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Rearing studies with a spider exhibiting a variable phenology: no evidence of substantial genetic variation

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Summary

Previous research has uncovered variation in life history phenology within populations of the filmy dome spider, *Neriene radiata* (Walck.). Some hatchlings that emerge from egg sacs laid in the spring overwinter as juveniles and mature the next year, whereas other progeny of spring-maturing adults develop rapidly and mature before autumn (Wise, 1976, 1984). Rearing experiments were conducted to determine whether or not a genetic polymorphism may contribute significantly to the variable phenology. The results provided no evidence of substantial genetic variation in developmental rate in *N. radiata*. The major factor determining the course of development appears to be the time of the season that hatchlings emerge from the egg sac.

Introduction

Substantial life history variation exists within populations of the filmy dome spider *Neriene radiata* (Walckenaer) [= *Linyphia (Prolinyphia) marginata* C. L. Koch] (Araneae: Linyphiidae) in Michigan and Maryland, USA (Wise, 1976, 1984). These spiders overwinter as juveniles, maturing and mating during May and June. Eggs hatch a few weeks after being laid. In early July very few adults remain, and the population consists almost entirely of spiderlings that have recently emerged from egg sacs. Hatchlings that appear during June and July have two different fates: (1) Some develop slowly, overwinter as late-stage juveniles, and mature the following spring; (2) Others develop rapidly, reproduce by August or September that year, and then die before winter. Their progeny overwinter as earlier-stage juveniles that mature later the following spring, before summer. Filmy dome spiders that complete a generation within one season mature at a smaller size and have a lower fecundity than the progeny of spring adults that develop more slowly and overwinter before maturing.

I report here the results of rearing studies designed to provide preliminary evidence of whether or not this variable phenology is an evolved genetic polymorphism. Several rearing studies with other spiders have uncovered substantial variation in growth and development under controlled laboratory conditions (Browning, 1941; Eason, 1969; Levy, 1970; Reed & Witt, 1972; Ramousse, 1973; Jackson, 1978). Breeding studies with one species have demonstrated that offspring of a female may be either fast or slow developers, resulting in either annual or biennial life cycles (Tretzel, 1961 — cited by Toft, 1976). Evidence in other spiders of variable developmental rates under laboratory conditions suggested the hypothesis that the mixture of slow and rapid developers in populations of *N. radiata* reflects a high amount of genetic variance maintained by balancing selection associated with a heterogeneous environment. In such models (e.g. Hedrick, 1983) rapid development is not consistently favoured because unpredictable environmental changes alter the relative fitnesses of rapidly and slowly developing genotypes. For example, in a constant environment alleles promoting rapid development should have a selective advantage because they reproduce at a faster rate. Rapidly developing genotypes would be favoured, even though they mature at a smaller size and thus have a lower fecundity than the other progeny of spring adults, which overwinter before maturing (Wise, 1984). However, unpredictable temporal variation in spiderling survival could select against rapid development in some years. Genes promoting rapid maturation overwinter in smaller juveniles than do genes that favour slower rates of development, and smaller stages of the filmy dome spider and other linyphiids are more susceptible to low temperatures than later stages (Martyniuk & Wise, 1985; Buche, 1966 — cited by Toft, 1976). Younger stages of spiders are also more vulnerable to prey shortages (e.g. Deevey, 1949; Turnbull, 1962), which may vary more unpredictably, and may be more severe, later in the season. Thus sufficient fluctuation in limiting factors, particularly those that affect summer-maturing spiders and their progeny, might maintain a genetic polymorphism for developmental rate in *N. radiata*.

Indirect evidence of genetic variation derived from laboratory rearings potentially suffers from two problems of interpretation: (1) differences may not reflect genetic variation, but instead, uncontrolled environmental variation in the laboratory; (2) the variation may be primarily genetic, but may only be expressed in a type of stressful environment that characterises the laboratory, not the environment in which the species has evolved. I removed this latter problem of interpretation by rearing *N. radiata* hatchlings under conditions of temperature, humidity, and photoperiod that were as close to natural as feasible, and at a super-abundance of prey. The other criticism of laboratory rearing studies can be answered only by measuring genetic variation directly, i.e. by comparing developmental rates of half-sibs and full-sibs (Falconer, 1981). However, direct measurement is needed only if preliminary rearing studies uncover substantial phenotypic variation. Disappearance of the phenotypic variation when animals are raised under natural conditions constitutes strong evidence that the variation observed in nature does not reflect a genetic polymorphism maintained by natural selection.

Methods

Spiderlings that had emerged from egg sacs deposited by spring-maturing females were reared under similar physical conditions, as close to natural as possible, and at different controlled feeding levels. Food supply was varied in order to determine whether

or not expressed genetic variation is a function of feeding rate, and also to determine the response of the developmental programme to food shortages. The research was conducted in 1982 with a population of *N. radiata* at the Patuxent Wildlife Research Center, Prince Georges County, Maryland, USA. Further description of the study site and the biology of *N. radiata* appears elsewhere (Wise, 1984).

Mature females were collected during May and June and were placed in individual jars on a covered, screened porch in the forest at Patuxent. The spiders deposited an egg sac within several days after being collected. Each egg sac was removed and placed in a similar jar at 85% RH. After approximately 2-3 weeks, hatchlings emerged and constructed a communal web. Within a few days after emerging, spiderlings to be reared were removed and isolated in 2.2 × 9.5 cm glass vials with a moistened plaster of Paris bottom.

I conducted three rearing experiments, each with hatchlings from sacs laid at a different time during the 1982 spring reproductive period. Hatchlings will be referred to as stage 1, which is actually the second instar, the first moult having occurred in the egg sac. Experiment 1 started with 164 progeny of 7 females that had been among the first to mature that spring. Similar numbers of offspring of each female were randomly assigned to three different feeding treatments: low (1 fruit fly (*Drosophila* sp.)/3.5 d), medium (1 fly/d) and high (3 flies/d). Feeding started 3 June. Due to their relatively small size, spiders in stages 1 and 2 were fed recently killed flies. These stages were passed in the vials on the screened porch. Each stage-3 spider was transferred to its own cage of 20 × 22 mesh (*c.* 72 openings per sq. cm) aluminium insect screening with a top of fine-meshed nylon cloth. The cages, 15 cm high and 8 cm in diameter, were placed in *N. radiata*'s microhabitat on the forest floor. Feeding continued with living flies.

Experiments 2 and 3 utilised hatchlings from the end of the spring reproductive period. Logistics were similar to those of Experiment 1, except for two modifications designed to increase the number of different families represented by spiders that reached maturity. The first modification was elimination of the intermediate feeding level. The second was a change in the container used to house the stage-3 and older spiders. This latter change was prompted by the large

Exp. No.	Starting date	Different mothers	Hatchlings isolated	Matured	Immature
1	3 June	7	164	63	1
2	1 July	10	186	1	64
3	15 July	12	241	0	78

Table 1: Developmental fates of progeny of early-spring maturing females (Exp. 1) and of offspring of females that matured later in the spring (Exps. 2 and 3). Given are the numbers of offspring that had matured, or that were still immature and alive, by mid-September. By this time of the season no filmy dome spiders were moulting to maturity in the natural population (Wise, 1984). Feeding continued through October, and none of the progeny that were immature in mid-September had matured by the end of the season.

	Mean	S.D.	S.E.
Time to stage 3 (days):			
Low prey	27.4	5.04	0.91
Medium prey	25.2	4.39	0.75
High prey	24.0	3.93	0.61
Age at maturity (days):			
Low prey	67.7	4.91	1.27
Medium prey	60.7	4.57	0.93
High prey	58.6	4.91	1.00
Size of tibia at maturity (mm):			
Low prey	2.22	0.092	0.025
Medium prey	2.30	0.181	0.037
High prey	2.42	0.179	0.037

Table 2: Effects of food supply upon developmental rate and size at maturity, Exp. 1. Food supply significantly affected the time required to reach stage 3 ($p < 0.05$, 1-way ANOVA). Two-way ANOVA (sex × food supply) of the spiders that reached adulthood revealed that food supply significantly affected age at maturity, defined as days from emergence from egg sac to adult moult ($p < 0.001$); and size, measured as length of the fourth tibia ($p < 0.01$). Differences between males and females were not statistically significant ($p > 0.7$); therefore, statistics presented here are for the sexes pooled.

number of spiders (42) that unaccountably had disappeared from the wire cages during Experiment 1. For the last two experiments, the 3rd stage juveniles were transferred to 240cc jars that had a wire framework inside for web attachment. The tops were covered with fine-meshed nylon cloth. These jars were kept on the covered porch at Patuxent and were periodically sprayed with water. Monitoring with thermistor probes confirmed that temperatures in the jars were similar to those at web sites in the forest. Experiment 2 started 1 July with 186 progeny of 10 females. The third experiment began two weeks later with 241 recently emerged offspring of 12 females.

In all three experiments rearing continued until all spiders had matured or died, or until the end of the season.

Results and Discussion

The developmental fates of the progeny of early- versus late-spring maturing females were strikingly different. With the exception of two individuals, all spiders that hatched at the same time of the season had similar developmental patterns. Those from the earliest egg sacs matured by August, whereas those that emerged from egg sacs laid later were still immature at the end of the season (Table 1). They had not matured even though adequate time for developing to adulthood was available (Wise, 1984). It might be argued that part of the difference in developmental fates resulted from different rearing conditions. Spiders ≥ stage 3 were reared in cages on the forest floor in Experiment 1, whereas these stages were raised on the porch in the last two rearing experiments. Although the porch might have been sub-optimal compared with the cages, this is unlikely for two reasons: (1) many field-collected spiders of all stages were reared to maturity on the porch as part of a related study (Wise, 1984); (2) I have reared filmy dome hatchlings to maturity under entirely artificial laboratory conditions (unpubl. data).

As is true of other spiders studied to date (e.g. Browning, 1941; Jones, 1941; Deevey, 1949; Turnbull, 1962, 1965; and several other studies), rate of feeding also affected developmental rate of *N. radiata*. Spiders receiving the low amount of prey in Experiment 1 required approximately a week longer to mature than those in the other two feeding treatments, and tended to mature at a smaller size (Table 2). Availability of prey also affected rates of development and growth in Experiments 2 and 3 (Table 3). However, as in the first experiment, increasing the food supply did not alter the basic developmental pattern. The only exception was the one spider in Experiment 2 from the high-prey treatment that had matured by the end of the season (Table 1).

Variation in developmental rate within a feeding treatment was relatively small, as indicated by the low standard deviations of age at maturity (Table 2) and rates of development to the first two stages (Tables 2, 3). Such low innate variation suggests that this population possesses small amounts of genetic variance in developmental rate. ANOVA did uncover some statistically significant differences between offspring of different females in developmental rate and size. Though possibly reflecting genetic variation, these differences probably result primarily from maternal effects, particularly since sizes of egg and hatchling are correlated in *N. radiata* (Wise, 1984). Even if all of the unexplained variation in Experiments 1-3 did result from genetic differences, this amount of variation in developmental rates is inadequate to explain the majority of the variation in phenology observed in natural populations of *N. radiata*. The presence of both slow and rapid developers from egg sacs laid at the same time of the season would have led to the conclusion that genetic variation contributes significantly to the developmental variability observed in natural populations. The absence of such variation is strong evidence that the variable phenology observed in natural populations of *N. radiata* does not result from a genetic polymorphism maintained by natural selection.

The lack of evidence for substantial genetic variation in developmental rate suggests that directional selection has favoured genotypes capable of rapid development in this population of *N. radiata*. Even spiders fed at the low rate in Experiment 1 continued to develop, though more slowly than those receiving abundant prey. Opposing selective pressures have not led to the evolution of a developmental genetic polymorphism, as apparently has occurred in some insect species (e.g., Campbell, 1966; Morris & Fulton, 1970; Giesel, 1976; Istock *et al.*, 1976; Tauber & Tauber, 1976, 1981).

One might argue that the *N. radiata* population could have consisted of two genetic strains that differed markedly in rates of development, and that the experimental design utilised in this research would have failed to detect such a situation. Suppose that summer-maturing adults produce offspring that mature early the next spring. Hatchlings in Experiment 1 would be the offspring of such rapid developers and would complete two generations per year. Also suppose that hatchlings from late-spring maturing females (Experiments 2 and 3) comprise a slow-developing strain that requires a full year to mature, not becoming adult until late the following spring. Such hypothesised strains would have to be genetically isolated, perhaps even sibling species, because any gene exchange should lead to a high genetic diversity in developmental rate within a sample at one time of the season. The absence of evidence in this study for such genetic diversity, however, does not suggest the presence of sibling species. Other observations indicate it to be unlikely that populations of filmy dome spiders consist of two reproductively isolated groups. For example, two distinct peaks of adult abundance do not occur during the spring (Wise, 1984). Furthermore, early-spring maturing females and males do not appear to be noticeably smaller than adults later in the spring (pers. obs.). Adults of both sexes live in the laboratory for many weeks, with females continuing to lay viable egg sacs. It is thus likely that some early-spring maturing spiders live long enough to mate with late-spring maturing spiders, most of which are probably the progeny of the previous year's summer adults (Wise, 1984). All this evidence considered together makes it improbable that *N. radiata* populations consist of two genetically isolated strains that differ in developmental rate.

The results of this study corroborate the conclusion, based upon detailed examination of natural populations, that *N. radiata*'s variable phenology is environmentally induced, resulting mainly from differences in the timing of egg-laying by the spring-maturing females (Wise, 1984). Early in the season all *N. radiata* hatchlings developed rapidly (Experiment 1). However, those hatching from eggs laid at the end

	Experiment 2			Experiment 3		
	Mean	S.D.	S.E.	Mean	S.D.	S.E.
Age at stage 2 (days):						
Low food	14.9	5.28	0.60	14.1	4.76	0.47
High food	12.2	2.64	0.30	12.8	2.90	0.30
Size of tibia at stage 2 (mm):						
Low food	0.41	0.04	0.005	0.44	0.04	0.004
High food	0.42	0.04	0.005	0.45	0.04	0.004
Age at stage 3 (days):						
Low food	32.7	8.07	0.95	31.9	7.90	0.90
High food	23.2	3.77	0.41	24.3	3.84	0.46
Size of tibia in Sept (mm):						
Low food	1.22	0.204	0.030	1.13	0.199	0.032
High food	1.41	0.163	0.040	1.27	0.103	0.017

Table 3: Effects of food supply upon rates of development and growth, Exps. 2 and 3. Increasing the food supply significantly increased the rate of development as measured by the time required to reach stage 2 ($p < 0.05$) and stage 3 ($p < 0.001$). Differences between feeding treatments in the size of stage-2 spiderlings were also statistically significant ($p < 0.05$). Sizes of juveniles in September at ages of 77 days (Exp. 2) or 69 days (Exp. 3) also differed significantly between feeding treatments ($p < 0.001$). Levels of statistical significance are based upon the F statistic or Welch statistic (for unequal variances) of 1-way ANOVA.

of the spring-maturing females' reproductive period (Experiments 2 and 3) had not reached maturity by the end of the season, even though adequate time for developing to adulthood was available. This result supports the conclusion that a developmental switch occurs sometime in the middle of the summer (Wise, 1984), and that it is an example of developmental conversion (Smith-Gill, 1983). The variable phenology of the filmy dome spider is not a genetic polymorphism, but is, in Smith-Gill's terminology, an environmentally induced polymorphism that results from specific environmental cues causing a shift from one developmental programme to another.

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