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Limited Dispersal and its Effect on Population Structure in the Milkweed Beetle *Tetraopes tetraophthalmus*

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Summary. The movement patterns of adult milkweed beetles, *Tetraopes tetraophthalmus*, were monitored via a mark-recapture technique. Movement or dispersal patterns were studied in two natural populations, one in which the host plant, *Asclepias syriaca*, was nearly continuously distributed over a 250 × 90 m area and another where *Asclepias* was distributed in 17 small discrete patches. In both populations dispersal distances resulting from the flight patterns of the adult beetles were quite short, averaging less than 40 m from the point of first encounter 10 days after marking. Males were shown to be more vagile than females. The distribution of dispersal distances collected from one of the populations was fit to three statistical distributions cited in the literature as expected from dispersal by many small-scale movements or observed in other species. It was found that an equation describing an exponential decay gave the best statistical fit to the data collected here for milkweed beetles. The data is discussed in the context of the effects of the limited dispersal power of the beetles and the distribution of suitable habitat on the population structure of *Tetraopes*.

Introduction

This is a study of dispersal of the adult stage of the milkweed beetle *Tetraopes tetraophthalmus* (Coleoptera: Cerambycidae). Dispersal is defined here as the distance traveled by an organism, with respect to some point of origin, due to its day to day activities. The distances moved by organisms between the location where they are born and the point of occurrence of episodes of mating and reproduction are important determinants of population structure. From a population genetic perspective, the vagility of an organism can be a strong influence on rates of gene flow, especially in species whose populations are physically structured by discontinuities in the distribution of suitable habitat or resources. Restricted gene flow can, of course, lead to genetic differentiation of local populations as a result of locally differing selection pressures or genetic drift. Mathematical models of genetic differentiation (eg. "stepping stone" or "isolation by distance") require information concerning the mean and distribution of distances moved by dispersing organisms.

A priori, flying insects would appear capable of long distance dispersal and individuals of many species do, in fact, move large distances during their lifetime (see Rabb and Kennedy 1979; and Johnson 1969 for reviews). Some species of insects, however,

show surprisingly restricted movement patterns despite their flight ability. For example, Dobzhansky and Wright (1943) found that female *Drosophila pseudoobscura* may only move several hundred meters during their lifetime. Ehrlich (1961) showed that adult checkerspot butterflies on Jasper Ridge, California exhibit restricted patterns of movement to the degree that individuals remain in highly localized populations despite access to nearby favorable habitat.

The present study of dispersal in milkweed beetles was motivated by several aspects of the biology of the organism which indicated that it could live in highly structured populations. *Tetraopes tetraophthalmus* feeds almost exclusively on the common milkweed *Asclepias syriaca*; the adults feeding on leaves and flowers and the larvae on the rhizome system (Chemsak 1963). The host plant grows in patches ranging in size from several to several thousand stalks across the central and eastern United States. Often these milkweed patches are rather discrete in their distribution with patches separated by intervals devoid of milkweed. Limited movement in the beetle could generate populations structured so that beetles inhabiting a specific milkweed patch could be considered a breeding unit or deme, partially isolated genetically from other nearby demes of *Tetraopes*. In electrophoretic studies, Eanes et al. (1977) found that local populations of *Tetraopes tetraophthalmus* located in Suffolk County, New York exhibited statistically significant variation between localities in the allelic frequencies of several polymorphic gene loci. This would indicate restricted gene flow whether the mechanism of differentiation is natural selection or genetic drift.

Because *Tetraopes* has grub-like fossorial larvae it is unlikely that significant dispersal could occur at any life-stage other than the adult. Thus, if a cohort of adult beetles can be followed through their entire lifespan, this should reflect the dispersal power of an entire generation of beetles and provide information on the degree to which dispersal behaviors would be expected to contribute to local genetic differentiation. The present study examines movement patterns of adult *Tetraopes tetraophthalmus* within large continuously distributed milkweed patches as well as between smaller patches separated from one another by 10–100 m. Particular attention is paid to sex differences in movement patterns.

Materials and Methods

Studies on natural populations of *Tetraopes* were performed in the vicinity of the Mountain Lake Biological Station in Giles County, Virginia in 1980. Movement patterns of beetles were followed by a mark-recapture technique. Adult beetles were marked on their elytra

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Table 1. Pairwise distances in meters between 17 small milkweed patches at Study Site II

Patch #	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	—															
2	19.9	—														
3	32.1	16.8	—													
4	62.7	45.9	30.6	—												
5	67.3	53.6	36.7	19.4	—											
6	52.0	32.1	21.4	15.3	32.1	—										
7	90.3	71.9	61.2	36.7	53.6	39.8	—									
8	88.7	70.4	64.3	49.0	68.9	45.4	21.4	—								
9	59.7	45.9	53.6	61.2	79.6	47.4	59.7	45.9	—							
10	39.8	24.4	33.7	50.5	64.3	33.7	61.2	53.5	21.4	—						
11	42.8	35.2	49.0	67.3	82.6	52.0	76.5	65.8	21.4	18.4	—					
12	29.1	36.7	53.6	81.1	90.3	65.8	99.4	91.8	50.5	38.2	27.5	—				
13	52.0	53.6	68.9	90.3	104.0	75.0	99.4	87.2	41.3	41.3	24.5	24.5	—			
14	64.3	58.1	70.4	85.7	102.5	70.4	85.7	70.4	26.0	36.7	23.0	42.8	23.0	—		
15	64.3	68.9	84.2	108.6	100.9	93.3	117.8	105.6	59.7	59.7	42.8	33.7	18.4	36.7	—	
16	87.2	100.9	117.8	146.9	153.0	133.1	166.8	157.6	111.7	104.0	91.8	67.3	71.9	93.3	56.6	—
17	42.8	61.2	70.4	99.5	96.4	90.3	130.1	131.6	101.8	81.1	81.1	56.6	79.6	99.5	82.6	76.5

with a small spot of acrylic based paint, color coded to represent the location where they were originally found. After marking, beetles were placed on the ground adjacent to the milkweed stalk where they were captured. At each study site all beetles were marked within a 24 h period beginning several days after the emergence of the first adult beetle. Thus, the study populations represent similarly aged cohorts of adult beetles. Though *Tetraopes tetraophthalmus* is univoltine, some adult beetles continued to emerge for several more weeks. It was not feasible, however, to continue to mark large numbers of beetles and account for variation in adult age in estimates of distances moved. Subsequent to marking, beetles were recaptured and re-released at intervals ranging from 1–5 days.

Two separate studies were carried out. At study site I milkweed was abundant and continuously distributed over an area 250 m long and 90 m wide. This area was arbitrarily divided into four contiguous sectors of approximately equal size. All of the beetles found in a given sector were marked with the same color; a total of 716 beetles being marked in the 24 h period. Recaptures were made daily for 6 days and then at intervals of 3–5 days for a total period extending 23 days after marking. Censuses noted the sector the beetle was marked in, the sector it was recaptured in, and, after day 3, its sex. At study site I, a second milkweed patch was located about 75 m from the main patch, separated by milkweed free pasture. No beetles were marked in this patch but it was censused periodically for marked beetles that had migrated in from the main patch.

Study site II was located about 2 km from study site I. Here the milkweed was much more patchy in its distribution. By weeding, we further enhanced the patchy distribution of the plants so that 17 discrete patches, each about 5 m in diameter, were created. Table 1 gives the distance from each patch to all other patches. At study site II over 1,200 *Tetraopes* were marked in a 24 h period with beetles found in each patch given a specific color code. While most patches contained about 50 beetles, it should be noted that patch 6 contained over 300. Censuses were performed 3, 4, 6 and 9 days after marking. Each census noted the patch where the recaptured beetle was originally marked, its present location, and its sex.

Results

Study Site I

Recapture rates at study site I remained rather constant at approximately 25% for the first 14 days of the study but declined to about 5% by the end of the 23 day period. This decline in the number of beetles recaptured no doubt reflects natural mortality of the adults. Price and Willson (1976) and Hartman

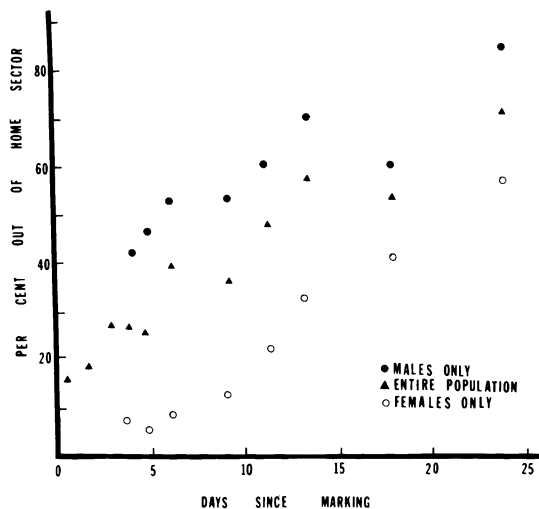


Fig. 1. The per cent of adult *Tetraopes tetraophthalmus* found out of the sector of study site I in which they were originally marked

(1977) estimate the average adult lifespan in this beetle to be about three weeks though a small minority have been observed to live well beyond this time (Edgren and Calhoun 1958). The proportion of adults recaptured in sectors of study site I other than where they were marked is presented in Fig. 1. The proportion of recaptures found out of the home sector increases nearly linearly with time. Figure 1 also shows that when the movement patterns in this population are examined on the basis of sex, males are much more mobile than females.

Extremely limited mobility could cause a population of beetles occupying a large milkweed patch to be genetically structured on a scale finer than would be detected by between patch comparisons alone. That is, populations with a continuous distribution but limited dispersal can be structured by "isolation by distance" (Wright 1943). With these data we can test the hypothesis that, over time, the distribution of beetles across study site I becomes random with respect to the sector where they were originally marked. The random expectation is that the proportion of each color type found in its home sector should reflect the proportion of each type originally marked. Should this random expectation be met there is little likelihood that limited dispersal could cause

Table 2. The number (N) of adult *Tetraopes* of each sex collected on 6 census days at study site I and chi-square value (X^2) calculated for the fit of the observed proportions of beetles in and out of their home patch to the proportions expected under the random mix hypothesis presented in the text

Days since marking	Males (N , X^2)	Females (N , X^2)
6	87, 18.77**	44, 56.57**
9	110, 8.19**	89, 103.25**
11	91, 7.85**	64, 53.21**
13	114, 1.34	70, 44.73**
18	55, 2.05	34, 9.77**
23	28, 1.81	18, 5.03*

* denotes $P < 0.05$, ** denotes $P < 0.01$ with one degree of freedom

Table 3. The proportions of male and female adult *Tetraopes* captured out of the milkweed patch where they were originally marked at study site II

Recaptured beetles	Days since marking			
	3	4	6	9
Males out of patch	0.65	0.66	0.72	0.70
Females out of patch	0.37	0.59	0.60	0.57

an internal structuring of a population of beetles occupying a large milkweed patch.

Using the random expectation stated above we calculated the number of beetles expected to be found in and out of their home sectors, summed across all color types. This sum was compared to the observed numbers of beetles found in and out of their home sector, summed across color types, by a chi-square test with 1 degree of freedom. This was done for each sex separately starting on census day 6. The results are presented in Table 2. For the males, no more beetles were found in their home sectors than would be expected based on random mixing from day 13 onwards. For the females, however, a statistically significant excess of recaptures were found to be in their home sector up to and including day 23, after most of the females had died. Movement by adult female *Tetraopes* is quite restricted even within a continuously distributed milkweed patch measuring 250×90 m in area. Movement by adult males, however, very likely precludes any internal structuring of this population.

The additional milkweed patch located about 75 m from one edge of study site I was censused periodically. Marked beetles who had migrated to this patch from study site I were removed

Table 4. Mean (\bar{Y}) and variance (S^2) of distances (in meters) moved by adult *Tetraopes tetraophthalmus* at study site II

Days since marking	Sex	\bar{Y}	S^2
3	male	22.2	592
	female	13.6	543
4	male	25.7	739
	female	24.3	886
6	male	32.4	901
	female	26.7	998
9	male	30.1	860
	female	24.4	887

as they were discovered. Only 19 beetles were found to have migrated between patches when recaptures were summed across the entire experiment. Fifteen of these were males; a result consistent with the sex differences in movement noted in Fig. 1 and Table 2.

Study Site II

Recapture rates at study site II were somewhat higher than at site I, ranging from 39–44%. Table 3 shows the proportion of recaptures of each sex made in and out of home patch on each of the four census days. Statistical tests of the equality of these percentages on each of the census days reveal the sex differences to be significant ($P < 0.01$) on all census days except day 4 ($0.2 > P > 0.1$). As in study site I, males are more mobile than females.

Because the size of patches is small relative to the distance between patches at study site II, and because the distances between all pairwise combinations of patches are known (Table 1), an estimate can be made of the means and distributions of flight distances 3, 4, 6 and 9 days after marking. Means and variances of the flight distances are shown in Table 4, distributions in Table 5. Beetles who remain in their home patch are assumed to have moved a distance of zero. Between patch distances given in Table 1 are pooled into class intervals along with the zero distance assigned to stay-at-homes and the number of beetles found in each interval related to the class mark. This gives an idea of the shape of the distribution of distances moved. The data for day 9 is also graphed in Fig. 2 so that the shape of the distribution can be more easily visualized. Note the differences between sexes.

The shape of the distribution of distances moved by dispers-

Table 5. Numbers of adult *Tetraopes* recaptured varying distances from the point at which they were originally marked at study site II

Days since marking	Sex	Distance in meters										
		0	16.2	28.8	41.2	53.8	66.2	78.8	91.2	103.8	116.2	128.8
3	male	101	86	36	17	24	10	8	5	0	2	0
	female	145	35	15	12	9	7	3	2	0	0	2
4	male	104	67	43	35	25	15	8	4	1	4	2
	female	104	59	21	13	23	12	6	8	3	1	3
6	male	77	43	37	44	36	9	13	8	1	4	4
	female	99	42	30	20	24	13	6	4	1	1	8
9	male	79	46	36	38	27	13	8	4	6	3	2
	female	87	37	18	12	13	22	3	3	1	1	3

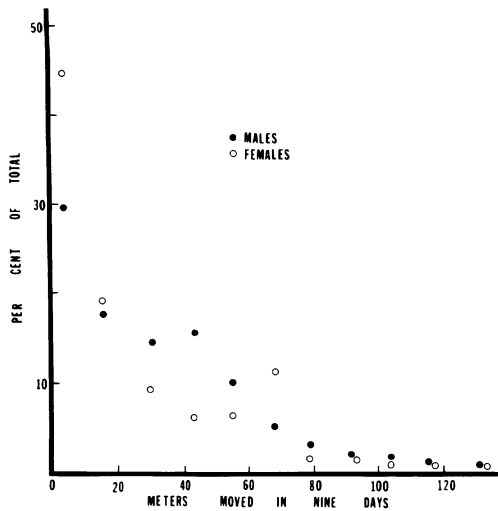


Fig. 2. The distance moved by adult *Tetraopes tetraophthalmus* nine days after being marked at study site II

ing organisms is of relevance both to the theory of island biogeography (MacArthur and Wilson 1967) and to the theory of population genetics (Bateman 1950; Skellam 1951; Cavalli-Sforza and Bodmer 1971; Richardson 1970; Endler 1977; and others). In organisms dispersing by many small scale movements, the distribution of distances moved from point of origin should resemble a half-normal shape if individual flight distances are constant and at random with respect to direction. A more leptokurtic distribution resembling an exponential decay is typically found, however, in natural and experimentally manipulated populations (Endler 1977). Bateman (1950) and Taylor (1978) point out that these two alternatives can be easily distinguished statistically because the equations describing half-normal and exponential decay distributions can take the form of simple linear regressions of numbers (N) on distance moved (X) given the appropriate transformations of the variables. Thus, a half-normal distribution can be generated by the equation:

$$\text{Log } N = a + b X^2 \quad (1)$$

and an approximation of an exponential decay by:

$$\text{Log } N = a + b X. \quad (2)$$

In addition, Wallace (1966) and Taylor (1978) found that the equation:

$$\text{Log } N = a + b X^{1/2} \quad (3)$$

gave a good fit to Dobzhansky and Wright's 1943 data on *Drosophila* dispersal as well as data from several other insect species. In all of these equations a and b can be thought of as the intercept and slope of a regression line. By appropriate transformations of X and N the data from Table 5 were fitted to equations 1–3. Data for two sexes taken 4 different times gives 8 separate comparisons of Eqs. (1)–(3). Obviously, these comparisons are not entirely independent since the distribution on any one day partially determines the distribution the next. Since a recapture rate of 40% indicates only partial overlap of individuals recaptured in successive censuses, however, it was felt that these multiple tests were of value. In all cases the fit to all three regressions is quite good (r^2 ranging from 0.62 to 0.97). Figure 3 presents the fit of males and females recaptured on day 9 (raw data shown in Table 5) to Eq. (2). In order to compare the fit of the data to the three equations, the data as well as

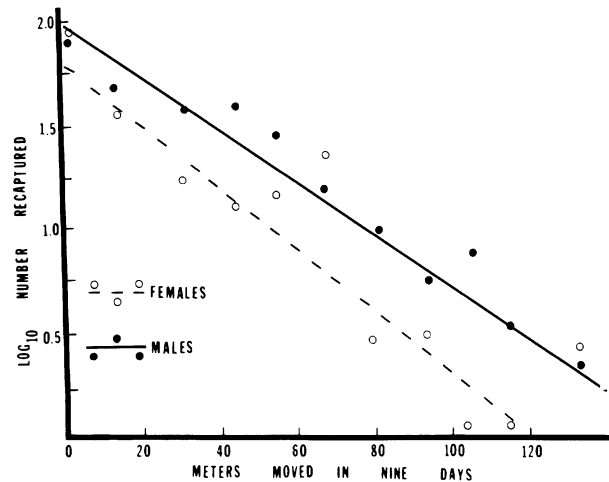


Fig. 3. Least squares regression of the \log_{10} number of adult *Tetraopes tetraophthalmus* on meters moved in nine days (eg. 2 from text)

Table 6. The value of the coefficient of determination (r^2) calculated when the observed numbers of adult *Tetraopes* recaptured varying distances from where they were marked is paired with expected values predicted by Eqs. (1)–(3)

Days since marking	Sex	Eq. (1)	Eq. (2)	Eq. (3)
3	male	0.81	0.94	0.71
	female	0.45	0.86	0.99
4	male	0.85	0.99	0.77
	female	0.63	0.94	0.88
6	male	0.84	0.88	0.70
	female	0.65	0.95	0.92
9	male	0.87	0.96	0.78
	female	0.58	0.91	0.92

the values of N predicted by the regressions at the various distances measured were backtransformed and a coefficient of determination (r^2) was calculated for each set of paired observed and expected values. This statistic calculates the per cent of the variation in one variable explained by the variation in a second variable. A good fit of Eqs. (1)–(3) to the data would result in r^2 near unity. The calculated values of r^2 are given in Table 6. It appears that Eq. (2) gives the best fit to the backtransformed data. Certainly, Eq. (1) gives the worst fit. Thus, the shape of the distribution of dispersal distances most closely resembles an exponential decay.

Discussion

Dispersal in *Tetraopes tetraophthalmus* is quite limited. Most adult beetles occupying a milkweed patch in which the host plant is either continuously distributed or distributed in sub-patches spaced at intervals of 10–20 m move less than 100 m in their lifetime. One could infer, then, that movement between widely separated milkweed patches must be quite rare. The small number of beetles that moved the relatively short distance of 75 m that separates study site I from the outlying patch tends to support this inference. Of course, the distances moved by any beetles that left either study site entirely were not measured. All known milkweed patches within several km of both study

sites were visited periodically for other reasons, however, and no marked beetles were encountered. Neither were any beetles found to have moved the 2 km between study site I and II.

Adult male beetles move greater distances than do females. This may result from mating patterns found in this insect. Adult males fight with each other in the presence of females with the loser being driven from the milkweed stalk (McCauley 1982). Movement in females is probably associated with oviposition which takes place in grasses found in close association with milkweed (Hartman 1977).

Given the limited dispersal of *Tetraopes* and the oviposition habits of females, it appears that beetles occupying a milkweed patch or a collection of small, closely spaced milkweed patches represent a breeding unit semi-isolated from other units. Given also the potential long life of a patch of *Asclepias syriaca*, the effects of isolation of *Tetraopes* populations could be of some consequence in determining the genetic structure of *Tetraopes* populations. Generally speaking, the greater the degree of isolation of two populations of the same species the greater the potential for them to become genetically differentiated. The true measure of the genetic isolation of two populations is the rate of gene flow between them. Gene flow is usually difficult to measure, however, and so it is often estimated by rates of dispersal or migration of individuals.

Movement of an individual from one population to another does not necessitate gene flow. That individual must give birth to viable offspring if a female and mate if a male. In *Tetraopes*, movement by males may be precipitated by failure at mating. Males that lose fights are forced into flight. Since copulation can last a matter of hours (Mason 1964), males that do mate are likely to remain stationary for a considerable period. Thus, it is possible that the males moving the greatest distances are those least successful at mating and least likely to convert migration between populations into actual gene flow.

The data presented here for *Tetraopes* indicates that two populations separated by as little as several hundred meters would exchange very few migrants. Care should be taken, however, in predicting genetical structure in terms of dispersal rate. Single locus population genetics theory states that a moderate level of gene flow can act as a powerful homogenizing force. A distribution of movement distances resembling an exponential decay implies that while most individuals move very little, a few could move quite a distance. Conversely, a distribution with the same mean but resembling the half-normal shape would imply more intermediate dispersal distances and fewer at the extreme tail. Statements about low mean dispersal distances presented in the absence of information about the tails of the distribution may not be very meaningful in predicting the homogenizing effect of gene flow.

Given the theoretical importance of the shape of the distribution of dispersal distances, a discussion of the biological forces that could generate an exponential decay is in order. A distribution of dispersal distances resembling an exponential decay can be generated when two types of flight distances are represented in the population (Skellam 1951). This could be due to differences between individuals, some individuals always flying short distances and other long, or due to a heterogeneous distribution of resources whereby the individual keeps flying until the appropriate resource is located. There is evidence in support of both possibilities in *Tetraopes tetraophthalmus*. Hartman (1977) proposes several egg-laying strategies in females of this species, one involving ovipositing in the area of adult eclosion and another involving considerable flight before oviposition. These contrasting strategies could provide the two flight types, in females at

least, necessary to generate the observed distributions. Hartman (1977) does not present actual flight distances nor does he differentiate between males and females in his mark-recapture data, however, so the validity of his hypothesis in the context of the dispersal distances presented here is unclear. Davis (1980) reported that in laboratory studies individual *Tetraopes* differ in the duration of their flight times and that these differences persist throughout the adult lives of the individuals. No sex effect was detected. This could partially explain the observed dispersal distributions if the laboratory results hold true under field conditions.

A second factor possibly influencing the shape of the distribution of dispersal distances is the distribution of favorable habitat or resources. Organisms may tend to remain in favorable habitat or keep moving until new favorable habitat is located. Milkweed was distributed into small patches at study site II and it is probable that *Tetraopes* wandering out of their home patch keep moving until a new patch is reached. If individuals have no knowledge of the direction to the next nearest patch then many of them must move a relatively long distance before encountering another patch. Thus, flights of intermediate distance are not particularly common. The two hypothesis are not mutually exclusive and more information is needed to test either or both of them.

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Announcement

XVth Pacific Science Congress, 1983

The XVth Pacific Science Congress will be held in Dunedin, New Zealand, 1-11 February 1983. Its theme is to be "Conservation, development and utilization of the resources of the Pacific".

A session is planned on the diversity, distribution, abundance and management of vertebrate populations in the Pacific region. Joint sessions will be arranged with related disciplines. Speakers are now invited to offer papers (with title and short summary) on such topics as:

Biogeography	Ecosystem studies
Species diversity	Man-induced changes
Habitat requirements	Endangered species
Migration and movements	Conservation and management
Population ecology	

For further information, please write to Dr CW Burns, Section Convener, (Ecology and Environmental Protection), c/-Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand