Factors affecting numbers and kinds of prey caught in artificial spider webs, with considerations of how orb webs trap prey

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Summary

Comparisons of catches by "control" and modified artificial spider webs showed that the following factors influence the functioning of the traps: (a) height above the ground (more insects lower down); (b) inclination of the trap (more insects in more nearly vertical traps); (c) quantity and quality of adhesive (more insects with more, fresher adhesive); and (d) density of threads (more and smaller insects in denser traps, but fewer insects/thread). It is possible that their greater visibility makes traps imperfect mimics of nocturnal orb webs at sites with relatively high nocturnal light levels.

Orb webs must both intercept and at least momentarily retain prey in order to function. At night, when webs are probably invisible to prey, interception is improved by wide spacing between sticky threads, while retention is improved by closer spacing. The designs of some nocturnal orbs can be interpreted as specialisations for prey which are difficult to retain, and those of others for prey which are easily retained. The process of prey retention should probably be divided into three subprocesses: stick to the prey; absorb its momentum; and hold it until the spider arrives. The relative importance of each of these subfunctions will be different for different kinds of prey, and the variety of orb web designs in nature may thus at least partly be due to adaptations to different arrays of prey.

Introduction

A trapping technique was recently described which was designed to mimic some characteristics of orb webs in certain situations (Eberhard, 1977). The traps, which consist of arrays of threads coated with adhesive, are thought to measure the numbers of insects likely to contact spider webs, but not the numbers actually captured (which probably vary according to the web's ability to retain them and the spider's ability to attack them quickly and effectively). The present paper is a supplement, in which insect capture data are used to clarify the effects of certain variables on the technique. The same data also have interesting implications regarding the effectiveness of different orb web designs. There is one other study known to us involving traps with sticky threads (Roth, 1963), but those traps were set out during the day, so only limited comparisons can be made.

Materials and Methods

Data were collected between July 1977 and January 1978 in a large, approximately 100 x 150m open field of grass and weeds on the Melendez campus of the Universidad del Valle in Cali, Colombia. The campus is situated in the midst of extensive sugar cane fields. The traps were placed in a barbed wire fence running through the field (Fig. 1)

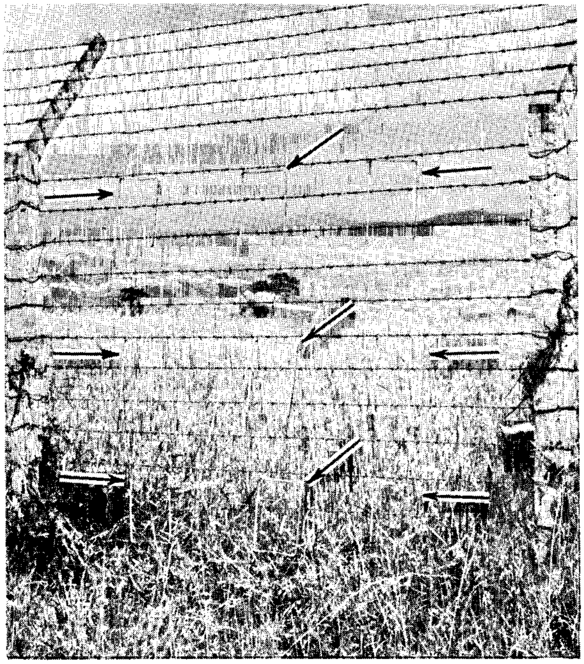

Fig. 1: Traps hung in fence in study field.

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on a total of 25 nights between 18.30 and 21.30. This time period was chosen because it yields the largest numbers of insects at night (Barreto & Eberhard, in prep.). Temperature and wind velocity were measured each night at 18.30, 19.00, and 21.30.

All the insects captured were identified to order, and most to family. The order Homoptera (principally Cicadellidae, Cercopidae and Cixiidae) was the most abundant, followed by Diptera (especially Nematocera) and Coleoptera (mostly Elateridae, Curculionidae, Bostrichidae, Chrysomelidae, Carabidae, Staphylinidae, Anthicidae and Scarabaeidae) (Fig. 2). Others, in order of decreasing abundance, were Lepidoptera (especially microlepidoptera), *Hemiptera (Reduviidae, Nabidae, Coriscidae and Corizidae)*, Hymenoptera (Formicidae, Ichneumonidae and Chalcidoidea) and Orthoptera (Acrididae). Specimens of the commonest species have been placed in the collection of the Departamento de Biología, Universidad del Valle.

The length of each insect was determined under a dissecting microscope according to size classes (0-0.99mm, 1.00-1.99mm, etc.). There was a relatively uniform distribution of insects in the various classes, with the exceptions of 2.00-2.99, which was more abundant, and > 8 which was much less common (Figs. 3 and 4). Some insects of the largest size class probably escaped after being caught in the

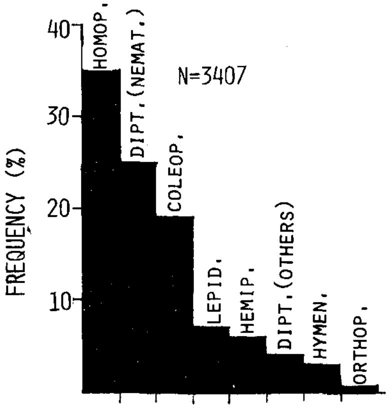

Fig. 2: Frequency of captures of insects of different orders.

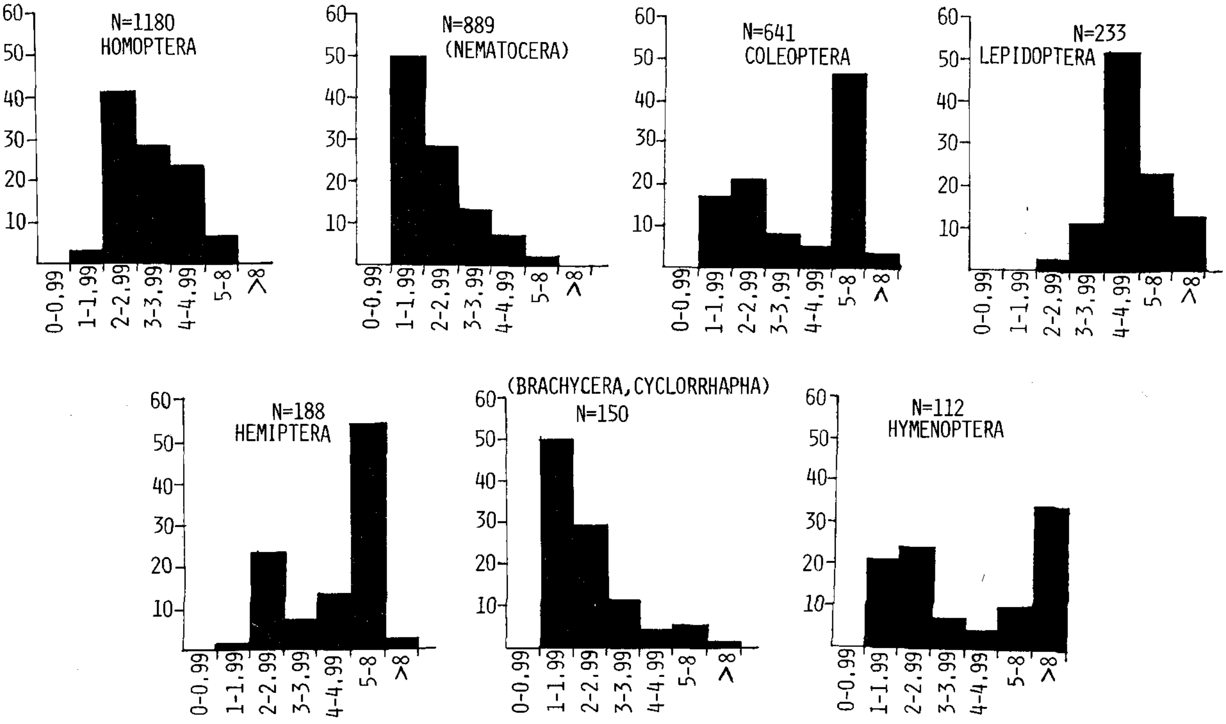

Fig. 3: Sizes of insects captured in traps, separated according to order (frequency (%) vs. length in mm).

traps (Eberhard, 1977), so the figures for this class are probably underestimates. Roth (1963) also found that larger insects were under-represented in catches from traps with adhesive lines.

In order to determine whether the samples obtained were sufficiently large, the coefficient of variation (standard deviation/mean) was calculated for each group of traps receiving a given treatment on a given night. The average of these coefficients for all experiments was 32%. The average catch per trap night was 16.3 insects for all traps, so the average coefficient of variation corresponds to ±5.2 around this mean. The formula given by Southwood (1968: p.19) to estimate the number of samples needed as indicated by the mean and the standard deviation gives approximately 36. In some cases we did not take this many samples, and in these instances we only accepted as significant two-tailed Chi^2 tests which gave $p < 0.01$.

"Control" traps, built and coated as described by Eberhard (1977) (metal frames 32 x 22cm with 40 threads 32cm long spaced 0.5cm apart and coated with "Tack Trap" were used in each experiment. They were treated in the following way:

(1) The adhesive was applied less than three hours before the trap was set out.

(2) Each set of threads was coated with a brisk movement of the plastic box along their length, as described by Eberhard (1977); the movement was completed in about one second, and left an average of 0.02g of adhesive on each thread (the speed of application strongly influenced the quantity of adhesive applied).

(3) The trap was hung so that its top edge was 0.71m above the ground.

(4) Each trap hung vertically (0° with vertical – Fig. 1).

Each night, catches in control traps were compared with those in experimental traps which were modified as described in the next section.

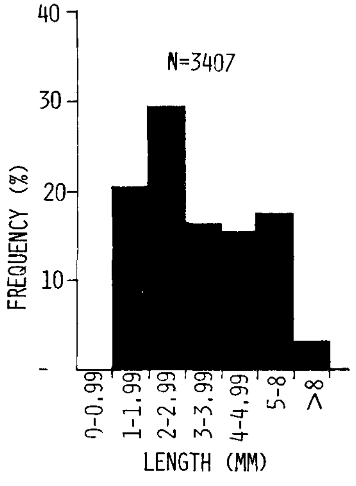

Fig. 4: Distribution of sizes of insects captured in traps.

Results

Effect of height of trap above ground

Control traps were compared with similar traps placed at two other heights, 1.30m and 1.90m (top edge) (Fig. 1). This experiment was performed on three nights, with three traps at each height, giving a total of 27 trap nights; a total of 547 insects was captured.

The two most common orders, Homoptera and Diptera, were captured in greater numbers in the lowest traps ($p < 0.01$) (Fig. 5), while there was no significant difference in the numbers of Lepidoptera, Coleoptera or Hemiptera caught at the three heights. Among the Diptera, smaller animals were most frequent in the lowest traps ($p < 0.01$), but there was no relationship between size and height in any other order.

Effect of the inclination of the trap

Traps identical to the controls were placed at two additional angles with respect to gravity, 90° (horizontal) and 45° (inclined); the traps at different angles were hung in alternating order along the fence. The experiment was performed on five nights, with three traps at each inclination, giving 45 trap nights; 428 insects were captured.

There was a clear tendency to capture more insects in the more vertical traps ($p < 0.01$ comparing vertical with the others). Taking the catch in vertical traps as standard, the horizontal traps caught only 32%, while the inclined traps caught 56%. All sizes and orders of insects followed more or less the same pattern.

Effect of the quantity of adhesive

In this experiment traps with double coatings of adhesive were compared with controls. Double coatings were applied by passing the plastic box twice along the length of the threads, giving each thread a coating of adhesive weighing 0.04g or slightly less. In some cases a little adhesive was added after the second pass with the box in order to obtain approximately double the quantity. The two types of trap were hung in alternating sequence along the fence on three nights with five traps for each treatment, giving 30 trap nights; 791 insects were captured.

There was a clear tendency for most orders to be caught in greater numbers in the traps with more adhesive ($p < 0.01$ for the totals), with the double-coated traps capturing 38% more than the controls. Catches for some orders were more affected than others (Table 1), but the differences were not significant when compared with the totals. There was no clear difference with respect to size (totals for all orders).

Effect of freshness of the adhesive

This experiment compared controls with similar traps in which the adhesive had been used once three nights previously, and the threads had not been washed and recoated as usual after the insects were removed. Again the two types of trap were hung in alternating order. On two nights five traps of each kind were put out, and on a third night three of each were used, giving a total of 26 trap nights; 516 insects were captured.

Group	% in doubly coated traps	% in control traps	N
Nematocera	65	35	113
Lepidoptera	63	37	71
Homoptera	59	41	380
Coleoptera	54	46	145
Others	59	41	84

Table 1: Effect of double coating of adhesive on numbers of insects captured.

Again the stickiness influenced the catch, with the traps with old adhesive catching 18% fewer insects ($p < 0.01$ for the totals).

Effect of the space between threads

"Dense" traps, with only 2.5mm between threads and 80 threads per trap, and "sparse" traps with 10mm between threads and only 20 threads per trap were compared with controls. The sparse traps were coated with control quantities of adhesive (0.02g/thread), but threads in dense traps had approximately only half of this quantity. The three types of trap were hung in alternating order on six nights with three traps of each kind, giving 54 trap nights; 838 insects were captured.

The orders Homoptera, Diptera and Coleoptera were all captured in greater numbers in the dense traps, but Lepidoptera did not show this pattern (Fig. 6), and Hemiptera showed the reverse ($p < 0.01$). It is difficult, however, to evaluate the Hemiptera data since half (15) of those captured in "sparse" traps

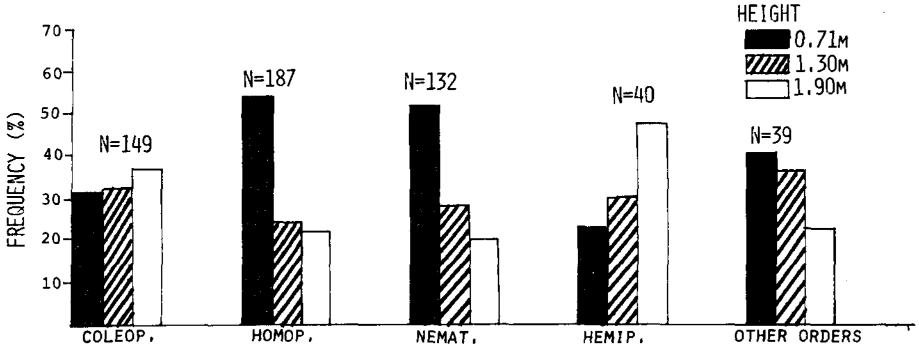

Fig. 5: Percentages of insects of different orders captured at different heights above the ground.

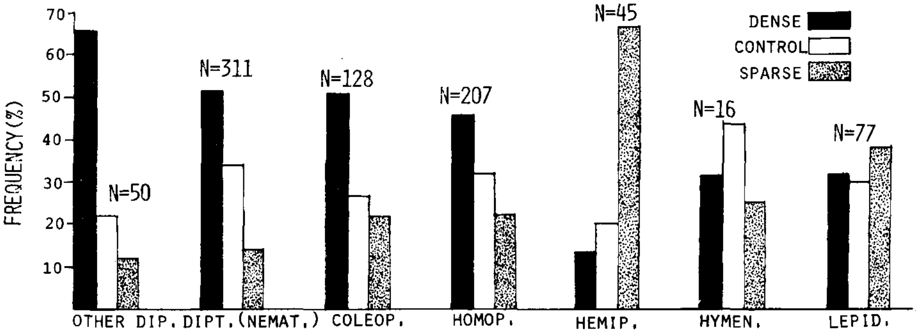

Fig. 6: Percentages of insects of different orders captured in dense, control and sparse traps.

were a single species of reduviid caught in one trap on one night, suggesting some sort of swarming activity. In addition, larger insects of all kinds tended to be captured relatively more often in sparse traps (Fig. 7), so it is possible that Lepidoptera and Hemiptera differed from the rest owing to their larger sizes (Fig. 3); this explanation seems less likely, however, because Coleoptera, which were also relatively large, were captured more often in dense traps.

Effect of mowing the adjacent field

The captures by control traps suffered a dramatic reduction which coincided with a mowing of the grass and weeds in the study field, and then a gradual increase (Fig. 8) which accompanied a recuperation by the vegetation. The dry season (which is not as severe in Cali as in many parts of the tropics) ended relatively abruptly in the last week of September, but this did not have a strong influence on the captures.

Effect of habitat

Control traps were placed in three other sites. In a pasture at 1500m elevation in the Andes near Cali, only 32 insects were taken by 9 traps on a drizzly evening. In a grove of guyaba trees (*Psidium guajava*) at about 1000m near Cali, only 35 insects were caught in 9 traps on a non-rainy night. And large numbers of insects (principally Trichoptera) were caught in three traps left all night (18.00 – 06.00) on two different nights just above the surface of a pool in a small stream near the guyaba trees. In this last experiment, there was a significant ($p < 0.01$) tendency for larger numbers of insects to be caught in the lower halves of the traps.

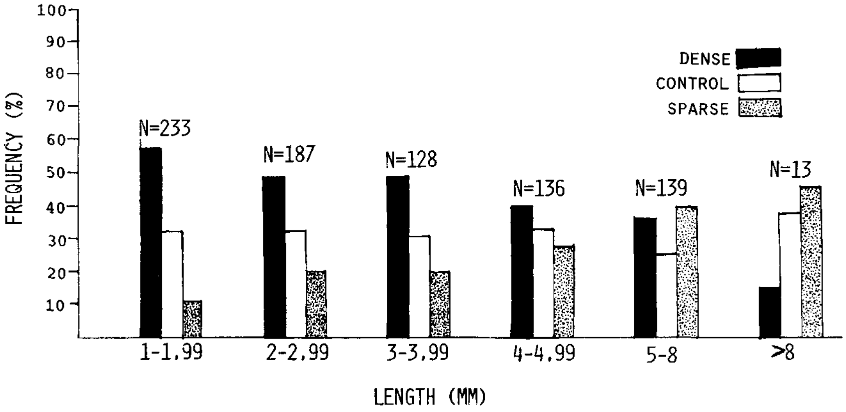

Fig. 7: Percentages of insects of different sizes captured in dense, control and sparse traps.

Discussion

The results can be analysed from two points of view. On one hand they show which factors are critical to the functioning of the trapping technique, and which must therefore be standardised to permit comparisons to be made. It is clear that the height of the trap over the substrate (land or water), the quantity and freshness of the adhesive, the inclination of the trap and the density of threads all influence both the numbers and the kinds of insects captured. An additional study (Barreto & Eberhard, in prep.) has shown that the hour of the night also influences both numbers and kinds of insects captured. It is also possible that the direction of the wind with respect to the trap may also influence captures. The technique is thus sensitive to a number of variables, and care must be taken to permit valid comparisons. The traps are sufficiently large to give reasonable sample sizes in some habitats, but in others the density of insects is apparently so low that either more or larger traps are necessary. Non-uniform distribution of insects, as illustrated by the apparent swarming of reduviids near one sparse trap, is another source of error in estimates of prey numbers.

The results can also be analysed in terms of the probable effects of different variables on the quantity of prey which orb weaving spiders can capture in their webs. For example, the fact that vertical traps were approximately three times as effective as horizontal ones for catching all sizes and groups of insects suggests that insects (at least those at the study site) tend to fly more horizontally than vertically, and that with respect to prey *interception*, vertical webs would be about three times more effective. Since prey *retention* is also greater in vertical than in horizontal webs because gravity pulls prey free of horizontal webs but pulls them into contact with other threads in vertical webs (Eberhard, 1972), the problem is raised of explaining why some groups of spiders (e.g. list in Eberhard, 1972; others include species of *Metabus, Spilasma, Dolichognatha, Azilia,* Anapidae and Theridiosomatidae) typically build more or less horizontal orbs. In some of these cases (e.g. some *Tetragnatha*) the advantage may lie in the possibility of getting more of the web closer to the substrate where prey are more abundant (Buskirk, 1975, in her study of *Metabus gravidus,* also found insects to be more abundant just above the surface of a stream); but many other species build horizontal orbs at elevated sites, and other factors such as perhaps wind damage (Eberhard, 1971) or prey falling from above must be involved.

One unsuspected result was the 38% increase in captures by traps with extra adhesive on the threads, and the reduction in catches in webs with 3 day old adhesive. It would seem that the *interception* efficiency of a trap should be very little affected by moderate changes in the quantity or quality of adhesive on the threads (the diameter of the doubly coated threads would be very slightly larger, but this increase is minimal compared with the space between threads). The increase in captures must therefore be due to a change in *retention* efficiency, but we have observed repeatedly that insects which touch a thread remain firmly stuck to threads coated with even less than "control" amounts of adhesive. The only explanation we can present for the increased captures with extra adhesive derives from observations of mosquitoes (*Aedes* sp., *Culex* sp.) which fly with a slow bobbing flight, holding their legs extended, and which avoid becoming entangled in spider webs by apparently touching them gently with their legs and immediately swerving sharply away, thus avoiding collisions. A large quantity of adhesive, or a less viscous adhesive could be more effective in trapping this kind of insect by sticking more firmly to the legs the moment they touch a thread. To a certain extent the results support this idea (Table 1). The group which showed the greatest tendency to be trapped more in traps with extra adhesive was Nematocera. Another group which was also particularly common in these traps was Lepidoptera, and this was also to

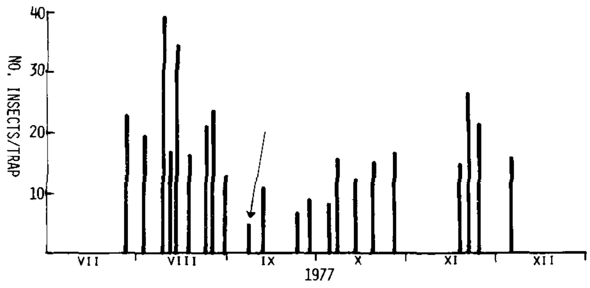

Fig. 8: Average catches in control traps (at least three control traps per night) at different dates. Arrow indicates the day the field was mowed.

be expected owing to adhesive considerations; their covering of loosely attached scales makes them difficult to capture with sticky thread (see Eisner *et al.*, 1964). These differences were not statistically significant, however, and this interpretation is thus still uncertain.

Other results can be related to captures in real spider webs only after taking into account the different functions which an orb web performs in prey capture. First, the path of the prey must cross a thread or threads (interception), and then the prey must be retained long enough for the spider to capture it (retention) (these correspond to the "trapping" and "restraining" functions of Lubin, 1973). The retention function can in turn be divided into subfunctions (see below). With the exception of the instances in which the quantity and quality of adhesive was varied, the experiments performed with artificial traps measured variations only in the *interception* function, since the traps were made of threads which were unbreakable for the prey, and were covered with abundant adhesive. As noted previously (Eberhard, 1977), almost all insects weighing less than about 40mg which fly into a trap and become stuck to a thread are held there indefinitely, so that *retention* in artificial webs is near 100%. This included the experiments comparing fresh and used adhesive, as we verified that insects weighing less than 40mg flying from an insect net into a trap with old adhesive were immediately stuck so tightly that they could hardly struggle. This contrasts with spider webs, which usually retain most insects for only a short time (e.g. Barrows, 1915; Robinson *et al.*, 1969; Suter, 1978).

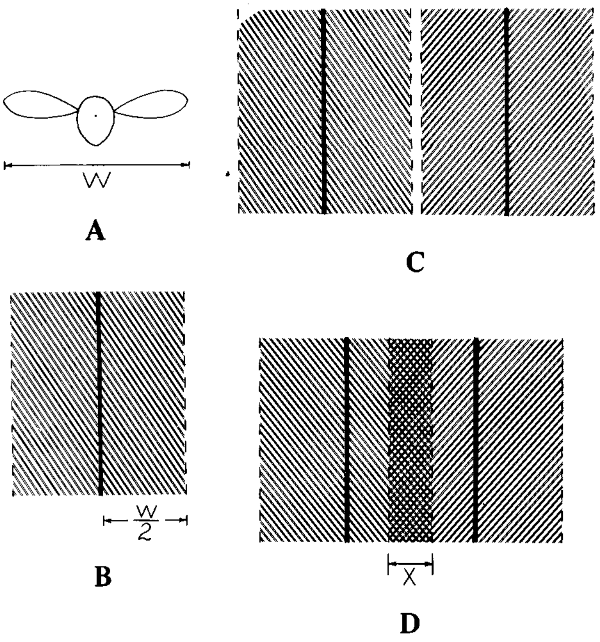

Fig. 9: Illustration of why lines spaced farther apart than the widest dimension of the prey are more efficient interceptors. Consider a prey (A) with a maximum width of w. If its centre (dot in A) passes within w/2 of the line in B, some part of its body will hit the line; one can thus draw (shaded) an "interception area" extending w/2 on either side of the line. For a line of unit length, the interception area would be w. When two lines are placed side by side but farther apart than distance w (C), the total interception area is 2w. But if the lines are placed closer together, as in D, their interception areas will overlap (x), and the total area covered will be reduced (2w – x). In other words, the interception area of the threads is wasted in the zone of overlap where a prey will encounter both threads. The major implication is that closely spaced sticky lines in spider webs probably function to increase *retention* of relatively large, difficult prey rather than *interception* of small ones (see text).

Comparing the catches in traps with different thread densities illustrates the importance of this distinction between interception and retention. Assuming that prey move randomly with respect to a trap, maximum interception would theoretically be obtained by spacing the threads farther apart than the widest dimension of the largest prey. This is because wider spacing would increase the area covered by the web, and avoid "wasting" threads by having more than one contact a given prey (Fig. 9). Comparisons of catches in control and sparse traps bear this out, since the sparse traps caught 73% of the total captured by the controls with only 50% of the thread and adhesive ($p < 0.01$ assuming half control captures; quantitative comparisons with the dense traps are not possible since they had only half as much adhesive/thread). This same tendency to capture more insects/thread in sparse traps was found by Roth (1963) using traps with two densities of sticky threads. These results do not, however, show that the most efficient web design for spiders is necessarily a very open mesh, because their webs do not retain all prey as well as the traps, and must therefore have design features (e.g. higher thread densities) to improve their retention capacity.

There was also a clear tendency for traps with more closely spaced threads to capture relatively more small prey (Fig. 7). (The results probably even underestimate this tendency, since the threads in the dense traps had lighter coatings of adhesive). This was also to be expected from considerations of interception efficiency. Very sparse traps would have maximum efficiency for all sizes of insect; as the distance between threads is reduced, the efficiency would be lowered first for insects of large sizes, and then progressively for those of smaller and smaller sizes. In other words, a trap with moderately spaced threads would "waste" threads intercepting large prey (two or more threads make contact), but would still be maximally efficient for intercepting small prey.

Some nocturnal spiders, however, spin webs with the spaces between the sticky spirals substantially smaller than the sizes of the smallest prey they are likely to capture (e.g. *Acacesia hamata* (Eberhard, 1976), *Scoloderus tuberculifer* (Eberhard, 1975) and *S. cordatus* (Stowe, 1978); see Stowe for food items of *S. cordatus*). These webs probably represent adaptations to improve *retention* of "difficult" prey (large, fast moving, covered with scales) rather than *interception.* Conversely, the webs of other nocturnal spinners, which have very widely spaced sticky threads, like those of some *Tetragnatha* species and *Hypophthalma* sp. (Eberhard, unpublished obs.) are probably designed to maximise the *interception* of relatively small and/or weak prey which are easily retained. This kind of interpretation can probably also be made with diurnal webs, but it is complicated by the possibility that some prey can see the threads. If they see them only at close range and swerve to avoid individual strands (see below), closer spacing between threads could improve interception as well as retention. If they are able to see the web from farther away and then avoid it entirely, closer spacing could lower interception by making the web as a whole more visible.

These ideas run counter to the intuitive notion that webs with more closely spaced lines are designed to catch smaller prey. More seriously, they appear not to agree with the only published data available on this point – those which Uetz *et al.* (1978) collected in their study of two species of *Argiope* and one each of *Leucauge, Mangora* and *Micrathena,* in which they found a positive relationship between prey size and distance between spiral turns for the five species. The sizes of these spiders vary widely, however (*A. aurantia* is about ten times heavier than *Mangora placida*). Since larger species generally spin stronger threads which are capable of stopping and holding larger prey, it seems possible that this factor was responsible for a major part of the differences in prey size; since the larger species in this study (*Argiope* spp.) also spun webs with wider meshes, the size factor could lead to an apparent correlation of prey size with mesh width. In fact the data of Uetz *et al.* can be tentatively interpreted to support the idea proposed here. *M. placida* spins a more tightly meshed web than *Leucauge venusta,* and despite the fact that it is substantially smaller (comparative weights of approximately 15mg and 30mg), it catches slightly larger prey. *Micrathena gracilis* is subequal in size to *L. venusta;* it spins a more tightly meshed web, and catches larger prey. Thus, at the very least the available data do not contradict the hypothesis that, given more or less equal spider sizes, smaller mesh widths represent adaptations for larger prey. More studies of prey found in spider webs are obviously of great interest.

The tendency for denser traps to capture relatively more small insects was even stronger than expected. Assuming conservatively, for instance, that interception efficiency for insects 1.00-1.99mm long was still maximum in dense traps (and ignoring the reduction in captures due to less adhesive), one would expect dense traps to capture four times more insects of this size than sparse traps, since they had four times more thread. Actually they caught more than six times as many insects in this size class (129 vs. 20). This difference from expected values is significant ($0.05 > p > 0.02$), and since the observed difference was actually a distinct underestimate owing to the smaller amount of adhesive/thread in dense traps (doubling the amount increased the catches by 38% in the experiment we performed), it seems probable that the difference is real. The most likely explanation is that the assumption that the insects flew randomly with respect to the traps was not quite correct. Smaller insects (mostly Nematocera in this study) could escape being captured in sparse webs by sensing threads they were approaching and changing their trajectories slightly to avoid collisions, but such evasive behaviour would only result in their being intercepted by adjacent threads when the encounter was with a dense trap. The study site was an open field which was always at least faintly lit due to distant street lights and moonlight, and it does not seem improbable that some prey could sense traps at least at close range and try to avoid them. Whether they could also sense spider webs with their much thinner threads with diameters of only a few microns (e.g. Witt *et al.*, 1968) (trap threads were nearly 1mm in diameter) is not clear; it seems unlikely to us that spider threads are seen at night, even though it is probable, from observations of avoidance behaviour (e.g. Turnbull, 1960; data of Robinson & Robinson, 1973 for Lepidoptera; Buskirk, 1975) that many insects can see them in the daytime. There thus may well be a difference between the traps and spider webs in this respect, and inasmuch as it exists, the traps fail as mimics of spider webs, at least in illuminated sites.

The data and arguments presented here suggest that in addition to separating interception and retention of prey as web functions, the retention function should be divided into at least three subfunctions: (a) adhere to the prey; (b) absorb the momentum of the movement which brought the prey into the web (i.e. stop it); and (c) hold it in the web until the spider arrives to attack it. Different characteristics of the threads and their arrangements could affect these functions in different ways. For example, greater quantity and viscosity of adhesive would improve (a) and (c), but probably, since they represent greater material investment, they would decrease the total area covered by the web and thus reduce interception; greater elasticity of both sticky and non-sticky threads would improve (b) and (c); and increased density of threads (smaller mesh size) would improve all three, but decrease the area covered by the web. In addition, the rapidity with which a spider arrives at newly trapped prey and the effectiveness of its attack behaviour would affect the relative importance of (c) (see Robinson *et al.*, 1969; Lubin, 1973).

Different prey must make different demands on a web. For example, smaller and slower prey would be easier to stop, and function (b) would be less important, while weaker prey (smaller or with longer appendages) would escape less and make function (c) less critical. One can thus imagine that the diversity of orb web designs is at least partly a result of adjustments that spiders have made to different arrays of potential prey. When one adds to this already complicated picture energetic considerations associated with material invested in the web and the cost of building behaviour, simplicity of construction behaviour (the relative difficulty of evolving a given set of behaviour patterns), structural stability of the web, and the ease of prey detection and localization (see Witt, 1965; Eberhard, 1969, 1972; Peakall & Witt, 1976; Denny 1976; Suter, 1978), the complexity of the selective pressures acting on an orb weaver with regard to its web becomes nearly overwhelming.

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