FREQUENCIES OF COLOR MORPHS IN FOUR POPULATIONS OF *ENOPLOGNATHA OVATA* (ARANEAE: THERIDIIDAE) IN EASTERN NORTH AMERICA*

BY DAVID H. WISE AND PAUL R. REILLO

DEPARTMENT OF BIOLOGICAL SCIENCES
UNIVERSITY OF MARYLAND BALTIMORE COUNTY (UMBC)
CATONSVILLE, MARYLAND 21228, U.S.A.

INTRODUCTION

Several types of spiders exhibit conspicuous color polymorphisms. Reiskind (1970) has discovered mimetic polymorphisms among clubionids. Examples in which only one sex is polymorphic occur among the jumping spiders, which have keen vision and often show marked sexual dimorphism (e.g. Galiano 1981a, b). In these species the sex-limited polymorphisms may be related to differential predation pressures upon the sexes and/or sexual selection (Stamps and Gon 1983). Many theridiid spiders are polymorphic (Levi 1957; Stamps and Gon 1983), though in this group the eyes are not well developed and recognition of colors or patterns during courtship probably does not occur. Polymorphisms in theridiid species appear not to be sex-limited, though the frequencies of certain morphs may differ between the sexes (Hippa and Oksala 1977, 1981). By far the most extensively studied color polymorphism among spiders is that found in the theridiid *Enoplognatha ovata* (Clerck).

Populations of *E. ovata* frequently contain three distinctive types of adults. The most common morph has a pale yellow abdomen, often with several pairs of dorsolateral dark spots, but with no red stripes (form *lineata*); another form has two dorsolateral red stripes running the length of the abdominal dorsum (form *redimita*); and the least common morph has a solid red band running the length of the abdominal dorsum (form *ovata*) (Bristowe 1958). This striking variation in a common species has long fascinated naturalists. Early arachnologists considered the forms to be three species, but by early last century the three varieties were considered to be conspecific

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(Hippa and Oksala 1979). The three morphs will mate readily in the laboratory, and Seligy (1971) discovered that *lineata, redimita* and *ovata* could be obtained in the progeny of a single female. Although the morphs are usually distinct, recent research of Hippa and Oksala (1979, 1981, 1982) indicates that the genetics of the color polymorphism is more complicated than previously thought; a brief summary of recent findings appears in the Appendix.

Ecologists have uncovered two intriguing aspects to the distribution of these morphs in Europe. Local populations often differ in the frequencies of the three morphs, yet a given population will maintain remarkably constant frequencies over several generations (Oxford 1976). Furthermore, a latitudinal cline in morph frequencies exists, with the red forms tending to be more common in northern populations of continental Europe (Hippa and Oksala 1979).

E. ovata also occurs in parts of North America (Levi 1957), but has not been extensively studied on this continent. Seligy (1971) provided information on the natural history of the species in North America and described details of postembryonic development; however, he did not give data on morph frequencies in different locales. In 1983 we determined morph frequencies in *E. ovata* populations in Maine, Massachusetts, and two regions of New York. We discovered that frequencies varied between local populations within an area, and also found that the overall frequencies for each geographical region were not the same. Most striking was the presence of the *ovata* morph in Maine and a mountainous area of Massachusetts, and its absence from two populations in widely separated regions of New York State.

METHODS

Natural History of *E. ovata*

This brief account is based primarily upon Nielsen (1932), Bristowe (1958), Seligy (1971) and personal observations.

Middle through adult instars are found underneath the leaves of many species of brambles, small saplings and herbs such as golden rod (*Solidago*). *E. ovata* occurs along roadside ditches, open fields and in the forest understory. It is often highly aggregated, with dense clumps sometimes being referred to as "colonies". The spider builds a small, inconspicuous tangle web underneath a leaf, the edges of which are often pulled down slightly by silk lines. This retreat is readily noticeable when examining vegetation, and the one constructed by the female for her egg sac is particularly obvious. Most females deposit a single sac in July or August, which they guard in a rolled leaf. The 2nd instar spiderlings emerge after several weeks and disperse in September through October. These instars overwinter in the leaf litter and in early spring build small webs in the curls of dead leaves. At this stage they were the most abundant spider in the litter community of one ecosystem studied (Stevenson and Dindal 1982; the population that they studied was the same central New York population that we examined). As the juveniles begin to molt they move into living vegetation where they build small webs similar to those of adults, though the younger instars do not consistently curl down the edges of leaves.

Sampling the North American Populations

During 13–17 July 1983 we surveyed morph frequencies of penultimate and adult *E. ovata* in several local populations in each of four different regions: Mt. Desert Island in Maine, October Mountain State Forest in the Berkshire Mountains of western Massachusetts, Huyck Nature Preserve in eastern New York, and the Lafayette Experimental Station of SUNY Syracuse in central New York (Fig. 1). Local populations were defined primarily as dense aggregations of *E. ovata* in contiguous stands of vegetation. After locating an aggregation, we continued to move systematically through that patch of vegetation until *E. ovata* was no longer common, or until we had scored approximately 50 spiders. This latter criterion was used primarily in Syracuse, where the vegetation suitable for habitation by *E. ovata* was continuous over large areas of the forest. The local populations were 50m to several km apart. We examined each patch carefully, but did not make an exhaustive survey of each geographical area to determine the number of local populations. Instead, we attempted to examine as many different geographic regions as possible, spending from under a day (Syracuse) to two days (Maine) in each area. We scored a total of 1107 spiders in these four areas, but in presenting frequencies in local populations within each region we have only included those with 20 or more individuals.

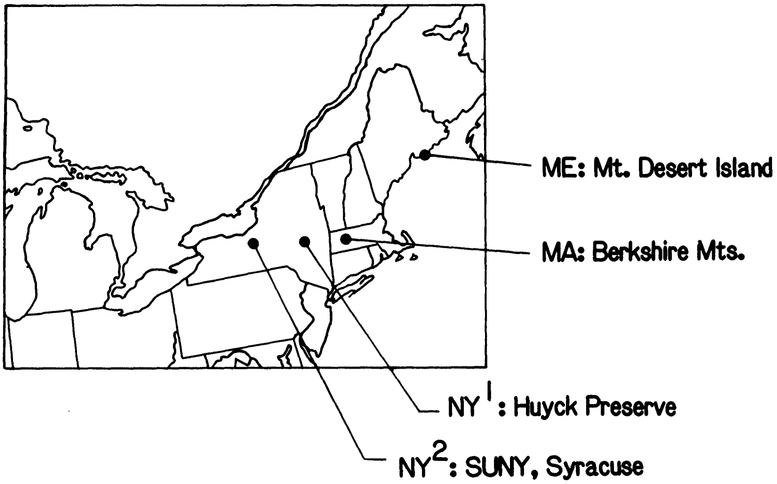

Fig. 1. Sites at which morph frequencies in local populations of *Enoplognatha ovata* were scored.

RESULTS AND DISCUSSION

Pooled local populations from the four geographic regions differed in overall morph frequencies (Fig. 2). Proportions of the yellow morph, *lineata*, differed significantly among the four regions sampled (chi-square = 11.41, $p < .01$, $df = 3$), due to the lower frequency of *lineata* in Massachusetts compared to the other three areas. The most striking difference involved the solid red morph *ovata*. This form was absent from both New York populations, but occurred in both Massachusetts and Maine. The differences in the frequency of *ovata* among the four regions was significant statistically (chi-square = 34.49, $p < .001$, $df = 3$).

We uncovered similar differences in morph frequencies between local populations within one of the regions that we sampled (Fig. 3). Variation in representation of the morphs among populations on Mt. Desert Island in Maine was statistically significant (chi-square = 13.2; $p < .05$, $df = 5$, 2×6 contingency table; comparison of *lineata* frequencies). The frequency of *lineata* varied from .70 to .96, and that of *ovata* from 0 to .15. The difference between population "A" and several of the others was quite striking, in that "A" had no *ovata* and very few *redimita,* whereas the others contained large numbers

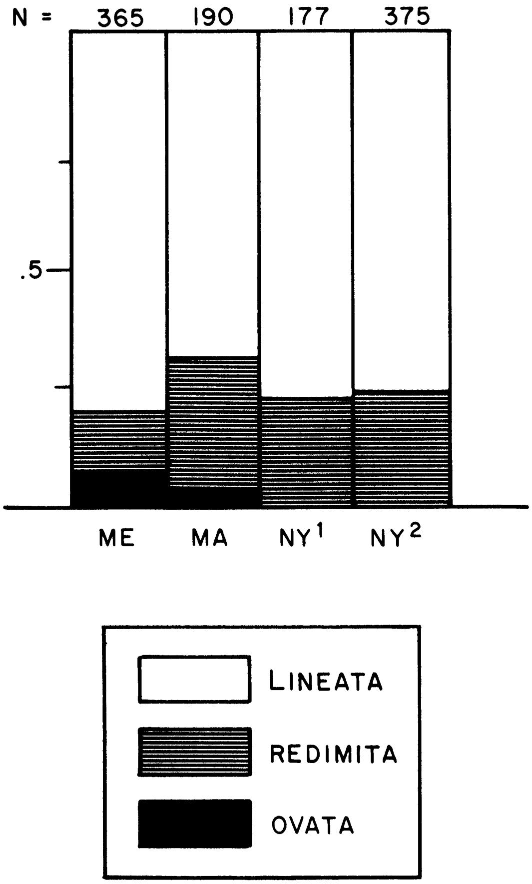

Fig. 2. Morph frequencies in the four different regions that were sampled. Individuals from the local populations (i.e. aggregations ⩾ 20) and also spiders found in aggregations with fewer than 20 individuals have been pooled to calculate the proportion of each morph. Thus, with the exception of SUNY Syracuse, the sample used to derive proportions for each region is larger than the sum total of local populations that appear in Fig. 3.

of both the striped and the solid-red morphs. The number of populations from October Mt. State Forest in Massachusetts and from the Huyck Preserve in New York is too small to make any generalizations about local differences in morph frequencies. Additional sampling might indicate that some local populations in western

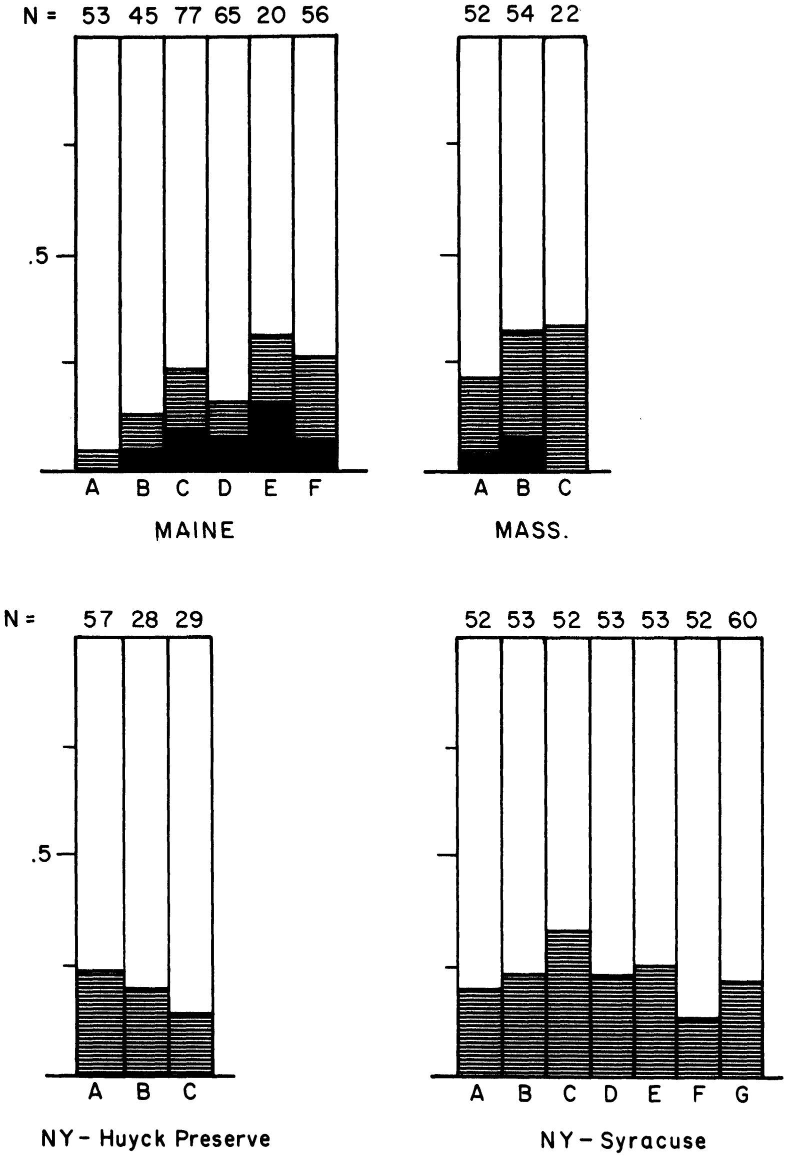

Fig. 3. Variation in morph frequencies among local populations. Key same as for Fig. 2.

Massachusetts differ in the proportion of the *ovata* phenotype. The three populations from the Huyck Preserve were quite similar; they all lacked the *ovata* morph and had similar frequencies of *redimita*. Populations from the forest in Syracuse, New York also lacked *ovata* and did not differ significantly in the proportion of *redimita* (chi-square = 6.0, $p > .4$, df = 6, 2 × 7 contingency table). This constancy likely reflected both the continuity of the habitat and the proximity of the local "populations" to one another. Each group that was defined as a population was no more than 50 m from another, with continuous vegetation also inhabited by *E. ovata* existing between them. Unlike the local populations in the other three regions, those in the central New York site were not physically separate aggregations.

These preliminary observations of morph frequencies in *E. ovata* populations in eastern North America suggest that patterns similar to those in Europe will be uncovered if more areas are sampled. In the region most extensively researched, Mt. Desert Island, significant differences in morph frequencies occurred among local populations. European workers have reported similar differences (Oxford 1976, Hippa and Oksala 1979). Morph frequencies also differed between widely separated regions. This preliminary evidence is insufficient to judge whether North American *E. ovata* exhibits a morph-ratio cline similar to that found in Europe by Hippa and Oksala (1979), but the absence of the *ovata* morph from both regions in New York is striking. A more detailed examination of *E. ovata* populations along latitudinal and longitudinal gradients in North America might uncover a consistent pattern of variation.

Apparently *E. ovata* is a relatively recent arrival to North America (Levi 1957). Our initial studies indicate that morph-frequency patterns in North America may be equally as intriguing as those already documented in Europe. More detailed examination of the pattern in a recently colonized area could provide comparative data useful to understanding the evolutionary forces responsible for the patterns of variation in morph frequencies occurring on both continents.

SUMMARY

The spider *Enoplognatha ovata* exhibits a conspicuous color polymorphism characterized by three morphs: *lineata* (yellow abdomen with no stripes), *redimita* (two dorso-lateral red stripes on

the abdomen) and *ovata* (medial red band on the dorsum). European researchers have found that local populations often differ in morph frequencies, and that average frequencies differ between geographic regions. We found preliminary evidence of similar variability in North American populations of *E. ovata*. We recorded the phenotypes of 1107 spiders from several local populations, 50m to several km apart, in each of four areas: eastern Maine, western Massachusetts, eastern New York, and central New York. The overall frequency of *lineata* was .70 among the spiders from Massachusetts, but was close to .80 in the other three regions. The most striking geographic differences in frequency involved the *ovata* morph. This form was absent from all New York populations sampled, but occurred in all but two of the local populations from Massachusetts and Maine. Overall frequencies of *ovata* in the Massachusetts and Maine samples were .03 and .06, respectively. In Maine, the most intensively sampled region, morph frequencies differed significantly among local populations. The proportion of *lineata* varied from .70 to .96; *ovata* frequencies ranged from 0 to .15. These observations suggest that further examination of *E. ovata* in North America may uncover morph frequency differences between populations comparable to those in Europe. Since *E. ovata* is likely a recent immigrant to North America, more detailed information from this continent could yield valuable comparative data on a curious phenomena whose evolutionary basis is still unexplained.

APPENDIX

Oxford (1976) found variation in coloration and patterning of the three morphs, particularly among laboratory-reared spiders. Hippa and Oksala (1979, 1981) also found that morphs were not always distinct, and furthermore, that in some groups the red coloration was not expressed until either the third instar or the final molt. Recently, Hippa and Oksala (1982) cited evidence from studies of variability in genitalia structure that some populations of *E. ovata* may consist of more than one species, contrary to previous interpretations of Levi (1957, 1967).

This recent information complicates the situation, but does not detract from the usefulness of our findings, for three reasons:

(1) Only a very few intermediate forms appeared in our sample of over 1000 spiders.

(2) Only the Maine populations appeared to have had significant numbers of penultimate females; however, they were a minority. Most spiders appeared to be mature. Development was more advanced in the southern populations, with many females guarding egg sacs. Thus in Maine we may have slightly underestimated the frequencies of the red morphs (Hippa and Oksala 1979); however, this possible bias makes our conclusion of significant morph frequency differences between regions conservative, since the sample from Maine had the highest frequencies of *ovata,* the phenotype with the most red coloration.

(3) Definition of new species in the *E. ovata* group by Hippa and Oksala (1982) is based upon relatively few museum specimens. This type of information does not indicate whether or not expressions of the red morphs differs between *E. ovata* and the newly recognized *Enoplognatha* species, nor does it indicate the extent of niche differences.

The most extensive sets of data available on morph frequencies in European populations are based on the assumptions of three distinct morphs and one species (eg. Oxford 1976, Hippa and Oksala 1979). Hence our data are directly comparable to that collected by European researchers. Future, more detailed research on both continents will have to take into account the possible existence of more than one species in some *E. ovata* populations. However, this taxonomic problem does not prevent one from making preliminary statements about patterns in morph frequencies.

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LITERATURE CITED

BRISTOWE, W. S.

1958. *The World of Spiders.* London, Collins.

GALIANO, M. E.

1981a. Revisión del género *Phiale* C. L. Koch, 1846 (Araneae, Salticidae) III. Las especies polimorficas del grupo *mimica.* Journal of Arachnology **9:** 61 86.

1981b. Revision of the genus *Phiale* C. L. Koch, 1846 (Araneae, Salticidae) IV. The polymorphic species of the *gratiosa* group. Bulletin of the British Arachnological Society **5:** 205 216.

HIPPA, H. AND I. OKSALA.

1979. Colour polymorphism of *Enoplognatha ovata* (Clerck) (Araneae, Theridiidae) in western Europe. Heriditas **90:** 203-212.

1981. Polymorphism and reproductive strategies of *Enoplognatha ovata* (Clerck) (Araneae, Theridiidae) in northern Europe. Annales Zoologici Fennici **18:** 179 190.

1982. Definition and revision of the *Enoplognatha ovata* (Clerck) group (Araneae: Theridiidae). Entomologica Scandinavica **13:** 213-222.

LEVI, H. W.

1957. The spider genera *Enoplognatha, Theridion* and *Paidisca* in America north of Mexico (Araneae, Theridiidae). Bulletin of the American Museum of Natural History **112:** 1-123.

1967. Cosmopolitan and pantropical species of theridiid spiders (Araneae: Theridiidae). Pacific Insects **9:** 175-186.

NIELSEN, E.

1932. *The Biology of Spiders, with Especial Reference to the Danish Fauna.* Vol. I. Copenhagen, Levin and Munnksgarad.

OXFORD, G. S.

1976. The colour polymorphism in *Enoplognatha ovatum* (Clerck) (Araneae: Theridiidae)—Temporal stability and spatial variability. Heredity **36:** 369-381.

REISKIND, J.

1970. Multiple mimetic forms in an ant-mimicking clubionid spider. Science **169:** 587-588.

STAMPS, J. A. AND S. A. GON III.

1983. Sex-biased pattern variation in the prey of birds. Annual Review of Ecology and Systematics **14:** 231-253.

SELIGY, V. L.

1969. Postembryonic development of the spider *Enoplognatha ovata* (Clerck) (Araneae: Theridiidae). Zoological Journal of the Linnean Society **50:** 21-31.

STEVENSON, B. G. AND D. L. DINDAL.

1982. Effect of leaf shape on forest litter spiders: Community organization and microhabitat selection of immature *Enoplognatha ovata* (Clerck) (Theridiidae). Journal of Arachnology **10:** 165-178.