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BLACK-STRIPE PHENOTYPES IN THE SPIDER *ENOPLOGNATHA OVATA* (ARANEAE, THERIDIIDAE)

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ABSTRACT

In this paper we describe black-stripe phenotypes of the polymorphic theridiid *Enoplognatha ovata* (Clerck) found among reared broods and natural populations from coastal Maine. Among reared spiders, black stripes were deposited over the typical color phenotypes *lineata*, *redimita* and *ovata*, and appeared to assort independently of the typical color morphs. Black stripes occurred more frequently among males than females, although the difference in incidence between the sexes was not statistically significant. Among 17 natural populations, black-stripe morphs were far more frequent among males than females, suggesting the possibility that black striping is associated with sex determination in *E. ovata*.

INTRODUCTION AND METHODS

The theridiid spider *Enoplognatha ovata* (Clerck) displays a conspicuous color polymorphism characterized by three distinct phenotypes: (1) *lineata*, with a creamy yellow opisthosoma (Fig. 1a); (2) *redimita*, exhibiting two dorsolateral red stripes (Fig. 1b); and (3) *ovata*, characterized by a solid red shield covering most of the dorsal opisthosoma (Fig. 1c). The genetic basis of color expression is detailed in a model by Oxford (1983) in which three color alleles (C^l, C^r, C^0) at a single autosomal locus determine the phenotypes *lineata, redimita* and *ovata.* The alleles exhibit a dominance hierarchy whereby *ovata* (C^0) is dominant to *redimita* (C^r) which is in turn dominant to *lineata* (C^l). A linked regulatory gene determines the timing of red pigment deposition in *redimita* and *ovata* during development (either early, during third or fourth instar, or late, upon final ecdysis to maturity). Biochemical aspects of pigment deposition in *E. ovata* are addressed elsewhere (Seligy 1969, 1972), and the reader is directed to many discussions of the ecological and evolutionary aspects of this color polymorphism (Oxford 1976, 1983, 1985; Oxford and Shaw 1986; Hippa and Oksala 1979, 1981; Wise and Reillo 1985).

Oxford (1976) reported that some *E. ovata* exhibit black stripes in addition to one of the typical color phenotypes just described. We recently discovered black-striped phenotypes among the offspring of field-collected broods of *E. ovata* from eastern North American populations. Below we describe the patterns observed and present preliminary estimates of the incidence of the black-stripe trait in natural populations.

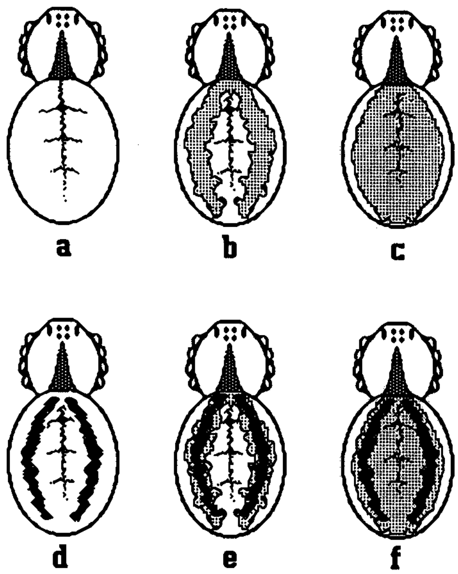

Fig. 1.—Typical color morphs (a) *lineata* (b) *redimita*, and (c) *ovata*, with corresponding black-stripe morphs below (d-f).

Fifty-seven *E. ovata* females with egg sacs were collected from several locations in Acadia National Park, Maine, USA during August 1985. None of these females exhibited the black-stripe character. Over the following year broods from these phenotypically known females were reared in cages based on a design by Oxford and Pitts (1981) or in individual glass vials as described in Seligy (1971) and Oxford (1983). Spiderlings from caged broods were isolated into individual glass vials upon reaching 4th instar, where they remained until maturity (6th instar) or death.

RESULTS AND DISCUSSION

The black-striped phenotype appeared in broods of five field-collected females. Black-striped individuals appeared with *lineata*, *redimita* and *ovata* background phenotypes. The black-stripe character results from a dark pigment deposited over the typical color morph patterns. Figure 1(d-f) depicts the combination black stripe/color morph phenotypes for the background patterns *lineata*, *redimita* and *ovata*. In individuals with a background *lineata* pattern, the striped morph appears as two dark lines that vary from dull grey to shiny black. The stripe width is also variable. Some individuals exhibit thin stripes, whereas others show broad bands with occasional horizontal bars bridging the two main stripes. In black-striped *redimita* individuals, the black stripes often coincide so completely with the dorsolateral red stripes that this phenotype can easily be mistaken for the black-striped *lineata* morph. Closer examination may reveal a triangle of red pigment left unmasked by the stripes at the anterior end of the opisthosoma or occasional patches of red along the margins of the black stripes. The pattern in black-striped *ovata* individuals is readily identified by the black stripes circumscribing the *ovata* red shield; occasionally red pigment can also be detected beyond the margins of the black stripes.

Black-stripe pigmentation was deposited by the end of the fourth instar and was detected in second and third instars in some individuals. Not all striped

PROGENY PHENOTYPES

MOTHER'S PHENOTYPE		lin.	red.	ova.	b/l	b/r	b/o	n	N	#b/n	tot.#b/N
OVA	♂	4	-	3	2	-	1	10	17	3/10	4/17
	♀	6	-	-	-	-	1	7		1/7	
LIN	♂	6	-	-	4	-	-	10	22	4/10	4/22
	♀	12	-	-	-	-	-	12		0/12	
RED1	♂	7	4	-	3	-	-	14	21	3/14	7/21
	♀	2	1	-	2	2	-	7		4/7	
RED2	♂	1	3	-	2	1	-	7	12	3/7	5/12
	♀	1	2	-	1	1	-	5		2/5	
RED3	♂	1	-	-	2	2	-	5	8	4/5	5/8
	♀	2	-	-	1	-	-	3		1/3	

OVA = *ovata* RED = *redimita* LIN = *lineata*

Fig. 2.—Summary table for broods exhibiting black-stripe phenotpyes: b/l = black-stripe morph over *lineata* pattern, b/r = black-stripe morph over *redimita* pattern, b/o = black-stripe morph over *ovata* pattern, "b" in last two columns refers to black stripes over any pattern.

young instars retained the black stripes. Some black-striped spiders changed phenotype during the fourth instar or upon ecdysis to fifth instar: three black-striped *lineata* spiders became indistinguishable from typical *lineata*, and one black-striped *redimita* spider became a typical *redimita*. Spiderlings that developed both black-stripe and red pigments indicate that black pigments can be deposited earlier in development than *redimita* or *ovata* pigments. Careful scrutiny of some third- and fourth-instar black-striped *redimita* and black-striped *ovata* spiders revealed that red pigments were deposited beneath black stripes already in place.

The distribution of phenotypes among the five broods exhibiting the black-stripe trait is given in Fig. 2. The character appears to assort independently of the *lineata, redimita* and *ovata* traits, suggesting that it is controlled by a locus (or loci) independent of the autosomal locus controlling the typical color phenotypes. The black-stripe trait is more frequent among male than female offspring from broods exhibiting the character (37% vs. 24%, respectively, Fig. 2), although this difference is not statistically significant (Chi-square = 1.64, df=1, $P = 0.200$).

Preliminary field census data from 17 populations reveal a sex-based bias in appearance of the trait. In all populations sampled, black-stripe morph frequencies were dramatically higher among males (Fig. 3). However, these frequencies should be interpreted with caution. Black-stripe frequencies in males may be over-estimated due to observers confusing the black-stripe morphs with dark patterns associated with the digestive diverticulae showing through the body wall (Seligy 1969; Oxford 1983). Laboratory examination of specimens is required to confirm phenotype assignments. Despite possible identification problems, the census data indicate that the black-stripe phenotype is more frequent among males than females and hence may be associated with sex-determination in *E.*

SITE	SEX	BLACK STRIPE	N	FREQ. BLACK STRIPE
DC	M F	17 -	245 383	.069 -
OCR1	M F	6 -	15 35	.400 -
OCR2	M F	3 1	14 37	.214 .027
OCR3	M F	3 1	14 37	.214 .027
OCR4	M F	4 1	19 31	.211 .032
OCR5	M F	8 1	22 28	.364 .036
OCR6	M F	8 -	12 38	.667 -
C	M F	8 -	51 102	.157 -
FT2	M F	3 -	17 36	.176 -
FT3	M F	7 1	15 35	.467 .029
OTT.PT.	M F	12 -	51 73	.235 -
TI	M F	20 1	36 66	.556 .015
G	M F	18 -	37 73	.486 -
J	M F	17 1	38 66	.447 .015
MP	M F	13 1	39 61	.333 .016
NL1	M F	7 -	34 66	.206 -
GCP	M F	4 -	23 41	.174 -
TOTAL	M F	158 8	668 1208	.237 .006

Fig. 3.—Frequencies of black-striped morphs from seventeen Maine populations, censused mid-July 1986.

ovata. G. S. Oxford also found the black-stripe trait more frequently among males in both reared broods and field populations (G. S. Oxford, unpublished data).

The genetic mechanism underlying the inheritance of this trait is unclear. The genetics of black-stripe expression in *E. ovata* may resemble the recessive, sex-linked inheritance of dark pigments of *Eupteryx* leafhoppers (Stewart 1986). Alternatively, gene(s) for the trait may be autosomal and its expression may be partially sex-limited (G. S. Oxford, pers. comm.). The most direct method of determining the inheritance of black striping would be to cross black-striped spiders of known ancestry; unfortunately, matings with lab-reared *E. ovata* have proven mostly unsuccessful (personal observation; Oxford 1983). In view of the difficulties of obtaining black-stripe crosses and censusing the morphs in natural populations, we feel it is worthwhile to present patterns based on preliminary data. We hope these data and ideas serve as incentives for future research.

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