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A COMPARATIVE STUDY OF PHENOLOGY AND DAILY ACTIVITY PATTERNS IN THE WOLF SPIDERS *PARDOSA MILVINA* AND *HOGNA HELLUO* IN SOYBEAN AGROECOSYSTEMS IN SOUTHWESTERN OHIO (ARANEAE, LYCOSIDAE)

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ABSTRACT. We studied the phenology and the daily activity patterns of *Pardosa milvina* Hentz 1844 and *Hogna helluo* (Walckenaer 1837) in replicated soybean fields in southwest Ohio over three years (1994–1996) using pitfall traps. For the phenology study we established an array of five pitfall traps in 12 replicate 0.42 ha fields. These traps were either set for two days at two-week intervals (1994), or for three days at three-week intervals (1995 & 1996), over the field season from May–October on a total of 20 trap dates. We found that *P. milvina* was more common overall, and found evidence for one population peak per year. Numbers of *H. helluo* tended to be lowest in the earlier censuses, and we found evidence for one peak of male activity per year. The immature male and female, and adult female *H. helluo* were larger (based on carapace width) than the immature male and female, and adult female *P. milvina* on most trapping dates. For the circadian activity periodicity study we used two different drift-fence trap designs, both with dry-cup pitfall traps set for two or three days and checked at 12 h intervals. For three sampling periods in 1994 we found *H. helluo* to be more frequently trapped at night, and for two sampling periods *P. milvina* was more frequently trapped during the daylight hours.

Keywords: Agroecosystem, *Pardosa*, *Hogna*, phenology, soybean, circadian

Spiders are common components of agricultural ecosystems wherever found (Luczak 1979; Young & Edwards 1990). Because spiders often attain high population densities in crop systems, there exists the potential for pest insect population suppression (Riechert 1999; Sunderland 1999). For this reason, there has long been interest in the population dynamics of spiders in agricultural ecosystems (Whitcomb 1967; Breene et al. 1993; Draney 1997; Greenstone & Sunderland 1999), and the ways in which crop management practices impact spider abundance and diversity (Bishop & Riechert 1990; Balfour & Rypstra 1998; Rypstra et al. 1999). Despite this interest, there have been relatively few studies which focus on the biology of specific spider taxa.

Wolf spiders (Araneae, Lycosidae) are one of the most abundant components of the spider community in agroecosystems (LeSar & Unzicker 1978; Luczak 1979; Young & Edwards 1990; Bishop & Riechert 1990). One wolf spider genus in particular, *Pardosa* C.L. Koch 1847, is a relatively well-studied inhabitant of agroecosystems across the northern hemisphere (e.g., Nyffeler & Benz 1988; Nyffeler & Breene 1990; Marshall & Rypstra 1999 a, b; Kiss & Samu 2000; Samu et al. 1998). The relatively large body of research on *Pardosa* is probably a result of its relatively high abundance in agricultural fields. The reasons for *Pardosa*'s conspicuous success in the structurally-simple and seasonally-barren habitats provided by crop fields may lie in an evolved adaptation to life in riparian corridors and other periodically flooded habitats, which would pre-adapt them to the annual cycle of disturbance found in most row-crop systems (Luczak 1979; Wissinger 1997; Marshall & Rypstra 1999 a, b).

We have found *P. milvina* Hentz 1844 to be the most common vagrant spider in the

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fields in which we work, and have observed densities of over 100/m^2 (Marshall & Rypstra unpublished data). We have also found the ecologically-divergent *Hogna helluo* (Walckenaer 1837) in these fields, but at much lower densities. We have found that these two spider species use the same microhabitats in similar ways (Marshall & Rypstra 1999 b), yet their behavior (Walker et al. 1999 a, b) and ecology (Marshall et al. 2000) make for a revealing contrast. *Pardosa milvina* is much more vagile than *H. helluo* (Walker et al. 1999 a), is more of a habitat generalist (Marshall & Rypstra 1999 a, b), and lives in the agricultural fields year-round (Marshall & Rypstra 1999 b). In addition, *P. milvina* exhibits complex anti-predator behaviors when exposed to *H. helluo*-associated cues (Persons et al. 2001), which suggests a shared evolutionary history.

In this paper we report on the population dynamics of *P. milvina* and *H. helluo* in an array of 12 replicate soybean fields as revealed by a study of pitfall trap samples. We conducted our studies in fields managed for research into the impact of tillage regime on the spider community structure of the fields. We present data on the impact of tillage regime on spider numbers elsewhere (Marshall & Rypstra 1999 b).

METHODS

Field site.—The soybean plots used in this study are located at the Ecology Research Center of Miami University in Butler County, Ohio, USA. The data were conducted within 12, 0.42 ha soybean monoculture plots. The plots are in a 2 by 6 rectangular array oriented in a north-south direction. Each plot measures 60 x 70 m with a 15 m mowed grassy strip border separating them from one another and the surrounding habitats (Kemp & Barrett 1989). Six of the plots were planted and maintained using conventional tillage practices, and the other six were managed using conservation tillage practices (see Marshall et al. 2000 for details). In 1994 this tillage regime was combined with a "no-herbicide treatment" in half of the plots for a total of four treatments. This elaboration was dropped in subsequent years (1995 & 1996). Tillage treatments were assigned randomly the first year and maintained between years in the same plots. The conventional tillage plots were tilled in early May. Soybeans were planted in late May. Pre-emergence herbicides were applied immediately after planting. In early June post-emergence herbicide was applied to the conservation tillage plots to control ragweed. The conventional tillage plots were again cultivated in July. No insecticides were applied to any plot at any time.

Phenology.—We used a pitfall trap that includes an elevated wooden cover to exclude rain and vertebrates (Cady & Sugg 1998). We placed five traps in each of 12 replicate plots. In each plot there was one trap in each corner, placed approximately 10 m from each side, and one trap in the center of the plot. Each trap contained several cm of a 50/50 ethylene glycol/water solution.

In 1994 the traps were set at two week intervals for 9 two-day trapping periods. In 1995 and 1996 we ran the traps at three week intervals for 5 and 6 three-day trapping periods respectively. We counted and measured the size of all the *H. helluo* and *P. milvina* under a dissecting microscope to the nearest 0.1 mm using an ocular micrometer. We used carapace width as an estimator of spider body size (Hagstrum 1971; Marshall & Gittleman 1994).

In our fields we also have a small number of *P. saxatilis* Hentz 1844 and *H. aspersa* (Hentz 1844). These two taxa may be confused with *P. milvina* and *H. helluo*, respectively, when immature. Because these two congeners were rare in the soybean agroecosystem (< 1%, based on abundances of the easily-identified adults) we categorize all immature *Pardosa* as *P. milvina* and all immature *Hogna* as *H. helluo*.

Daily activity periodicity.—We used drift fence traps in 1994 to test for differences in activity periods in *H. helluo* and *P. milvina*. The traps were constructed of 25 cm wide sheets of metal 3.05 m long. At 0.75 m intervals along each side of the fence 250 ml plastic cups were buried flush with the ground surface against the fence. Between 2–6 August we set up two drift fences approximately 18 m long. We placed one in a conservation tillage plot and the other in a conventional tillage plot. During the August trapping period each drift fence trap had a total of 48 cups (24 on each side). Between 6–9 September and 3–6 October we ran six smaller trap arrays in six plots, three in conventional tillage plots and

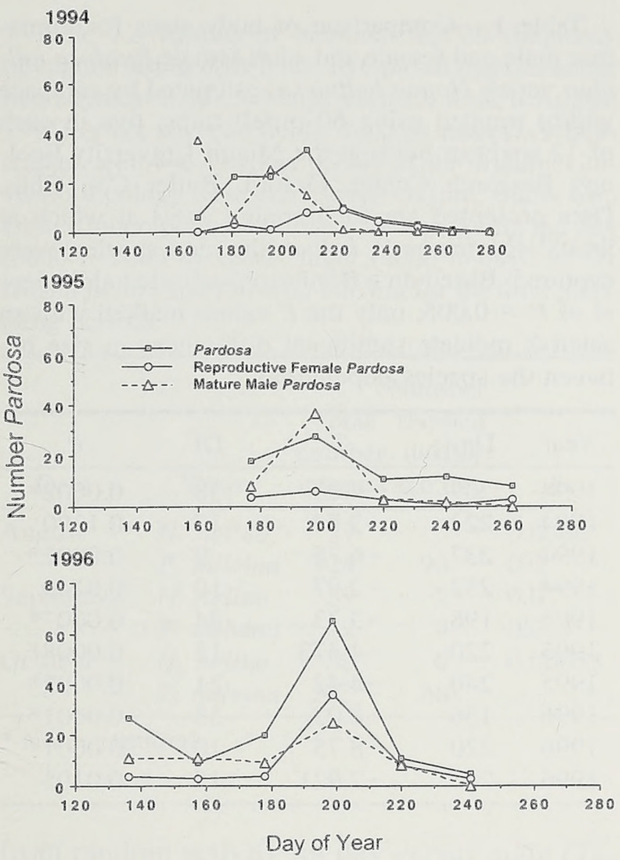

Figure 1.—Total *Pardosa milvina* collected in 60 pitfall traps set in 12, 0.4 ha soybean fields (five per field) at the Miami University Ecology Research Center, Oxford, Butler Co., Ohio. "*Pardosa*" refers to immature and non-reproductive adult female *P. milvina*, "Reproductive Female *Pardosa*" refers to adult female *P. milvina* carrying eggs or spiderlings, and "Mature Male *Pardosa*" refers to sexually mature male *P. milvina*.

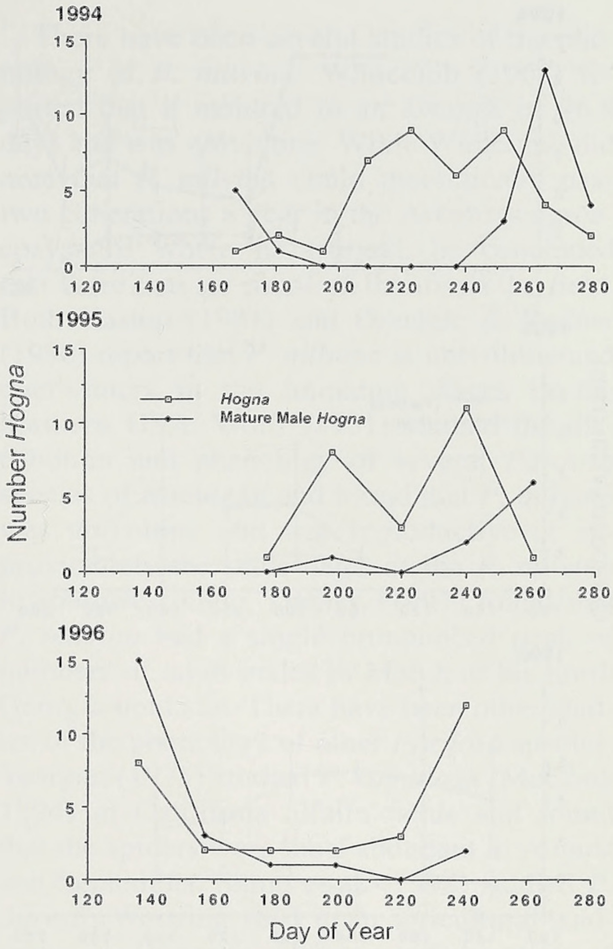

Figure 2.—Total *Hogna helluo* collected in 60 pitfall traps set in 12, 0.4 ha soybean fields (five per field) at the Miami University Ecology Research Center, Oxford, Butler Co., Ohio. "*Hogna*" refers to all immature and adult female *H. helluo* and "Mature Male *Hogna*" refers to adult male *H. helluo*.

three in conservation tillage plots. Each trap array was approximately 9 m long and each had a total of 24 cups, 12 to a side. At all dates each drift fence trap array was oriented row-wise (east-west) at an arbitrarily selected spot in the plot. Traps were set in the evening on the first day (ca. 2000 h) and all cups checked at 12 h intervals thereafter. Each time the trap was checked any *H. helluo* and *P. milvina* captured were counted and released on the opposite side of the trap from which they were captured. In August we checked the traps four times for two sampling days, in September and October we checked the traps 6 times for three sampling days. We analyzed the data using a binomial test for an expected proportion of 0.5 trapped during the day versus night sampling period for each species to test the null hypothesis of no difference between the total numbers trapped during the day versus night. All spider collections made during this research are in the collections in the Hefner Museum of the Department of Zoology, Miami University.

RESULTS

Phenology.—We found that *P. milvina* was overall more common than *H. helluo* (Figs. 1, 2). *Pardosa milvina* exhibited a consistent population peak around Julian date 200 (in mid June). Captures of both immature and adult *P. milvina* peaked around this date in all three years, as did the numbers of female *P. milvina* carrying eggs or spiderlings.

The population trends for *H. helluo* are less clear. In general there were greater numbers trapped both early and late in the year than during mid-season. We were unable to assess

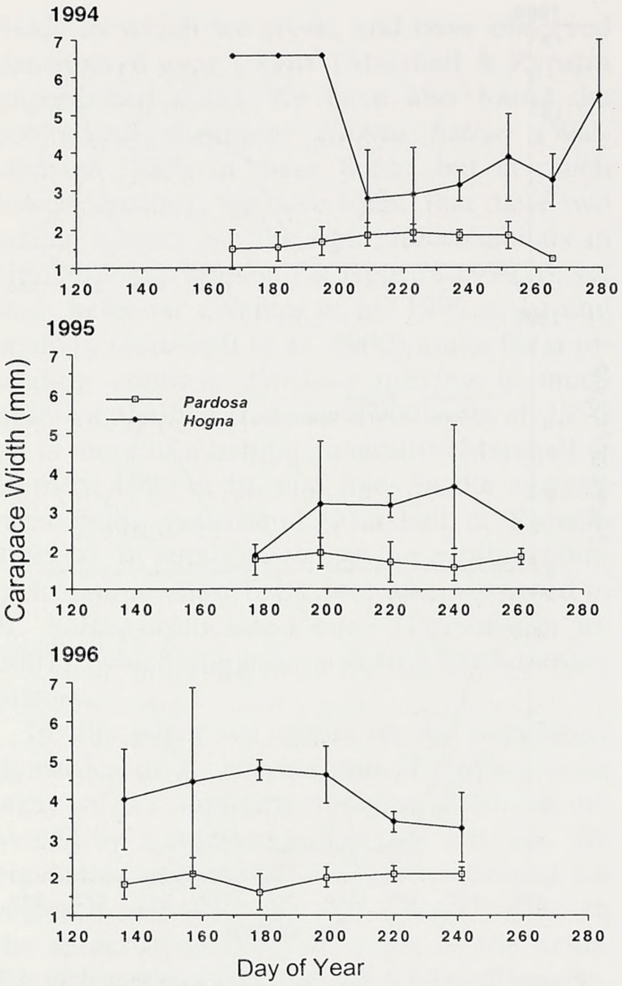

Figure 3.—Comparison of carapace widths for all immature and adult female, and all immature male *Hogna helluo* and *Pardosa milvina* collected at each date in 12, 0.4 ha soybean fields at the Miami University Ecology Research Center, Oxford, Butler Co., Ohio. Expressed as means ± 1 SD.

Table 1.—Comparison of body sizes for immature male and female and adult female *Pardosa milvina* versus *Hogna helluo* (as estimated by carapace width) trapped using 60 pitfall traps, five in each of 12 soybean fields at the Miami University Ecology Research Center, Oxford, Butler Co., Ohio. Data presented are for trapping dates at which at least 3 specimens *H. helluo* (the rarer species) were captured. Based on a Bonferroni-adjusted alpha level of $P = 0.005$, only the P values marked with an asterisk indicate significant differences in size between the species populations.

Year	Day	T	Df	P
1994	209	−4.05	38	0.0002*
1994	223	−2.74	17	0.1390
1994	237	−6.75	9	0.0001*
1994	252	−2.97	10	0.0140
1995	198	−3.73	34	0.0007*
1995	220	−4.478	12	0.0008*
1995	240	−4.42	21	0.0002*
1996	136	−8.03	33	0.0001*
1996	220	−8.75	10	0.0001*
1996	241	−2.921	15	0.0105

female reproduction since adult female *H. helluo* with egg sacs or spiderlings were rarely found because they take refuge in burrows when reproductive (Dondale & Redner 1990; Walker et al. 1999 b). There seemed to be a uniform increase in the numbers of adult males in the fall and spring. This indicates that males may mature at the end of the summer and over winter as adults, or over winter as subadults that mature in the spring. The unimodal timing of sexually mature males indicates that *H. helluo* may be seasonal in its breeding.

We were able to compare mean body size of the trapped populations of the immature stages of both sexes and adult females between *H. helluo* and *P. milvina* (Fig. 3). We arbitrarily selected a minimum of three of the rarer species on a given trap date as a cut-off for inclusion in a statistical comparison of carapace widths. Using these criteria, we were able to make a comparison on 10 out of the total of 20 trapping dates over the three years (Table 1). Because we were performing replicate statistical tests (10) and because our selected alpha level of $P = 0.05$ means that 1 in 20 tests could indicate significant differences based on chance alone, we used a simultaneous Bonferroni adjustment procedure. This entailed dividing the selected alpha level by the number of tests performed. Thus, our adjusted alpha level was now $P = 0.005$. Using these criteria, we found that the *H. helluo* we trapped were significantly larger than the *P. milvina* on 7 of the 10 dates for which this test was performed.

Daily activity periodicity.—There was an obvious trend for *H. helluo* to be more active at night, and *P. milvina* during the day. There were a total of 98 *H. helluo* and 138 *P. milvina* captures over the three sampling dates. Some of these were likely to be recaptures, but during pilot studies when we marked *P. milvina*, we had recapture rates approximating 5%. No *P. milvina* were captured during the October trapping period. For the three dates for *H. helluo* there was a significant deviation

Table 2.—Results of binomial test on frequency of capture using drift-fence live pitfall traps in either two soybean fields, 48 cups each (2, 4, & 6 August 1994) or six soybean fields, 24 cups each (7–9 September and 4–6 October 1994) at the Miami University Ecology Research Center, Oxford, Butler Co., Ohio. Data reported are total captures during the day (0800 h–2000 h) versus night (2000 h–0800 h) for *Hogna helluo* and *Pardosa milvina* for the three sampling periods.

Date	Taxon	Total number trapped	Number trapped during the day	*P*
August	*H. helluo*	27	5	0.0006
	P. milvina	124	90	0.0
September	*H. helluo*	39	2	0.0
	P. milvina	12	9	0.054
October	*H. helluo*	30	6	0.00055
	P. milvina	NC*	NC	

* None captured.

from random activity for day versus night (Table 2). For *P. milvina* there was only a significant deviation for one of the two dates for which there were data (Table 2).

DISCUSSION

Pardosa milvina and *H. helluo* were both common elements of the spider fauna of the soybean fields under study. All life stages of both species are found in the fields throughout the summer growing season. *Pardosa milvina* overwinters in the fields as subadults, and can even be observed active in the fields in midwinter on warm days (December–February; S. Marshall, pers. obs.). The circannual pattern for *H. helluo* is less clear, other than the higher numbers of adult males trapped at the beginning and end of the field season. It may be that *H. helluo* mate in the fall or early spring, with females producing successive egg sacs during the summer. The comparison of body sizes of the adult female and subadult female and male population did not reveal any strong pattern. We had hoped to see evidence of growth of the spiders through the year as increased mean body size for the trapped population. We are left to guess about the number of generations of *H. helluo*. Based on data from laboratory rearing studies (R. Balfour unpublished data) we tentatively conclude that *H. helluo* has at least a two year life cycle.

There have been several studies of the phenology of *P. milvina*. Whitcomb (1967) reported that it matured in an average of 96.8 days and was univoltine. While Whitcomb did note that *P. milvina* could theoretically pass two generations a year in the Arkansas agroecosystems where he worked, he concluded that there was no proof of this from the field. Both Kaston (1981) and Dondale & Redner (1990) report that *P. milvina* is univoltine and overwinters in the immature stages in the northern USA. Wolff (1981) studied the distribution and phenology of several *Pardosa* species of Michigan and found that *P. milvina* was univoltine and was reproductive at approximately the same dates as the *P. milvina* in southwest Ohio. Draney (1997) found that *P. milvina* had a single pronounced peak of numbers of adult males in March at his north Georgia field site. There have been other studies of the phenology of other *Pardosa* species. Yeargan (1975) studied *P. ramulosa* (McCook 1894) in California alfalfa fields and found that the spiders were most abundant in August and September. Samu et al. (1998) studied *P. agrestis* Westring 1861 in an agricultural landscape in Hungary. Using a combination of suction sampling and pitfall traps they found evidence for two peaks in abundance during the summer. They also observed that *P. agrestis* overwintered as subadults. They generated two hypotheses to explain the pattern: 1. There are two generations a year, and 2. the two peaks represented the maturation of early and late season cohorts of spiderlings. Buddle (2000) studied the phenology of *P. moesta* Banks 1892 and *P. mackenziana* Keyserling 1877 in a deciduous forest ecosystem in Alberta, Canada. He also found that *Pardosa* overwinters as a subadult, and found a single peak in the abundance of juveniles. Based on field enclosure studies he proposed that these two *Pardosa* species may take two years to mature.

In addition to the pitfall trap returns we report on here, we also have direct-observation hand-census data for the same fields. Using hand census techniques we found evidence for two population peaks in the field. The second peak occurred around the 270th day of the year, in late August (Marshall & Rypstra 1999 b). This was after we had closed the pitfall traps for the season in the present study. We did not record adult males in our hand censuses, nor did we record the size of the spiders trapped. The time intervals between the observed population peaks were approximately 65 d (1995), 70 d (1996) and 90 d (1996). Would this be long enough for a *P. milvina* spiderling to mature and produce young of its own? The only data we have for time to maturation for *P. milvina* are from Whitcomb's 1967 study, which reported a maturation time of 86.1 d for males (n = 8) and 107.5 d for females (n = 9). It is always hard to interpret laboratory data on time to maturation in spiders because factors such as temperature and feeding regime can have a tremendous impact on the duration of each instar. However, the times Whitcomb reports are long enough to suggest that the length of time between population peaks we observed in the previous study (Marshall & Rypstra 1999 b) are not the result of an over-wintering cohort of immature spiders giving rise to a summer cohort which in turn produced the over-wintering cohort for the following year.

In contrast to the relatively well-studied *Pardosa*, the phenologies of *Hogna* (formerly *Lycosa*) species wolf spiders have not been studied in agroecosystems. Nappi (1965) studied the mating behavior of *H. helluo* in natural habitats in Connecticut. He reports on his observations of the frequency of adult males and females over three years (1961–1963). His data show a peak in numbers for both sexes in mid-summer (approximately late June-early July). This unimodal peak at mid-summer is the opposite of what our traps revealed for the adult males. On the other hand, Kaston (1981) remarking on *H. helluo* in natural ecosystems in Connecticut, noted that females may be found throughout the year, and males in the summer months. Kaston believed that *H. helluo* mates in the spring. He also inferred that the females overwinter as adults and males as immatures. This is not in agreement with our data, where mature males seem to be more prevalent in the late and early season. An alternative hypothesis is that the males are merely more active at this time, which could also account for their prevalence in the pitfall trap samples.

For our 12 h trapping interval studies we found clear evidence that *P. milvina* is most active during the day, and *H. helluo* at night. We have observed both species to be on the soil surface or in the vegetation throughout the day and night, but each species is evidently most mobile at different times of the day. Other researchers have also noted that *Pardosa* species are conspicuously active during daylight hours. Dondale (1977) found that the *P. saxatilis* in an Ontario meadow were most active between 1100 and 1600 h. Yeargan (1975) found that the *P. ramulosa* he studied in alfalfa fields were most active between 0700 and 1700 hours. In contrast, workers in the southern US have noted nocturnal foraging activity by *P. milvina*. Whitcomb et al. (1963) noted that they observed spiderlings active on cotton plants at night in Arkansas. Hayes & Lockley (1990) observed *P. milvina* with prey during nocturnal surveys of the wolf spider fauna of cotton fields in Mississippi. We have also noted nocturnally active *P. milvina*, observing large numbers of spiders sitting on the upper surface of the leaves of the soybean plants nocturnally during warmer weather (overnight temperatures > 22 °C).

Both *H. helluo* and *P. milvina* are successful colonists of soybean agroecosystems, despite the fact that they exhibit such divergent ecological strategies. Of the two spiders, only *P. milvina* might be viewed as a true "agrobiont" (Luczak 1979), or a species that resides in the fields year-round. *Hogna helluo* may need to recolonize the fields each spring after the cropping manipulations are over and the crop plants start to develop (Marshall & Rypstra 1999 b).

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