VERTICAL STRATIFICATION IN ORB-WEB SPIDERS (ARANEIDAE, ARANEAE) AND A CONSIDERATION OF OTHER METHODS OF COEXISTENCE[1]

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Abstract. Measurements of the web height and counts of the number of webs on randomly selected plots in lespedeza fields reveal that immature *Argiope aurantia* and *Argiope trifasciata*, very large araneid spiders, place their webs at different heights. In late summer this vertical stratification disappears, while the numbers of the two species on plots become positively correlated. Coexistence of the two spider species may depend in part upon the usual occurrence of high mortality during the immature stages. Invasion of webs by araneids is reported as possible competitive interference. The two largest species of European araneids also show vertical stratification only as immatures. However, the niches of most Polish *Araneus* species in fields seem differentiated by parameters related to prey size: season of breeding and size differences between species.

Key words: Behavior; interference; niche; spider; survivorship; web.

INTRODUCTION

Cody (1968) showed that species of grassland birds coexist by a combination of specializations both vertical and horizontal in use of food and use of space. Horizontal space may be a dummy variable for habitat or other subtle differences in the needs of the species. Temporal separation completes Cody's exhaustive list of schematic parameters of the niche. His success in characterizing bird niches using such schematic parameters suggests that similar analyses of "communities" of species of other taxa may provide a framework for understanding the natural history of such groups.

Slobodkin (1961) suggested that predation must permit the coexistence of more prey species than that allowed by competition for a limiting resource. Paine (1966, 1971) demonstrated that horizontal space limits sessile intertidal organisms, so that predation upon the dominant competitor increases the number of species that can coexist in a particular area. Ricklefs and O'Rourke (1973) consider the possibility that appearance to predators may be treated as another parameter of niche space, for sessile, cryptic animals.

The use by web-building spiders of fixed webs for foraging can provide clearcut data for investigations of the use of space. In most of North America, two species of *Argiope*, a genus of large orb-web spiders, coexist in fields: *Argiope aurantia* Lucas (the "garden spider") and *Argiope trifasciata* (Forskal) (Levi 1968). These species overlap greatly in the range of habitats (Fitch 1963, Enders 1973) and in phenology (Muma and Muma 1949, Fitch 1963,

Enders 1973). These two species are also similar in body size (Kaston 1948, Levi 1968), the size and general appearance of the web and fangs (the trophic apparatus), and the prey actually taken (Bilsing 1920). Thus, the two species actually coexist in most field-type habitats, while apparently using the same prey resource. Vertical stratification or a predation effect would be necessary to allow their coexistence. During a study of web site selection, I found both species abundant in stands of sericea lespedeza (*Lespedeza cuneata*), a dicot perennial whose stems die back each year. As the spiders were abundant there, I was able to investigate the height at which webs of the two *Argiope* species are placed and the absolute numbers of each species. On occasion, the species reach a similar abundance in more natural vegetation (Enders 1973). I noted invasion of other spiders' webs, while observing marked individuals of various species; the behavior can serve as the proximate mechanism of the spatial separation of niches. The annual decline in numbers of the two *Argiope* species I observed suggests that, within a habitat, these two competitors can coexist as adults because of high mortality in the vertically stratified immature stages. To determine whether coexistence via a predation effect (Slobodkin 1961) was common among araneid spiders, I then analyzed the season of breeding, the adult size, and the stratum of vegetation used by a group of ten species of the genus *Araneus* found by Luczak (1963) in stands of heather with young pines.

METHOD

Random sampling of numbers and location of Argiope *webs*

I chose the five largest adjacent road cuts along U.S. Highway 1 Bypass northwest of Raleigh, North Carolina. Despite the apparent uniform growth of

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TABLE 1. Correlations between no. of *Argiope aurantia* and *A. trifasciata*. Correlation coefficients calculated between the no. of webs per m² at the N randomly selected locations. No. of plots searched 2N in Aug. and 3N in Sept. Numbers of the two species become positively correlated by late summer

		Dates of sampling				
		May	June	July	August	September
	1970		30/6–2/7/70	26/7–13/8/70	24/8–29/8/70	29/9–6/10/70
	1971	26/5–3/6/71	30/6–2/7/71	2/8–4/8/71	31/8–5/9/71	
Correlation coefficients	c	−.04	.13	.12	.48**	.27**
Both 1970 and 1971 data	N	29	93	158	143	79

c = correlation coefficient.
N = number of locations.
** Correlation statistically significant at the .01 level.

sericea lespedeza (80% cover, planted about 10 years ago), these areas had additional plants, mainly intrusive herbaceous "weeds" in the first four meters from the road's edge, including, in descending abundance, *Lactuca*, *Oenothera*, *Aster*, *Ambrosia*, *Rubus*, and *Phytolacca*. The shoulder of the highway and a distance of two meters up the road cuts were covered by Kentucky Tall Fescue Grass (*Festuca* sp.) and were mowed every month. Occasional trees, principally Loblolly Pine (*Pinus taeda*), were present, especially near the upper edge of the road cuts.

The total length of the areas sampled was 845 m, excluding parts where the ditch at the edge of the road was concrete; the width averaged 25 m. At monthly intervals, the length of the areas was systematically sampled, with a random start, by transects taken up the slope of the road cuts. Dates of sampling are given in Table 1. Monthly sampling began 1 week after the young *Argiope aurantia* were last to be found in cocoons in order to find the maximum number of this species on webs and ended in September to avoid the heavy mortality from frost in October. In 1971 samples were taken from only the two largest road cuts, 660 m long.

At each transect I searched successive plots of 1 m² for spider webs. Taking the ditch as zero, the first plot was between the roadside ditch and 2 m towards the road, on alternate transects between 0 and −1 m, or between −1 m and −2 m. Since the next meter of vegetation up the slope was trampled during the search for webs, the lower edge of the next plot was located 1 m up slope from the previous plot (on alternate transects 1–2 m or 0–1 m). The last plot searched was entirely within the lespedeza which had a clear separation from adjacent forest.

To find webs, I first looked along the top of a plot and also underneath, without disturbing the vegetation. Then I carefully parted the vegetation from top to bottom and from edge to center, till I had searched the entire volume of vegetation.

For each plot, I recorded the number of webs of each *Argiope* species, the height of placement of each web (distance in cm from the ground to the hub), the height in cm of the vegetation where each web was, and the instar[1] of each spider. The instar was estimated from comparison with the size of preserved laboratory-reared specimens of *Argiope aurantia*. Since the instar of *A. trifasciata* was judged using specimens of *A. aurantia*, the estimates for instars of *A. trifasciata* were less accurate. When collected specimens of both species were reexamined in the laboratory using a dissecting microscope, it was found that the field and laboratory estimates differed by no more than one instar.

Data were gathered only after 1000 (to avoid dew), before 1700 (to avoid heavy highway traffic), and on sunny days (to help see webs). In August and September, one and two additional plots, respectively, were searched immediately next to each plot, because of the low densities of spiders. Statistics were computed with programs by A. J. Barr and J. H. Goodnight (Department of Statistics, North Carolina State University, Raleigh) and the facilities of the Triangle Universities Computing Center.

Incomplete information was gathered for some webs because of: (1) destruction of the web or distortion of the vegetation to which the web was attached, (2) failure to find a spider on the web (such webs were counted, but the spider's instar could not be described), (3) lack of sufficient time to examine all webs, mainly in May, 1971, because the spiders were very numerous (on such occasions I examined only every second or third web). These deviations from strict randomness are considered minor.

Correlations of numbers of the Argiope species

In the lespedeza areas, the numbers of individuals of the two species became significantly positively

[1] The first instar is that stage which remains inside the cocoon after eclosion, while the second instar is that which emerges from the cocoon and first builds a web (Kaston 1948). As McCook (1889) noted, araneids can mature at various unequally-sized late instars.
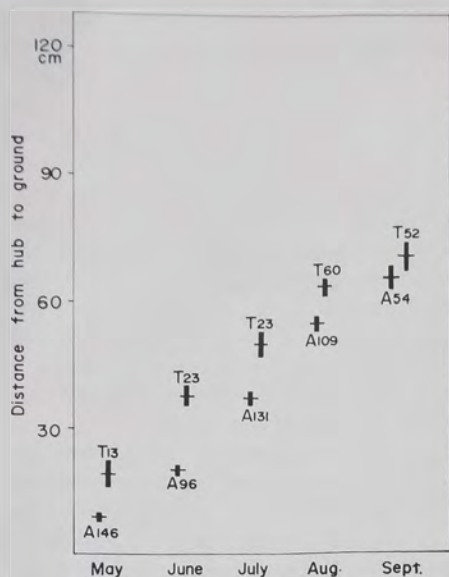
FIG. 1. Height above ground at which webs of *Argiope aurantia* (A) and *A. trifasciata* (T) were located. The bars = one SE on either side of the mean, near the bars are the no. of webs. The ht of location of webs increases with successive months, especially by *A. aurantia*. The two species differ significantly in the ht of location of webs, except in Aug.–Sept.
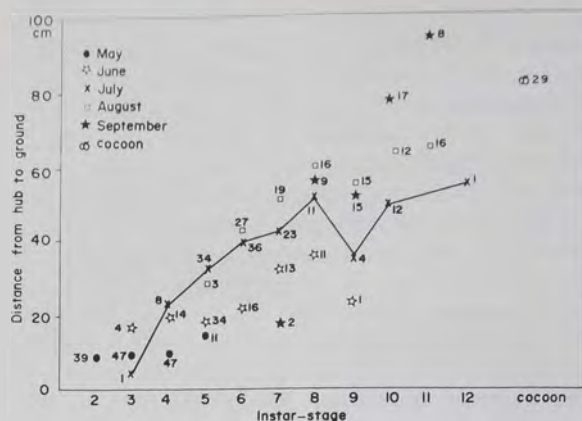

FIG. 2. The dependence of ht above ground on instar in *Argiope aurantia*. A solid line connects the data for the sample taken in July. Numbers are the sample sizes for instars within each sampling month.

correlated by the end of the summer. Sums of data for the months of sampling are analyzed in Table 1.

Height at which web was built

Fig. 1 shows the height at which the webs of *Argiope aurantia* and *A. trifasciata* were found in the random sampling of webs at the end of each month in 1970 and in May of 1971. For *Argiope aurantia* Fig. 2 shows the web heights of the various instars and height of location of the egg sacs, for data from the same months. The positive slope of the data shows that the increase in height in the later months of the year is related to the increase of instar from one month to the next. The fact that the lines which might be drawn connecting data for later months in Fig. 2 lie ever higher up indicates that growth of the vegetation during the summer had the effect of increasing the height at which all instars situate the web.

For both species, the height of the vegetation in which the web is built is shown in Fig. 3. The lack of a consistent difference between the two species shows that the difference in the height at which the webs of the two species are built early in the year (Fig. 1) is not due to a choice of vegetation that differs in height. Fig. 1 reveals that *A. trifasciata* webs are consistently located higher up than *A.*

aurantia webs. But, by September, the webs are no longer at significantly different heights, when compared by the use of a *t*-test (Snedecor and Cochran 1967).

Interference among araneids

Independent exploitation is the method of allocating resources ordinarily assumed. But interference
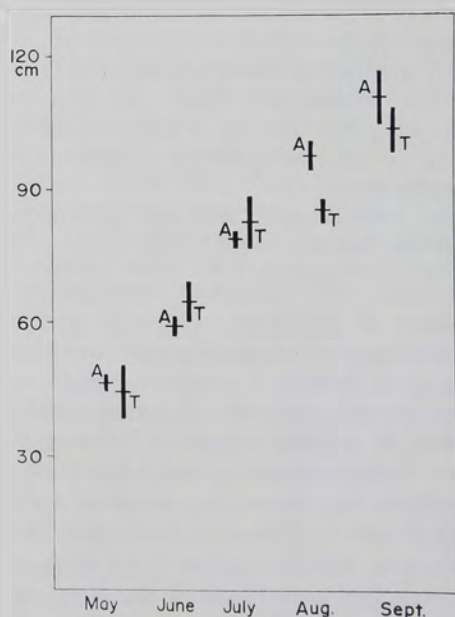

FIG. 3. Height of the vegetation in which *Argiope aurantia* (A) and *A. trifasciata* (T) webs were located. The ordinate is the distance between the top of the vegetation directly above the web and the ground, in cm. The bars = one SE on either side of the mean.

may occur, to prevent the success of the most efficient competitor (Miller 1967). Web spiders may be subject to interference by intrusion onto their webs and preemption of web sites by larger individuals. Bilsing (1920) recorded cannibalism by *Argiope trifasciata* upon individuals of the same species in less than 1% of 621 webs examined for prey. Late in the year I also observed a very few cases (less than 1% of prey) of *A. aurantia* feeding on *A. aurantia, A. aurantia* on *A. trifasciata*, and *A. trifasciata* on *A. aurantia.* These cases are females being eaten by females. Since the prey of araneids ordinarily must contact the web, this suggests that females of either species of *Argiope* will intrude onto the web of either species.

I have made observations of the invasion of unoccupied webs: 39 adult female *Argiope aurantia* were removed from their webs for an hour between 0220 and 0100 hr, to be weighed; five of the unoccupied webs were invaded, all by conspecifics. At a fishing pier, 38 similar cases of removal of *Araneus cornutus* Clerck (Araneidae) from their webs resulted in another five invasions of webs: three conspecifics, one *Eustala* sp. (Araneidae), and one *Tetragnatha laboriosa* Hentz (Tetragnathidae). Of these intruders, one conspecific was followed and captured off the web by the original occupant. On later occasions, I chased the intruder away before returning the original occupant. The *Eustala* had a web on the previous night at the site which it invaded, though no web was found the evening the invasion occurred. The large *Tetragnatha* which invaded an *Araneus cornutus* web had probably left the very large horizontal web immediately under the large vertical *Araneus* web, thus allowing a much smaller *Tetragnatha* to invade the otherwise inordinately large *Tetragnatha* web.

Finally, even occupied web sites are invaded and used for the intruder's web:

1) I made 800 successive observations (total spider-days) of 118 *Argiope aurantia* marked with model airplane paint at the edges of lespedeza areas. In five cases (0.6%) a marked *Argiope aurantia* definitely invaded the web of another spider, one the web of an *Argiope trifasciata*, the others of conspecifics. In the single case where a long-term record was available, the invader left a site where it had obtained 29 prey in 13 days, to take a web site where only one prey had been taken in 13 days: the invader's web had been blocking the other web site from obtaining the honeybees pollinating the lespedeza at that time. In 166 observations of 29 *Argiope trifasciata* at the edge of lespedeza, only the one invasion mentioned above was noted.

2) In the laboratory, four *Argiope aurantia* were placed in an indoor cage (4 m × 2 m × 2 m), and

maintained there several months; one of the spiders eventually lingered at the edge (frame threads) of another's web, for several days, until I found it being eaten by the inhabitant of the web. It was not possible to mark very young spiders, but in crowded, small (0.06 m³) boxes, used to rear *Argiope aurantia* from the egg sac, I regularly noted that two small spiders (usually second instar) were on one web, usually in the normal head-down position at the hub, but one on either side. In these rearing boxes I also occasionally noted that small spiders' webs were taken by others, distinguishable by being two instars larger. (While molting was very frequent in the young spiders, no cases of two molts in one day have ever been noted in isolated individuals.)

3) In 162 observations of 16 individuals of *Araneus cornutus* in lakeshore vegetation and pier, one double invasion (0.6%) of occupied web sites was noted. A subadult *Araneus cornutus* invaded, within 15 minutes, the webs of two smaller subadult *Neoscona arabesca* (Walckenaer). This marked *Araneus cornutus* had been present several days, its web closer to the vegetation than the *Neoscona* webs and within 15 cm of their vertical faces. In each invasion, the *Araneus* climbed rapidly up the *Neoscona* web from below, and then from the sides, until it could not find silk on which to climb. Meanwhile, the *Neoscona* ran down from the hub and seemed to cut away the silk in front of the *Araneus*, jerking itself back toward the hub (and the *Araneus* away) by the release of the tension of the web each time. In one case, the invasion began while the *Neoscona* was handling prey at the hub of the web, and, in this case, the *Araneus* was able to advance further onto the web. That night, after invading, and somewhat later than the usual time for building, the *Araneus* built a very large web at the site of the *Neoscona* webs. In 18 observations of eight *Neoscona arabesca*, no other web invasions were noted.

These observations suggest that araneid spiders may interfere with the use of space by competitors, by intruding upon one another's webs. While one might object that these observations of web invasion occurred under "crowded conditions," that is precisely the point: spiders probably tend to invade webs, even those of other species, mainly under "crowded" conditions, so that this behavior must function as a form of competition for space. I have not observed that the invaders of webs are undernourished, judging from the relative width of abdomen and cephalothorax; I have noted, judging from length of leg or other hard part, that successful intruders seem to be larger than the original occupant of the web.

Thus, invasions of occupied webs occurred in 0.6% of my observations, both in *Argiope aurantia* and in
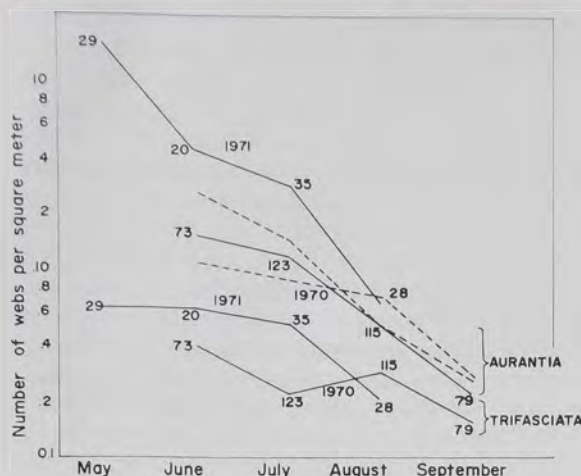
FIG. 4. Survivorship curve for *Argiope aurantia* and *A. trifasciata*. Solid lines connect the months of sampling in 1970 and 1971 for each species, and show the number of locations searched for webs. Dashed lines show the survivorship at the two largest road cuts during 1970 separately for *A. aurantia*.

Araneus cornutus. This figure is considered a minimum estimate, because if one of the participants in the invasion was unmarked (and was not two instars larger) or had been at an unmapped web site, my methods would not record web invasion. If invasions occur at a rate of 0.6% per web-day, since each adult spider has spent about 110 days on an individual web, most araneids, at least of these species, must have contended with web invasion during their lives.

Mortality: a partial life table

Fig. 4, illustrating survivorship curves (webs per square meter) on a semilogarithmic plot, approximates a straight line, usual for invertebrate animals. While no *marked* difference in the rates of mortality (the slopes of the lines) between the two species is evident, *Argiope trifasciata* does appear to have a slightly lower rate of mortality. The latter could be an artifact of the later emergence of *A. trifasciata* from the egg sacs: the peak numbers of *A. trifasciata* on webs may have occurred in early June rather than late May. Then a steeper, but unobserved, decline in numbers, as sharp as that for *A. aurantia* would have resulted.

The downward curve of the graph of the data for *A. aurantia* in September may be due to the disappearance of the (shorter-lived) males by then; doubling the number of spiders in September eliminates the curve, and so provides a better fit to a straight line.

In 1971, only road cuts 4 and 5 were sampled. For *Argiope aurantia* in 1970, data from 4 and 5 (dashed lines) are shown separately. Fig. 4 shows that the marked increase in numbers of *Argiope*

aurantia from 1970 to 1971 cannot be due to the sampling of these areas only. Also, Fig. 4 shows some compensatory mortality: the increase of *Argiope aurantia* from 1970 to 1971 is much reduced by August.

In 1970 *Argiope aurantia* from road cut 3 declined in numbers more precipitately than the other areas. During observations of marked spiders, more activity by spider-hunting wasps (Psammocharidae) had been noted at the edge of that area than in other study areas. Besides various species of psammocharid wasps, predators observed attacking *Argiope aurantia* (immatures) include *Mimetus* (probably *epeiroides*) spiders, and one *Lycosa* (probably *carolinensis*) spider. Also, the cocoons of *Argiope aurantia* were subject to mortality from several predators upon eggs:

1) During August and September several *Chauliognathus* beetle larvae (Cantharidae) were collected from cocoons in which they had partially eaten the egg masses; most of the cocoons found later in the year had holes similar to those made by *Chauliognathus'* entrance.

2) In many cocoons the insides were completely removed, including the silken lining between the eggs and the outside parchment-like silk. As this regularly occurred even when the cocoons remained attached about 90 cm above the ground, this sort of damage was probably done by birds. Eight of 66 cocoons collected in spring, 1971, when care was taken to obtain even those heavily damaged egg sacs, had more than half of the silk removed. Still more such cocoons can be supposed to have been torn completely loose from their supports, and so not recorded—several such egg sacs were found.

3) Salticid spiders were found in 4 of 58 cocoons which had not been torn open, in two cases, with their own eggs. These salticids were observed to eat young *Argiope* when the cocoons were warmed to room temperature.

4) In late autumn, 1969, 26.5% of 34 cocoons collected from lespedeza-covered road cuts near Raleigh were parasitized by *Tromatobia rufopectus* (Cr.) (Ichneumonidae, Hymenoptera). In autumn 1970, 26.0% of 100 cocoons collected were so parasitized. A chalcid hyperparasite occurred in 44.4% and 69.2% of the cocoons attacked by *Tromatobia* in the 2 years.

5) *Pseudogaurax signatus* (Lw.) (Chloropidae, Diptera) occurred in 17.6% of the cocoons in 1969, and only in 4% in 1970. The cocoons were not collected on the study areas, though parasitized cocoons were encountered during September sampling. These last two sources of mortality did not vary considerably in the 2 years of study: the infestation of cocoons on the next large road cut to the

northeast of road cut 4 (5 faced 4) varied only from 22.7% to 23.8% for *Tromatobia*, and from 9.1% to 4.8% for *Pseudogaurax*, of 22 and 21 cocoons collected there from 1969 to 1970. *Tromatobia* and *Pseudogaurax* often left many *Argiope aurantia* alive in the cocoons, possibly because they are able to eat only the eggs. In only one cocoon were both egg parasites present.

6) Cocoons up to 4 m up the side of the road cuts were destroyed by annual winter mowing.

I have no information for *Argiope trifasciata* regarding predators, other than the observation of a web-invading predatory theridiid spider (*Rhomphaea* sp.) at the edge of an *Argiope trifasciata* web. Moreover, I found only four cocoons of *A. trifasciata*, none of them damaged; these cocoons were located considerably lower down than those of *A. aurantia*.

GENERAL DISCUSSION

Muma and Muma (1949) collected *Argiope trifasciata* on trees and shrubs, but *A. aurantia* from herbs. Contrary to their findings, Fitch (1963) reported that *Argiope aurantia* usually builds its web higher up than *A. trifasciata*. However, this is probably an artifact of *A. trifasciata*'s occurring in more open areas where vegetation is shorter (Fitch 1963, Enders 1973). In all habitats, therefore, the average adult *A. trifasciata* web might be closer to the ground than the web of the average adult *A. aurantia*. However, my data (Fig. 1) show that the immature *A. trifasciata* in the habitat studied build webs higher up than immature *A. aurantia*. In fact, wherever I have found both species in the same stand of vegetation, mainly roadside vegetation and old fields, the immature *A. aurantia* built webs closer to the ground, on the average. I have confirmed this difference in height chosen experimentally in outdoor cages (Enders 1972).

The positive slope of web height of *Argiope aurantia* graphed against instar (Fig. 2) suggests that the spiders must choose different heights at different instars. I have evidence that this depends upon sexual maturity rather than body size (instar) per se.

The cocoons of *Argiope trifasciata* were generally lower down and hidden under leaves more than those of *Argiope aurantia*. The absence of predation upon any of the four *A. trifasciata* egg sacs, contrasted to the high rate of damage to egg sacs of *A. aurantia*, suggests that the location of the former may prevent birds from seeing them, while the colder weather late in the year when this species lays its eggs may preclude predation by the arthropods. Wilder (1873) reported a high infestation of *A. aurantia* cocoons with egg parasites, possibly the same as I found. While an outdoor life table is available for no other web spider, Abalos and Baez (1967) reported similar

high levels of mortality from egg parasites on various black widow spiders (*Latrodectus*, Theridiidae).

Fig. 4 indicates that the numbers of *Argiope aurantia* differed considerably in the 2 years of my study. While this may, in part, merely be the result of the later phenology of the cold spring of 1971, similar fluctuations in population levels of *A. aurantia* were noted by Fitch (1963) and Levi (1968). I observed some mortality of *A. aurantia* at the time of molting in the field; possibly Levi's (1968) idea is applicable, that the fluctuations in numbers of *Argiope* spiders are related to drought. I suggest via increased water loss during molting, which may increase mortality in protracted dry weather.

The positive correlations between the numbers of the two species of *Argiope* indicate that the two species are occupying the same horizontal component of the microhabitat. Niche separation by Cody's (1968) scheme must therefore be either by vertical space or prey items taken.

Turnbull (1964) reported that *Achaearanea tepidariorum* (Theridiidae), a web-building spider, had a positive aggregation response to prey abundance. Enders (1972) found no such response for *Argiope aurantia*, and the little data for *Argiope trifasciata* also show no aggregation where success at prey capture is higher. This indicates that the positive correlation between the two species is not due to local prey abundance; the correlation may be due to the similar needs of the two species for suitably stout attachment points for webs and for an open space between the attachment points of sufficient diameter for the adult web.

Here I use ecotope, niche and habitat range as suggested by Whittaker et al. (1973). Late in the year, the two *Argiope* species seem to be, in effect, using the same niche, including food and location of the web. These species may be able to do so because they are few, as adults, although, in the case of an encounter, the larger species (in my experience, ordinarily *A. aurantia*) will physically interfere with, and even eat, the smaller. *Argiope trifasciata*, as a species, has a habitat refuge in those stands of vegetation which are too sparse for the use of *A. aurantia* (Enders 1973). Early in the year, these two species are vertically stratified. Late in the year, the two species compete directly for web sites, in most of their ecotopes, due to the changed vertical distribution of *A. aurantia*. However, since both species are becoming fewer, the number of encounters may be reduced to a tolerable level.

Thus, these spiders are an example of the importance of both spatial and temporal coincidence for competitive encounters. Griffiths (1969) pointed up the importance of such coincidence for predatory interactions. In general, spatial coincidence must be less frequent in less mobile organisms, which encoun-

ter other individuals less often the less either species moves; spatial coincidence in sedentary organisms must regularly decline during their lifetimes, if geometric increase in the size of the web (or other measure of living space) is overmatched by the logarithmic decline of numbers due to predation or other source of mortality. Slobodkin (1961) predicted that more species than the number set by competition can exist as a result of predation upon one of the competing species; Paine (1966, 1971) has confirmed this prediction for benthic intertidal organisms. Perhaps this phenomenon is restricted to sedentary organisms, due to the reduction in spatial coincidence discussed above: a predation effect has so far been reported for trees (Janzen 1970), and resting moths (Ricklefs and O'Rourke 1973). Most of the animals studied by Paine (1971), and web spiders also, can be described as *sessile* filter feeders. Conceivably, if predation regularly allows species of invertebrates to coexist, such predation by the vertebrates may partially explain the great number of species among such invertebrate groups as the Arthropoda.

Evolution of the ecotope of Argiope trifasciata

The situation of the two *Argiope* species is comparable to that studied by Murray (1971): in different geographical areas, two sparrow species dominate a third, fugitive species (Hutchinson 1951), which seems to depend for its survival upon the chance reduction in numbers of the domineering species. As a result, the subordinate member of the species pair comes to be adapted to what were originally "suboptimal" habitats for the genus. For arthropods (and the intertidal benthos) the chance reduction in numbers is great in the immature stages and has a high probability; in fact, for one of the domineering sparrows, catastrophic mortality due to excessively high tides has been found in 2 of 4 years of one study (Post and Enders, unpublished data).

The vertical separation of *Argiope trifasciata* from *Argiope aurantia* can be interpreted both as an evolutionary displacement from the niche of *A. aurantia*, and as an adaptation for the use of early stages of succession: *A. trifasciata* can colonize cultivated fields abandoned only 1 year, because it accepts web sites exposed to more wind, including habitats with sparser vegetation as well as web sites higher up than those acceptable to *A. aurantia* (Enders 1972).

That *Argiope trifasciata* evolved after *A. aurantia* is supported by the fact that, on morphological grounds, *A. trifasciata* is a recent offshoot from *Argiope bruennichi* of southern Europe (Levi 1968); the latter seems more like *A. aurantia* in preferring a web site near the ground as an immature (Tilquin 1942). The number of mutually allopatric *Argiope* species which are sympatric with the cosmopolitan

A. trifasciata in the Americas in different areas (Levi 1968) also supports the recent derivation of *A. trifasciata*, and implies that its niche is displaced from that of the primitive *Argiope*, which, I suggest, is a large orb-weaver, near the ground as an immature but higher up as an adult.

Consideration of the *Araneus* spiders collected by Luczak (1963) suggests that *Argiope trifasciata* must have evolved to fill the niche of *Araneus diadematus* in the New World field-type habitats, in the presence of *Argiope aurantia* (which fills the niche of *Araneus quadratus*) and *Araneus marmoreus*. *Araneus diadematus* has been successfully introduced to the western hemisphere, but its range here is mainly restricted to north of that of *Argiope trifasciata*. This is as expected—*Araneus diadematus* in the New World should occupy a different range of habitats but the same niche in those colder areas, as the genus *Araneus* is probably physiologically adapted to a cooler climate, *Argiope*, to a warmer. (Compare the ranges of the genera, as described by Levi 1968, 1971.)

Coexistence of araneids: specialization for microhabitat (stratum) or for prey size?

As Bristowe (1958, p. 247) pointed out, there are two groups of araneid spiders in Europe, spring and autumn breeders. Within these two groups one expects to find the species separated by successive increases of 28% in size, reflecting a doubling of prey size, and sufficient specialization for food size only (Hutchinson 1959). Because specialization for season of breeding also results, in spiders, in distinction of the spiders' sizes, the season of breeding may be taken also to reflect specialization for prey size. Luczak (1963) collected ten species of *Araneus* from stands of young pine trees and heather. Here, I analyze her data to test: (1) what fraction of araneid species depend mainly upon specialization for prey size for coexistence (via differences in season of breeding and in size), (2) what fraction of the araneids show a vertical stratification of species and, with age, a change of stratum used (specialization for microhabitat), and (3) whether there is a large residuum of species apparently coexisting by differences along some other, undetermined niche parameter.

In Table 2, I list for these *Araneus* species the length of the adult female spider, the season of breeding, the increase from the size of the next smaller species breeding in that season, and the stratum of vegetation used by immatures (shrub or heather). In the springtime, one would expect to find most obvious the differences among species critical for their coexistence: in spring the spiders are most abundant, most similar in size (the larger fall-breeding species present as immatures), and most

TABLE 2. Ecological differences among the species of *Araneus* found by Luczak (1963) in stands of heather with young pine trees. Sizes of adult female spiders taken from Menge (1866) and Locket and Millidge (1953), the latter the source of data on months of breeding as well. Figures in parentheses are the calculated increase in size from the next smaller species breeding in the same season; the last columns on the right give the location of the small spiders taken by Luczak (1963) by beating the vegetation during Aug. and Sept. 1959. Two species of *Araneus* are excluded because only two specimens of each had been taken by Luczak

| | | Length of adult female, in mm | | | | Location of young collected by Luczak | |
| | | Locket & Millidge | | | Average increase in size | No. in heather/no. in shrubs | Majority in |
Species of *Araneus*	Months of breeding	Range	Midpoint of range	Menge			
A. sturmi	April–June	3–5	4	4.5		16/31	shrubs
A. cucurbitinus	May–July	4–6	5 (25%)	7 (56%)	41%	81/124	shrubs
A. redii	April–May	5.5–7	6.3 (25%)	not given	25%	60/14	heather
A. patagiatus	all year	5–8	6	9		9/11	shrubs
A. adiantus	July–Sept.		6	6		none/8	shrubs
A. marmoreus	Aug.–Sept.	5–8	6.5 (9%)	13 (117%)	63%	2/4	shrubs
A. diadematus	Aug.–Oct.		11 (69%)	15 (15%)	37%	16/25	shrubs
A. quadratus	Aug.–Sept.		12 (9%)	15 (zero)	5%	44/10	heather

compressed in their vertical distribution (due to the presence of only previous years' growth of vegetation). Though data for the spring is not available, it is certain that the largest autumn-breeding species will be smaller than the smallest spring-breeder at that time. I assume that the sizes of the immatures will be isomorphically related to the sizes of conspecific adults, as seems to be true for araneids I have worked with. (Possibly the sexual size dimorphism of spiders causes males and females to represent two ecological "species," males the smaller. Then, one would demand more than 28% difference in size, from Table 2, before one accepts that size is the only significant niche parameter. According to this view, sexual dimorphism may explain some of the high values for difference in size among adult females in Table 2. But, as young spiders do not show sexual size dimorphism, the size differences of immatures may be only 28%; we must remember that the figures in Table 2 do represent only a first approximation to their sizes.)

Table 2 suggests that most araneid spiders coexist by differences related to prey size: season and size of spider. Most species' niches are sufficiently distinguished on the basis of size of spider (and so of prey) alone. Only one medium-sized species, *Araneus patagiatus*, breeds throughout the year, and it also has the most even distribution of numbers of immatures between the two strata, heather and shrubs. This species thus seems to be a generalist which is less efficient at using the limiting resource (MacArthur and Connell 1966, p. 67), and, as such, may depend upon the occurrence of unusual mortality

of (any of seven) specialist species to reduce competition. It must also be able to interfere with the other species whenever they happen to be smaller than itself.

Table 2 shows that the smaller spider species breed, on the average, before larger, except where microhabitat differences (shrub or heather used by immatures) obviate the need. Thus, in spring, *Araneus sturmi* breeds before *A. cucurbitinus*, and, in autumn, *A. adiantus* breeds before *A. marmoreus*, which is before *A. diadematus*. This is contrary to what one expects from Hutchinson (1959). And, if, as seems to be true, the young of smaller species are smaller than the young of larger species, the reason behind any pattern of phenology is obscure.

The three largest *Araneus* species, of the autumn-maturing group, do not show the sufficient differences in size: Locket and Millidge (1953) show more than the 28% size difference between *Araneus marmoreus* and *A. diadematus*, but Menge (1866), Kaston (1948) and my own experience indicate that *A. marmoreus* is smaller than *A. diadematus*, but not by the full 28%. But, since Menge (1866), Kaston (1948) and Locket and Millidge (1953) all indicate that *A. marmoreus* uses a retreat in leaves, usually in damp localities, the coexistence of this species with the other two large species may be due partly to its smaller size and partly to the use of a specialized site for its web.

Luczak (1963) collected large and small specimens of *Araneus* by different methods. She states (p. 203) that in contrast to small specimens of the *Araneus* species "the community of large spiders . . . matures-

cent and adult forms (*A. diadematus* Cl., *A. quadratus* C., *A. marmoreus* Cl.) is distributed in another living space, occupying ecological niches between pine trees." Luczak's data on the distribution of the *small* spiders, Table 2, shows that 61% of the 41 *A. diadematus* were taken from shrubs, but only 18.5% of the young *A. quadratus*. Thus the evidence suggests that these two species of *Araneus* coexist by the use of different sites for webs while immature. That 42.5% more of the young *A. diadematus* use the shrub layer indicates sufficient specialization for stratum, as shown by qualitatively measured web sites in the same way that Reynoldson and Davies (1970) analyzed kinds of food.

The adults of *Araneus diadematus* face competition from the similarly sized *Araneus quadratus* and *Araneus marmoreus*. But, as I have argued above for *Argiope* species, the few individuals which survive to adulthood, and the consequent low number of possible competitive interactions between the species, must allow coexistence of the large *Araneus* species using the same prey resource in the same stratum of the vegetation as adults. *Araneus quadratus* may be considered an ecological equivalent to *Argiope aurantia* (and *Argiope bruennichi*), while *Araneus diadematus* similarly is equivalent to *Argiope trifasciata*.

Vertical stratification and aggression

While vertical stratification has been reported in several insectivores, Morse's work (1968) reveals that much of the vertical stratification of warbler species (MacArthur 1958) must have been due only to the choice of particular song perches by males. Andrews (1971) found vertical stratification in lizards, which also was partly confounded with the use of certain heights by males when displaying. Additionally, Handley (1967) has noted vertical stratification of species of bats. A vertical stratification similar to that of the largest orb-weaving spiders in fields is known to occur between species of the large widow spiders (*Latrodectus*, Theridiidae), which weave three-dimensional webs (Shulov and Weissman 1959; McCrone and Levi 1964; Abalos and Baez 1967). The *Latrodectus* species actively choose their characteristic strata (Szlep, 1966), as do the *Argiope* (Enders 1972). Richter (1970a, 1970b) has demonstrated vertical stratification of errant *Pardosa* species. Nonetheless, my analysis of Luczak's (1963) data suggests that vertical stratification is secondary in importance to specialization for food size, at least for spiders. If the animals specializing for stratum are eating different foods, then vertical stratification may only be a derived phenomenon, secondary to food partitioning. E. Waldorf (1973, unpublished data) finds that, in an evergreen forest herb, different size classes of spiders are located differentially,

according to the vertical distribution of insect size classes.

Murray (1971) suggested that *horizontal* stratification of birds, especially of closely related species, may reduce aggression-eliciting encounters between look-alike males rather than reduce competition for food. Edington and Edington (1972) have suggested that aggression must play a role in spacing within guilds even distantly related birds. In warblers (MacArthur 1958, Morse 1968) and lizards (Andrews 1971), *vertical* stratification also may be the result of aggression (interference) rather than the result of exploitive competition.

Luczak and Dabrowska-Prot (1970) have observed cases of inter- and intraspecific invasion of webs of theridiid spiders, like the invasions of araneid webs reported here. In neither observations do spiders show any sense of the "home" web or any knowledge of the surroundings such as occurs in home ranges of the vertebrates. Generally, the larger spider is dominant. Spiders thus may engage in interference, like carnivorous birds (hawks and owls), which have been reported to devour competitors (Bent 1938, pp. 60, 115, 149, 191, 308, 318) in the course of interference, rather than like passerine birds, which engage in contests of display.

A graded series of invasions of webs is known to occur, within the family Theridiidae, and again among the superfamily Epeiroidea (Kaston 1948) of the order Araneida (spiders). One family of epeiroid spiders (Mimetidae) and several species of conopisthine theridiids (genus *Rhomphaea*) make their living by invading webs of other spiders to eat the "host." Another group of theridiids (genus *Conopistha*) within the Epeiroidea are kleptoparasites which invade the webs of other spiders to eat the prey of the host. Thus, the occurrence of web invasion during the lifetime of web building epeiroid spiders, both theridiid (Luczak and Dabrowska-Prot 1970) and araneid (this report), may originally represent only interference by species specialized in size, season, and stratum. A second step may be the use of physical interference by a generalist species (such as *Araneus patagiatus* or *Araneus cornutus*, distinguishable by breeding all year), as a principal method of survival in a world of specialists. McCook (1889) and Tilquin (1942) noted an affinity for silk structures by spiders ("sericophily"). Once the behavior of searching for structures of silk and invading webs was well-developed, successive arachnophagous and parasitic specialist spider species may have evolved from these generalist species. Thus, competition for space may occur among web-building spiders, though interference with webs. This interference seems based upon similarity of web type, as the vertebrate's aggression may be directed by similarity of visual

and aural appearance of the species. In fact, I have recently found invasion of webs across family lines: *Latrodectus* spiders (Theridiidae) having invaded the webs of *Diguetia* (Diguetidae), a family of distant relation, but with similar three dimensional web structure.

Changes of vertical stratum by insectivores

Changes of the vertical stratum used by an animal at different ages have not frequently been noted. Handley's (1967) data imply that male *Anolis polycelis* lizards must change perch heights as they grow up. Judging from the data presented by Eberhard (1971) and Luczak (1963), the web-building spiders *Uloborus diversus* (Uloboridae) and *Araneus quadratus* may also. I have herein demonstrated that a change of stratum used occurs in *Argiope aurantia*. I recently observed immature and adult *Argiope argentata* in different strata. Perhaps any other geographic replacement of *Argiope aurantia*, which serves as the largest orb-weaving spider in a particular locality, may also change the stratum in which it places its web. Edgar (1971) and Hallander (1970) have shown that errant *Pardosa* spiders (Lycosidae) change the locality of their search for food from within the litter layer to above the litter as they mature. These authors suggest that a change in food may partly explain the change of stratum with increase in size.

Why should changes of stratum occur so often in spiders? Spiders are active predators long before they are fully mature, and the size of the prey taken is correlated with the size of the spider. Therefore, (1) young spiders of larger species are potential competitors with the adults of smaller species, as Hutchinson (1959) pointed out for corixid bugs which have similar life histories, and (2) a change of prey size must occur as the spider increases in size, assuming prey size and spider size are correlated. Should the prey of different sizes occur in different places, a change of the stratum during the life of the spider is understandable. In fact, one might expect the lowest stratum of herbaceous vegetation to have the most insects, especially of the smaller sizes[2] (and so be a preferred habitat for small spiders, as noted in the discussion of the evolution of the niche of *Argiope trifasciata*), while larger, more active flying insects occur higher up, even above the mass of the vegetation. This hypothesized distribution of insects could explain why smaller *Uloborus diversus* (Eberhard 1971) and *Argiope aurantia* build webs lower than do larger conspecifics. This reasoning should also apply to insectivorous reptiles, which change size

[2] More small insects may occur near the ground because individuals from the detritus food chain and those falling from higher up add to those already on the plant at that height.

after leaving the parents. During revision of this manuscript, I discovered that E. Waldorf (unpublished data) studying a woodland perennial herb supported the ideas developed here: arthropods taken on sticky traps show a rise in numbers at higher locations the larger the size of the arthropods. I have suggested that the significant parameters of smaller web spiders' niches may be reduced to prey size alone. From the data presented above, I conclude that large web spiders, in addition, use space as a distinct resource.

MacArthur and Levins (1964) show that searching animals should specialize for habitat while pursuers should specialize for the size of prey. Therefore, the latter occur in arrays of species of different sizes (Rosenzweig 1966). These theoretical considerations imply that the smaller species of araneids are acting as pursuers, since they occur in arrays, while the larger species of araneids are acting as searchers, since they specialize in a particular stratum (microhabitat) when young. The *Pardosa* species of wolf spiders (Richter 1970*a* and *b*, Vogel 1972) also specialize in habitat, and their searching method of hunting is in line with theory. While the fairly large *Latrodectus* species (Theridiidae) also act as searchers (judging from their vertical stratification), it would be of interest to know if smaller species of theridiids occur in sets, as pursuers. That the larger araneids appear to be searchers for prey may be because they are so big they take so large a range of prey sizes that they are unable to expand their food niches vis-a-vis one another by size differences; instead they must show spatial segregation.

It is of some interest that the small araneids appear to be pursuers rather than searchers. Originally, I had anticipated that the use of webs would place them either in a separate category from searchers or pursuers, or as searchers, like filter-feeders that ought to take any size prey once extracted from the fluid. Very tiny prey are regularly ingested by araneids when the web is eaten prior to renewal. However, hindsight suggests that capture of prey is a major struggle for a tiny spider; as the spider becomes larger a larger proportion of its prey will take relatively less energy in actual capture, so the spider spends relatively more energy in making contact with some prey. Thus, a change from a "pursuing" mode of behavior to one of searching may occur in the lives of filter-feeding organisms, and, indeed, in the lives of any organism which retains the same manner of feeding as it increases in size.

27152 to W. F. Blair. K. S. Babu cooperated in rearing spiders, and R. Pulliam, M. Mares, and E. Yensen made helpful comments on draft versions of the paper. H. W. Levi (Museum of Comparative Zoology) has confirmed the identification of the araneid species, and I must also thank C. W. Sabrosky and R. W. Carlson (Smithsonian Institution) and D. Stephens (N. C. State University Extension) for identifying insects.

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