

ORIGINAL PAPER

Stephen F. Matter

Interpatch movement of the red milkweed beetle, *Tetraopes tetraophthalmus*: individual responses to patch size and isolation

Received: 5 December 1994 / Accepted: 12 September 1995

Abstract Individual movement patterns and the effects of host plant patch size and isolation on patch occupancy were examined for red milkweed beetles, *Tetraopes tetraophthalmus*, residing in a heterogeneous landscape. Male beetles were found to move both more often and farther between host plant patches than female beetles, and this difference affected the patterns of patch occupancy observed. Overall, unoccupied milkweed patches were smaller and more isolated than patches occupied by beetles. Patches uninhabited by females tended to be more isolated, but not necessarily smaller, than patches with female beetles, indicating that females may be affected more by patch isolation than patch size. Presence of male beetles on patches showed a stronger response to patch size than to patch isolation. Differences in movement between males and females illustrate the need for demographically based dispersal data. Comparisons of *Tetraopes* interpatch movement patterns between landscapes composed of patches of different size revealed that landscapes with overall smaller patches may have greater rates of interpatch movement.

Key words *Asclepias* · Dispersal · Landscape · Patch · *Tetraopes*

Introduction

Empirical and theoretical studies have highlighted the importance of dispersal for single species population dynamics at regional (between-population) scales (Levins 1970; Brown and Kodric-Brown 1977; Hansson 1977, 1991; Connor et al. 1983; Fahrig and Merriam 1985; Pulliam 1988; Fahrig and Paloheimo 1988; Pulliam and

Danielson 1991; Hanski and Gilpin 1991; Kareiva 1990). Movement between local populations may produce patterns apparent only from a regional perspective (e.g., metapopulation, source-sink). Much recent research in population ecology has been devoted to understanding under what conditions, and to what degree, regional dynamics are prevalent in nature.

However, the identification of when dispersal may be important in creating regional dynamics has been limited in part by a lack of good dispersal data. Most studies of dispersal have focused on movement within local populations in homogeneous habitats, not on movement among populations (Vance 1984; Porter and Dooley 1993). How individuals move within a population may not adequately reflect movement among local populations. That is, observations of local movement patterns may not provide the data necessary to make predictions concerning between-population processes. Furthermore, local populations can be affected by the demographic makeup of dispersers, which may not be representative of local populations to or from which they are dispersing. The loss or gain of a particular demographic class of individuals may result in movement-based stochasticity (Myers and Krebs 1971). To adequately describe and quantify the effects of dispersal at a regional scale, information concerning the frequency and distances that individuals move between local populations is needed (Wiens et al. 1993).

A rich literature suggests that two landscape features, habitat patch size and isolation, can influence population structure by affecting dispersal (MacArthur and Wilson 1967; Wilson and Simberloff 1969; Root 1973; Williamson 1981; Kareiva 1982, 1983). Immigration (colonization) rates are predicted to be higher for large than for small habitat patches, as larger patches may be easier for dispersers to locate. Less isolated habitat patches may receive more immigrants than distant habitats, if dispersal frequency declines with distance. At one end of the spectrum, small, isolated habitats may be uninhabited due to lower rates of colonization. However if small, isolated habitats also have lower population sizes, these popula-

S.F. Matter¹
University of Virginia, Department of Environmental Sciences,
Charlottesville, VA 22902, USA
Fax: (804) 982-2137, email: sfm2z@faraday.Virginia.EDU

Present address:

¹ The Blandy Experimental Farm, Boye, VA 22620, USA

Table 1 Summary of patch attributes for this and previous studies of interpatch movement for *Tetraopes tetraophthalmus*. Patch size was evaluated as the number of ramets in a patch and interpatch distance (m) as the distance from the edge of one patch to another

Study	Patches	Patch size			Interpatch distance			Proportion dispersing		Mean distance moved	
		Max	Min	Mean	Max	Min	Mean	Male	Female	Male	Female
McCauley et al. (1981)	17	(5 m dia.) ^a			167	17	65	0.70	0.57	30	24
Lawrence (1982)	7	600	100	N/A	200	20	121 ^b	0.24	0.18	44	25
Lawrence (1986)	6	186	24	76	140 ^b	10 ^b	40	0.19	0.13	14	10
This study	61	96	1	14	593	10	248	0.53	0.44	170	154

^a A diameter of 5 m corresponds to a patch size of approximately 10–30 ramets (personal observation)

^b Indicates a value calculated from the available data

tions may be more prone to stochastic extinction (Richter-Dyn and Goel 1972), and may also be less likely to be 'rescued' from extinction by immigration (Brown and Kodric-Brown 1977; Faeth and Simberloff 1981). Thus small, isolated habitats are predicted to be uninhabited more frequently than large, less isolated habitats either due to more frequent extinction or less frequent colonization.

The objectives of this research were twofold. The first was to examine interpatch movement of *Tetraopes tetraophthalmus* in a heterogeneous landscape and to make comparisons among movement patterns of this species in landscape of differing structure. A number of previous studies have focused on *T. tetraophthalmus* movement both among and within milkweed patches (Table 1). McCauley et al. (1981) created, through selective weeding, 17 distinct patches of milkweed each approximately 5 m in diameter. Over 1,200 beetles were marked and censused after 3, 4, 6, and 9 days to determine interpatch movement distances. Lawrence (1982) observed the within and between-patch movement patterns of 21 male and 19 female beetles in eight large unmanipulated milkweed patches over a 24-day period. In a separate study at a different site Lawrence (1986) marked 1682 beetles residing in six patches. Beetles were individually marked and movement patterns were observed over one season.

In general, previous studies have shown that interpatch movement is infrequent (McCauley et al. 1981; Lawrence 1982, 1986, 1987, 1988; Davis 1981, 1984; McCauley 1991), that males tend to move farther and initiate more interpatch movements than females (McCauley et al. 1981; Lawrence 1982, 1986), and that male movement may be related to mating opportunities (Lawrence 1986).

The second objective of this research was to test the hypothesis that small and/or isolated habitats would be uninhabited more frequently than larger, less isolated habitat patches. Additionally, because males and females differ in movement patterns, they may also differ in their response to habitat isolation and size. I predicted that small, isolated patches should be less likely to have beetles present than larger, less isolated patches. I would also expect that if females move shorter distances than males, females should show greater sensitivity to patch isolation than males.

Methods

Natural history and study site

Tetraopes tetraophthalmus (Forster) (Coleoptera: Cerambycidae) is distributed throughout eastern and midwestern North America (Chemsak 1963). The beetle is a univoltine, monophagous herbivore of common milkweed, *Asclepias syriaca* (Asclepiadaceae). During the summer, adult beetles mate repeatedly and feed on the leaves, buds, and flowers of milkweed. After mating, females oviposit, generally 8–20 eggs per clutch, into hollow stems of nearby grasses (McCauley and Reilly 1984). After 6–10 days larvae emerge, burrow into the soil, and begin to feed on milkweed rhizomes until late autumn when they leave the root mass to form overwintering cells. Larvae pupate near the soil surface and emerge during early June in northern Virginia.

I conducted this research in a 40-ha meadow at the Blandy Experimental Farm, Clarke County, Virginia. The study site is typical of rural Virginia, containing common milkweed, *Asclepias syriaca*; many grasses such as *Festuca* sp., *Poa* sp., and *Dactylis* sp.; and several dicots including *Carduus nutans*, *Solanum carolinense*, and *Galium* sp. Periodic burning or mowing of the meadow during the winter, approximately every other year, is practiced to reduce woody plants.

Field methods

An exhaustive search of the study site revealed 61 discrete patches of *Asclepias syriaca* (each separated by at least 10 m) which were monitored for beetle activity. Patches ranged in size from 1 to 95 ramets. The location of each milkweed patch was mapped and all interpatch distances calculated. Mark-recapture censuses of beetles began 9 June 1992 after first appearance of adult beetles on patches, and continued until 3 August 1992. Upon initial capture, beetles were placed into individual vials and taken to the laboratory where they were sexed, weighed, and marked. Each beetle was given a unique color code painted on the elytra using Testors model enamel (McCauley et al. 1981). I returned beetles to the patch in which they were found no later than 12 h after capture. Censusing and replacement of beetles was conducted either early in the morning or evening to minimize disturbance to the beetles (Lawrence 1982, 1986). Initially all patches were censused daily, but during the third week beetle abundance became too great to complete censusing in one day. After this time the field was divided in half, and each patch was censused approximately every other day.

Data analysis

A history of individual movements, total distance moved, and longest move was compiled for each beetle. Number of interpatch moves, censuses, and patches in which an individual was observed were also recorded. Frequency distributions of movement distances were generated using the single longest distance moved by an individual. Frequencies were adjusted by multiplying the observed

number of movements in a distance interval (10-m intervals) by the reciprocal of the number of interpatch distances in that interval. This method gives each interpatch distance an equal weight (Porter and Dooley 1993). Linear, negative exponential, and geometric models were fit to the adjusted movement distributions for male and female beetles using linear and non-linear regression (NLR) procedures (cf. Porter and Dooley 1993 for methods).

Tests for differences in movement between the sexes were analyzed for all individuals in the population and separately for individuals making interpatch movements. Because number of censuses in which a particular beetle was observed was strongly correlated with other variables, such as longest and total distance moved ($r > 0.50$, in all cases), number of censuses was used as a covariate in all movement analyses. Analysis of covariance (ANCOVA) was used to test for differences in movement between male and female beetles within both the dispersing and total populations.

I used multivariate analysis of variance (MANOVA) to test the effects of patch isolation and size on the presence or absence of beetles on patches. I conducted separate analyses for the total population, male beetles, and female beetles. The areal extent of a patch is strongly correlated with the number of ramets in a patch ($r = 0.70$, $P < 0.001$, $df = 57$); however, beetle abundance shows a stronger relationship to number of ramets ($r = 0.93$, $n = 57$) than patch area ($r = 0.72$, $n = 57$) (Matter 1994). Therefore the number of ramets per patch was used as a measure of patch size. Isolation was measured as the sum of the distances from a patch to all other patches. This method of determining isolation gives each patch in the landscape an equal "weight" as a potential source of immigrants. Other methods for determining isolation were also employed (e.g., distance to the nearest occupied patch) and provided qualitatively similar results.

Results

A total of 1390 beetles was marked (678 females and 644 males, 68 beetles were not sexed). Sex ratio over all patches and census dates did not differ from an expected 1:1 ($\chi^2 = 0.874$, $df = 1$, $P = 0.350$). No bias in number of observations was found between the sexes; males ($\bar{x} = 1.87 \pm 1.30$ SE) and females ($\bar{x} = 1.88 \pm 1.37$) had equal mean number of observations per individual (Mann-Whitney U -test large sample approximation, $Z = -0.1161$, $P = 0.9076$).

Interpatch movement for both male and female *Tetraopes tetraophthalmus* was moderate. Of those beetles that were recaptured ($n = 628$), and therefore whose movement could possibly be observed, 48% made at least one interpatch move. However, the beetles that did move generally made only one interpatch move, and no beetle made more than four (Fig. 1). A significantly greater proportion of males (0.53) than females (0.44) made interpatch moves ($G_{adj} = 22668$, $P < 0.001$). Males and females also showed differences in interpatch movement distances. Using only beetles that were observed at least twice, and adjusting for the number of censuses per beetle, I found that males moved significantly farther than females both in total distance moved ($F_{1,581} = 6.25$, $P = 0.013$) and single longest move ($F_{1,581} = 6.43$, $P = 0.011$) (Fig. 2). Males also made more interpatch moves ($F_{1,581} = 5.26$, $P = 0.022$) and were found on a greater number of patches ($F_{1,581} = 7.73$, $P = 0.006$) than were females (Fig. 3).

Analyses limited to individuals making interpatch movements showed no significant differences between the

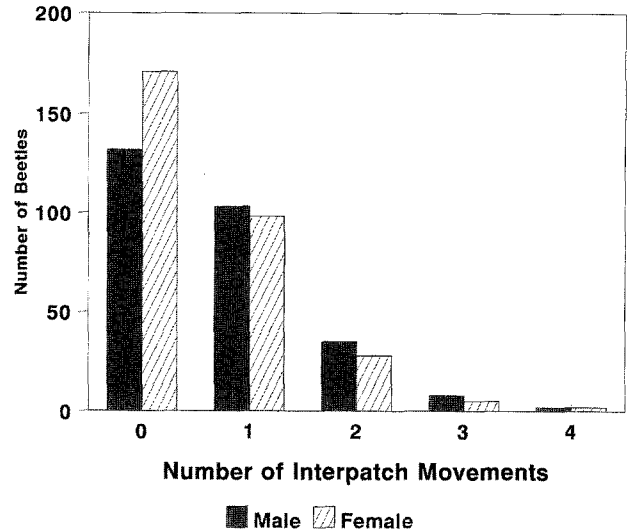


Fig. 1 The number of *Tetraopes tetraophthalmus* making interpatch movements. Only beetles for which sex could be determined and that were recaptured at least once were included. No beetles made more than four interpatch moves

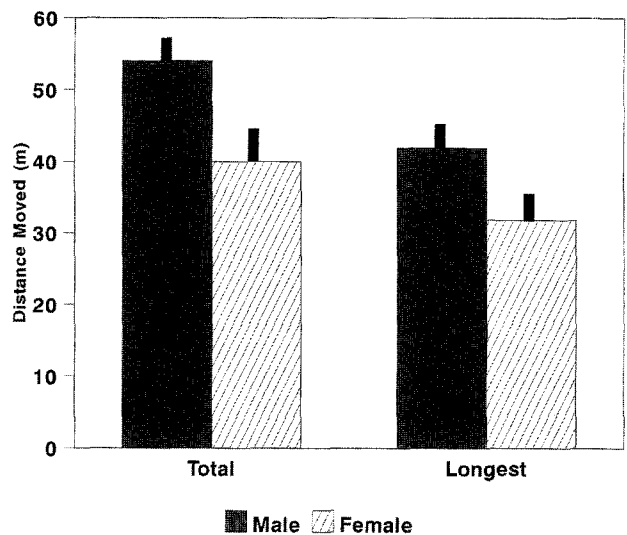


Fig. 2 Mean (\pm SE) total interpatch distance moved and single longest interpatch move for male and female *T. tetraophthalmus*. Means are unadjusted for the covariate, number of censuses. Analysis of covariance showed significant differences between males and females for both total and longest movements

sexes for single longest move ($F_{1,278} = 1.96$, $P = 0.162$), total distance moved ($F_{1,278} = 2.46$, $P = 0.135$), number of interpatch moves ($F_{1,278} = 0.851$, $P = 0.357$), or number of different patches ($F_{1,278} = 3.62$, $P = 0.058$). However the same trends seen in the total population for males to move farther and more often were also present in the dispersing fraction. Although insect mass is often correlated with flight ability (Davis 1981), no movement variable for either the total or dispersing population showed a significant correlation with mass; however, females were significantly heavier than males ($\bar{x} = 0.128 \pm 0.001$ g, $\bar{x} = 0.110 \pm 0.001$ g, respectively; $t = 18.84$, $df = 1310$, $P < 0.001$).

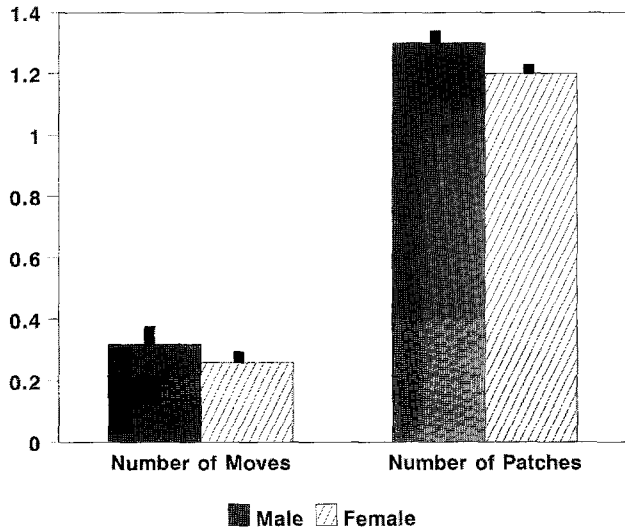


Fig. 3 Mean (\pm SE) number of interpatch movements and number of different patches occupied by male and female *T. tetraophthalmus*. Means are unadjusted for number of censuses. Analysis of covariance showed significant differences between males and females for both number of interpatch movements and number of different patches occupied

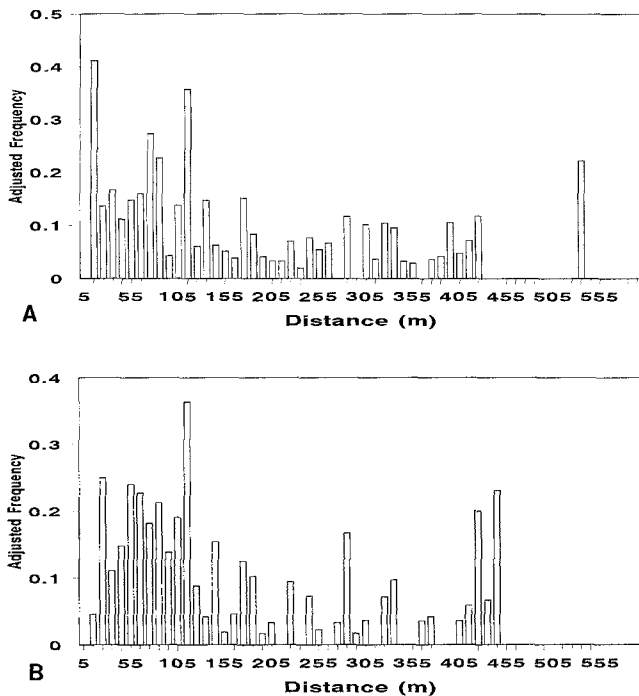


Fig. 4A, B Adjusted frequency of interpatch distances moved for **A** male and **B** female *T. tetraophthalmus*. Interpatch distances were grouped into 10-m intervals; midpoints of every 5th interval are indicated on the x-axis. Frequencies were adjusted by multiplying the observed number of movements in each distance interval by the reciprocal of the number of interpatch distances in each interval. This method gives each interpatch distance an equal weight (Porter and Dooley 1993)

Table 2 Goodness of fit (r^2) of linear, negative exponential, and geometric models, for adjusted male and female dispersal frequencies. A dash indicates that the model has less explanatory power than a simple mean (Porter and Dooley 1993)

	Model		
	Linear	Negative exponential	Geometric
Male	0.359	0.421	–
Female	0.360	0.248	–

Table 3 Summary of the means (\pm SE) of patch size (ramets) and interpatch distance for patches occupied and unoccupied by males, females, and both (total population)

	Interpatch distance (m)	Ramets	n
Overall	47871 \pm 10622	14.1 \pm 19.4	61
Total population			
Unoccupied	61463 \pm 6675	4.0 \pm 4.0	5
Occupied	46657 \pm 10077	15.0 \pm 19.9	56
Male			
Unoccupied	53050 \pm 11771	3.8 \pm 3.0	9
Occupied	46974 \pm 10269	15.9 \pm 20.5	52
Female			
Unoccupied	54975 \pm 1161	4.8 \pm 4.2	8
Occupied	46798 \pm 10153	15.5 \pm 20.4	53

The adjusted frequencies of movement for male and female beetles both show a general decline as distance increases (Fig. 4). However, there was a large proportion of long-distance movements for both males and females, producing a nearly bimodal pattern. Of the three models tested a linear model best fit the distribution of female movement distances, while a negative exponential model best described male movement (Table 2).

Analyses of the effects of patch size and isolation on beetle presence or absence reflect both the beetles' dispersal ability and the sexual bias in movement. Of the 61 patches 5 (8.2%) had no beetles of either sex throughout the study. Nine patches (14.8%) had no male beetles and eight patches (13.1%) had no females. The probability that 5 of 61 patches will be uninhabited given 1390 beetles with an equal chance of being on any patch is $P=2.32 \times 10^{-43}$ (Feller 1968, p. 105). When patches are weighted for number of ramets in a particular patch the simulated probability of having 5 empty patches rises to $P=2.08 \times 10^{-4}$, indicating that the distribution of beetles on patches is non-random. The unoccupied patches tended to be significantly smaller and more isolated than were occupied patches (Tables 3 and 4). Univariate tests of patch size and isolation revealed that males and females respond differently to these patch attributes. Patch size had a greater effect on male beetle absence than did patch isolation, while patch isolation showed a stronger effect on female absence than did patch size (Table 4).

Table 4 MANOVA table of univariate F tests comparing mean distance from all other patches and patch size (number of ramets) between occupied and unoccupied patches for the total population, male, and female beetles

	Hypo. SS	Error SS	$F_{1,59}$	P
Total				
Distance	1.0×10^9	5.8×10^9	10.299	0.002
Patch size	559	22061	1.145	0.226
Male				
Distance	2.8×10^8	6.5×10^9	2.58	0.114
Patch size	1131	21489	3.11	0.083
Female				
Distance	4.7×10^8	6.3×10^9	4.35	0.041
Patch size	810	21811	2.19	0.144

Discussion

The expectations that habitat isolation and size are important determinants of presence or absence were supported by these results and analyses. However, the degree to which patch size and isolation affect presence and absence may differ between the sexes. The statistics for the total populations of males and females reveal that males tend to move more often and greater distances than females. Because the female population as a whole does not move as often or as far as the male population, greater isolation of patches may contribute more to female than to male absence.

Within the dispersing fraction of the total population there were no significant differences in movement patterns between males and females. This result may be interpreted as evidence that the only important difference between male and female movement is the greater propensity to disperse seen in male beetles. If males move more often they will tend to move greater distances. However, the lack of significant difference between male and female movement in the dispersing population may be purely statistical. The trend for males to move farther and more often is present in the dispersing populations, but restricting the data set reduces the sample size and hence the statistical power. On average the power and effect sizes (f) for tests concerning the total population were 0.70 and 0.10, respectively, while for tests of the dispersing fraction power was in the neighborhood of 0.30, and effect sizes were only slightly lower, 0.08 (Cohen 1977).

The difference between male and female dispersal patterns is further reflected by the fact that their dispersal frequencies are best described by different equations (Table 2). This result is significant because models of spatially distinct populations usually model dispersal using "average population parameters" (Wiens et al. 1993). Such an approach may be oversimplistic and illustrates the need for dispersal data for different demographic categories. If, as these results show, demographic groups move different distances or with different frequencies, predictions of local population presence/absence, persis-

tence, or dynamics can be altered. It is important to note that in situations where females tend to move less frequently and/or shorter distances, and because females are potential colonizers, population models using data from the entire population would tend to overestimate actual (re)colonization rates and potentially persistence times.

The results presented here generally concur with previous studies of milkweed beetle dispersal (Table 1). All studies showed male beetles to move both farther and proportionally more often than female beetles, regardless of the landscape. Consequently, the sexual bias in movement appears to be unrelated to landscape features and may be genetically based or linked to other ecological factors such as mating opportunities (Lawrence 1986). A comparison of patch size and proportion dispersing across studies of milkweed beetle dispersal (Table 1) suggests that landscapes with smaller patch sizes may increase the amount of interpatch movement, while greater isolation may increase overall distances moved. The effect of small patch sizes on interpatch movement may be particularly strong for male beetles. Males initiate more intrapatch movements than females (Lawrence 1982), and thus may leave a patch by random movement at a greater rate than females (Turchin 1986). The greater effect of patch size on male movement is supported by a greater increase in the proportion of males than females dispersing with decreasing patch size (Table 1). Lawrence (1982), however suggests that *T. tetraophthalmus* can detect patch edges and alter their behavior to avoid leaving host patches. Previous studies of insect movement have demonstrated that emigration decreases with increasing patch size (Root 1973; Kareiva 1985; Turchin 1986; Bach 1988). However comparisons of *landscapes* composed of patches of differing size have not, to my knowledge, been conducted. The collective results of these studies in different landscapes suggest that landscapes with overall smaller habitat patches may have greater rates of dispersal than landscapes containing predominantly larger habitat patches. Because dispersal can link local dynamics, landscapes with small patches may be more "integrated" than landscapes with large patches. By this token factors affecting dynamics in one patch in a small-patch landscape may be felt more keenly in other patches than in a large-patch landscape.

Comparisons between this and previous studies of *Tetraopes* indicate that greater dispersion of host plants patches may elicit an increase in distance moved. However, comparisons of movement distances between studies may be somewhat suspect. In all studies, the observed movements are constrained by the represented interpatch distances. In this study because the range of interpatch distances in this study extended 60 m farther than the longest observed movement and 100 m farther than the second-longest observed movement, thus the problem of representing all possible movement distances should be minimal. However the possibility of long distance movements carrying beetles out of the system cannot be ruled out. Unfortunately, this type of data is not available from other studies for comparative purposes.

Kareiva (1982), using two species of flea beetles, *Phyllotreta cruciferae* and *P. striolata*, demonstrated that increased isolation of habitat patches reduced the overall amount of dispersal for both species. This is not the case for *T. tetraophthalmus*. Perhaps the difference lies in the fact that *T. tetraophthalmus* possess the ability for long distance movements, whereas the flea beetles used in Kareiva's study are limited in their dispersal ability. Further discrepancy may lie in the fact that patch size was constant in the experimental design of Kareiva (1982). Patch size may be a more important determinant of the rate of interpatch movement than patch isolation for *Tetraopes*.

Effects of dispersal in the *Tetraopes*-*Asclepias* system

Matter (1994), using the same system of milkweed patches, over the same time period found that beetle density increased with milkweed patches size, but dispersal had no effect on local population size. The average net flux of beetles per patch (immigration – emigration) was zero, and was unrelated to either patch size or isolation. However, within a landscape dispersal may directly affect the number of occupied patches through colonization. Patches that are devoid of beetles may be a result of a lack of colonization rather than extinction. This notion is supported by the observation that once beetle populations become established on a patch they tend to remain; beetle populations rarely become extinct without the destruction of the milkweed patch (McCauley 1989; S.F. Matter, personal observations).

The fact that uninhabited patches tend to be small may introduce an interesting dynamic. Newly established milkweed patches are small; only one "ramet" is produced from a seed. Thus new patches may be free of beetles for some time until they are colonized. This lag-time until colonization may allow milkweed patches to increase in size relatively quickly until the patch is either large enough that it is apparent to dispersing beetles, or it is inevitably found over time. Once colonized the rate of patch growth may be affected by herbivory by adult and larval beetles. However, little is known concerning the impact of herbivory on milkweed growth. It is safe to assume that a small number of beetles (one or two) could easily seriously damage a milkweed seedling. Additionally, seedlings or small patches may be unfavorable to colonists. Survival of offspring may be reduced in small patches owing to their potentially smaller rhizome network. Thus there may be a "critical patch size" needed to support populations (Kareiva 1983).

The results of this study have many implications for landscape scale studies. If demographic groups respond differently to habitat isolation and size, as my study suggests, much care must be taken in projecting how a species will respond to a patchy environment. *T. tetraophthalmus* may provide an extreme example of the need for individual movement data in landscape scale studies because of the sexual bias in movement. However, many

species exhibit both demographic and habitat-based differences in dispersal frequency or distances, which may affect landscape scale predictions (Myers and Krebs 1971; Gaines and McClenaghan 1980; Otronen and Hanski 1983; Pulliam 1988; Pulliam and Danielson 1991). The comparison of milkweed beetle dispersal in different landscapes provides some evidence that movement may be qualitatively similar between landscapes, but the distances and rates of movement may be landscape-specific.

Acknowledgements I would like to thank M. Beck, M. Bowers, E. Connor, J. Dooley, C. Sacchi, and an anonymous reviewer for their advice and critical evaluations of an earlier version of this manuscript. I would also like to thank the individuals at the Blandy Experimental Farm who assisted with this project. This research was supported by a grant from the Eugene and William Odum Foundation to the author.

References

- Bach CE (1988) Effects of host plant patch size on herbivore density: patterns. *Ecology* 69:1090–1102
- Brown JH, Kodric-Brown A (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58:445–449
- Chemsak JA (1963) Taxonomy and bionomics of the genus *Tetraopes* (Cerambycidae: Coleoptera) University of California Publications, Berkeley
- Cohen J (1977) Statistical power analyses for the behavioral sciences. Academic Press, New York
- Connor EF, Faeth SH, Simberloff DS (1983) Leafminers on oak: The role of immigration and *in situ* reproductive recruitment. *Ecology* 64:191–204
- Davis MA (1981) The flight capacity of dispersing milkweed beetles, *Tetraopes tetraophthalmus*. *Ann Entomol Soc Am* 74:385–386
- Davis MA (1984) The flight and migration ecology of the red milkweed beetle *Tetraopes tetraophthalmus*. *Ecology* 65:230–234
- Faeth SH, Simberloff DS (1981) Experimental isolation of oak host plants: effects on mortality, survivorship, and abundances of leaf mining insects. *Ecology* 62:625–635
- Fahrig L, Merriam G (1985) Habitat patch connectivity and population survival. *Ecology* 66:1762–1768
- Fahrig L, Paloheimo J (1988) Determinants of local population size in patchy habitats. *Theor Popul Biol* 34:194–213
- Feller W (1968) An introduction to probability theory and its applications, vol 1, 3rd edn. Wiley, New York
- Gaines MS, McClenaghan LR Jr (1980) Dispersal in small mammals. *Annu Rev Ecol Syst* 11:163–196
- Hanski I, Gilpin M (1991) Metapopulation dynamics: brief history and conceptual domain. *Biol J Linn Soc* 42:3–16
- Hansson L (1977) Spatial dynamics of field voles *Microtus agrestis* in heterogeneous landscapes. *Oikos* 29:539–544
- Hansson L (1991) Dispersal and connectivity in metapopulations. *Biol J Linn Soc* 42:89–103
- Kareiva P (1982) Experimental and mathematical analyses of herbivore movement: quantifying influence of plant spacing and quality on foraging discrimination. *Ecol Monogr* 52:261–282
- Kareiva P (1983) Influence of vegetational texture on herbivore populations: resource concentration and herbivore movement. In: Denno RF, McClure MS (eds) *Variable plants and herbivores in natural and managed systems*. Academic Press, New York, pp 259–289
- Kareiva P (1985) Finding and losing host plants by *Phyllotreta*: patch size and surrounding habitat. *Ecology* 66:1809–1816
- Kareiva P (1990) Population dynamics in spatially complex environments: theory and data. *Philos Trans R Soc Lond B* 330: 53–68

- Lawrence WS (1982) Sexual dimorphism in between and within patch movements of a monophagous insect: *Tetraopes* (Coleoptera: Cerambycidae). *Oecologia* 53:245–250
- Lawrence WS (1986) Movement ecology of the red milkweed beetle *Tetraopes tetraophthalmus* (Forster). Dissertation, Yale University, New Haven, Connecticut
- Lawrence WS (1987) Effects of sex ratio on milkweed beetle emigration from host plant patches. *Ecology* 68:539
- Lawrence WS (1988) Movement ecology of the red milkweed beetle in relation to population size and structure. *J Anim Ecol* 57:21–35
- Levins R (1970) Extinction. In: Gerstenhaber M (ed) Some mathematical problems in ecology. American Mathematical Society, Providence, Rhode Island
- McArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton
- Matter SF (1994) Patch population dynamics of the red milkweed beetle, *Tetraopes tetraophthalmus*. M.S. Thesis, University of Virginia, Charlottesville
- McCauley DE (1989) Extinction, colonization, and population structure: a study of a milkweed beetle. *Am Nat* 134:365–376
- McCauley DE (1991) The effect of host plant patch size variation on the population structure of a specialist herbivore insect, *Tetraopes tetraophthalmus*. *Evolution* 45:1675–1684
- McCauley DE, Reilly LM (1984) Sperm storage and sperm precedence in the milkweed beetle *Tetraopes tetraophthalmus* (Forster) (Coleoptera: Cerambycidae). *Ann Entomol Soc Am* 77:526–530
- McCauley DE, Ott JA, Stine A, McGrath S (1981) Limited dispersal and its effects on population structure in the milkweed beetle *Tetraopes tetraophthalmus*. *Oecologia* 51:145–150
- Myers JH, Krebs CJ (1971) Genetic, behavioral, and reproductive attributes of dispersing field voles, *Microtus pennsylvanicus* and *Microtus ochrogaster*. *Ecol Monogr* 41:53–78
- Otronen M, Hanski I (1983) Movement patterns in *Sphaeridium*: differences between species, sexes, and feeding and breeding individuals. *J Anim Ecol* 52:663–680
- Porter J, Dooley J (1993) Animal dispersal patterns. a reassessment of simple mathematical models. *Ecology* 74:2436–2443
- Pulliam HR (1988) Sources, sinks, and population regulation. *Am Nat* 132:652–661
- Pulliam HR, Danielson BJ (1991) Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *Am Nat* 137:S50–S66
- Richter-Dyn N, Goel N (1972) On the extinction of a colonizing species. *Theor Popul Biol* 3:406–433
- Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards, *Brassica oleracea*. *Ecol Monogr* 43:95–124
- Turchin PB (1986) Modelling the effect of host patch size on Mexican bean beetle emigration. *Ecology* 67:124–132
- Vance RV (1984) The effects of dispersal on population stability in one-species, discrete-space population growth models. *Am Nat* 132:230–254
- Wiens JA, Stenseth NC, Van Horne B, Ims RA (1993) Ecological mechanisms and landscape ecology. *Oikos* 66:369–380
- Williamson M (1981) Island populations. Oxford University Press, Oxford
- Wilson EO, Simberloff DS (1969) Experimental zoogeography of islands: defaunation and monitoring techniques. *Ecology* 50:267–278