

HOST PLANT MORPHOLOGY, SPECIATION, AND THE ECONOMICS OF MATE CHOICE IN  
THE SOLDIER BEETLE CHAULIOGNATHUS PENNSYLVANICUS

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ABSTRACT: Mate choice in populations of the soldier beetle is examined with reference to the model of economic mate choice developed by Wilson and Hedrick (1982, *Evol. Theory* 6: 15-24). Several major predictions of the model are borne out: 1) as the cost of selective mating increases, selectivity decreases, 2) choice in intertype (nonassortative) matings involves phenotypic evaluation at multiple levels, which may compensate for genetic disharmony, and 3) females, which are presumed to invest more per progeny than males, are more selective than males. Host plant morphology determines local population density. Under conditions of high beetle density the cost of selective mating is high, and, as a consequence, speciation is inhibited.

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# INTRODUCTION

Recently, Wilson and Hedrick (1982) described an economic analysis of mate choice derived from ecological foraging theory. They note that the rate of return on a mating is important not the absolute quality of a mate. The rate of return can be modeled as  $e/t$  where  $e$  is the combined fitnesses of offspring from a mating and  $t$  is the total time in which additional matings cannot take place. Thus, whether a mate is accepted depends upon the abundance of more desirable mates and the cost of selective mating. The conclusion is that some matings may be selectively favored even if fitnesses of offspring are not maximized. Therefore, economic factors may retard or prevent speciation (premating reproductive isolation).

The present study examines mate choice and speciation in the soldier beetle Chauliognathus pennsylvanicus (Cantharidae) and provides an example from natural populations where selection for economic mate choice mediates the degree of assortative mating. An ecological factor, host plant morphology is shown to determine local population density, altering  $t$ , and, thus,  $e/t$ , selecting for different mate choice strategies.

Wilson and Hedrick (1982) note that an economy of mate choice appears to exist for many species. However, the present study represents the first empirical analysis of the economics of mate choice with reference to speciation.

# METHODS

Mating beetles were randomly collected in September, 1982 at two old fields in the Piedmont physiographic province of north Georgia. The field sites, located near Braselton and Monroe, contain numerous herbaceous species upon which the beetles forage, apparently for pollen or nectar. The host plant and density of the beetles were recorded.

The length of the elytra and the length of the elytral spot were measured to the nearest 0.125 mm with a hand held ruler. Beetles fall into two modal classes on the basis of  $(\text{length of the elytral spot})/(\text{length of the elytron}) = p$ ,  $p = 0.40-0.60$  (short spots) and  $p = 0.80-1.00$  (long spots). A smaller number of intermediates occur,  $p = 0.60-0.80$ . In the mountains of far north Georgia the two modal classes exist without intermediates. In this area, mating pairs were collected from an old field near Cornelia. All collections were made between 1400-1800 h when courtship activity

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peaks. Assortative mating on the basis of  $p$  was measured by Pearson's correlation coefficient,  $r$ , from the linear regression of  $p$  of mating pairs. The length of the elytron correlates very strongly with dry weight ( $r > 0.9$ ; McLain, 1982) and is, therefore, utilized as a measure of size.

## RESULTS AND DISCUSSION

There is tremendous variation in beetle density at the Braselton and Monroe field sites, and density is strongly associated with host plant choice (Table 1). The floral structure of different host plant species determines the number of beetles which can forage and mate on a single plant (Figure 1). Thus, beetle density and mating dynamics vary greatly over distances of only 2-3 m. Plants which support high beetle densities possess inflorescences of multiple racemes or cymes such that many flowers or flower heads are present at the top of the plant. This provides the broad horizontal substrate necessary if many beetles are to interact upon the same plant. On the other hand, plants supporting only small beetle densities characteristically possess only one or a few flowers or flower heads per inflorescence at the end of a long slender peduncle. Here, it is physically impossible for more than a few beetles to simultaneously occupy the same plant. When females are courted on these plants they can readily assess male phenotype and mate or fly from the plant. However, within the matrix of a dense inflorescence many beetles interact simultaneously and continuously. This surely alters the cost of selective mating.

In contrast to the situation in Monroe and Braselton, beetle density at Cornelia is low and independent of host plant choice.

The strength of assortative mating is strongly density dependent. At high density mating is not assortative, but it is significantly so at low density (Table 1). At first, one might expect that at high density beetles would mate assortatively if selection favors economic mate choice since there is a higher probability of encountering high quality mates than at low density. Thus,  $t$  would decrease and  $e/t$  would increase. However, the cost of selective mating is probably high for beetles at high density since a single female is frequently courted by several males simultaneously (McLain, 1982). As a result, males may not be selective because of intense competition for females, and females may not be selective because the opportunity to assess the phenotype of courting males is rare. Thus, to be selective would increase  $t$ , the investment per mating, and decrease the rate of return on the mating,  $e/t$ . Females may also benefit from mating rapidly, even if indiscriminately, if this increases foraging efficiency through decreased harassment from males seeking mates (see McLain, 1981). Thus, low density is more favorable to assortative mating. Of course, there may also be threshold densities below which beetles would be selected to mate with the first available potential mate.

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Table 1. Density of beetle on host plants at the three field sites. Measure of assortative mating is given by  $r$  (\* indicates statistical significance,  $P < 0.05$ ).

Field Site	Plant Species	Density/0.25 m <sup>2</sup>	$r$
Monroe	<u>Eupatorium</u> sp.	200-300	0.22
	<u>Heterotheca subaxillaris</u>	1-5	0.75*
Braselton	<u>Bidens</u> sp.	1-10	0.87*
	<u>Erigeron canadensis</u>	20-50	0.41
	<u>Solidago</u> sp.	50-100	0.26
	<u>Mikania scandens</u>	200-300	0.18
Cornelia	<u>Eupatorium</u> sp.	1-5	0.93*
	<u>Solidago</u> sp.	1-5	0.95*

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The phenotypic distributions of  $p$  in north Georgia populations suggest disruptive selection (Figure 2). The distributions are strongly bimodal, especially in Cornelia where there is absolute premating isolation between long and short spot length

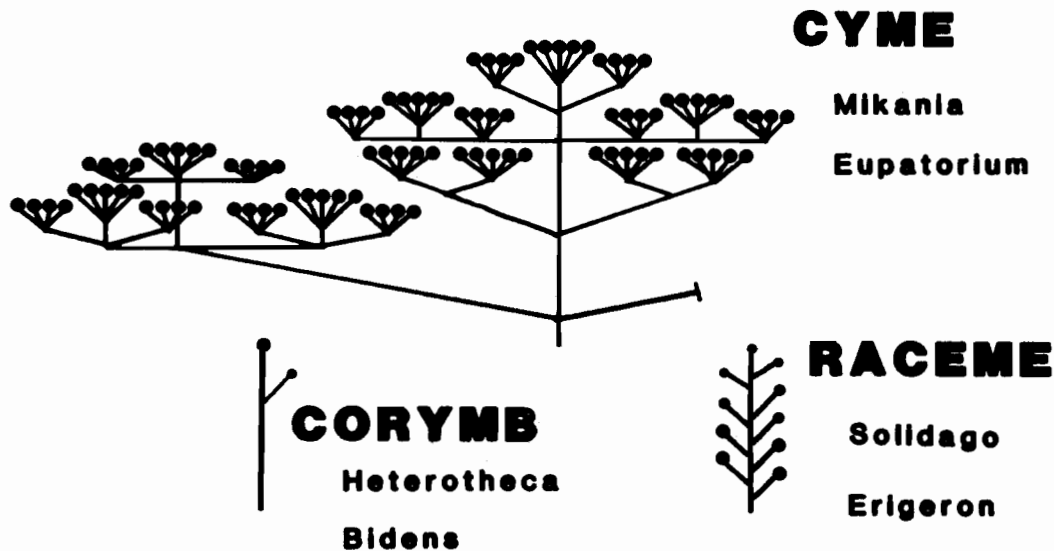


Figure 1. Schematic representation of inflorescences of the soldier beetle host plant species. See Table 1 for densities of beetles on each type of inflorescence.

\* \* \* \* \* individuals. The assortative mating observed at low density in Monroe and Braselton suggests that selection could favor speciation in these populations as well were the beetle densities generally low.

If there is an additional criterion for mate choice (such as body size) which does not correlate with attributes under disruptive selection, the acceptability of intertype (nonassortative) matings may increase (Wilson and Hedrick, 1982). This obtains because if mates of larger size are of higher quality, for instance through the production of more eggs or a larger spermatophore (McLain, 1981), variance would be produced around the fitness of intertype matings. Indeed, both in Monroe and Braselton, males from intertype matings are significantly larger than assortatively mating males (Table 2). This suggests that there are multiple criteria affecting mate choice and that in intertype matings larger males are more favorable as mates.

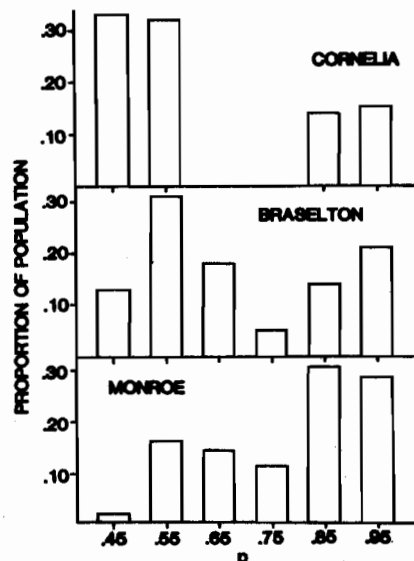


Figure 2. Phenotypic distribution of  $p$  (elytral spot length)/(length of elytron) at the three field sites.

Larger males may transfer more nutrients to females via the spermatophore or they may mate for a longer period, increasing female foraging efficiency. Preference by males for larger females is not observed (Table 2). There was no significant difference in male size between areas of low and high density (Table 2). Therefore, these results are not an artifact of size differences in males between low and high density areas.

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 Table 2. Length of elytra (mm  $\pm$  SD) of assortatively and nonassortatively mating males and females at Monroe and Braselton field sites. ANOVA yields significant differences in size of assortatively and nonassortatively mating males ( $F=22.71$ ;  $P<0.01$ ), but no significant difference on the basis of density for all males, mating and nonmating ( $F=3.35$ ;  $P>0.05$ ). Differences among females were not significant. N=sample size.

	MALES		FEMALES	
	Assortative	Nonassortative	Assortative	Nonassortative
Monroe	7.27 $\pm$ 0.39	7.42 $\pm$ 0.32	7.78 $\pm$ 0.38	7.90 $\pm$ 0.55
N	58	22	58	22
Braselton	7.28 $\pm$ 0.40	7.55 $\pm$ 0.29	7.89 $\pm$ 0.45	7.75 $\pm$ 0.42
N	120	80	120	80
	Low density	High density	Low density	High density
Monroe	7.40 $\pm$ 0.30	7.39 $\pm$ 0.35	7.84 $\pm$ 0.61	7.86 $\pm$ 0.44
N	45	77	39	86
Braselton	7.57 $\pm$ 0.41	7.54 $\pm$ 0.37	7.78 $\pm$ 0.53	7.81 $\pm$ 0.50
N	55	210	65	199

\* \* \* \* \*  
 Wilson and Hedrick (1982) also suggest that selection for optimal mate choice will more strongly favor intratype mating in the sex that invests more per offspring. Since it is generally true that females invest more heavily than males, even if one just considers the cost of gamete production in species without parental care (Trivers, 1972), females are expected to prefer intratype (assortative) matings more strongly than males. Since any intertype mating would involve both a male and a female, such matings cannot be used in this analysis. Therefore, in the present study comparison is made between the proportion of matings in which males and females mated with beetles of intermediate spot length ( $p=0.60-0.80$ ). Males were 1.56 X as likely to mate intermediates as females ( $P_{\text{♂}}=0.192$ ,  $P_{\text{♀}}=0.123$ ;  $P<0.001$ , t-test for proportions). Thus, it appears that females are more selective than males, as predicted from economic considerations. Potential mates of intermediate spot length are equally available to males and females since the sex ratio of individuals of intermediate spot length is not significantly different from 50:50 (proportion of males = 0.511;  $P>0.05$ , t-test).

Thus, beetle density and mating dynamics vary tremendously within local populations. The population density of soldier beetles in the Piedmont of northern Georgia is very high. Therefore, beetle density is high on plant species with dense inflorescences. Plants with dense inflorescences, such as a cyme or multiple raceme, are among the most abundant flowering species in the fall in this area. Were beetle density low in the Piedmont as it is in the Blue Ridge Mountains of far north Georgia host plant morphology would not affect mate choice. This is the case in *Cornelia*.

The data presented here indicate that selection favors an economic approach to mate choice. Where the cost of selective mating is high, mating is not selective and intertype matings are common. However, there are multiple criteria for mate choice in the soldier beetle, and in intertype matings larger males mate more frequently than smaller males. This may be selectively favored if mating of larger

males ultimately translates into greater energy intake by females. Finally, it appears that females, which probably invest more than males in the production of gametes, are more selective than males, as economic theory predicts. The absence of selective (intratype) mating at high density appears to prevent speciation between long and short elytral spot length types as has occurred in low density populations.

Of course, the validity of these conclusions rests on several important assumptions. First, it is assumed that selective mating is more costly at high density, and although inferences based on field observations and other published studies suggest this is true, no direct measurements were made to test this assumption. Second, there is only indirect evidence that females employ multiple criteria in the evaluation of potential mates. Thus, while the data are consistent with the models, they represent only an indirect link between economic mate choice and speciation.

#### LITERATURE CITED

- McLain, D. K. 1981. Interspecific interference competition and mate choice in the soldier beetle, Chauliognathus pennsylvanicus. Behav. Ecol. Sociobiol. 9: 65-66.
- \_\_\_\_\_. 1982. Density dependent sexual selection and positive phenotypic assortative mating in natural populations of the soldier beetle, Chauliognathus pennsylvanicus. Evolution 36: 1227-1235.
- Trivers, R. L. 1972. Parental investment and sexual selection. In: Sexual Selection and the Descent of Man (B. Campbell, ed.). Aldine. pp. 136-179.
- Wilson, D. S. and A. Hedrick. 1982. Speciation and the economics of mate choice. Evol. Theory 6: 15-24.