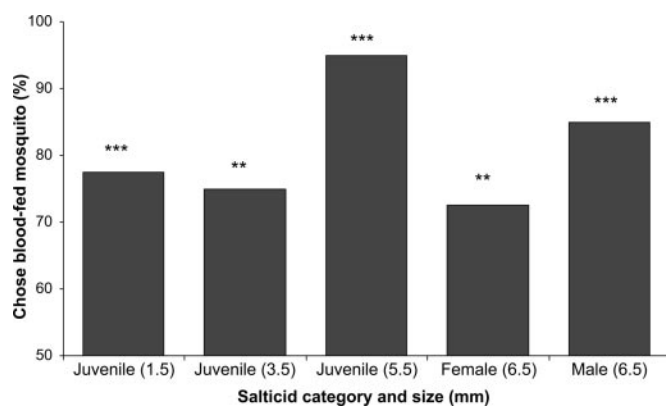

Fig. 11. Percentage (y axis) of test spiders (adult males, adult females, and juveniles; see x axis) that chose the odor of blood-fed female *A. gambiae* instead of that of conspecific male mosquitoes. $n = 40$ for each bar. Size on x axis, body length of test spider in mm. Odor source, hidden immobilized insects at the ends of a Y-shaped olfactometer. χ^2 tests of goodness of fit (null hypothesis, choose each prey type equally often). ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.

erence (i.e., they chose large, not small, female mosquitoes) (Fig. 7). When the small female mosquito had been feeding on blood, whereas the large female mosquito had been feeding on sugar, larger juveniles, adult males, and adult females of *E. culicivora* reversed their prey-size preference (i.e., they chose small, not large, female mosquitoes) (Fig. 7).

Odor-Based Prey Choice Using Nonimmobilized Prey. When the alternative was the odor of arthropods other than mosquitoes, juveniles, adult males, and adult females of *E. culicivora*, regardless of size class, chose the odor of blood-fed female mosquitoes significantly more often (Fig. 8). Pooling all data from these tests, 727 (87%) of the spiders chose blood-fed mosquitoes, whereas only 114 (13%) chose the alternative prey.

When the alternative was the odor of conspecific male mosquitoes, *E. culicivora* chose the odor of blood-fed female mosquitoes significantly more often. This trend held regardless of the mosquito species and regardless of the sex–age–size category of the individual of *E. culicivora* being tested (Fig. 9). Pooling data from these tests, 626 (84%) of the spiders chose the odor of blood-fed female mosquitoes, whereas only 124 (16%) of the spiders chose the odor of male mosquitoes.

When the alternative was the odor of sugar-fed conspecific female mosquitoes, *E. culicivora* chose the odor of blood-fed female mosquitoes significantly more often. This trend held regardless of the mosquito species and the sex–age–size category of the individual of *E. culicivora* being tested (Fig. 10). Pooling data from all of these tests, 252 (90%) of the spiders chose the odor of blood-fed female mosquitoes, whereas only 28 (10%) of the spiders chose the odor of sugar-fed female mosquitoes.

Odor-Based Prey Choice Using Immobilized Prey. When the alternative was the odor of conspecific male mosquitoes, *E. culicivora* chose the odor of blood-fed female mosquitoes significantly more often. This trend held regardless of the sex–age–size category of the individual of *E. culicivora* being tested (Fig. 11). Pooling data from all of these tests, 162 (81%) of the spiders chose the odor of blood-fed female mosquitoes, whereas only 38 (19%) chose the conspecific male mosquitoes.

Discussion

Our testing methods in the laboratory eliminated potentially confounding effects from prey behavior, and our data showed that, by means of its prey-choice decisions, *E. culicivora* feeds indirectly on vertebrate blood. By sight, *E. culicivora* consistently chose lures made from blood-carrying female mosquitoes instead of lures made from prey that were not carrying blood (sugar-fed female mosquitoes, male mosquitoes, and a variety of arthropod species that do not feed on blood). *E. culicivora* also consistently chose the odor of blood-carrying female mosquitoes instead of the odor of prey that were not carrying blood.

Although presenting these data is beyond the scope of the present paper, we have tested individuals of *E. culicivora* that had been denied any prior experience with blood meals (i.e., individuals that had been maintained since hatching on a diet of lake flies only, *A. gambiae* males only, or sugar-fed *A. gambiae* females only), and the data from these studies rule out prior experience with blood meals as a necessary factor determining *E. culicivora*'s preference for blood-fed female *A. gambiae* when the alternative prey during testing were lake flies or conspecific male mosquitoes (i.e., these individuals had a significant inclination to choose the blood-fed mosquitoes). Data from other studies in progress imply that maternal effects (30) and other indirect genetic effects (31) are unlikely alternative explanations for our findings (individuals of *E. culicivora* from the second and third generation of laboratory rearing had a significant trend toward choosing the blood-fed mosquitoes, not only when the feeding regime of the culture was as in the present study but also when the feeding

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regime of the culture was lake flies only, males of *A. gambiae* only, or sugar-fed females of *A. gambiae* only).

Our experiments imply that *Evarcha culicivora's* prey-choice behavior is driven by an innate preference for blood-fed female mosquitoes and also show that *E. culicivora* has a remarkable ability to make the same highly specific prey identifications by sight alone and by odor alone. This appears to be the first predator that has been shown experimentally to select prey on the basis of what the prey has recently eaten, to single out mosquitoes as preferred prey, and to feed, indirectly, on vertebrate blood.

By sight alone, *E. culicivora* also made prey-size choices. When all lures were made from blood-fed female mosquitoes and when all lures were made from sugar-fed female mosquitoes, 1.5-mm juveniles of *E. culicivora* chose the smaller lures, but all other size classes of *E. culicivora* chose the larger lures. However, *E. culicivora's* preference for the blood-carrying prey evidently took precedence over preference for particular prey sizes (i.e., *E. culicivora* chose blood-fed female mosquitoes even when they belonged to the nonpreferred size class).

It is known that, after feeding on blood, females of *A. gambiae* become more vulnerable to attack by generalist salticids (32), presumably because the mosquito becomes sluggish when engorged. The mosquito's sluggishness, however, is not a proximate explanation for our findings, because the data we present are from using only immobile lures and prey odor, not from using living prey (i.e., our data are not confounded by effects deriving from prey behavior). These findings do not rule out impaired prey defense as part of the ultimate explanation for *E. culicivora's* preferences (i.e., *E. culicivora* may be adapted to choose prey that are especially easy to capture). However, work in progress suggests that the blood meal itself is important to *E. culicivora* and imply that advantages deriving from ease of capturing the prey do not fully account for the adaptive significance of *E. culicivora's* prey-choice decisions.

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