Differences in maturation rates of *Schizocosa ocreata, Schizocosa rovneri,* their F_1 and F_2 hybrids and backcross progeny (Araneae: Lycosidae)

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Summary

Schizocosa ocreata and *Schizocosa rovneri* are very similar to each other in morphology, ecology and rate of development. When given a variety of temperature:light regimes, they respond in an essentially identical manner. Their reciprocal F_1 hybrids showed a slightly slower development time, given a warm LD 12:12 environmental regime. The F_1s did not mature at all in regimes involving longer dark cycles and/or cooler temperatures. F_2 hybrids took longer to mature than the F_1 hybrids in a warm LD 12:12 regime. Backcross progeny were more similar to the parental populations than to either the F_1s or F_2s. Differences in the hybrids indicate a degree (although small) of genetic incompatibility in the parental species populations. There were no apparent differences in viability at other stages of the life cycles.

Introduction

The growth and development of spiders have been studied by a variety of researchers, especially with respect to life histories (Jackson, 1978; Workman, 1978, 1979; Edgar, 1972; Eason, 1969; den Hollander, 1971; Van Dyke & Lowrie, 1975), feeding requirements (Greenstone, 1979; Edgar, 1969, 1970), and embryological development (Austin & Anderson, 1978; Vachon, 1957; Eason, 1969).

There have been fewer experimental studies examining the effect of environmental conditions on the rate of maturation of spiders. Hagstrum (1970) found that *Tarentula kochi* Keyserling matured in the fall of their second year in response to shorter day length. He found that the spiders did not require a period of lower temperature before the final moult. The rate of development was correlated with temperature, as stadia were 12, 29 and 42 days long at 30, 20 and 12°C, respectively. Hagstrum defined the "ecological zero point" to be near 10°C since moulting did not occur at this temperature or below. Edgar (1972) reared *Pardosa* in the laboratory at 22°C and exposed some to a "cold shock" of 6°C for several weeks. He found that the cold shock was not essential for the maturation of the spiders, but that the rate of development was slightly increased for those animals that received the cold shock.

Schizocosa ocreata (Hentz) is a wolf spider common throughout the Eastern United States in deciduous leaf litter (Dondale & Redner, 1978; Cady *et al.*, 1980). Its sibling species, *Schizocosa rovneri* Uetz & Dondale is found within the range of *S. ocreata* (Stratton & Uetz, 1981) but its preferred habitat appears to be floodplain leaf litter (Uetz & Dondale, 1979). The current study was part of a larger behaviour study (Stratton & Uetz, 1983, Stratton & Uetz, in review) and while the animals were being reared in the laboratory, the opportunity was taken to study the effects of varying temperature and light:dark cycles on the rate of maturation of these spiders and their hybrids. F_1 hybrids were obtained from forced crosses between the two species (Stratton & Uetz, 1981), and F_2 hybrids and backcross progeny were likewise obtained. While the hybrids appeared to mature normally, this study provides quantitative measures of the maturation rates, which may give further insight into the genetic similarities or differences between the two species. In addition, this study elucidates some important aspects of rearing wolf spiders successfully in the laboratory.

Methods

Individuals of *S. ocreata* and *S. rovneri* were collected as immatures in October and November 1980. *Schizocosa ocreata* was collected from the Cincinnati Nature Center, Clermont County, Ohio, in deciduous leaf litter. *Schizocosa rovneri* was collected from the flood plain of the Ohio River, one mile west of Taylorsport, Boone County, Kentucky. To ensure virginity all spiders were individually housed in plastic boxes. Water was provided via a cotton-stoppered

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glass vial (Uetz & Denterlein, 1979).

Hybrids were obtained by forcing crosses between the two species of *Schizocosa* (Stratton & Uetz, 1981) in June 1980, using individuals which had been collected as immatures from the above localities. The method of forcing crosses between the species involved anaesthetizing the female with carbon dioxide and placing her in a receptive position in front of a courting heterospecific male. Typically, the male would mount the female in the manner typical of wolf spiders (his venter against her dorsal surface) and he would begin scraping the sides of the female's abdomen with his palp, which normally elicits a swivelling of her abdomen, permitting the insertion of the male's palp. When she "awoke", usually within two-three minutes, she would respond to the scraping of the male's palp by swivelling her abdomen, he would then successfully insert his palp, and the copulation would proceed normally. Reciprocal crosses each produced living young, and were named by their maternal species. That is, offspring of a female *rovneri* x male *ocreata* were called Hybrid-*rovneri* or Hrov. Purebred spiderlings were obtained by mating conspecific spiders. Spiderlings hatched in mid July 1980 were isolated into small glass tubes (diam. 1 cm) when they dispersed from the back of the female. The tubes were stoppered on one end with wet cotton while the other end was stoppered with dry cotton. Spiderlings were fed weekly either pinhead crickets (*Acheta domestica* L.) or collembola. The temperature of the rearing room was 23.3 ± 1.6°C. Light was 464.8 ± 2.4 lumens/m^2. Relative humidity in the environment of the spiderlings was 100% owing to the damp cotton. After two months, the spiderlings were placed in larger glass tubes (diam. 1.5 cm), similarly stoppered, and were fed twice weekly. At this phase, the spiderlings were fed both crickets and vestigial-winged fruitflies (*Drosophila melanogaster*). Just before the onset of the experimental regime, the spiderlings were placed in the plastic boxes described above.

In December 1980, when most spiders were in the antepenultimate instar, the temperature-light experiment was started. Four treatment groups were organized and were designated by temperature and light: dark regimes (Table 1). The four treatment groups were: Warm LD 12:12, Warm LD 10:14, Cool LD 12:12, Cool LD 10:14. Individuals from each of the four groups of spiders (i.e. *S. ocreata, S. rovneri,* Hocr. and Hrov.) were selected randomly and placed in each treatment.

1. Warm LD 12:12. This treatment was the room in which the hybrids were reared. Fluorescent room lights were on an automatic timer with about 10 minutes to change from full light (464.8 ± 2.4 lumens/m^2) (Table 1). Likewise, in the morning, when the lights came on, it took about ten minutes to go from subdued light to full light. Light readings were made with a Litemate Photometer System (Photo Research Division, Kollmorgan Corp., Burbank, CA). Temperature was recorded on a continuously monitoring hydrothermograph (model H311 Weather Measure Corporation, Sacramento, CA). Temperature averaged 23.3 ± 1.6°C. Relative humidity in the room was also recorded by the hydrothermograph and ranged from 7-60%. However, relative humidity in the spider boxes was continuously high because of the cotton-stoppered water bottle in each box.

2. Warm LD 10:14. Spiders in plastic boxes were placed in a growth chamber (General Electric Model 808) which was lighted with 6 fluorescent bulbs (902.1 ± 191.4 lumens/m^2). The lights were on an automatic timer, but unlike the room light, the switch from light to dark was abrupt. The mean temperature was 19.5°C (as measured by a max./min. thermometer) and fluctuated between 26.3 and 12.7°C. Note that while the mean temperature was similar to the Warm LD 12:12 treatment, it

Treatment group	Light (lumens/m^2 ± S.D.)	Temperature (°C ± S.D.)
Warm LD 12:12	464.8 ± 2.4	23.3 ± 1.6
Warm LD 10:14	902.1 ± 191.4	max. 26.3 ± 2.7 min. 12.7 ± 4.6 mean = 19.5
Cool LD 12:12	1314.7 ± 173.1	max. 16.2 ± 5.1 min. 2.7 ± 5.1 mean = 9.4
Cool LD 10:14	1314.7 ± 173.1	max. 16.2 ± 5.1 min. 2.7 ± 5.1 mean = 9.4

Table 1: Summary of treatment groups testing effects of temperature and light/dark cycles on rate of maturation in spiders.

varied greatly in comparison to that treatment. Also, the overall light intensity was greater in the Warm LD 10:14 treatment group.

3/4. Cool LD 12:12/Cool LD 10:14. Both of these treatment groups were in the same growth chamber (General Electric Model 805). Two lighting systems were set, each on a shelf lit by two fluorescent bulbs, with the two sections shielded by heavy black plastic. The average light in both sections was 1314.7 ± 173.1 lumens/m^2. The average temperature was 9.4°C with an average high of 16.2 ± 5.1°C, and an average low of 2.7 ± 5.1°C. Note that the light levels for both of the cool treatments were higher than the warm treatments. Although the effects of these light levels are not known, they are within the normal range of light levels found in the field.

The experiment lasted 4 months. All spiders were fed 5 mm crickets (*Acheta domestica*) twice weekly, and at the time of feeding, they were checked for moults. Each spider was examined microscopically for development in the pedipalps and epigynes at the beginning of each month. The differences between the groups were tested by a Chi-Square test with the 0.05 level chosen as the level of significance.

When the F_1s were mature, they were cross-mated with each other to obtain F_2s and they were backcrossed with both parental species to obtain backcross progeny. These matings were in March to April 1981, and were done using the same "forced-mating" technique described above. All these spiderlings were reared in the warm LD 12:12 treatment, with the exception of two months immediately after hatching when they were kept in a house and given an approximate LD 12:12 light regime (June-July).

Results

1. Comparison of S. ocreata and S. rovneri

There were no differences in the percentage of spiders maturing when *S. rovneri* was compared with *S. ocreata* across all treatment groups (Table 2). Neither species needs a cold shock to mature. The photoperiod is of primary importance to both species, as 100% of the spiders from both species matured in the LD 12:12 regimes. However, given the cooler and more variable temperature, it took four months longer for 100% of the spiders to mature (Fig. 1). Given a longer dark period (i.e. LD 10:14), a lower proportion of the spiders matured (Fig. 2).

2. Comparison of F_1 hybrids

The two groups of hybrids, Hrov and Hocr, were compared to each other across all treatment groups and were not found to differ from each other (Table 2). The hybrids show a very low % maturation in all treatment groups except the Warm LD 12:12 treatment. In the Warm LD 12:12 treatment, while most individuals did mature, it took two months longer for maturation than in the purebred spiders (Fig. 3, cf. Fig. 1).

3. Comparison of F_2 hybrids and backcross progeny

F_2s and backcross progeny were reared in the Warm LD 12:12 regime; thus comparisons are only possible in the regime where the highest proportions from the other groups matured. A significantly higher proportion of the backcross progeny matured more quickly than either the F_1s or the F_2s (Fig. 4). By month 8, the F_1s and backcrosses were 90% mature, but in the F_2s, only 38% were mature. These differ-

Treatment group	Spider type			
	S. rovneri	*S. ocreata*	*Hrovneri*	*Hocreata*
Warm LD 12:12	8 (8)a	18 (18)a	9 (9)a	13 (15)a
Warm LD 10:14	2 (5)a	2 (5)a	0 (9)b	1 (11)b
Cool LD 12:12	5 (5)a	6 (6)a	0 (7)b	0 (11)b
Cool LD 10:14	4 (5)a	4 (6)a	0 (7)b	1 (12)b
Totals	19 (23)	30 (35)	9 (32)	15 (49)

Table 2: Number of spiders maturing and sample size (n) for each group of spiders over the full experimental period. Groups that are not significantly different from each other (at $p < 0.05$) are followed by the same small letter.

ences were significant at $p < 0.005$. By month 10, nearly 100% of the F_2 s were mature.

Discussion

In many groups of arthropods, photoperiod is the primary inducer of diapause. Factors such as temperature and diet are often of secondary importance (Lees, 1955; Beck, 1968; Clark & Platt, 1969). This is also true of the few spiders that have been studied (Hagstrum, 1970), although there are several studies which suggest that the amount of food is important in determining how many moults a spider will have (Levy, 1970). My study indicates that two species of wolf spiders, *S. ocreata* and *S. rovneri*, also depend primarily on photoperiod to mature. Both species matured when given an LD 12:12 regime (and sufficient food). In the midwestern United States, this photoperiod would correspond to spring, the time when these spiders naturally mature.

A large proportion of the genes in an organism are regulatory (involved with turning on or off various metabolic processes or developmental expressions). They are thus impossible to measure by means of electrophoresis, or by the structure of an organism. Oliver (1979a) emphasized that the only means available for studying the differences in regulatory genes is by hybridization studies and subsequent observations in the laboratory. Oliver suggests that much of the driving force of speciation may be through small differences in metabolic integration. Genetic incompatibility, and subsequent speciation, can potentially occur with only a slight change in the genetic material. Small differences in the metabolic integration of parental populations may be important in affecting hybrid viability. Thus, small changes in the regulatory genes may affect different aspects of development and maturation, and have profound consequences on hybrid individuals.

Tauber & Tauber (1977) and Tauber *et al.* (1977) have proposed a model of genetic change for sympatric speciation that involves changes in 2 or 3 genes. They found that single allele differences at two unlinked autosomal loci caused significant differences in photoperiod response, which effectively isolated two groups of neuropterans. They suggest that these changes are sufficient to explain the divergence of two species of *Chrysopa* (Neuroptera). Thus, this may be an example of how a change in a small number of genes can explain divergence in reproductive time and subsequent reproductive (seasonal) isolation.

It is interesting that while the two species of *Schizocosa* in this study showed no differences in their development rate under different regimes, both reciprocal F_1 hybrids differed significantly from the parental populations. Thus, there is some degree of basic developmental incompatibility between the species, although this appears to be slight (compared with studies in Lepidoptera – Oliver, 1979b). These differences are further emphasized in the F_2 generation in which the spiders become an additional 2 months out of synchronization with the parental groups. The differences between the hybrids and the parental populations can possibly be attributed to differences in the regulatory gene complex. Clearly

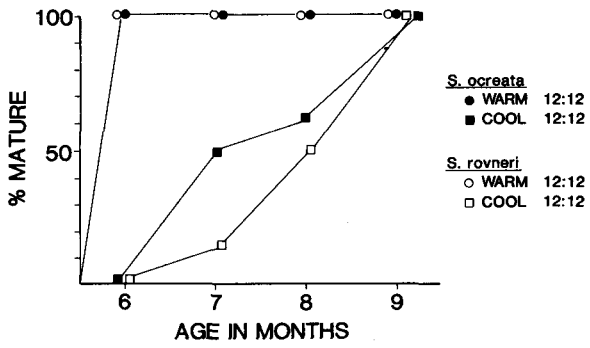

Fig. 1: Maturation of *Schizocosa ocreata* and *S. rovneri* given a warm LD 12:12 regime and a cool LD 12:12 regime.

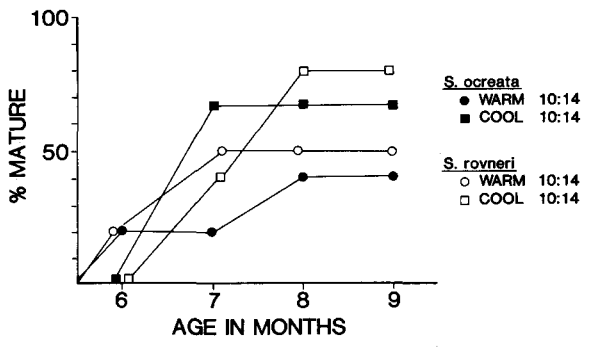

Fig. 2: Maturation of *S. ocreata* and *S. rovneri* given a warm LD 10:14 regime and a cool LD 10:14 regime.

the backcross progeny mature more quickly than the F_1s or the F_2s, and are thus most like the parental groups. Oliver (1978) indicates that inviability later in development may be due to an inability to produce sufficient quantities of a growth hormone to cause metamorphosis at the proper stages. It is possible that the cooler and darker regimes affected hormone production in the F_1 hybrids to a greater extent than is seen in the parental species. This in turn could account for the reduction of maturation in the hybrids.

Reciprocal hybrids (i.e. hybrids with different maternal species) may differ extensively from one another. There may likewise be disharmony between the X chromosomes from the father and the cytoplasm from the mother. There were no apparent differences (and thus no maternal or paternal effects) between the reciprocal hybrids of *S. ocreata* and *S. rovneri*.

The literature suggests that there is extensive phenotypic plasticity with respect to developmental rate, number of moults, size and fecundity in spiders (Wise, 1976; Deevey, 1949; Turnbull, 1962, 1965). Eason (1969) found that the time for an individual to mature varied greatly for siblings raised in similar laboratory conditions. Females of *Pardosa lapidicina* Emerton took from 80-299 days, and males took from 80-163 days to mature. She suggests that factors other than food and environment affect the rate of maturation. It would appear that there is a genetic polymorphism in this group for rate of development. Den Hollander (1971) found that the time of the final moult in *Pardosa pullata* (Clerck) subgroups varied between populations and between years. He suggests that a relationship exists between the stability of the microclimate and the degree of synchronization in the moulting time of the respective populations. Individuals from a subgroup which had a highly synchronized final moult were from a relatively stable microclimate, while individuals from a subgroup that was much less synchronized were from a relatively unstable microclimate. Levy (1970) found large differences in the development time of males and females of the crab spider *Thomisus onustus* Walckenaer. Because of this asynchrony, it was impossible for siblings to mate. Also, in rearing thousands of spiders, he found great variance in the number of moults and in the time spent in any one stadium. Other workers have also found there to be great variation in the number of times wolf spiders moult (Bonnet, 1930; Eason & Whitcomb, 1965; Miyashita, 1968). While data are not available for the number of moults in *Schizocosa*, it would appear that given constant conditions, the variation in development time is not as great as is seen for other spiders. While this alone suggests only slight differences in the genes regulating development, it does suggest a means of further differentiation between hybrids and purebreds if crossbreeding were to occur in the field. Although these differences alone may not be sufficient to isolate the various groups genetically,

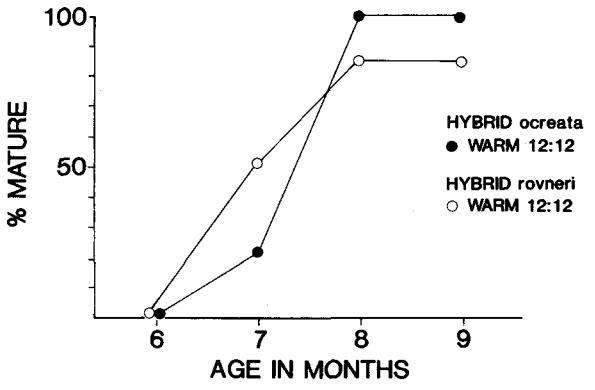

Fig. 3: Maturation of F_1 hybrids given a warm LD 12:12 regime and a cool LD 12:12 regime.

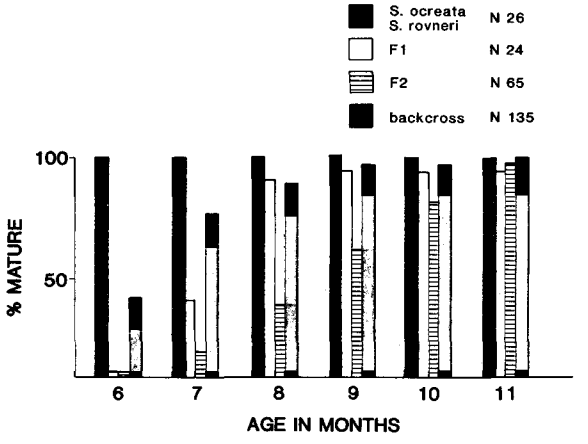

Fig. 4: Comparison of the rate of maturation of *S. ocreata*, *S. rovneri*, F_1, F_2 hybrids and backcross progeny. All given a warm LD 12:12 regime.

the longer maturation time may put the hybrids in reproductive jeopardy compared with the faster maturing purebreds. The sexual behaviour of the two species remains the critical and defining difference between the two species (Uetz & Denterlein, 1979; Stratton & Uetz, 1981; Stratton & Uetz, in review).

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