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SHORT COMMUNICATION

The rare large prey hypothesis for orb web evolution: a critique

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Abstract. Several recent studies emphasize, correctly, that the biomass of prey captured by an orb web is likely more important than the number of prey in driving the evolution of web designs. Using equations that estimate prey mass from the lengths of captured prey, one study concluded that rare, long-bodied prey contribute the large majority of energy obtained by orb weavers in general, and thus that the designs of orb webs should generally reflect selection favoring the capture of larger insects, especially the ability to absorb high-energy impacts. I show here that the weights of long prey have sometimes been seriously overestimated by these equations. In addition, the longer prey captured by spiders probably represent highly biased samples, in terms of both low weight/body length and low momentum/body weight, of the longer prey available in the environment, leading to overestimates of the kinetic energy that the orb needed to absorb to stop them. Deductions concerning how selection acts on orb designs that have been based on the prey captured are also flawed, because additional data on prey availabilities and prey escapes are needed to evaluate the possible gains and losses from different orb designs. Still another complication is that data on prey abundances in natural rather than altered environments are needed to understand past selection pressures that produced present-day web forms. I conclude that a dominant importance for rare large prey in orb web evolution has not been conclusively demonstrated to be a general rule for orb weavers. A more inclusive approach regarding orb functions is prudent, especially because many traits that improve some functions have opposite effects on others.

Keywords: Orb web evolution, rare large prey hypothesis

Orb webs perform multiple functions. These include intercepting prey, stopping them without breaking, retaining them until the spider can attack, transmitting prey vibrations to the spider, facilitating the spider's movements across the web, and others (Witt 1965; Blackledge et al. 2011). The traits that will improve some functions of an orb are likely to make it less able to perform others (Table 1), complicating understanding of orb evolution. In addition, some functions are very complex. For instance, retention is affected by the positioning of the glue droplets on the axial fiber, the mechanical properties of the axial fiber, the arrangements of the sticky lines, the surface of the prey, the prey's impact velocity (higher velocities make the line stickier), and the humidity of the environment (Blackledge et al. 2011). The optimum balance of web traits is likely to vary for different prey, for different body conditions of the spider, and in different environments (Table 1; Blackledge 2011). It has thus been difficult to determine the net advantage or disadvantage of particular orb traits. Recent emphasis on the possibility that rare, large prey dominate the nutritional payoffs to orb weavers (Venner & Casas 2005; Blackledge 2011) promises to simplify this problem by focusing on the abilities of orbs to promote the capture of large prey, thus justifying special emphasis on the stopping function (Sensenig et al. 2010). In this note I argue, however, that such a focus is not well justified by currently available data.

Prey weight: important but difficult to determine.—A spider's basic payoff from an orb is nutritional, and larger prey organisms offer greater nutritional reward than smaller prey organisms. Small prey, however, are generally more abundant than large prey, but of course they weigh less and have less digestible material per gram, due to their having relatively greater surface areas and hence a greater proportion of chitin. Thus the balance of benefits from having an orb designed to capture larger or smaller prey is not immediately obvious. Under some conditions, the relative frequencies of prey and the sizes of payoffs from prey of different sizes could result in the payoffs from rare, very large prey items to be so much greater than those from more common smaller prey that the smaller prey are nutritionally irrelevant for reproduction. The "rare large prey" hypothesis posits that this condition generally obtains for orb-weaving spiders. Other possible mixes of prey, such as higher numbers of medium-sized prey, or especially rare large prey, could result in a reduced relative importance for large prey (Nentwig 1985). The rare large prey hypothesis is important for understanding the evolution of spider webs, because it implies that natural selection consistently favors the designs of orbs and the physical properties of their lines that promote capture of especially large prey (see Sensenig et al. 2010; Blackledge 2011; Blackledge et al. 2011).

The rare large prey hypothesis greatly simplifies analyses of the possible evolution of orb web designs, because it allows one to navigate the complex array of tradeoffs between traits that can affect the many different possible functions of orbs (Table 1), and to focus on the ability of an orb to absorb high kinetic energy impacts without breaking. This opportunity was exploited recently in the important study by Sensenig et al. (2010) of 23 species in four families, where an orb's "performance" was defined as its ability to absorb high-energy impacts.

The validity of the rare large prey hypothesis depends on the masses of small and medium-sized prey being small enough, and/or their capture being rare enough that they make only relatively small contributions to the spider's dietary intake compared with the contributions of the rarer, large prey. Do these conditions occur in nature? In the most complete study to date, Venner & Casas (2005) found that large prey were indeed captured only rarely by spiders in the *Zygiella x-notata* (Clerck, 1757) population that they studied. They measured the lengths of all prey found in webs, and estimated their probable dry weights using a standard equation that converts insect length to dry weight (Schoener 1980). They made the assumption that a prey's dry weight is a good indicator of its contribution to the spider's nutritional intake. Although a previous control study showed that the dry weight equation of Schoener yielded only approximate indications of the amount of ingestible food for spiders (Tso & Severinghaus 1998), they increased the biological realism of their analysis by determining the maximum amount a spider could consume in a day (9.4 mg of dry weight) and held gains

Table 1.—This list of possible trade-offs in the advantages of alternative orb web designs illustrates the complex tangle of inter-relationships that probably exist between the advantages and disadvantages of different orb web designs. The supposition is made that the spider has only a finite amount of material resources that can be dedicated to alternative designs. The advantages and disadvantages marked with "*" are likely to be especially pronounced for relatively large prey. The list of trade-offs is undoubtedly incomplete.

Advantages	Disadvantages
Larger sticky spiral spacing and thus greater capture area	
More prey intercepted;	*Reduced ability to stop and retain prey
Web less easily perceived by prey	Reduced ability to survive environmental stresses such as wind
	Greater energy expended in building behavior
Nearer to an approximately vertical substrate[a]	
More difficult for prey to perceive web	Fewer interceptions (prey arrive from only one side)
*Prey flying more slowly	
Horizontal (rather than vertical)	
Less energy expended in construction	Reduced prey interception[b];
Reduce loading by wind	*Prey encounter fewer lines as they struggle free and fall from the web
More rapid attack[c]	
Greater portion of web close to a prey-rich horizontal substrate (e.g., surface of water)[d];	
Less distortion of web by spider's weight while building (more precise positions of lines)	
More equitable distribution of tensions from spider's weight at the hub (greater mechanical stability)	
Thinner lines	
Longer lines, thus increased area covered (improved interception) and/or *greater density of lines (improved retention)	*Reduced ability to stop and retain prey
Web less visible for prey	Reduced ability to survive environmental stresses
	Reduced ability to support spider
Greater amount adhesive on sticky lines	
*Increased retention times	Reduced sticky line length (reduce numbers of prey intercepted
Increase prey attraction to "sparkly" droplets[e]	Web easier for prey to perceive
Tighter web	
Better able to survive in wind because it flaps less	*Less able to stop and retain prey[f]
Less distorted less by spider's weight during construction (more precise positions of lines)	Less web movement in light wind[g]
Improved transmission of vibrations[h]	
More radii	
*Better able to stop prey;	Increased silk cost, or fewer interceptions because web smaller;
Improved resistance to environmental stress such as wind	Orb more easily perceived visually by prey[i]
	Greater energy expended in building web (at least in radius construction)
Larger spaces between sticky spiral loops near the edge	
Increased interception near the edge	*Reduced ability to stop and retain prey near the edge

[a] More or less planar substrates could include, for instance, a tree trunk or a large leaf.

[b] This prediction makes the assumption that the flight paths of prey are mostly horizontal. This trend in flight paths may be surprisingly small, however. When identical artificial sticky traps consisting of lines strung in frames made of strips of aluminum about 2 cm wide (Eberhard 1977) were hung vertically and horizontally at the same height in a barbed-wire fence across a uniform, open field, the horizontal traps captured nearly a third of the total number of insects captured in vertical traps, despite the fact that no prey travelling perfectly horizontally would have been intercepted by any of the sticky lines in the horizontal traps (Chacón & Eberhard 1980). In sites that are less open, non-horizontal flight paths (and thus interceptions by horizontal orbs) may be even more common.

[c] This is expected at least comparing prey impacts to the side of and above the spider in vertical orbs.

[d] Documented by Buskirk (1975) near stream surfaces in Costa Rica for *Metabus gravidus*; a similar trend was clear in artificial traps (Eberhard 1977) that were hung just above a stream near Cali, Colombia (el. 1050 m) (W. Eberhard, unpublished).

[e] Only a single species of prey (a stingless bee) was tested for attraction of "sparkle" (Craig & Freeman 1991).

[f] The hypothesis that lower tension increases prey retention is supported by the independently evolved active reduction of web tension by the spider when prey hit the web in *Hyptiotes, Epeirotypus, Micrathena,* and *Wagneriana* (for a discussion of the physics involved, see Craig 2003).

[g] Support for the hypothesis that flapping movements of webs in the wind play an important role in increasing the web's abilities to intercept prey (the "encounter model" of Craig 1986) was based on measurements that probably overestimated web movements (the webs were loaded with cornstarch), so the possible importance of this factor is not certain.

[h] This is surely true in the extreme case comparing lines under tension with slack lines, which scarcely transmit the longitudinal vibrations that are used by spiders (see Landolfa & Barth 1996).

[i] Craig & Freeman (1991) state, probably correctly, that the sticky spiral is largely responsible for determining an orb's visibility; but, at least to the human eye, the glint of radii when they are illuminated at an appropriate angle is also visible.

constant for prey with estimated dry weights above this value. They also measured the weights of egg masses, of females when they laid egg masses, and of spiders when they died of starvation, the rate of basal metabolism and assimilation of prey. Using these data, Venner & Casas (2005) calculated that without the rare captures of large prey, the spiders could not reproduce.

There are several complications in this study. The largest prey were reported to be "mainly" crane flies; these flies have long thin bodies, making the equation used to estimate a prey's weight on the basis of its length give overestimates of their weights. The error can be quite large. I measured and weighed 11 individuals of a large species of tipulid in Baton Rouge, LA (mean length = 14.4±3.1mm), and found that the dry weight calculated from the equation that Venner & Casas used, $W = 0.024 + L^{2.35}$, was on average 65 times higher than their measured dry weight (mean 10.2±7.1 mg). The use by Venner & Casas of an upper limit on prey consumption (which was also obtained when tipulids were the prey – S. Venner pers. comm.) probably reduced this type of error somewhat (to an unknown extent) in their estimates. This likely imprecision calls into question (but does not disprove) the claim that payoffs from large rare prey were determinant for reproduction in *Z. x-notata* (Venner & Casas 2005). Recalculations that correct for different body designs of prey or direct measurements of prey weights are needed. In fact, Schoener (1980:106) warned specifically against just this kind of problem ("Workers who use length-weight equations to estimate overall biomass are cautioned not to lump insects having markedly different body proportions into the same regression").

Biases in captured prey and their flight speeds.—Setting aside the unusual body design of crane flies, there is a more general problem with using an equation that gives a best general estimate of weight in general samples of insects to study selection on orb webs on the basis of the prey that they capture. This is because in general the largest prey captured (tipulids and others) are likely to be a highly biased subset of the large prey in the habitat, favoring prey with low weights with respect to their lengths, and they are thus especially likely not to follow the Schoener relationship. The species whose impacts involved the least energy and were thus most likely to fall prey to the spider were most likely to be captured (the heavier, faster prey of that same length will tend to escape due to their higher impact energies). Of the especially long prey in the environment, only the lighter ones are likely to be detained; of the shorter prey, in contrast, both relatively light and relatively heavy individuals are likely to be detained. In other words, the Schoener equation is designed to describe length-weight relations in a random sample of insects. But the prey captured by orb weavers are not expected to be a random sample (the larger ones are expected to have relatively low weights in relation to their lengths). Thus the equation is expected to be inappropriate for this subsample. This bias is likely to be especially strong for the largest, most difficult prey for the orb weaver to capture.

Still another problem in extrapolating from the Venner & Casas study is that a prey's flight speed also affects its momentum (and thus the energy the orb must absorb to stop it) (see Blackledge & Zevenberg 2006 for examples of differences in the momentum of different prey species). For instance, crane flies are atypical among insects with respect to flight speeds: they generally fly slowly, and have long, weak legs (Borror et al. 1989), making them especially easy to stop with an orb. Their slow, tentative flight constrasts, for example, with that of many flying beetles or grasshoppers of similar body lengths. In addition, the *Z. x-notata* webs in the Venner & Casas study were nearly all built close to and parallel to the windows of a building (S. Venner pers. comm.), making it likely that many of the tipulids, as well as other large prey that the spiders in this study captured, were flying relatively slowly. From my own incidental observations of the flight of several species of crane flies, I would guess that many of the tipulids that were capturd by the *Z. x-notata* orbs had "bounced" repeatedly against the windows; and that, as occurred in trials in captivity with the similarly long-legged and tentative flier *Hyalobittacus* sp. (Blackledge & Zevenberg 2006), most escapes from orbs were due to failures to retain the tipulids (and perhaps other insects) after their momentum had been absorbed by the webs, not to failures to stop them. The important general point here is that the impact of a large prey with an orb does not necessarily involve large momentum. Therefore, finding occasional large prey captured by orb weavers does not necessarily indicate that their orbs successfully resisted high-energy impacts.

In sum, these considerations do not argue against the validity of the important insight of Venner and Casas that prey mass is much more important than prey numbers to the survival and reproduction of orb weaving spiders. But the biomass of prey captured by *Z. x-notata* may not have been as heavily biased toward larger prey as they calculated; and, even accepting their biomass calculations, the capture of large prey clearly did not imply that *Z. x-notata* orbs successfully resisted high-energy impacts.

General trends in selection on orb webs?—Blackledge (2011) followed up the Venner & Casas (2005) study by asking whether or not it is a general rule that the mix of different-sized prey for different orb-weaver species is such that the payoff from small and intermediate-sized prey tends to be so small that natural selection consistently favors traits designed to capture larger, rarer prey (I will call this a "Venner & Casas mix"). He concluded, after classifying prey as "large" if they were >2/3 of the spider's body length and applying the same Schoener equation (again indiscriminantly to all prey) in a meta-analysis of 38 studies of the prey of 31 species in 18 genera of orb weavers, that the answer is yes: "The 'rare, large prey' hypothesis thus can apparently be generalized across orb spiders." (Blackledge 2011:205, abstract). He argued that this means that "… the latter metric (the ability to stop and retain insects rather than intercept them) is more likely to play a decisive role in determining fitness" (p. 209).

Two of the problems noted in the previous paragraphs are also relevant for this Blackledge study: prey weight cannot be reliably estimated from prey length, especially in a small, likely biased sample of the longer species captured by an orb weaver; and the capture of a large prey by an orb weaver does not reliably imply that its orb resisted high-energy impact. Even Blackledge's worst case equation to estimate prey weight, with an exponent of 2 for L, overestimates the dry weights of the tipulids I measured by >2500%. The correction used by Venner & Casas (2005) for the upper limit on the amount of food a spider can consume in one day was not applied in Blackledge's study, accentuating the potential for overestimates of the importance of longer prey.

In addition, there are questions concerning the evolutionary realism of the 38 studies. The list of habitats includes "orchards", "fields", "buildings", and "cotton field". The existence (or lack of existence) of a Venner & Casas mix in these types of unnatural settings has no logical implications for whether Venner & Casas mixes occurred in the natural settings where the orb designs of these species evolved.

The most basic problem with this study concerns the translation of data on prey captures into conclusions about how natural selection acts on orb web designs. I believe that the data used by Blackledge (2011) are not equal to the task of drawing convincing conclusions. The location of the optimum point in the tradeoff between interception and stopping is not expected to depend only on the frequencies with which large and medium prey were captured, but also on additional variables, including their relative abundances in the environment, their relative numbers of encounters with orbs, and their relative frequencies of escapes. These additional factors will determine the possible gains or losses to be expected from changes in web design. Simply counting up the prey captured and estimating their weights is not enough. Nor will it suffice to combine weights of captured prey with data on the numbers and weights of prey of different sizes in the environment, because attempts to assay the prey that are actually available to an orb weaver have had serious problems, and are generally unreliable (Castillo & Eberhard 1983; Eberhard 1990). Thus the data in Blackledge's meta-analysis, and indeed those in most if not all studies of prey captured by orb-weavers in nature, are not sufficient to test ideas regarding selection on different orb designs.

Evidence from web designs.—If the rare large prey hypothesis is generally true, the implication is that selection consistently favors orb designs that are better able to stop high-energy prey. But the web designs of a variety of species do not fit this prediction. The webs of the theridiosomatid genus *Olgunius* (Coddington 1986), of *Cyrtarachne* and its relatives *Pasilobus* and *Poecilopachys* (Shinkai 1979; Carran & Miyashita 2000; Robinson & Robinson 1975; Clyne 1972), and of *Meta reticuloides* Yaginuma, 1958 (Shinkai 1969) all have very low numbers of especially widely spaced radii and sticky spiral loops. The flimsy, open-meshed orbs of species in the large genus *Tetragnatha* also seem poorly designed for stopping high-energy prey (Comstock 1948; Kaston 1948; Shinkai 1979; Gillespie 1987). In at least one species, *T. kaestneri* (Crome, 1954), field observations of prey emphasized the importance of relatively small, low-energy flies (Chironomidae) (Crome 1954). In another species, *T. lauta* Yaginuma, 1959, an even sparser array of radii and sticky loops has evolved (Shinkai 1988).

Another, more taxonomically widespread example also calls into question the supposedly dominant role of the stopping function and, more generally, the trumping effect of stopping plus retention over interception (Blackledge et al. 2011). This concerns the pattern of sticky spiral spacing within the webs of many orb weavers. It is common for the spaces between sticky spiral loops to be larger in the outer portions of an orb than near the hub in Araneidae, Tetragnathidae, Theridiosomatidae, and Uloboridae (LeGuelte 1966; Herberstein & Heiling 1998; see also photos in Comstock 1948; Kaston 1948; Shinkai 1979; Coddington 1986; Shear 1986; Kuntner et al. 2008). That is, in just those portions of these orbs in which the orb's ability to stop high-energy prey with its radii is the lowest, the sticky spiral loops are placed farther apart, further reducing the web's abilities to stop and retain high-energy prey, but increasing its ability to intercept them. This raises the possibility of different balances between different functions in different parts of a single orb. Although it is possible that intra-orb differences (if they exist) in the properties of sticky and non-sticky lines (e.g., Crews & Opell 2006; Herberstein &Tso 2011; Blackledge et al. 2011) may complicate interpretations, this pattern does not seem likely to be the result of selection favoring stopping and retaining high-energy prey at the expense of interception.

Conclusions.—In sum, I believe that Blackledge's conclusion that the rare, large prey hypothesis is "… generalizeable across orb spiders" is overly ambitious. Where does this leave us regarding models concerning the evolution of orb webs? I am convinced of the importance of the insight of Venner & Casas that the biologically important variable for a spider is not the number of prey it captures, but the amount of resources that it receives from these prey. This insight renders irrelevant much previous work on orb webs that emphasized prey numbers, including some of my own (Castillo & Eberhard 1983; Eberhard 1986). But extrapolating from this insight to gain an understanding of selection on orb web designs is not simple. Constructing models based on a particular function such as stopping prey (Sensenig et al. 2011) can be useful as explorations of that particular function. And of course constructing models always involves making simplifying assumptions; there is no magic degree of biological realism that a model must fulfill. But omission of variables that are known to be important, especially when those variables have effects that run counter to a key variable such as the stopping function in a hypothesis (see Table 1), can reduce the likely usefulness of a model for understanding the real world.

The major conclusion of this note is that until better confirmations of the rare large prey hypothesis are available, it will be wise to keep in mind the multiple functions of orbs, and avoid emphasizing only the stopping function to the exclusion of all others, because of the perceived importance of large prey (Sensenig et al. 2011). This does not mean that there may not be species in which the importance of the stopping function trumps that of all others (I suspect that such cases probably exist). Nor do I wish to imply that it is not useful to explore traits affecting this (or any other) particular function. But the importance of studies that attempt to understand the evolution of orb web designs in general is likely to be compromised if their emphases are too narrow.

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