

## Effects of orb web orientation and spider size on prey retention

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### Summary

Struggling flies were retained longer in samples of *Metazygia* sp. webs held vertically than in those held horizontally, and longer in those of mature females than in those of subadults. Retention times varied substantially in each treatment. Moderate modification of web geometry did not affect retention times significantly.

### Introduction

Orb webs perform several different functions in prey capture: intercept prey; stop it; and then retain it until the spider arrives to attack (Chacón & Eberhard, 1980; Craig, 1987). Retention is important because orb weavers generally take several seconds to reach insects which fall into their webs. Average response times to prey flying or falling into their webs (from the moment of prey impact until initiation of biting or wrapping by the spider) were  $6.9 \pm 9$  s in *Nephila maculata* (Fabr.) and  $8.7 \pm 13.2$  s in *Cyrtophora moluccensis* (Doleschall) responding to blowflies (Lubin, 1973); about 5.5 s in *Araneus diadematus* Clerck responding to house flies (Witt *et al.*, 1978); and from 1.7 to 3.8 s in *Cyclosa turbinata* (Walck.) responding to different prey species (R. Suter, pers. comm.). These studies specifically excluded large prey which spiders probably tend to approach more slowly (Robinson & Mirick, 1971; Suter, 1978).

The general conclusion is that most orb webs need to restrain prey for at least 5-10 seconds before the spider arrives to attack. But prey often escape from orbs within this same range of times; it is not uncommon for more than half of those prey which hit an orb to escape in less than 5 s (Barrows, 1915; Lubin, 1973; Nentwig, 1982; Yoshida, 1987; Uetz & Hartsock, 1987; Eberhard, in prep.). Clearly web characteristics which increase prey retention times could be strongly favoured by natural selection. The experiments reported here were performed to test the effects of two variables, the web's orientation with respect to gravity and the size of the spider which made it, on the length of time an orb can retain prey.

### Materials and Methods

Samples of newly-spun webs of adult females and penultimate and antepenultimate instars (subadults) of *Metazygia* sp., a species which usually builds more or less vertical orbs, were collected in the early evening 15 km SE of Puerto Lopez, Meta, Colombia on rectangular wire frames (15 × 10 cm) which had been coated lightly with a viscous adhesive ("Tack Trap", Animal Repellents, Griffin, GA). The frame was pressed gently

against an undamaged portion of an orb (usually including both central and peripheral portions of several radii), and the web lines around the edge of the frame were then cut with scissors. Only a single sample was taken from each orb. Lines were observed closely as the frame was cut free; if there was any movement of the lines in the sample portion relative to each other or to the frame, the sample was discarded. In practice such movements were uncommon owing to the strong adhesive force of the Tack Trap relative to the tensions of lines in the orbs. Samples were stored individually in cardboard boxes and used the following day.

*Metazygia* sp. probably catches a wide variety of kinds and sizes of insects (see Castillo & Eberhard (1983) on the prey of *Metazygia gregalis*). The experimental prey species used here, a sepsid fly, was about 3 mm long and an estimated 10-25% of the weight of adult female *Metazygia*. I held the web sample on the frame in a more or less horizontal position about 15 cm above a fresh pat of cow dung where flies were abundant, started a tape recorder, simultaneously spoke into the recorder and waved my hand briskly near the pat to cause the flies to fly up in alarm, and then called out each time a fly escaped from the web. Some webs were tilted to a vertical position as soon as the flies flew into them, while others were kept horizontal. Tapes were later played back, and retention durations were noted to the nearest second. Occasionally flies freed themselves from one part of the web only to become entangled in another; these events were also noted. Final escape times were used in all analyses.

Flies which passed directly through the web or bounced off it were not counted. Thus the web functions described by Chacón & Eberhard (1980) as "stopping" (absorbing the prey's momentum without breaking) and "adhesion" (sticking to the prey on first impact) were not measured. The results measure only "retention" (holding the prey in the web once it has been stopped). Flies which touched the Tack Trap adhesive were not counted. Each web sample was tested at least once vertically and at least once horizontally; the order was changed for successive samples.

Response times of spiders were determined by holding a light near a newly-built web in the evening, and noting the time that elapsed between the impact of an insect (most were probably drawn by the light) and the moment the spider contacted it. Only a single prey was counted for a given spider on a given evening.

Voucher specimens labelled 1515, 1692, 1693 and 1694 of *Metazygia* sp. are deposited in the Museum of Comparative Zoology in Cambridge, Mass., U.S.A.

### Results

Webs tilted into a vertical position retained flies for longer than those held in a horizontal position (Fig. 1). When the numbers of flies which escaped after 1-5, 5-15, and > 15 s were compared, there were significant differences between vertical and horizontal webs of mature females, and similar but insignificant differences for subadult females ( $p < 0.001$  and  $0.1 > p > 0.05$

respectively for the combined totals of first and second trials using Chi-Squared test).

Webs of mature females also retained flies for longer than those of subadults (Fig. 1). When the times were grouped as above, the differences between matures and subadults were significant for both vertical and

horizontal webs ( $p < 0.001$  for both with Chi-Squared test).

Flies sometimes freed themselves and fell free, only to be intercepted by other web lines. Double entrapments were more common in vertical webs, occurring 138 times for 497 flies trapped, compared with 8 of 532

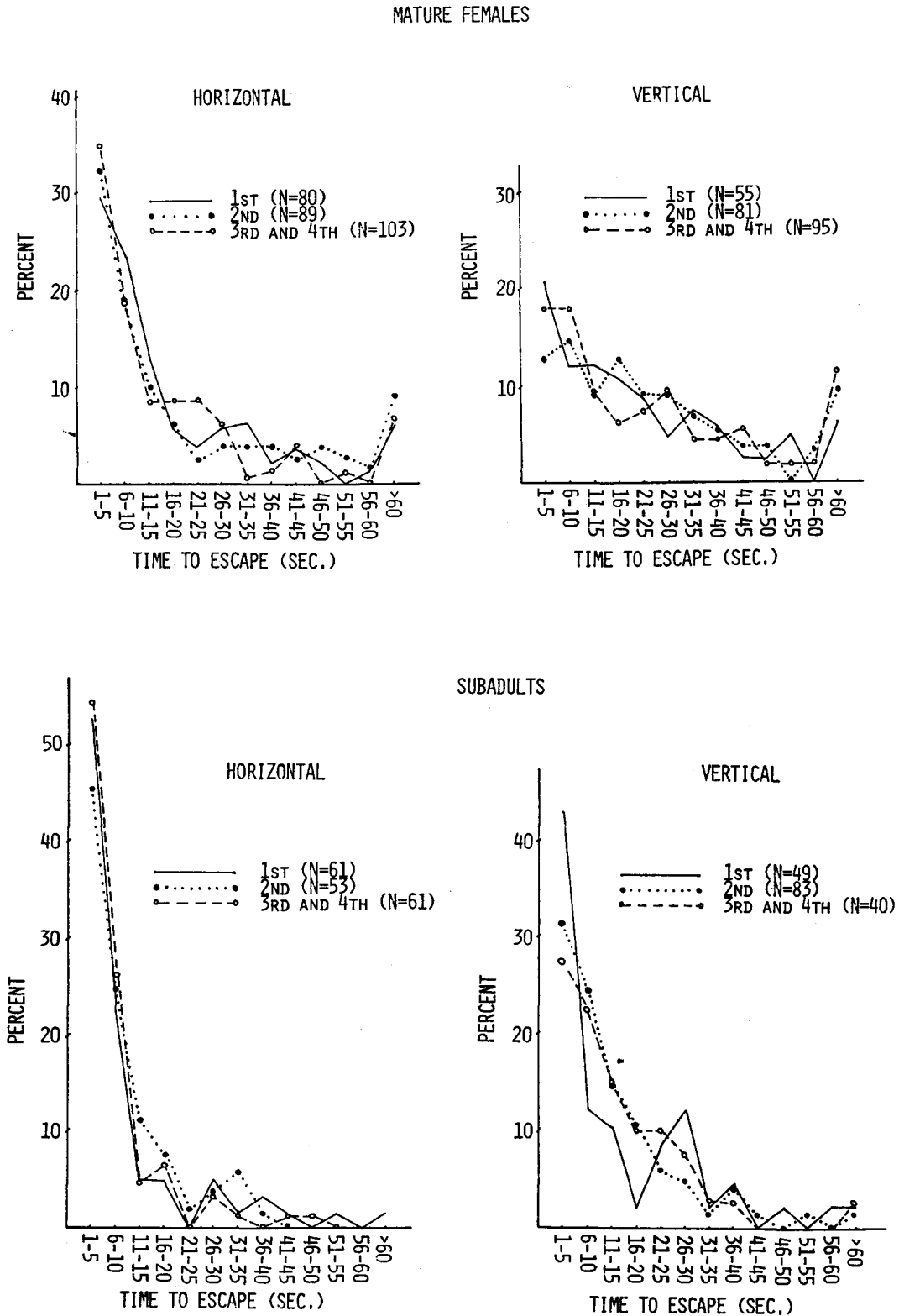


Fig. 1: Distribution of escape times for sepsid flies in *Metazygia* sp. web samples taken from mature females (top) held horizontally and vertically, and from subadults (bottom) also held horizontally and vertically (1st, 2nd, etc. refer to whether other prey had already been frightened into the web). Flies were retained longer in vertical than in horizontal webs, and longer in those of larger vs. smaller spiders.

flies in horizontal webs ( $p < 0.001$  with Chi-Squared test). In other cases flies in vertical webs became entangled in additional sticky lines as they sagged downwards after struggling only partially free.

Distributions of retention times were not influenced by whether or not the web had already been used (compare data for 1st, 2nd, and 3rd and 4th in Fig. 1). Thus the irregularities in the arrays of web lines produced by the struggles of previous flies did not affect distributions of retention times significantly.

Spiders took more than 4 s to reach 12 of 27 prey drawn to their webs (Fig. 2) (median delay was 4 s, average  $5.5 \pm 4.0$  s).

## Discussion

*Metazygia* sp. took more than 5 s to contact prey in its web in about 37% of the observed impacts, and  $> 10$  s in about 15%. The greatest variations in the retention time experiments were in the 0-5 s category, so the effects of spider size and web orientation measured in this study are probably functionally significant for this species of spider. The attack times of *Metazygia* sp. are neither unusually fast nor unusually slow compared with those of other araneids (see Introduction; also *Leucauge mariana* (Keyserling) averaged  $2.5 \pm 3.0$  s [median = 1 s,  $n = 23$ ], and *Gasteracantha cancriformis* (L.) averaged  $15.9 \pm 23$  s [median = 8 s,  $n = 24$ ] in responding to houseflies — W. Eberhard, unpublished).

Retention times documented here appear to be shorter than those for the webs of *Micrathena gracilis* (Walck.) (Uetz & Hartsock, 1987), though differences in data collection and analysis preclude direct comparisons. It is probable that different species of spider make orbs which retain prey for longer or shorter periods; if *M. gracilis* resembles its relative *G. cancriformis*, its long retention times may be associated with relatively slow attacks on prey.

Like other orb weavers, *Metazygia* sp. often jerks radii in response to prey vibrations. This may further entangle prey and increase retention times (e.g. Lubin, 1986), though I know of no data on this point for this or other species. Retention times given here may thus underestimate times in nature. It should also be noted that the flies in this study were generally exposed to vibrations produced by other prey struggling in the same web, an uncommon stimulus in nature. It is not known whether this factor affects struggling behaviour. Neither of these factors is likely to have affected the comparisons between horizontal and vertical, or between larger and smaller spiders.

Although the use of samples of orbs on wire frames rather than whole webs would be inappropriate for a study of how well webs intercept and stop prey (visibilities and overall mechanical and geometric characteristics of web samples undoubtedly differed from those of intact orbs), it is, however, appropriate for studying retention. The struggles of the flies broke only sticky spiral lines in the immediate vicinity of the fly, and almost never the radii, so the retention capacities for these prey were probably determined largely or

exclusively by the properties of lines very near the point of impact.

The large variance in retention times obtained with only a single prey species illustrates the difficulty of obtaining precise measures of selectively important properties of orbs, and thus the difficulty in establishing the functional significance of different design features. When one considers the wide spectrum of prey captured by orb weavers (e.g. Robinson & Robinson, 1970, 1973; Nyffeler & Benz, 1978, 1979; Olive, 1980; Castillo & Eberhard, 1983) and that different species are retained for different lengths of time (Nentwig, 1982), it becomes clear that it will be difficult to obtain overall measures of the retention capacities of webs under natural conditions.

Chacòn & Eberhard (1980) showed that artificial traps placed horizontally captured only about 32% of the total number of insects captured by identical vertical traps at the same site. Since most insects encountering these traps were probably retained (the traps had both abundant adhesive and lines which the insects could not break), the difference implies that horizontal webs probably intercept substantially fewer prey. This study showed that horizontal orbs are also poorer at retaining prey once they are intercepted, and thus compounds the mystery of why many orb weavers nevertheless make more or less horizontal orbs (genera include the araneids *Enacrosoma*, *Dolichognatha*, *Azilia*, *Leucauge*, *Tetragnatha* and *Mangora*, as well as several genera in the families Anapidae, Symphytonathidae and Uloboridae — Wiehle, 1927; Eberhard, 1987, unpub.). Perhaps speed of attack is at least part of the explanation: the shortest attack time yet determined is that of *Leucauge mariana*, which spins more or less horizontal orbs (different studies were admittedly done under different conditions and involved spiders running different distances) (see also Masters & Moffat, 1983 on attacks directed downwards vs. upwards on vertical orbs). More data are needed to clarify this point.

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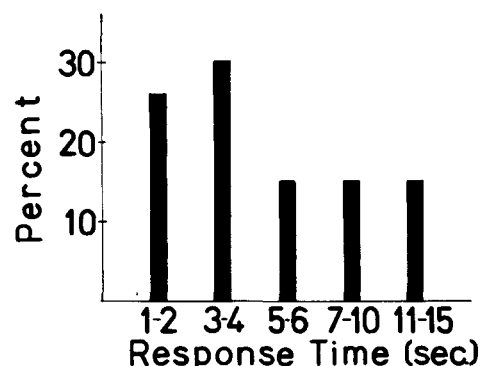


Fig. 2: Distribution of response times of *Metazygia* sp. spiders in the early evening to prey drawn to their webs by a light held nearby.

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