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Population density and area: the role of between- and within-patch processes

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Abstract The relationship between population density and the size of host plant patches was investigated for the red milkweed beetle *Tetraopes tetraophthalmus* inhabiting unmanipulated patches of *Asclepias syriaca*. The resource concentration hypothesis proposes that density-area patterns, specifically that of increasing herbivore density with patch size, are primarily a function of movement between host plant patches. This research investigated the degree to which movement accounted for density-area patterns. Poisson regression analysis of beetle abundance versus milkweed patch size revealed that beetle density tended to increase with patch size. The pattern of density and patch size resulted from local reproduction and residence time. The density of emerging beetles tended to increase with patch size while emigration rates were unrelated to patch size. Immigration rates were constant with patch size for male beetles, and decreased with patch size for female beetles. Net flux of beetles (immigration – emigration) did not vary with patch size for male beetles and decreased with patch size for female beetles. Comparisons are made between this system and previously studied systems where movement plays a significant role in forming density area patterns. Additionally, several hypotheses are presented which may account for greater in situ recruitment and residence time in large patches.

Key words *Asclepias* · Density-area relationship · Emigration and immigration · Resource concentration · *Tetraopes*

Introduction

The relationship between population density and habitat area is of fundamental interest to both basic and applied ecology (MacArthur and Wilson 1967; Simberloff and Abele 1982; Wilcox and Murphy 1985). Root (1973) proposed in the "resource concentration hypothesis" that a net movement of insects onto large and out of small patches would produce a pattern of increasing insect density with patch size. The bulk of observational studies has demonstrated a pattern of increasing density with patch size for herbivorous insects (Root 1973; Cromartie 1975; Raupp and Denno 1979; Denno et al. 1981; Kareiva 1981; MacGarvin 1982; Kindvall and Ahlen 1982; Bach 1988; Funderburke et al. 1990). Studies focusing on the mechanisms responsible for density-area relationships have generally explored only movement-based hypotheses, often finding lower rates of emigration from and greater immigration to large patches, supporting the resource concentration hypothesis (Kareiva 1985; Turchin 1986, 1987). However, other factors such as local reproduction (Capman et al. 1990), predation rates (Root 1973; Raupp and Denno 1979; Risch 1981; Risch et al. 1982), or residence time (Root 1973), may vary with the size of patches and contribute to density-area relationships, but have rarely been investigated simultaneously.

Here I report the results of a study that examined the patterns of movement, residence time, and reproduction among host plant patches for the red milkweed beetle, *Tetraopes tetraophthalmus*. Based on the resource concentration hypothesis, I predicted that (1) milkweed beetle density, immigration rates, and residence times should increase with increasing patch size, and (2) that emigration rates should decrease with increasing patch size. Additionally, I examined the relationship between local recruitment, estimated by beetle emergence, and patch size. The resource concentration hypothesis makes no predictions concerning the patterns of local repro-

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duction with patch size, so I expected that the number of beetles emerging per unit patch size would remain constant over the range of patch sizes. The goal was to determine how within and between patch factors contribute to beetle density in patches of different size.

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.* During the summer, adult beetles feed on the leaves, buds, and flowers of milkweed. The beetles mate repeatedly during the summer. After each mating females oviposit eight to ten eggs into the hollow stems of nearby grasses (Gardiner 1961; McCauley and Reilly 1984). After 6–14 days larvae eclose, burrow into the soil, and begin to feed on milkweed roots and rhizomes until late autumn when they leave the root mass to form overwintering cells. Larvae pupate near the soil surface and adult beetles emerge in 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 carolinese*, and *Galium* sp. The meadow is burned or mowed during the winter, approximately every other year, 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. Milkweed patches ranged in size from one to 95 ramets. The site was isolated from other milkweed patches by at least 400 m. Mark-recapture censuses of beetles began on 9 June 1992 when adult beetles first appeared on patches, and continued until 3 August 1992. Upon initial capture, beetles were placed in individual vials and taken to the laboratory where they were sexed, weighed, and marked. All beetles found on patches were marked with a unique color code painted on the elytra using model airplane paint (McCauley et al. 1981). I returned beetles to the patch in which they were found no later than 12 h after capture. 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 (census 15) the field was divided in half, and each patch was censused approximately every other day. Each patch was censused a total of 25 times over the study.

Data analysis

Beetle abundance on each patch was estimated as the minimum number known alive (MNKA) for each census period. A beetle was assumed to be on a particular patch, even if unobserved, if it was found in a prior and subsequent census of that patch, but was not found on another patch during intervening censuses. This assumption is justified by the relatively low rate of interpatch movement demonstrated by these beetles (Lawrence 1982, 1986; Matter 1996). Immigration and emigration were only counted for known events, i.e., when a previously marked beetle appeared on a different patch. This method may underestimate the total amount of movement due to unmarked beetles moving, but should be unbiased with regard to patch size patterns. Net flux of beetles on a patch was calculated as the total number of beetles immigrating minus the total number emigrating. Because of the clumped distribution of emerging beetles within a patch, direct measurements of beetle emergence would require total or near total enclosures impeding estimates of dispersal. Therefore the number of beetles emerging on a patch was estimated as the number of beetles first appearing on a patch over the first 15 censuses (9 June–28 June). While this method may confound immigration with emergence to some degree, daily censusing and infrequent movement of beetles, should have minimized this problem (Fig. 1). Individual residence times were calculated as the number of consecutive censuses that each beetle remained on a patch. Patch residence time was calculated as the mean of the individual residence times over the entire season for a particular patch. Only patches in which beetles were present were included in residence time analyses.

To evaluate the relationships between patch size and beetle density, emergence, immigration, and emigration, I used Poisson regressions (Vincent and Haworth 1983; Connor et al. 1997). This technique was adopted because most standard regression approaches (e.g., linear, non-linear, quadratic) violate the assumption of homoscedasticity for this type of data. Log area-log abundance transformation plots necessitate excluding patches with zero abundance, as the log of zero is undefined. The "traditional" solution to this problem, adding a small number to each value before log transformation, alters the slope of the relationship in an unpredictable manner, making tests involving the slope ambiguous (Williams 1995).

The Poisson model used to examine density-area relationships when habitat areas vary in size is:

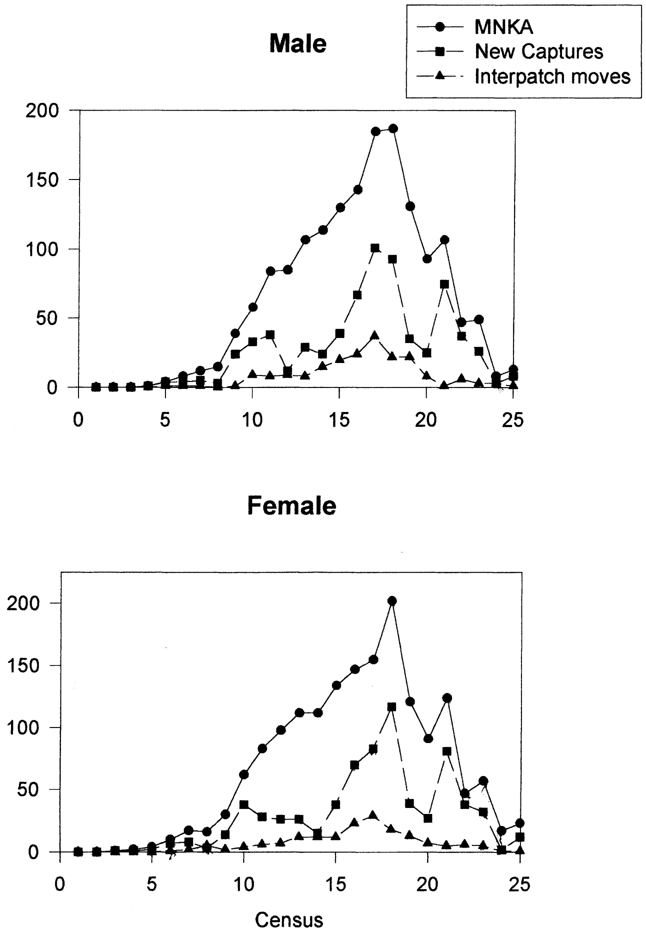

Fig. 1 The number of male (*top*) and female (*bottom*) beetles known to be alive, (*MNKA*), number of new beetles marked, and number of beetles making interpatch movements (earliest estimable time of emigration) for each census period

$$P(Y = k) = \frac{e^{-\lambda A^{\beta}}(\lambda A^{\beta})^{k}}{k!}$$

where k is the number of individuals, A is the area (patch size), λ is the number of organisms (or, e.g., immigrants) per unit area, and β is a parameter that can be used to examine the relationship with area (Connor et al. 1997). When $\beta = 1$ density is constant with area, $\beta > 1$ indicates increasing density with area, and $\beta < 1$ indicates decreasing density with area. To examine the relationship between density and patch size two models were fit, one including β, and one in which β was not included (e.g., $\beta = 1$, an assumption of constant density with area). Generalized linear models, weighted for over-dispersion where necessary, were fit to the data (Wedderburn 1974; McCullagh and Nelder 1989; Crawley 1993). The deviance difference between the two models is approximately χ^2 distributed with 1 *df*, and can be used to test whether β differs from one (Connor et al. 1997).

The relationship between density and patch size was examined for each census period in which more than five beetles were known to be alive. The total number of immigrations per patch over all census periods and the number of emerging beetles per patch over the first 15 census periods were also tested using Poisson regressions. A similar procedure was used to examine the relationship between emigration and patch size, however patches with zero abundance were excluded from these analyses. Number of ramets within each patch was used as the measure of patch size (Lawrence 1982, 1986; Matter 1994, 1996).

The relationships between mean residence time and net flux (immigration − emigration), and patch size were examined using simple linear regression. Here the test of interest was simply whether the slope was significantly different from zero. All analyses were conducted separately for male and female beetles, as previous research has shown that the sexes may differ in their responses to patch attributes (Lawrence 1982; Matter 1996).

Results

A total of 1455 beetles was marked (708 females and 686 males, 61 beetles were not sexed). The number of observations per beetle did not vary between the sexes [males, $\bar{x} = 1.82 \pm 0.05$ (SE); females, $\bar{x} = 1.83 \pm 0.05$, Mann-Whitney *U* large sample approximation, $Z = -0.1613$, $P = 0.8719$). Capture probability, estimated as the probability that a beetle marked in census t would be found in census $t + 1$ (Skalski and Robson 1992) showed no relationship with patch size across both sexes ($r^2 = 0.000$, $df = 52$, $P = 1.000$).

Emigration rates did not vary with patch size for both male and female beetles (Table 1). Immigration rates were also constant with patch size for male beetles, however female beetles immigrated to smaller patches at a proportionally higher rate than to larger patches (Table 1). The density of beetles emerging tended to increase with patch size for both males and females, although the relationship is only marginally significant (Table 1). The relationship between beetle density and patch size was erratic during early censuses, and as time progressed gradually shifted to that of increasing density with patch size, reaching a maximum at census 13 (Table 2). After this point the relationship for females gradually moved toward constant density with patch size, and later in the season decreasing density with patch size. For males, a similar, but less pronounced late-season trend toward decreasing density with patch size occurred. For abundance summed across all census periods, females showed a fairly strong pattern of increasing density with patch size; male density tended to increase with patch size although the relationship is not as strong.

The slope of the relationship between mean residence time and patch size was significantly greater than zero for both males ($t = 2.84$, $df = 50$, $P = 0.007$) and females ($t = 3.11$, $df = 51$, $P = 0.003$). The flux of males was unrelated to patch size ($t = -0.231$, $df = 59$, $P = 0.818$), and female flux was negatively related to patch size ($t = -4.95$, $df = 59$, $P < 0.001$).

Table 1 Parameter estimates for total number of immigrations, emigrations, and emergenences per patch. The deviance difference is used to test whether β differs from 1

	β (±SE)	Deviance difference	*P*
Male			
Immigration	0.922(0.104)	0.561	0.454
Emigration	0.882(0.111)	1.118	0.290
Emergence	1.234(0.125)	3.585	0.058
Female			
Immigration	0.789(0.102)	4.428	0.039
Emigration	0.925(0.106)	0.500	0.480
Emergence	1.234(0.147)	2.618	0.106

Discussion

The pattern of increasing insect densities with host plant patch size, is usually explained by movement from smaller to larger patches (Root 1973; Kareiva 1981; Turchin 1987). The results of my study support the pattern, milkweed beetle densities tended to increase with patch size, especially at times of high abundance. However, the underlying mechanisms involve increasing emergence rates and increasing residence times with patch size, not directional movement. For movement to affect local densities the flux of individuals must vary systematically with patch size, and it must comprise a substantial fraction of the population. In this system, slightly less than half of the population made at least one interpatch move (Matter 1996), but the tendency for directional movement was toward smaller patches for females and unrelated to patch size for males. Such movement patterns could not increase density in large versus small patches.

The movement pattern exhibited by females may counterbalance the positive density area relationship created by emergence. This pattern can be seen in the temporal trends (Table 2). Early in the season, the density relationship is somewhat erratic due in part to asynchronus emergence between patches. As emergence continues the density-area relationship becomes positive. However, after the emergence period (approx. census 18 on) the tendency for females to immigrate to smaller patches creates a negative density-area relationship.

Table 2 Male (*top*) and female (*bottom*) abundance and parameter estimates for each census period in which > 5 individuals were known to be alive. The deviance difference is used to test whether β differs from 1. An asterisk indicates that the data were not significantly over-dispersed and unweighted models were used. (*MNKA* minimum number known alive)

Census	MNKA	β (±SE)	Deviance difference	*P*
Male:				
1	0			
2	0			
3	0			
4	1			
5	4			
6	8	0.973(0.461)	0.004	0.950
7	12	1.261(0.430)	0.382	0.537
8	15	1.053(0.345)	0.024	0.877
9	39	0.982(0.197)	0.008	0.929
10	58	1.309(0.148)	4.593	0.032
11	84	1.379(0.153)	6.708	0.010
12	85	1.386(0.162)	6.175	0.013
13	107	1.406(0.155)	7.566	0.006
14	114	1.365(0.152)	6.153	0.013
15	130	1.237(0.168)	2.050	0.152
16	143	1.097(0.352)	0.078	0.780
17	185	1.174(0.158)	1.241	0.265
18	187	1.373(0.182)	4.204	0.040
19	131	1.124(0.145)	0.744	0.388
20	93	1.236(0.148)	2.644	0.104
21	107	0.921(0.150)	0.269	0.604
22	47	0.990(0.206)	0.002	0.964
23	49	0.872(0.176)	0.516	0.473
24*	8	0.824(0.345)	0.286	0.593
25*	13	1.166(0.276)	0.383	0.536
Total	1620	1.207(0.113)	3.432	0.064
Female:				
1	0			
2	0			
3	1			
4	2			
5	4			
6*	10	0.761(0.289)	0.668	0.418
7	12	0.978(0.294)	0.006	0.938
8	16	1.098(0.312)	0.100	0.752
9	30	1.103(0.218)	0.225	0.635
10	62	1.496(0.170)	9.612	0.002
11	83	1.376(0.140)	7.794	0.005
12	98	1.456(0.159)	9.097	0.003
13	112	1.429(0.177)	6.336	0.012
14	112	1.387(0.166)	5.222	0.022
15	134	1.285(0.196)	2.183	0.140
16	147	1.110(0.353)	0.101	0.751
17	155	1.260(0.159)	2.776	0.096
18	202	1.463(0.206)	5.642	0.018
19	121	1.169(0.147)	1.350	0.245
20	91	1.028(0.132)	0.044	0.834
21	124	0.868(0.132)	0.976	0.323
22	47	0.723(0.171)	2.596	0.107
23	57	0.895(0.158)	0.438	0.508
24*	17	0.528(0.217)	4.509	0.034
25	23	0.912(0.251)	0.118	0.731
Total	1655	1.218(0.104)	4.561	0.033

However the temporal shift in density-area relationship is curiously present for both females and males. While, Lawrence (1987) found that males tend to emigrate from male-biased patches, I did not observe a similar pattern. For males whose exact time of emigration was known (i.e., they were on a particular patch at time t and on another patch at time $t+1$, without any intervening absence) the mean sex difference (males − females) on these patches did not differ from zero ($t = -0.166$, $df = 58$, $P = 0.869$). Possibly the temporal trend in the male density-area relationship may be due to increased male residence time on patches with a female biased sex ratio. If males tend to emigrate and immigrate randomly, but remain or survive for longer periods of time on patches with numerous females, the area density pattern for males may resemble that for females.

The "enemies hypothesis" offers an alternative mechanism to the resource concentration hypothesis (Root 1973; Risch et al. 1982). If predator efficiency is greater in smaller patches, prey densities may be reduced relative to larger patches. If residence time is correlated with survival, it may be an indicator of higher predation rates on small versus large patches. However, *Tetraopes* has very few natural enemies and the primary predators of adult *Tetraopes*, assassin bugs (McCauley and Lawson 1986), were seldom seen throughout the study, but may be important. Additionally, predation or parasitism on larvae is unlikely because of the larvae's fossorial nature (Hawkins 1994). Rather, the increase in residence time with patch size may be related to the presence of milkweed flowers. Large milkweed patches tend to have a higher percentage of flowering ramets, and a greater number of flowers per ramet (Matter unpublished). Hartman (1977) found that the lifespan of beetles feeding on both flowers and foliage was drastically longer than beetles feeding on foliage alone. Thus beetles on large patches may survive longer and have longer residence times because of the presence of milkweed flowers.

Dispersal may play a significant role in population dynamics despite the lack of effect on density patterns. The density of beetles emerging increased with patch size and beetle populations on small patches had relatively little local reproduction. In small patches a few immigrants may constitute a large fraction of the local population. The pattern of movement into small and out of large patches for females would imply that large patches are "sources" and small patches are "sinks" (Pulliam 1988; Pulliam and Danielson 1991). This observation is in contrast to McCauley (1991) who postulated that small patches are sources and large patches sinks for *Tetraopes*. He based his hypothesis on the observation that residence times increased with patch size, as I also found, but concluded that the pattern of residence time reflected greater emigration out of small patches presumably directed toward large patches.

That emergence tended to increase with patch size suggests greater in situ recruitment in large patches than small patches. There are a number of possible explanations for this pattern. First, because abundance is greater on large patches less time may be spent searching for mates, possibly increasing the reproductive output per individual. Second, if large patches contain more rhizomes per unit area, or larger diameter rhizomes than small patches, larvae may either have a higher probability of finding a rhizome after eclosion, and/or there may simply be more rhizome on which to feed in large patches. Additionally, greater amounts of rhizome on which to feed may produce larger adult beetles. Larger female *T. tetraophthalmus* produce a greater number of offspring than smaller females (Lawrence 1986, 1990). I found that larger patches tend to produce larger females ($t = 2.842$, $df = 47$, $P = 0.005$), thus females on larger patches may have slightly higher per capita reproductive rates than on small patches. Third, because large patches cover a greater area they may potentially contain a greater number of favorable oviposition sites. Fourth, because large patches have more flowers, the longevity and reproductive output (Hartman 1977) may be greater for beetles residing on large patches.

Two interesting longer term temporal effects may also lead to positive density-area relationships. Larger patches may be older than smaller patches, given the clonal nature of *Asclepias syriaca*. If beetle abundance builds over generations, larger, older milkweed patches may have had more time to accumulate beetles than smaller patches, leading to increasing beetle density with patch size. Thus time since colonization may affect beetle abundance to a greater degree than patch size, though they may be highly correlated. However, the relative importance of patch age and size on beetle densities may depend on milkweed patch growth rates. Increasing beetle density with patch size may arise if milkweed patch growth is a decreasing function of patch size. For example, if the absolute numbers of beetles on each patch remained constant from year one to year two, but smaller patches increased their size at a proportionally greater rate than large patches over the same time period, the result would be that of increasing beetle density with patch size.

Previous studies examining the resource concentration hypothesis may be biased toward over-estimating the importance of movement in generating area-density patterns and underestimating longer term responses. Most previous studies have been conducted either in 'agricultural' situations where plants are harvested, or over short time frames within which no insect reproduction is occurring (e.g. Root 1973; Kareiva 1985; Turchin 1986; Bach 1988; Funderburke et al. 1990). Studies of this type allow for only two mechanisms to affect density, movement (resource concentration) or survival (enemies hypothesis). Thus, the generality of movement creating density patterns in natural systems may be called into question. A number of mechanisms besides dispersal can affect relationships between insect density and host plant patch size (Kareiva 1983). Dispersal, residence time, or predation acting within generations or the between generation process of reproduction may affect density. The challenge is to identify which and when potential factors are important. For agricultural systems, when hosts are annual plants, or insects spend only part of their life-cycle on a particular host, the between-patch processes of dispersal may be dominant in determining density-area patterns (Root 1973; Kareiva 1985; Turchin 1986; Bach 1988; Funderburke et al. 1990). However, as this study illustrates, in situations where host plant patches and insect populations maintain a more permanent relationship, local reproduction may be of greater importance in forming density-area relationships.

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