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INTERFERENCE BY WEB TAKE-OVER IN SHEET-WEB SPIDERS

I. Introduction.

Web invasion and take-over have been reported in several families of webbuilding spiders (Araneidae: Wise (1981,1983), Spiller (1984); Agelenidae: Riechert (review in 1982); Linyphiidae: Toft (1987). In several of these cases both intra- and interspecific invasions were observed. However, detailed studies have been completed only for the intraspecific case of the agelenid, Agelenopsis aperta (Gertsch) (Riechert 1978a,b, 1979, 1981, 1982, 1984). These revealed strong intraspecific competition for high-quality web-sites, and at the same time led Riechert (1981) to suggest that spacing of individuals due to territoriality produce population limitation, preventing any significant role of interspecific interactions. Other authors, following different lines of study (Wise (review in 1984), Hoffmaster (1985) and others), agree with the general conclusion of an insignificant role for interspecific interactions, whereas Spiller (1984a,b) and Toft (1986) found opposing evidence. In the orb-weavers studied by Spiller (1984a,b) both exploitative competition for food and interference competition are infered, but neither here, nor in Toft (1986) was the precise mechanism of interference determined.

This paper describes a simple experiment designed to demonstrate the occurrence of web invasion and take-over in the sheet-web spider Linyphia triangularis (Clerck). It further analyses the data in terms of the ecological consequences of this behaviour. The experiment was performed in order to test an hypothesis proposed to explain why adult females of L.triangularis occupying different microhabitats were of different sizes.

Published (Toft 1987) and preliminary data on the same behaviour taking place interspecifically and its possible role in the structuring of sheet-web spider assemblages will then be discussed. Finally, web invasions will be viewed in relation to other mechanisms of interference competition. Most of this is merely speculation.

II. Study area and methods.

The field work took place on a coastal plain called "Sletten" belonging to the Mols Laboratory, Eastern Jutland, Denmark. The area is grazed all year round by cattle (Scottish Galloway) for habitat management; therefore higher vegetation of junipers (Juniperus communis L.), wild apple (Malus silvestris (L.) Mill.), oaks (Quercus robur L.) and several other bushes and trees, form islands separated by a network of short, grazed sward. Junipers occur here in two different morphological types: (1) low-broad ones, with several main stems radiating from a common base, about 120 cm high and one to several meters in diameter, and (2) columnar ones, with a single main stem, 3-4 m high and rarely more than one meter in diameter. The two types occur mixed between each other within the whole area. L.triangularis is found in both kinds. In the low-broad junipers the webs are very large (the sheet may exceed 1000 cm^2) filling the large spaces between different main stems of the bush. Most potential web-site spaces seem occupied. In the columnar junipers webs are situated between small shoots at the perifery of the bush, and the rarely exceed 200 cm^2.

Adult female L.triangularis were collected from webs in each of these microhabitats, and their size measured under the binocular microscope as length of the cephalothorax.

Field experiment.

The experiment was performed in mid-September, i.e. in a period of active growth after all females have become adult, but before egg-laying starts (Toft 1978).

Adult female L.triangularis were removed from 83 large webs in low-broad junipers and their size was measured under the microscope as length of tibia I (this is an easier measure than cephalothorax length when working with live specimens). At the same time colour-marked individuals of known size (tibia I) were released into the webs. The spiders released had been collected from both kinds of junipers and were selected to represent more evenly the full range of sizes in the habitat. No spider was released in its own web. The spiders were not individually marked, but the webs into which they were released were so dispersed that movement between experimental webs was unlikely. During the following week the webs were inspected regularly; then observations were terminated as the webs were destroyed by heavy winds. If a web was inhabited by the marked spider, this was just noted. If inhabited by an unmarked spider, this was collected and measured (tibia I). If on succeeding inspections a marked spider was followed by an unmarked, a take-over is assumed to have taken place (though see discussion); if an unmarked individual followed an empty web, it is regarded a floater.

III Results

Female L.triangularis collected from low-broad junipers had cephalothorax lengths (mean ± 1SD) amounting to 2.70 ±0.24 mm (n=128), those from columnar junipers 2.48 ±0.23 mm (n=166). Spiders from the low-broad junipers are considerably larger than those from columnar ones, the difference being highly significant (Mann-Whitney U-test, $p<0.001$).

As noted the juniper types are so mixed in the locality that there is no reason to believe that spiders encountered in one type have also developed in this type; any change of web-site confers a fair chance of bringing an individual from one type to the other. The difference then should not be explained by their developing in habitats of different quality (Vollrath 1988).

Field experiment.

The spiders released in the webs were smaller and also more variable in size than the original web-owners (fig. 1). However, during the week following release the size of released spiders still present in the web increases, though not reaching the pre-experimental level. This is due to the also observed fact (fig. 1), that individuals expelled from their webs as a result of take-overs obviously are the smaller ones, whereas the larger individuals seem better able to keep their web. On each inspec-

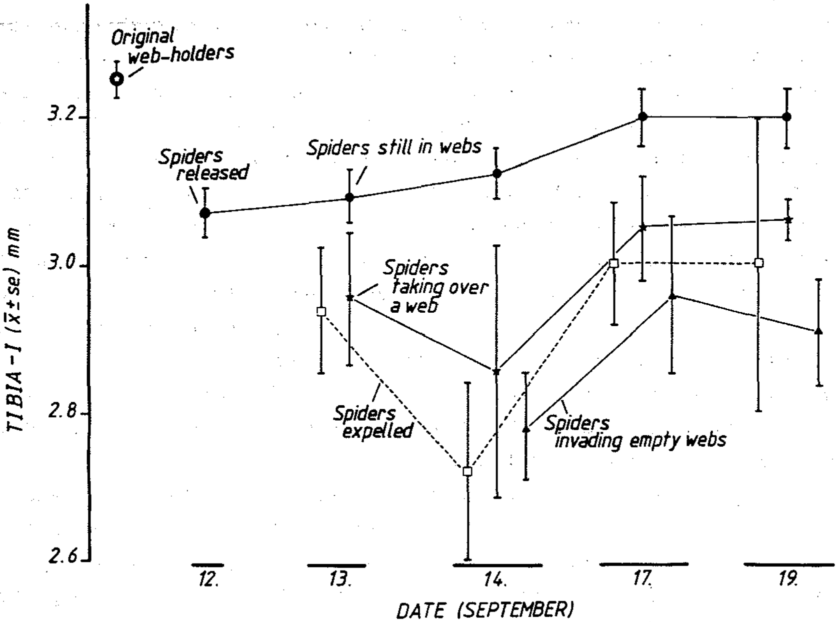

Fig. 1.Variations in size of various groups of adult female Linyphia triangularis following experimental manipulation: "Original web-holders" were removed from their webs and replaced by "Spiders released". Some of these deserted the webs, while others ("Spiders expelled") were ousted by "Spiders taking over a web". "Spiders invading empty webs" are floaters turning up in deserted webs or webs from which an intruder had been removed.

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tion date the mean size of individuals taking over a web is slightly larger than those expelled.

Finally, fig. 1 shows that individuals invading empty webs are among the smallest of the whole size range.

Discussion of field experiment.

By releasing individuals of the full range of sizes available in supposedly high-quality webs the experiment intended to set back the situation to the "pre-competition state", in the hope that the following events would show comnpetition at work and a return to the pre-experimental situation. This expectation was only partly fulfilled. However, the mechanisms supposed to be at work were found actually to be so. Thus, competition for webs or web-sites by means of web take-overs did take place and there was a clear indication that taking-over requires the invader to be larger than web-holder. (As webs were not under constant inspection, situations in which webs were abandoned and later inhabited by a floater, all between two insepctions, have also been classified as take-overs. Two cases in which the intruders were much smaller than the residents, probably can be explained this way; though see Hodge 1987). Large spiders have a good possibility of keeping their web, or of obtaining an already existing web if they chose to leave their own. Small spiders, on the other hand, run a great risk of being expelled by a slightly larger floating individual invading its web, becoming floaters themselves.

The number of web take-overs as well as the fact that empty webs usually are occcupied very soon, points towards the existence of a large floating population. It appears from fig. 1 that these floaters are small compared to the web-holders (compare to "original web-holders" that represent the non-experimental surrounding situation from which they are recruited). In the experimental situation, the largest individuals of these floaters were able to expel the small sized fraction of web-holders, thus raising the mean size of web-holders (not shown directly in fig. 1). Another small-sized fraction of the floaters turned up in empty webs created partly by my removal of individuals having taken over a web partly by voluntary desertion of webs (webs may be deserted for unknown reasons, also in the undisturbed situation).

In the natural situation floaters must have two options: Either to keep searching for a high-quality web-site (that is either unused or inhabited by a smaller spider that can be ousted); or to go to a less productive microhabitat and occupy a low-quality web-site.

Sheet-webs are costly to produce (Ford 1977, Janetos 1982). The advantages of a take-over are not only saving the investment in a new web, but also saving time to find an unoccupied web-site, providing extra foraging time (i.e. time to find new web-site plus time until new web is functional), and most probably the site will be more productive than an unoccupied one. The costs are the energy used in direct fight plus possible risks of injury. The relative benefit-cost-balance of the alternative choices must depend on the size of the spider. For a large spider web invasion is likely to be the most profitable choice much more often than for a small spider. Furthermore, once in possession of a web a large spider have greater chances of keeping the web, whereas a small spider runs a great risk of being expelled itself very soon. Thus, it is likely that a large floater will go for an existing web rather than seeking an empty web-site, whereas a small floater may do better chosing a less competitive, though also less productive microhabitat (cf. Rubenstein 1987). The idea of a size-dependent predisposition for different choices remains untested, however.

IV. Interspecific web take- overs.

Toft (1987) reported on web-take-overs between the two sheet-weavers *L.triangularis* and *L.tenuipalpis* Simon, occurring together in a *Calluna* habitat. As indicated in fig. 2 size superiority seem to play the same role in these interspecific encounters as found for intraspecific ones. Only one out of 22 interspecific take-overs were performed by a smaller individual ($p<<0.001$, sign test, Siegel 1956). Though *L.triangularis* on average is the larger of the two, they do have overlapping sizes. Thus, because of this size difference, only 2 out of the 22 take-overs were done by *L.tenuipalpis*.

Fig. 2 indicates that the occurrence of take-overs by smaller individuals is largely confined to the first two days after the start of the experiment. Later, they virtually do not occur. This indicates that the spiders do not defend an unaquainted web as vigourously as they will later defend an aquainted web. However, even including these early data the positive size difference between winner and looser is highly significant ($p<0.0001$, one-tailed sign test, corrected for continuity, Siegel 1956).

It is reasonable to suppose that the more equal in size two species of related sheet-web spiders are, the more similar are

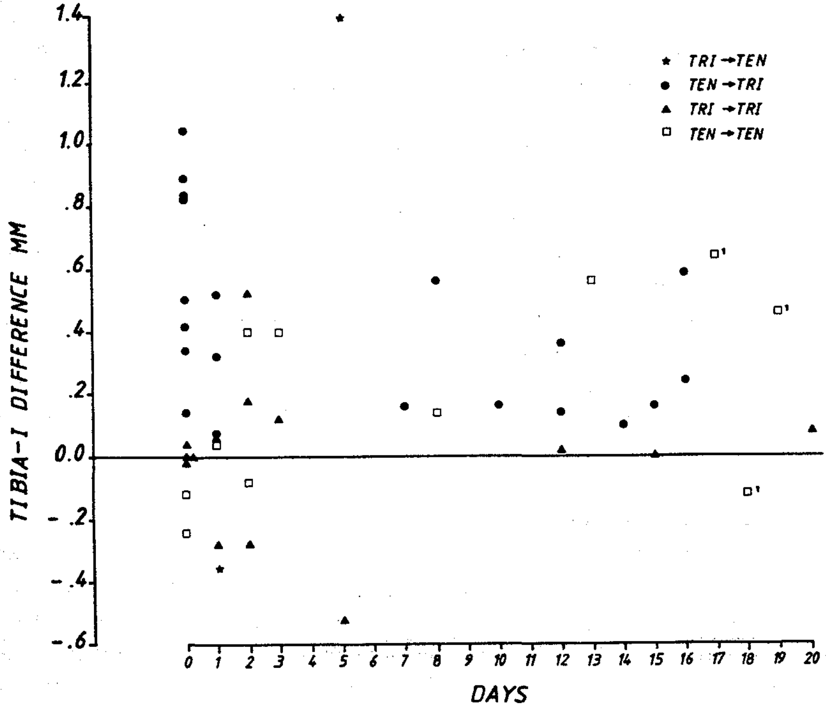

Fig. 2. Difference in size between intruding and expelled Linyphia females in an experimental field situation, plotted against time (days) since expelled females were released in webs. Symbols should be read as, for example, *: L.triangularis expelled by an L.tenuipalpis. 1: intruding female had finished egg-laying (shrunken abdomen).

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also their requirement for web sites. In line with this, I have documented identity of web-site requirements in L.triangularis and L.tenuipalpis (Toft 1987). This identity is what leads to interspecific web take-overs in dense populations. All data so far indicate that the larger species is the stronger in this competition for webs. Preliminary results from experiments, in which I transfered additional specimens of L.triangularis into habitat patches naturally dominated by L.tenuipalpis, show that even here L.triangularis took over at the expense of L.tenuipalpis. The logical inference from this is that numerical dominance of the smaller species in the natural situation was not created by interspecific competition for web-sites, though its decline during the experiment certainly was.

Web invasion with subsequent take-over thus have at least the potential of being a force in the dynamics of both single-species populations within a habitat as well as in the interactions between different species forming an assemblage of related species within a habitat. In both intra- and interspecific cases there is a competitive disadvantage to the smaller part which a) may be driven away from high-quality web-sites, and thus b) may be forced to accept low-quality web-sites (i.e. different microhabitats), and/or c) may form a relatively large fraction of the total floating population. However, microhabitat displacement caused by interspecific interference still has to be documented.

V. Web take-over vs. other kinds of interference.

Riechert (1984) notes that if an intruding Agelenopsis is much smaller than the web owner, it retreats immediately. This is likely to be the case also in sheet-weavers, both intra- and interspecifically. Thus, webs of large species may occupy spaces being potential web-sites of smaller species, these being kept away from the web-sites simply by their being occupied. In my heathland studies I have frequently seen small juvenile Microlinyphia pusilla (Sund.) invade deserted webs of the larger Linyphias or to put up a new web between the rudiments of a spoiled Linyphia-web. This preoccupation of web-sites is probably strictly assymmetrical and probably one of the most widespread forms of interference competition among sheet-weavers. As size difference decreases I believe web invasions to get increased importance. As long as the size difference is still substantial, they may actually take the form of web removal, in which the larger species cleans the space to make room for its web.

However, as the size difference deminishes the structure of small species' web is likely to become more and more similar to that of the larger species, i.e. it becomes a more and more exploitable resource. Therefore, web take-over gradually will become more frequent.

The primary objective of web take-overs certainly is the fast and cheap possession of a functional web trap. The aggressive behaviours associated with fights over a web incur the possibility of getting a meal at the same time. "Intraspecific predation functions as an extreme form of interference competition" (Polis 1981). The same can be said about predation resulting from interspecific web invasions involving related species with similar web structure. However, in the case of the large Linyphia (L.triangularis and L.tenuipalpis) intra- as well as interspecific predation seem to be extremely rare. But in a study of the sheet-web spider assemblage of the beech-wood field layer (Toft, in prep.) I have found substantial interspecific predation by L.triangularis on the somewhat smaller Helophora insignis (Bl.). Direct observations revealed that at least some of this followed from web invasions.

I consider interference by interspecific predation to take two forms, that it will be useful to distinguish. First, it may occur as a regular feature of one species' food catching strategy. To some spiders other spiders form a substantial part of their diet and they may have special behavioural adaptations for spider catching. This interaction is classical predation. Riechert & Cady (1983) have described situations which appear to be of this type. In the other form, predation may be a more or less accidental result of web invasions, even if the effect on the prey population is substantial. The main purpose of invasions is to obtain web space or perhaps a web and probably result in predation only rarely. The behaviour is adaptive even if there is no predation. The main interaction, therefore, is interference competition. The behaviours described in this paper probably belong to this category.

Most kinds of interference probably favour the larger (individual/species) of two opponents. Interference thus incurs a size determined competitive gradient on the assemblage. The result of this will depend on the structure of the habitat. If very heterogenous, i.e. offering possibilities for displacement of inferior competitors into suboptimal microhabitats, the effect on populations may be minor and hard to detect. If the habitat is very homogenous, however, inferior competitors will become floaters, eventually die or emigrate to marginal habitats (cf. Jocqué 1981). Elsewhere (Toft, in prep.) I present evidence for these ideas. Thus, in woodland linyphiid assemblages in grassy (homogenous) vegetation, I found a positive correlation between species size and numerical abundance; no such correlation was found in assemblages of woody (heterogenous) vegetation.

All discussions here have been based on the assumption that a sheet-web spider can only feed if in possession of a web. As far as is known this holds true for the large Linyphias considered here. However, some species of web spiders are known or have been infered to abandon webbuilding and take up a wandering foraging mode in part of their life-cycle or as an alternative foraging tactic (Tetragnatha elongata, Gillespie 1987). Our minds should be held open for the possibility, then, that floating is not just "out of business", but may be an alternative foraging strategy in the case only low-quality web-sites are available.

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Jocqué: Could the intraspecific size differences in L. triangularis not be the result of some juveniles having grown up in more favourable habitats than others?

Toft: Probably not, because the habitat is mosaic and websites are often changed, so that the same spider will pass part of its life in favourable and another part in marginal habitats.