Interspecific Relationships among Three Species of Milkweed Beetles (*Tetraopes*: Cerambycidae)

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There recently has been considerable debate over the role of interspecific competition in the structuring of animal communities (8, 10, 13, 19, 31, 32). Some ecologists have considered competition as a relatively unimportant influence on community organization (2, 14, 20, 25, 26, 27, 29, 30, 34, 35, 37, 19). This view is one which has been traditionally espoused by insect ecologists. The consensus is that the structure of insect populations does not meet many of the assumptions of competition theory, most important of which is the fact that insect populations rarely occur at equilibrium (27). Habitat complexity, habitat heterogeneity, and dispersal (7, 15, 9, 23), and predation and parasitism (19) all act to severely limit insect populations. The combined effect of these factors is to greatly minimize the influence that interspecific competition has on the organization of insect communities (16).

These caveats do not appear to apply to the milkweed beetles of the cerambycid genus *Tetraopes*. These beetles complete their entire life cycle on various species of milkweed (Asclepiadaceae), with the adults congregating on the leaves and inflorescences to feed and mate, and the larvae feeding and overwintering in the milkweed root (4). No parasites of *Tetraopes* have been reported (4), and predation is rare (pers. obs.). The beetles apparently sequester cardenolides from the milkweed sap, which makes them highly distasteful to avian predators (17). Milkweeds are perennials and tend to occur in more or less discrete patches. Adult *Tetraopes* move infrequently between patches (18).

Chemsak (4) notes that when two sympatric species of *Tetraopes* utilize the same species of milkweed as the host-plant one of the *Tetraopes* species is decidedly less abundant than the other. Similarly, when two sympatric species of *Tetraopes* utilize different host-plants the two *Tetraopes* species occur with equal abundance. The depression of the population growth rate (r) or the carrying capacity (K) of one species in the presence of another, ecologically similar, species has been considered indirect evidence for interspecific competition (12). The purpose of this study was first to determine whether or not direct evidence for interspecific competition between species of *Tetraopes* could be obtained from field data, and, if so, to determine its importance in the dynamics of the *Tetraopes* guild.

Methods

Field work was done on a 100 m x 100 m study plot located in eastern Monroe Co., IN, from 16 June 1981 to 10 Aug 1981. The study plot included 420 *Asclepias syriaca* and 83 *A. tuberosa* plants, with *Solidago* sp. and assorted grasses comprising the bulk of the ground cover. Three species of *Tetraopes* were present on the study area: *tetrophthalmus* (Forster), *femoratus* LeConte, and *melanurus* Schönherr. A fourth species, *quinquemaculatus* Haldeman, has been reported from Indiana (1), but was not present on the study plot.

Daily censuses were taken on the study plot, during which time the entire plot was examined for the presence of *Tetraopes*. For each beetle the following information was noted: 1) species of *Tetraopes*, and 2) species of plant on which the beetle was found.

Figure 1
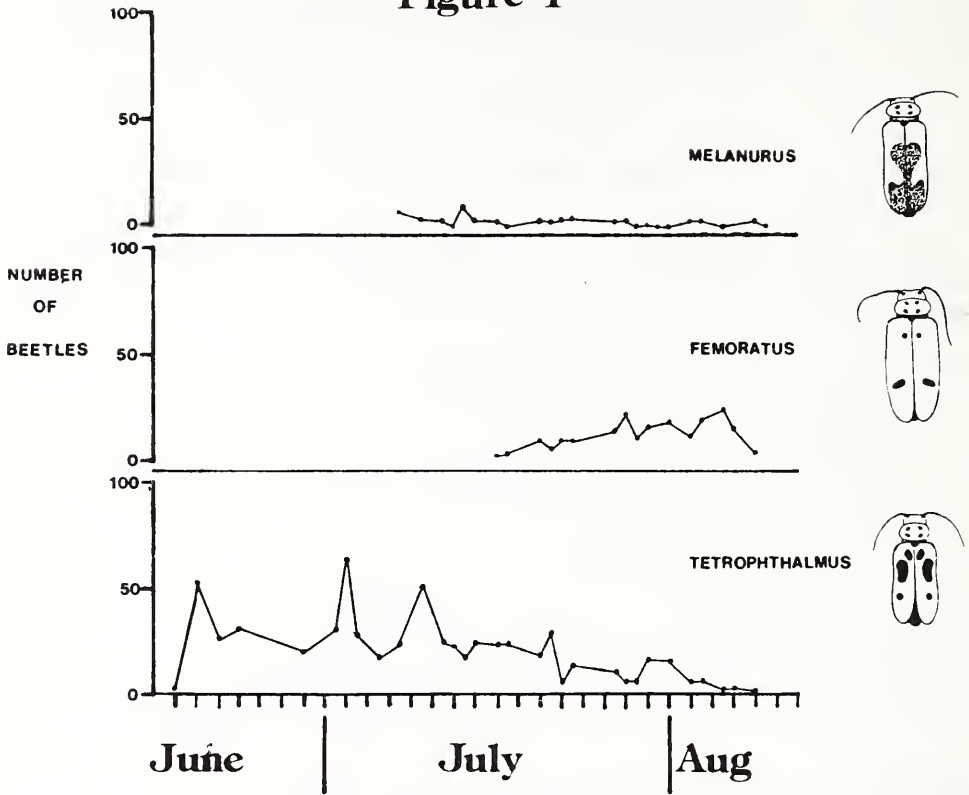
Results

Figure 1 gives the census data for the three species of *Tetraopes* present on the study site. *T. tetrophthalmus* was the most abundant species on the plot, first appearing on 16 June, when three individuals were noted. The peak count for this species was 64 on 2 July. *T. melanurus* was first noted on 7 July when six beetles were found, with a peak of nine individuals on 13 July. This species was the rarest *Tetraopes* on the site. The third species, *femoratus*, first appeared on 16 July. Two beetles were noted on this date, with the highest count being 24 on 6 Aug.

The distribution of the three species of *Tetraopes* on the host-plants is presented in Figure 2. *T. tetrophthalmus* specialized on *A. syriaca*, and *T. melanurus* on *A.*

Figure 2

Host Plant Preference
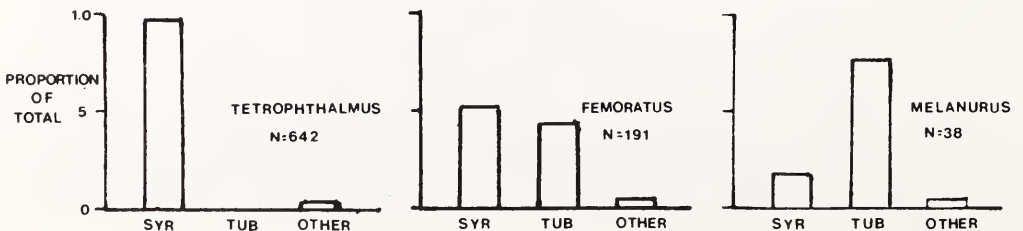
tuberosa. T. femoratus distributed itself nearly equally between the two milkweed speices. For all three species host-plant choice differed significantly from what would be expected if the beetles were distributing themselves randomly among the available *Asclepias* plants on the study plot (*tetrophthalmus*: $X^2 = 124.9$, df = 1, p ≪ .01; *femoratus*: $X^2 = 98.6$, df = 1, p ≪ .01; *melanurus*: $X^2 = 103.5$, df = 1, p ≪ .01).

From the census and host-plant data, niche breadth values were calculated using the formula:

$$B_{ij} = \frac{1}{\Sigma\ P_{ij}^2}$$

where B_{ij} is the niche breadth of species j on resource state i, and P_{ij} is the proportion of species j on resource state i (21, 24). This value was standardized, resulting in a range of 0 to 1.0 for the niche breadth values. A value of 1.0 represents the largest possible niche breadth. Comparison of the niche breadths for the three species of *Tetraopes* on the two resource dimensions, host-plant and time (Table 1), shows that

TABLE 1

| | Niche Breadth | |
	Host-Plant	Time
tetrophthalmus	0.36	0.65
femoratus	0.74	0.40
melanurus	0.54	0.28

for all species a wide niche breadth along one resource dimension is complimented by a relatively narrow niche breadth along the other

The amount of niche overlap between species pairs was calculated using the formula:

$$O_{jk} = \frac{\Sigma\ P_{ij}\ P_{ik}}{\sqrt{\Sigma\ P_{ij}^2\ \Sigma\ P_{ik}^2}}$$

where O_{jk} is the niche overlap between species j and k, P_{ij} is the proportion of species j on resource state i, and P_{ik} is the proportion of species k on resource state i (5, 24). The overall niche overlap is merely the product of the overlap values for all the resource dimensions (28). Two species whose niches totally overlap will have an O_{jk} of 1.0. The niche overlap values for the three pairs of *Tetraopes* species are presented in Table 2. For these species pairs overlap values are high on one resource dimension and relatively lower on the other, with the overall niche overlap between species pairs being small.

Finally, competition coefficients can be calculated for the species pairs using the index of MacArthur and Levins (22):

$$\propto_{ij} = \frac{\Sigma\ U_{ih}\ U_{jh}}{\Sigma\ (U_{ih})^2}$$

where $\propto_{ij}$ is the effect of species j on the population growth rate of species i, U_{ih} is the number of individuals of species i utilizing resource state h, and U_{jh} is the number

Table 2

	Host-Plant	Niche Overlap Time	Overall
tetrophthalmus vs *femoratus*	0.78	0.24	0.19
femoratus vs *melanurus*	0.79	0.29	0.23
melanurus vs *tetrophthalmus*	0.23	0.42	0.10

of individuals of species j utilizing resource state h. $\propto$ values of less than 1.0 indicate that intraspecific competition is more important than interspecific competition. From the Lotka-Volterra competition equations it can be shown that in order for two species to coexist the following inequalities must be true:

$$K_i < K_j / \propto ji$$
$$K_j < K_i / \propto ij$$
$$\text{or: } \propto ji \cdot \propto ij < 1$$

where K_i and K_j represent the carrying capacity for species i and j, respectively (12, 28).

The competition coefficients and their products for the species pairs are given in Table 3. In all three cases the products of the $\propto$'s are well below the critical value of 1.0.

Discussion

The preceeding analysis suggests that interspecific competition does not play an important role in the organization of *Tetraopes* communities, at least with regards to adult populations. For the two resource dimensions, host-plant and time, the three *Tetraopes* species were found to behave as specialists on one resource dimension, and as generalists on the other, with the resulting overall niche overlaps being quite small. This is a pattern similar to one found by Uetz (33) in a guild of wandering spiders.

Table 3

	Competition Coefficients		
	$\propto_{ij}$	$\propto_{ji}$	$\propto_{ij} \cdot \propto_{ji}$
tetrophthalmus vs *femoratus*	$\propto_{tf} = 3.29$	$\propto_{ft} = 0.16$	$\propto_{tf} \cdot \propto_{ft} = 0.53$
femoratus vs *melanurus*	$\propto_{mf} = 3.1$	$\propto_{fm} = 0.17$	$\propto_{mf} \cdot \propto_{fm} = 0.53$
melanurus vs *tetrophthalmus*	$\propto_{tm} = 0.01$	$\propto_{mt} = 4.9$	$\propto_{tm} \cdot \propto_{mt} = 0.05$

In this instance niche divergence along at least one resource dimension was found to occur, allowing potentially competing species to coexist.

The question still remains as to the cause of the differences in relative abundances shown by sympatric species of *Tetraopes* utilizing the same host-plant reported by Chemsak (4). Chemsak also notes that in the midwest, near the eastern extent of the range of *T. femoratus, T. tetrophthalmus* is always the more abundant species (36, 11), but the situation is reversed farther west near the western extent of the range of *tetrophthalmus* (4). Such a reversal of relative abundances may be expected to occur if individuals near the edge of the species' geographic range, and presumably near the biotic limit of the species, are less efficient competitors.

Interspecific competition may still be an important influence on *Tetraopes* communities, not during the adult stage, as this study suggests, but rather during the period of larval development. One aspect of *Tetraopes* biology which has not been investigated is the effect that different levels of cardenolides have on the development of *Tetraopes* larva. *Asclepias* plants vary in their relative cardenolide content (3, 6), and it is possible that not all available milkweed roots are equally suitable for the development of larval *Tetraopes*. If this is true, the larval period may be a time of intense intra- and interspecific competition for these insects.

Acknowledgments

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