

Use of Artificial Webs to Determine Prey Available to Orb Weaving Spiders



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dual purpose in field studies. They can be readily recovered from the field after a prolonged period, and their populations can be controlled by providing or withholding the required nutrient. It should be noted that not all auxotrophic mutations can be expected to perform in this way; a *C. heterostrophus* mutant requiring inositol (*ins2*) survived marginally but did not spread in the field when tested in experiments parallel to those described for *his1* (Tables 1 and 2).

Although genetic markers such as drug resistance (Brockwell et al. 1978, Kloepper et al. 1980), morphological mutations (Hausermann et al. 1971, Foster and Helman 1979), enzyme polymorphisms (Hanken and Sherman 1981), and auxotrophs (Van Alfen et al. 1975) have been used previously to track the presence of experimental organisms in the field, to our knowledge the work reported here represents the first use of a conditional mutant whose population dynamics can be manipulated under field conditions while simultaneously bearing genetic markers to detect gene flow or contamination of field plots by nonexperimental organisms. Research involving field studies of populations may be facilitated by use of genetically marked organisms under conditions that allow experimental control of population growth.

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USE OF ARTIFICIAL WEBS TO DETERMINE PREY AVAILABLE TO ORB WEAVING SPIDERS¹

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The success of web-weaving spiders in predation depends largely on the placement and design of their

webs. It would seem that simple traps similar to webs would give good estimates of both numbers and kinds of prey available to web weavers. However classical trapping techniques for insects (windowpane traps, sticky traps, sweeping) capture different proportions of prey species than those captured by spiders (Robinson and Robinson 1973). Although these unsatisfactory techniques have not been completely abandoned (e.g., Olive 1980), traps specially designed to function like spider webs have been used in recent studies (Eberhard 1977, Login and Pickover 1977, Chacón and Eberhard 1980, Uetz and Biere 1980, Biere and Uetz

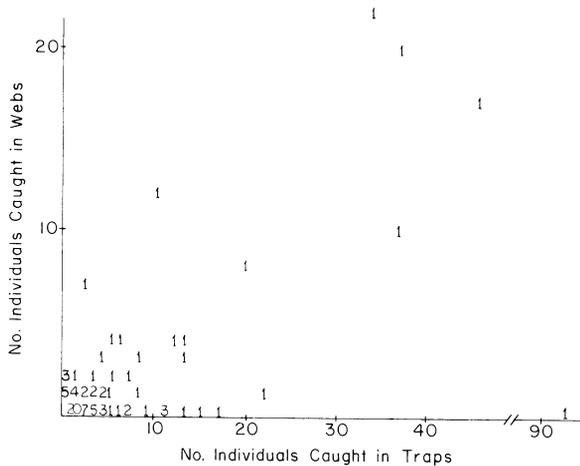


FIG. 1. Relationship between numbers of individuals of each species of insect which were captured by traps and by *Metazygia gregalis* spiders. The small numbers within the data field indicate the numbers of species at that point.

1981, M. Greenstone and A. L. Rypstra, *personal communications*). Uetz and Biere (1980) found that artificial webs captured relatively more small prey than did adult female *Micrathena gracilis*. Their calibration study was incomplete, however, because prey were identified only to order, and neither the height of the spider webs above the ground nor the angle between the web and vertical were equal in all cases to those of the traps. Chacón and Eberhard (1980) showed that web height and angle can greatly affect trap captures. In addition, Uetz and Biere (1980) did not check all spider webs at regular intervals, did not discount prey captured in webs before traps were in position, and conducted their study in a forest where microhabitat differences may have existed between web sites and trap sites.

The present study controlled for all of the factors just mentioned. We found that even under optimum conditions traps gave only very approximate estimates of the prey captured by spiders.

We used 10 traps with parallel nylon lines strung on aluminum frames, made according to the size and design of Eberhard (1977) and coated with Tack Trap (Animal Repellents, Griffin, Georgia) as described by Chacón and Eberhard (1980). We hung traps at ≈ 8 -m intervals along a 72-m portion of a 3-m vertical barbed wire fence in the middle of a large, open field of grass and weeds (see photograph in Chacón and Eberhard 1980) on the Melendez campus of the Universidad del Valle in Cali, Colombia, on the evenings of 3, 9, 11, 16, 18, 20, and 22 December 1980. A large population of the orb-weaving araneid *Metazygia gregalis*, a species which spins in the early evening, was present

in the fence. Each evening at ≈ 1900 the traps were hung in the fence 1.5 m above the ground (top of trap), and all prey captured previously by spiders in that section of the fence were removed. We used fine forceps and scissors to separate the prey from the spider and its web with a minimum of damage to the web. Only spiders with webs between 0.7 and 1.5 m above the ground were observed. All spiders were in the first four instars. (Larger individuals built higher in the fence.) The size of each spider was determined in the field by comparison with standard spiders of each of the five instars in vials. Every 10 min the spiders' webs were revisited and any prey the spiders had caught and were feeding on were removed and placed in alcohol. Prey taken from different spider instars were kept separate. Most sessions were terminated between 2100 and 2200, at which time the traps were removed and placed in a tightly closed styrofoam box. The prey were removed from the traps the next day, washed in gasoline, and stored in alcohol, and traps were washed and recoated as described by Chacón and Eberhard (1980).

All prey were measured to the nearest millimetre (front of head to tip of abdomen) and classified to species using a synoptic collection of the insects at the study site. This collection is stored in the Departamento de Biología of the Universidad del Valle. On 22 December additional insects were collected by sweeping near the fence (20 samples of 20 sweeps per sample) during the period the traps were up. Unless otherwise noted, statistical tests were two-tailed χ^2 .

A total of 238 individuals of 46 species in 25 families and 9 orders were collected from spider webs, and 654 individuals in 88 species in 43 families and 10 orders were caught in the traps (a list of the families and the numbers of species in each is available⁵). There was a significant correlation between trap and spider captures in the total numbers of each prey species, but only 23% of the mean squared variation in spider captures was explained by trap captures (Fig. 1).

We observed two probable causes of this low correlation. We never found the most common species in the traps (a cicadellid homopteran; 93 captured) being eaten by a spider. This insect, despite its lack of warning coloration, was apparently distasteful. One spider was observed rushing to attack an individual that had landed in its web, but after touching the insect the spider returned to the hub without completing the attack, and the insect escaped. Thus some of the species

⁵ See ESA Supplementary Publication Service Document No. 8412 for 2 pages of supplementary material. For a copy of this document, contact the second author or order from The Ecological Society of America, Cornell University, Ithaca, New York 14853 USA.

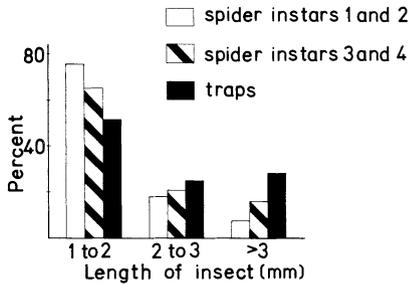


FIG. 2. Distributions of sizes of prey captured by traps, and by larger and smaller *M. gregalis* spiders.

in the traps were probably intercepted and retained by spiders' webs but subsequently not eaten by the spiders.

Second, spiders of different sizes captured different-sized insects. Larger spiders (instars 3 and 4) captured both larger prey than smaller spiders (instars 1 and 2) $P < .01$, comparing prey in the size classes in Fig. 2), and also a greater variety of prey sizes (Fig. 2). (The data from 16 and 18 December were excluded in these analyses, since the relative numbers of small and large spiders were different from the combined totals of the other nights, $P < .05$ and $P < .01$, respectively; none of the other nights were significantly different.) The prey captured in traps were significantly larger than prey captured by small spiders ($P < .05$) but not significantly different from prey captured by large spiders (comparisons of prey and spider size classes in Fig. 2). More data (82 additional prey) which included the prey captured by spiders immediately prior to the observation periods show the same statistically significant tendencies (Fig. 3).

Even when these sources of discrepancy were reduced by considering only the prey caught by larger spiders during the observation periods, and excluding the apparently distasteful cicadellids, the unexplained mean square variation was still 52%.

Although traps failed to mimic webs precisely, they were clearly superior to sweeping. A total of 500 individuals of 75 species were captured by sweeping. Only one of these species (1.3%) was also found in spider webs. This contrasts with 88 species captured in traps, of which 31 (34.8%) were also found in webs.

Habitat quality in terms of expected prey yield should be measured only in terms of those prey which the spiders can be expected to capture and feed upon. There are clearly many insect species present in the vicinity of spiders' webs which are not caught and fed upon by the spiders. Some prey probably avoid or fly through webs, others escape before the spider attacks, and others cause the spider to fail to complete attacks.

The traps in this study were unusually well placed

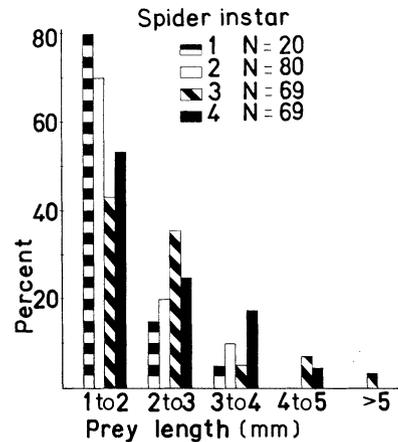


FIG. 3. Distributions of sizes of prey captured by different instars of *M. gregalis* spiders, including prey collected at the start of each observation period (N = all prey captured by spider instar).

to intercept the same prey as the spiders' webs. Webs and traps were in an extremely uniform environment, were at the same height above the ground, were present at the same time of day, were up only at night when both traps and webs are nearly invisible (both trap and web visibility may influence catches; Rypstra, *in press*), and were oriented exactly the same way with respect to both gravity and the wind (angle with wind direction affects trap captures; E. Alvarado, *personal communication*). Despite these extraordinarily favorable conditions, there were substantial differences between the insects captured by the spiders and by the traps. Failure to standardize any of the several difficult-to-control factors which were kept constant here can strongly affect the data obtained (Chacón and Eberhard 1980, E. Alvarado, *personal communication*). Thus it seems likely that other trapping programs, which have not been and will not normally be done under such favorable conditions as those of this study, will yield only imprecise estimates of habitat quality in terms of expected prey yield for orb-weaving spiders.

We believe that the best approach to determining habitat quality for web-weaving spiders is to take advantage of the spiders' own behavior (as has been done already by many authors, e.g., Turnbull 1960, Kajak 1965, Robinson and Robinson 1970, 1973, Nyffeler and Benz 1978, 1979, Lahmann and Eberhard 1980, Janetos 1982, D. Smith Trail, *personal communication*). Because spiders are sedentary on webs, one can locate a series of webs and then revisit them to observe what the spiders have captured. Using care not to flush prey into webs, correcting for the different handling times for different prey, and sampling on a schedule which

covers the entire active period of the web, such observations can yield data much better than those available for most other predators. Other less direct techniques which take advantage of the spiders' lack of mobility are also possible (e.g., Eberhard 1979).

Data from artificial traps is useful to evaluate natural selection on web design and attack behavior. Comparisons between what is caught in traps with different properties (height, slant, etc.) can suggest selective factors acting on web design and placement, and comparisons between trap and spider captures can indicate which prey are either escaping or not being attacked. In sum, traps can probably more accurately assess prey that is available in evolutionary than in ecological time.

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CONSTRUCTION AND OPERATION OF HEATED TAXIDERMIC MOUNTS USED TO MEASURE STANDARD OPERATIVE TEMPERATURE¹

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Previous papers have described the use of heated taxidermic mounts to make direct measurements of

standard operative temperature, T_{es} (Bakken et al. 1981, Buttemer 1981). The procedures used to construct and operate the mounts used in this studies were not entirely satisfactory, and were thus not detailed. This note describes improved methods for constructing multiple copies of a heated mount.

Standard operative temperature is a direct index of net sensible heat transfer, which provides a useful definition for the concept of "environmental temperature." The reader is referred to Gagge (1940), Gagge and Hardy (1967), Bakken (1976), and Bakken et al. (1981) for the theory behind T_{es} and its measurement with heated mounts. Applications of T_{es} in laboratory and field studies are described by Bakken (1980), Bak-