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POPULATION CONSEQUENCES OF RESTRICTED DISPERAL FOR AN INSECT HERBIVORE IN A SUBDIVIDED HABITAT

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Abstract. This paper addresses how dispersal ability of the geometrid moth Itame andersoni interacts with habitat subdivision to impact population structure, importance of different habitat types (e.g., patch sizes, habitat configurations), and regional distribution patterns in a subdivided habitat of patches of its host plant Dryas drummondii (Rosaceae). Habitat subdivision occurs both on the patch scale and on the larger spatial scale of sites due to patchy successional patterns. Itame distribution is patchy within areas colonized by Dryas. This research combines observational and experimental approaches to examine individual movement behavior, immigration, and emigration rates of both caterpillars and adult females at the scale of discrete Dryas patches. Itame caterpillars will cross bare ground separating plant patches; however, movement of caterpillars on bare ground was more restricted than predicted by a correlated random walk due to large turning angles which led to area-restricted search. Caterpillar immigration into patches previously cleared of Itame is usually low and is negatively affected by patch isolation when local Itame densities are high. Caterpillar emigration is also significantly greater from patches with high Itame density. Immigration of females, which have reduced wings, was positively influenced by patch isolation and negatively influenced by the presence of a barrier preventing adult females from walking into patches. All females emigrate from their point of emergence and continue moving as they oviposit. Females lay eggs singly on foliage, in leaf litter, and on rocks under and surrounding Dryas patches. Significantly more eggs are laid off of Dryas patches than within Dryas patches, but this is not a result of concentration of searching effort off of Dryas patches. Females move greater distances than predicted by a correlated random walk. Movement parameters combined with oviposition parameters lead to the prediction that the average female will lay all of her eggs within 5–15 m of her starting point. Restricted movement appears to demographically isolate sites separated by distances of as little as 0.5 km. Limited between-site dispersal may link these populations into metapopulations and may explain patchy regional patterns of distribution. Within sites, densities are likely to build up in smaller patches and subdivided habitat due to preferential oviposition on bare ground. These smaller patches may in turn be disproportionately important for population processes due to their contribution of dispersers through density-dependent emigration within and between sites. Thus, this research demonstrates how limited dispersal can impact patterns of distribution, abundance, and population structure in a natural system.

Key words: correlated random walk; Dryas drummondii; emigration; habitat patchiness; immigration; insect dispersal; Itame andersoni; metapopulation; oviposition behavior.

INTRODUCTION

Over the past decade an increasing emphasis has been placed on the importance of spatial patterns for population dynamics, particularly the spatial arrangement of habitats. To understand population level processes of species inhabiting fragmented landscapes, it is not only vital to document the spatial scale of habitat subdivision but also to study the movement of the species of interest (Kareiva 1990, May and Southwood 1990, Reeve 1990, Taylor 1990, Harrison 1991, Doak et al. 1992, Kuussaari et al. 1996, Ims and Yoccoz 1997, Stacey et al. 1997).

Although much of this work has concentrated on easy-to-measure aspects of habitat subdivision, what appears as subdivision to the observer may or may not be subdivision on a scale relevant to resident species. Even small scale subdivision may affect population dynamics (e.g., Gerber and Templeton 1996, Kindvall 1996, Kareiva 1987), however in other cases, dramatic subdivision may have little or no effect on population dynamics (e.g., Antolin and Strong 1987, Fahrig and Paloheimo 1988, Harrison and Thomas 1991, Stacey and Taper 1992, Neve et al. 1996). Sedentary organisms can be affected by very slight subdivision, whereas highly mobile organisms may not experience any impacts from even drastic large-scale fragmentation.
Understanding the interaction of dispersal capability and behavior on the one hand, and the qualitative and quantitative aspects of habitat subdivision on the other, is of interest for many aspects of basic population ecology, agroecology, and conservation biology. Although the questions apply to many taxa, most work on habitat subdivision has been conducted on insects due to their short generation time, ease of manipulation, and relative tractability (see Douk et al. 1992 for a review). However, even for insects, relatively few studies have rigorously investigated both habitat pattern and individual movement, and still fewer have studied naturally occurring patterns of habitat arrangement.

My research concerns the moth, *Itame andersoni* (Geometridae) (henceforth *Itame*), which inhabits patches of its host plant, *Dryas drummondii* (Rosaceae) (henceforth *Dryas*). Although *Dryas* patches are ubiquitous along river bars and glacial margins and occupy hundreds of miles of riverways in the Wrangell Mountains of Alaska, *Itame* populations are rare and limited in spatial extent. I examine immigration and emigration rates at the level of discrete *Dryas* patches as well as individual movement of both larval and adult life stages to address three issues relating to spatial population processes:

1) What can movement behavior and dispersal distances reveal about the connectivity of habitat patches and thus the spatial population structure of *Itame*?

2) How does movement behavior impact the influence of different patch types (e.g., small vs. large, isolated vs. surrounded) and habitat arrangements (e.g., highly subdivided vs. continuous) on *Itame* populations?

3) Can movement behavior help in explaining *Itame*’s patchy pattern of regional distribution?

A central question in the study of subdivided populations is the scale at which population processes occur (Hanski and Gilpin 1991). By examining both caterpillar and adult movement as well as oviposition patterns, I am able to address the scale of population processes and examine the possible impacts of habitat subdivision at two distinct spatial scales.

A less emphasized but related issue is how important different habitat types are for population or metapopulation maintenance (Root 1973, Shaffer 1981, Soule and Simberloff 1986, Wilcove et al. 1986, Kuussaari et al. 1996, Thomas and Hanski 1997). *Itame* populations appear to flourish in smaller *Dryas* patches and highly subdivided habitat (Doak 2000). I use investigations of larval and adult immigration and emigration, and of oviposition behavior to address the contribution of different patch types to population mixing and colonization of new patches.

*Itame*’s patchy regional distribution might be explained by variation in host-plant quality, abiotic factors, interspecific interactions, limited dispersal and colonization potential, or any combination of the above. Here, I examine displacements of both caterpillars and ovipositing females to shed light on whether dispersal is limited enough to play an important role in these regional patterns of distribution.

**Natural History and Study System**

**Habitat pattern**

I conducted this research on the east margins of the Kennicott Glacier in the Wrangell Mountains near McCarthy, Alaska (61° N, 143° W).

The host plant, *Dryas drummondii*, is an early successional, nitrogen-fixing subshrub (height ~5 cm) that grows on glacial moraine and river bars. It forms a two-dimensional habitat of distinct patches on gravel, rock, and silt substrates. At later successional stages these patches grow together, forming extensive mats that are then overgrown by later successional species. Individual *Dryas* patches range from minute to quite large with many discrete patches within the range of 0.1–2 m² (personal observation). In many locations *Dryas* exists in an almost complete monoculture.

In this system, subdivision not only occurs on the small patch-to-patch scale but also on a larger spatial scale due to patchy successional patterns. The glacial retreat at the study site has left a landscape of dry run-off channels interspersed with older vegetation “islands.” The dry channels and lower benches tend to harbor younger populations of *Dryas* than the older and higher island areas. Thus, there is a mosaic of very recent run-off channels with little or no vegetation, older channels with young patchy distributions of *Dryas*, island areas with older patchy or continuous growth of *Dryas*, and island areas in later successional stages that are being taken over by shrubs and trees. Additionally, there exists a great deal of seemingly suitable habitat that is not occupied by *Itame*. The distribution of *Itame* along the Kennicott Glacier and River is far from uniform, with areas of occupied *Dryas* interspersed with areas of unoccupied *Dryas*. This pattern of patchy occupation also occurs on a larger scale within the Wrangell Mountains with large regions of some drainages unoccupied by *Itame* despite extensive populations of *Dryas*.

**Life history**

*Itame andersoni* is univoltine. Caterpillars hatch from overwintering eggs in early to mid-May shortly after snowmelt. All larval instars feed on the foliage of *Dryas drummondii*. I never found *Itame* associated with any other host plant.

Fifth instar caterpillars pupate under rocks or in the litter beneath host plant patches in mid-June to mid-July. Adults emerge about two weeks after pupation. Neither males nor females feed. Males fly readily both diurnally and nocturnally. Females have smaller wings than males and seldom fly. Eggs are laid singly in leaf litter, on foliage and predominantly in gravel and rocks.
both under and surrounding *Dryas* patches. Adult females live for one to two weeks in captivity but lifespan in the field is unknown. The total flight period is approximately one month (Doak 1997).

**METHODS**

I conducted this research during the summers of 1994, 1995, and 1998. Related research on the distribution, abundance, and population dynamics of *Itame* occurred from 1991–1995 (Doak 2000). *Itame* was the only abundant herbivore on *Dryas* at my study sites from 1990–1998. In this paper “patches” refers to *Dryas* individuals or groups of individuals that have grown together to form a linked and discrete clump, whereas “sites” encompass groups of *Dryas* patches. Sites were delineated by natural features such as the extent of *Dryas* growth, gravel banks, forested areas, and boundaries where patchy areas merged into regions of huge continuous *Dryas* mats. The three study sites used for this research were approximately 3200, 5300, and 6400 m² (OR, IN, and GL sites respectively). Distances between the sites were 460 (GL and OR), 730 (GL and IN), and 760 m (OR and IN).

**Caterpillar movement**

_Caterpillar immigration and patch isolation._—To examine the colonization of vacant patches by caterpillars, I removed all caterpillars from experimental patches and then censused these extirpated patches to determine the arrival of immigrants.

In 1994, I marked 10 patches at each of two sites (GL and IN). These patches were small with mean patch size of 0.30 ± 0.02 m² (mean ± 1 se, n = 20) and were classified as either surrounded or isolated. The GL site had high caterpillar densities whereas the IN site had low caterpillar densities throughout my survey studies (Doak 2000). On 31 May, after virtually all eggs had hatched and when the majority of caterpillars were in the first and second instar, I sprayed each patch with Malathion 50 Plus (Ortho, Columbus, Ohio, USA; 3.91 mL/L of water). My observations indicated that Malathion was effective in killing these early instar caterpillars. I counted immigrants eight times from 11 June to 6 July, removing them and noting their instars. I also reared a subset of the immigrants to examine sex ratios (n = 47).

In 1995, I marked 15 patches at each of three sites and classified these patches as surrounded, isolated, or very isolated. I used the two sites from 1994 and added the OR site which in past years had caterpillar densities intermediate between the IN and GL sites (Doak 2000). In 1995 mean patch size was 0.35 ± 0.02 m² (mean ± 1 se). I sprayed these patches with Pyreneone (AgriEvo, Wilmington, Delaware, USA; 1.29 mL/L water) on 8 June 1995 when the majority of caterpillars were third instars (again the insecticide appeared effective). I checked each patch seven times from 14 June to 8 July, again counting and removing immigrants and noting their instar.

I switched from Malathion to Pyreneone because Malathion appeared to have a fertilizing effect on patches; this effect did not, however, appear to differ between patch types or sites.

The areas of all patches were estimated as ellipses based on their major and minor axes. Patch isolation, for surrounded and isolated patches, was quantified after inclusion of patches in the experiment, and this led to slightly unequal sample sizes (Table 1). To quantify patch isolation, I measured the areas of all patches with an edge within 2 m of the edge of each experimental patch. I calculated the sum of the areas of these neighbors. Since a larger patch encompasses a larger area by this measurement, I divided the summed neighbor areas by the area surveyed. This measure of isolation was used to classify patches into two categories (isolated < 0.2 < surrounded). This quantitative measure, developed to distinguish between the original two categories, did not apply well to very isolated patches. Very isolated patches were distinguished by having no or very few neighbors within at least a 5 m radius.

Number of immigrants was analyzed by ANOVA with effects of patch isolation, site, and the site by isolation interaction. Contrasts were done using sequential Bonferroni corrections (Rice 1989) at the overall α = 0.05 level. Model assumptions were examined and adequately met in this and all subsequent analyses.

_Caterpillar emigration._—To examine rates of caterpillar emigration from patches, I conducted an experiment in which I monitored the movement of caterpillars out of patches (size: 0.28 ± 0.01 m², mean ± 1 se, n = 36) containing three different initial population densities. The experiment had two phases: an initial set-up phase to manipulate population density and hence the amount of feeding damage and an experimental phase in which I followed emigration. I chose 30 patches in 10 blocks of three patches each. Within each block, patches were randomly assigned to a low, medium, or high density treatment. In addition, six of the blocks also contained a control patch.

During the set-up phase (beginning 10–13 June), when the majority of caterpillars were in the third and fourth instars, I adjusted densities in the patches so that low, medium, and high density patches contained 5, 15, and 25 caterpillars respectively. This initial treat-

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ment yielded different damage levels which may affect emigration. Because most damage to the host plant is done by late fourth and fifth instars, my adjustments were made early enough to impact damage levels.

I performed the experimental phase in two temporal sets, using one half of the blocks for each. On 15 June I removed all caterpillars in each patch of the first set of five blocks. I then placed 10, 20, and 30 caterpillars in low, medium, and high density patches respectively. Caterpillars were collected from nonexperimental areas, pooled, and randomly chosen for placement near the center of each patch. Each patch received half fourth and half fifth instars. The caterpillars in each patch within a block were dusted with a different color of dayglo fluorescent powder. There was no detectable movement between blocks. Caterpillars appeared to behave normally when marked (personal observation, this experiment, caterpillar movement experiment below, and unpublished data). Patches were censused each day from 16–20 June. The fluorescent powder was easily seen during both night and day censuses. At each census the number of marked caterpillars still present and visible in each patch was recorded. By doing destructive samples, I have found that my estimates of density correlate well with actual densities even when searching for unmarked caterpillars (Pearson correlation, $r = 0.79$; Doak 1997); therefore, I am confident that my censuses of these patches accurately reflect differences between treatments.

On 25 June I set up the second set of emigration patches in the same manner, but using only fifth instars (10, 20, and 30/patch), because the majority of caterpillars were in that stage by 25 June. The second set of patches was censused each day from 26 June to 1 July and all marked caterpillars were counted.

I also followed control patches to monitor the loss of caterpillars from sources other than emigration (e.g., the loss of marks when fourth instars molted to fifths, pupation of fifth instars). I marked six control patches, each within an experimental block. Control patches were surrounded by clear plastic barriers, buried at their base and approximately 12 cm high, with a thin strip of Tanglefoot (Tanglefoot Company, Grand Rapids, Michigan, USA) around the top to prevent caterpillars from leaving the patches (tame caterpillars will not walk into Tanglefoot so it does not increase mortality). These patches were manipulated in the same manner as medium density patches, receiving 15 caterpillars during the set-up phase and 20 marked caterpillars for the experimental phase. Three of the six control patches were followed during each experimental set and censused on the same dates as the experimental patches.

I used survivorship analysis (PROC LIFETEST; SAS Institute 1989) to examine the effect of density treatment on emigration times. Only data from the first three time intervals (days 0–3) were used due to the large numbers of caterpillars missing from patches by day three (>50% for many patches) indicating the breakdown of density treatments. Caterpillars still remaining on day three became right-censored observations.

I pooled the data across the two time sets and across blocks, leading to a conservative estimate of treatment effects. Both Wilcoxon and log-rank $\chi^2$ statistics were used to evaluate the overall treatment effect. I then calculated $Z$-statistics for multiple pairwise treatment comparisons with an experimentwise $\alpha = 0.05$ (Fox 1993). I also tested the set and block effects for association with the loss time using Wilcoxon $\chi^2$ (PROC LIFETEST).

Individual caterpillar movement.—On 8–12 July 1994 and 13–14 July 1998, I observed 20 fifth instar caterpillars (10 each year) to document their movement off of Dryas patches and thus their possible contribution to population mixing and long distance spread. Caterpillars that engaged in pre-pupation behavior (e.g., searching under rocks for pupation sites) were not included in these 20 observations. Each caterpillar was marked with dayglo fluorescent powder to make it easier to track. The caterpillar was placed on bare ground in an area with very few Dryas patches and, after a 10 min acclimation period, its location marked every 2 min until it stopped moving for 10 min, found a patch of Dryas, or, in 1998, for a maximum of 50 min. I measured the distance and compass direction between successive positions, and these data were used to calculate a caterpillar’s net displacement as a function of time.

To assess whether caterpillar movement could be described as a correlated random walk, I examined the relationship between mean squared displacement (MSD) and time. The correlated random walk model describes a situation in which there is neither correlation within or among move lengths or turning angles; both distance and direction of moves can be represented as random draws from frequency distributions of move lengths and turning angles (Kareiva and Shigesada 1983, McCulloch and Cain 1989, Cain 1990). Observed values of MSD vs. time can be compared to expected values under the assumption that movement fits a correlated random walk. Movement paths can be described by move lengths ($l$) for set time intervals and by clockwise turning angles ($\theta$) between moves. Under a correlated random walk model the expected mean squared displacement after $n$ moves is then:

$$E(\text{MSD}) = nE(l^2) + 2E(l)^2 \frac{c}{1-c} \left(n - \frac{1-c^2}{1-c}\right)$$

where $E(l^2)$ is the expected value of $l^2$, $E(l)$ is the expected value of $l$, and $c$ is the expected value of cos$\theta$ (Kareiva and Shigesada 1983). Expected values are calculated as the means over all moves and all individuals included in an analysis. This model is of particular interest because when movement fits a correlated random walk, MSD can be extrapolated as a linear function of $n$, thus allowing characterization of movement be-
yond the time period examined (Kareiva and Shigesada 1983).

Because the length of observations varied, I had data from few individuals for the later time periods (>50 min). For this reason, my analysis only included data for the 11 caterpillars followed for a full 50 min.

To further explore distance moved and the persistence of movement direction, I examined both clockwise turning angles and move lengths. For each individual I calculated the mean move length and the mean cosine of the turning angle for 10 min intervals. The cosine of the turning angle is a useful measure of persistence of direction, with values near 1 indicating small turning angles and a high degree of persistence. Values near −1 indicate frequent reversal of direction (Turchin et al. 1991). I used likelihood ratio chi-squared tests to examine these data for independence in the direction of successive turns (e.g., whether the direction of a turn at one time is independent of the turn direction at the previous time); if right turns are more often followed by left turns and vice versa, persistence of movement direction is increased. Parameters were examined for 10 min intervals both to aide in comparisons between the life stages and because smaller time intervals make it difficult to capture the overall pattern of movement.

**Adult movement**

**Adult female immigration.**—I could not accurately census unmarked females immigrating into host plant patches because female moths are inconspicuous, inactive for much of the day, and prone to hiding in the vegetation. Therefore, I measured immigration indirectly by censusing caterpillars one year after removing them from plant patches.

On 28–30 May 1994, I placed 12 cm high plastic barriers around 20 experimental patches distributed throughout an area dominated by smallish (<2 m²), discrete Dryas patches. These patches were classified (using the method described for the caterpillar immigration experiment) as either isolated (7 patches) or surrounded (13 patches) and were randomly assigned to either a treatment that allowed immigration of flying females only, or one that allowed immigration by walking and flying females. I hand-removed caterpillars from these patches on 11, 15, and 17 June. On 17 June I trimmed patches to an approximately 50 × 50 cm circle and sprayed them with Malathion 50 Plus (3.91 mL/L water). This first spraying resulted in some knock down without kill (this had not been a problem when spraying earlier instars as in the caterpillar immigration experiments), so I sprayed all patches again on 21 June with a higher concentration of Malathion (7.82 mL/L).

On 16 July when caterpillar activity had ended for the year and adult activity had begun, I removed barriers from half of the patches to allow female movement into these patches by walking as well as flight. I placed a Tanglefoot band around the top of each remaining barrier. Barriers were removed after all Itame activity ended for the season.

I replaced barriers as soon as I arrived at the field site in 1995 (15–16 May). First instar caterpillars were present in the field on these dates. Each barrier was topped with a band of Tanglefoot. I then counted and removed all caterpillars on the patches on 13 June and again on 17–18 June when caterpillars were predominantly fourth and fifth instars. I summed the counts from the two collection dates to obtain my estimate of caterpillar numbers.

Number of caterpillars was analyzed by ANOVA with effects of patch isolation, barriers to walking, and the interaction of these two effects.

**Adult female emigration.**—I tested whether female moths emigrate from patches by placing 10 female moths on each of six patches on the morning of 10 July 1995. Unmarked females were not observed on the experimental patches. The experimental moths had been reared from fifth instar larvae in captivity, were <5 d old, and many were virgins although some may have mated while in captivity. These moths were marked with fluorescent powder which did not appear to affect their movement. I censused the patches using a UV lamp on the nights of 11–13 July. During the early evening of 12 July, I placed eight captive-reared moths in each of six more emigration patches. These patches were then censused the following two nights, 13 and 14 July. I counted the numbers of marked individuals remaining in the experimental patches at each census.

**Individual female movement and oviposition behavior.**—In 1995 I followed individual female moths to document their movement and oviposition behavior and to examine the demographic spread and mixing of populations through adult female movement. All of the observations were conducted in areas where there were many small and medium sized patches (0.10–2 m²) interspersed with bare ground.

I performed two types of observations. First, I did individual “long observations” on 31 females (both captive-reared and wild) marked with dayglo fluorescent powder. I tried to follow each of these females for a minimum of 40 min, but some became inactive or were lost prior to that point; the average length of observation was 51 min. All females were released on host plant patches, usually in the morning when females were inactive. Observations began on an individual female after she became active.

I used a Tandy TRS-80 computer (Model 102; Tandy Corporation, Fort Worth, Texas, USA) to record behavioral data and the time of each event for all observations. I recorded when a female was on Dryas vs. the ground and each transition between substrates, behavior (sitting, walking, flying, oviposition), and her position at 10 min time intervals. I then measured the distance and compass direction between successive points and the length of each flight. Although eggs are difficult to see during oviposition, I was able to ac-
curately distinguish actual oviposition from probing by closely watching the females’ behavior and body movements.

I used data from the long observations to examine net displacement over time, movement parameters, and oviposition rates. My interest was in characterizing movement of active females. For this reason, I excluded four moths from the analysis; one appeared injured, and the other three all had long periods of inactivity. I also excluded all terminal time intervals where females were inactive for more than 70% of the interval.

To test whether adult female movement could be adequately described as a correlated random walk, I examined the relationship between mean squared displacement (MSD) and time and compared it to the predicted relationship under the correlated random walk model. As with the caterpillars, the length of observations varied, and I had data from few individuals for the later time periods. For this reason my analyses examined data from: (1) 16 females followed for a full 40 min, and (2) 10 females followed for a full 60 min. As noted earlier, whether the observed and expected relationships match is of interest because MSD can be extrapolated as a linear function of time if movement follows a correlated random walk.

For each individual I calculated the mean move length and mean cosine of the turning angles. I used likelihood ratio chi-squared tests to examine for independence in the direction of successive moves. I also compared move lengths for 10 min periods spent completely on Dryas to those spent completely on the ground. For all females that spent time both on and off of Dryas patches (n = 23), I calculated the total observation time spent on vs. off and the percent of time on and off that was active (inactivity was defined as rests of 3 min or more; shorter rests are common after oviposition events).

To examine oviposition rates I calculated the number of eggs laid per unit of time, as well as the number of eggs laid per move length. I also calculated the number of eggs laid per unit time on Dryas and on the ground for all females that moved on and off of Dryas.

The second type of observation was shorter, lasting a maximum of 15 min. I located 32 unmarked active females in the wild and followed them to gain more information on the frequency and length of flights. These data were combined with those from the long observations to characterize flight behavior.

Results

Caterpillar movement

Caterpillar immigration and patch isolation.—In 1994 no immigrants were found in extirpated patches on the first census date suggesting that censusing began prior to immigration. Immigration had diminished by the last census date although a few new arrivals were still found on this date. In 1995 a few individuals were found on the first census date suggesting that immigration had recently begun and one individual was found at the last census.

In 1994 I found a total of 116 caterpillars in 20 patches at two sites. In 1995 I found 185 caterpillars in 45 patches at three sites. In both years the majority of immigrants were fifth instars (83% in 1994, 82% in 1995). In 1994 I found one, and in 1995 two, third instar immigrants. The remaining individuals were all fourth instars. This indicates that the majority of caterpillar movement is carried out by fifth instars.

The majority of patches received very few immigrants (Fig. 1). I found no more than 8 immigrants in a patch, except at the high density GL site where a few patches had high numbers of immigrants in both 1994 and 1995.

In 1994 there was a significant effect of site and a significant site by isolation interaction (Table 2). Contrasts revealed a significant effect of isolation at the GL site (Fig. 1b, \( F_{1,16} = 14.01 \)) where isolated patches received fewer immigrants, but the isolation effect was not significant at the IN site (Fig. 1a, \( F_{1,16} = 1.70 \)) with experimentwise \( \alpha = 0.05 \).

In 1995 there were again significant site and site by isolation effects (Table 2). The patterns in this year were less clear than in 1994. At the GL site the very isolated patches received few immigrants, but at least one of the isolated patches received a great many colonists (Fig. 1c). No clear patterns emerged at either the IN or OR sites, although generally patches received few immigrants (Fig. 1c and d). Contrasts revealed that the only significant isolation effect was between surrounded and very isolated patches at the GL site (\( F_{1,16} = 13.17 \)).

In 1994, the sex ratio of emerging Itame was 45% male and 55% female (n = 47, mostly from GL site). These values are almost identical to those for a much larger sample (n = 206) reared from caterpillars collected at the GL and IN sites in 1994 (44% male, 56% female; unpublished data).

Caterpillar emigration.—My manipulations of caterpillar numbers for this experiment were successful in creating three distinct ranges of starting densities (Table 3). These densities were higher than average densities at many of my sites under natural conditions but within the range of naturally occurring densities (Doak 2000).

Density treatment, which combines effects of feeding damage and actual caterpillar density, had a striking effect on emigration rate (Wilcoxon \( \chi^2 = 27.37, df = 3, P = 0.0001 \); log-rank \( \chi^2 = 29.62, df = 3, P = 0.0001 \); Fig. 2). Pairwise treatment comparisons revealed that high density patches displayed a significantly different survivorship function than control, low, and medium density patches (\( Z = 5.40, Z = 4.05, \) and \( Z = 3.81 \) respectively) with an experimentwise error of \( \alpha = 0.05 \). While high density patches display more rapid loss of individuals, differences between the other treatments
are not significant (Fig. 2). Tests for association between the survivorship function and the temporal and spatial blocking factors indicate that while temporal set has a significant association (Wilcoxon $\chi^2 = 7.26, P = 0.007$), spatial block does not (Wilcoxon $\chi^2 = 3.21, P = 0.073$). Despite this effect of set, by combining data across the two temporal sets, my tests for density effects incorporate more noise and thus are conservative.

Individual caterpillar movement.—I observed no tendency for caterpillars to orient to Dryas patches (or any other objects) even at a distance of a few centimeters; it appeared that they had to touch their host plant before detecting it.

Comparison of observed and expected MSD for the 11 individuals observed for a full 50 min (Fig. 3a) shows that the observed values fall beneath the expected for all time periods. This indicates that caterpillars moved less from their initial positions than would be expected by a correlated random walk. The results from the analysis with all individuals were qualitatively indistinguishable. The low values of MSD most likely resulted from the tendency for many of the individuals to turn back on their paths.

Caterpillar move lengths for 10 min periods are distributed between 0 and 180 cm (Fig. 4a) with a mean of $74.30 \pm 7.67$ cm ($n = 20$). Turning angles for 10 min intervals were fairly evenly distributed between small and large turns (Fig. 4c). The mean cosine of the turning angle was negative for 8 of 18 individuals (where adequate data existed) and the overall mean was $0.14 \pm 0.10$ ($n = 18$) indicating an average turn of 82 degrees and a tendency for their paths to spiral back on themselves. When all turns for all individuals are pooled, the directions of successive turns were not independent with turns being autocorrelated (right–right 29, right–left 12, left–right 12, left–left 18; $G = 6.76, P = 0.009$), which further indicates a tendency to turn back on their paths.

**Adult movement**

**Adult female immigration.**—Immigration of adult females into extirpated patches (quantified as: In(number of caterpillars subsequently found in patch)) was significantly affected by both patch isolation and the presence of a barrier to walking, although the interaction of these two factors was not significant (Table 4). Patches without barriers had significantly more caterpillars than did patches with barriers, confirming that

---

**Table 2.** ANOVA for number of caterpillar immigrants (log transformed) vs. site and patch isolation in 1994 ($r^2 = 0.59$) and 1995 ($r^2 = 0.40$).

<table>
<thead>
<tr>
<th>Source</th>
<th>1994 df</th>
<th>F</th>
<th>P</th>
<th>1995 df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td>1</td>
<td>10.31</td>
<td>0.0054</td>
<td>2</td>
<td>3.40</td>
<td>0.0444</td>
</tr>
<tr>
<td>Isolation</td>
<td>1</td>
<td>3.10</td>
<td>0.0975</td>
<td>2</td>
<td>1.63</td>
<td>0.2093</td>
</tr>
<tr>
<td>Site x Isolation</td>
<td>1</td>
<td>12.87</td>
<td>0.0025</td>
<td>4</td>
<td>2.99</td>
<td>0.0316</td>
</tr>
<tr>
<td>Error</td>
<td>16</td>
<td></td>
<td></td>
<td>36</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Table 3.** Initial densities of caterpillars in emigration experiment patches.

<table>
<thead>
<tr>
<th>Density treatment</th>
<th>Density (individuals/m$^2$ ± 1 SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td>37.47 ± 2.41</td>
</tr>
<tr>
<td>Medium</td>
<td>68.30 ± 3.88</td>
</tr>
<tr>
<td>High</td>
<td>106.79 ± 5.63</td>
</tr>
<tr>
<td>Movement barrier controls</td>
<td>76.96 ± 7.56</td>
</tr>
</tbody>
</table>
movement by walking is an important alternative to flight in females (Fig. 5). Furthermore, isolated patches contained more caterpillars than surrounded patches, an unexpected result (Fig. 5). Isolated patches were not congregated in one region so spatial proximity and local conditions cannot explain this result.

**Female emigration.**—In the first set of emigration trials, all females disappeared from their release patch within three days. The second set was only censused for two days but at that time the majority of females had disappeared; one patch had two females and two patches had one female remaining when last censused. Although predation, as well as emigration, could contribute to this disappearance, these results strongly suggest that females leave their patches of origin.

In the first trial 23 of the 29 females that remained in patches on the first night were copulating when I surveyed the patches. None were seen copulating in subsequent surveys. This suggests that females mate before moving. Often when I released virgin females, swarms of males arrived immediately after release and copulation began within minutes.

**Individual female movement and oviposition.**—

1. **MSD.**—Comparison of observed and expected MSD for both the 16 females observed for 40 min and the 10 females observed for 60 min, revealed that the observed values were consistently higher than the expected line at later time intervals (Fig. 3b). This indicates more persistence of direction than would be obtained from a correlated random walk and presents a strikingly different pattern than seen for caterpillars (Fig. 3a).

2. **Movement parameters.**—Move lengths for 10 min periods tended to be short (Fig. 4b), and mean move lengths for individuals did not differ significantly between adult females (76.81 ± 9.90, n = 30) and caterpillars (74.30 ± 7.67, n = 20) (t test on ln transformed data: \( t_{55} = 0.51, P = 0.61 \)). An ANOVA examining only moves that were completely on or off of *Dryas* revealed significant effects of both substrate \( F_{1,31} = 21.81, P < 0.001 \) and moth identity \( F_{20,31} = 2.85, P = 0.004 \) on move length. The least squares mean move length per 10 min interval on *Dryas* was only 23.34 ± 0.98 cm (mean ±1 se, n = 30) while that on the ground was 70.39 ± 1.52 cm (n = 23).

Turning angles were skewed towards smaller angles (Fig. 4d), and comparison of mean cos(turning angle) for individual female moths (0.65 ± 0.06, n = 26) and individual caterpillars (0.14 ± 0.10, n = 18) indicates that females make significantly smaller turns \( t_{42} = 4.72, P < 0.0001 \). This likely contributes to the persistence of direction and the greater than expected values for MSD. If females alternated left and right turns, their movement paths would be even straighter; however, there was no evidence of nonindependence of turning directions when all data on adjacent turns were grouped \( G = 0.188, P = 0.664 \).

In the patchy landscape where these observations were made, there was no evidence that females spent more time on vs. off of *Dryas* patches (Table 5; paired t test: \( t_{22} = 1.006, P = 0.325 \)). However, on average 96% of the time on the ground was active while 86% of the time on patches was active; this difference is significant (Mann Whitney \( U = 157.50, P = 0.009 \)).

The contribution of flight to female movement was small. When all moths from the short and long observations are considered, 70% (44 out of 63) of females did not fly during my observation periods and those that did fly did so infrequently (Fig. 6a). Furthermore, flights were quite short, with 85% of them being no more than 1 m (Fig. 4d). I never observed females flying higher than 25 cm above the ground. Thus flight did not account for the majority of female movement. Although infrequent longer flights could have significantly impacted overall movement, I did not observe even rare long distance flights. I lost no females during
flights, thus there should be no bias towards recording only short flights.

3. Oviposition rate.—On average more than twice as many eggs were laid per unit time on bare ground than on Dryas (Table 5; paired t test: $t_{22} = -6.568$, $P < 0.001$). This surprising difference cannot be explained by the greater inactivity of females on Dryas, because the difference in oviposition rate was still significant when oviposition rate was calculated only for active periods. Calculated over all females and for all 10 minute intervals, eggs were laid at rates of 0.38 eggs/min and 7.72 eggs/m (note that these are meters traveled not displacements from the point of origin).

The dispersion of eggs over space is of great interest because it describes the demographic mixing of a population. While I cannot directly calculate this, I can estimate lower and upper bounds on egg dispersion by the average female. It is clear from my analyses, that females move more than what is predicted by a correlated random walk (Fig. 3b), so extrapolating displacement as a linear function of time (correlated random walk model) will underestimate movement distance and give a lower bound on displacement. A relationship between oviposition and distance can then be obtained by combining information on the squared displacement of moving females (m$^2$/unit of time) and the number of eggs laid (eggs/unit of time). For this,
Table 5. Comparison of time and oviposition on and off of Dryas patches for 23 females that spent time on both substrates.

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Percent time</th>
<th>Percent time active</th>
<th>Eggs/min</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dryas</td>
<td>0.54 ± 0.04</td>
<td>0.86 ± 0.03</td>
<td>0.24 ± 0.04</td>
</tr>
<tr>
<td>Ground</td>
<td>0.46 ± 0.04</td>
<td>0.96 ± 0.02</td>
<td>0.60 ± 0.06</td>
</tr>
</tbody>
</table>

Note: Values are means ± 1 SE.

I used the lowest estimate of MSD (regression forced through the origin for 10 females observed for 50 min: MSD = 0.082 m²/min) and the average number of eggs laid per minute (0.38 eggs/min) to arrive at 4.60 eggs/m². Fig. 7 shows this lower bound as the expected radius within which the average female spreads her eggs, based on an average egg load of 120 eggs per female (Doak 1997). I calculated an upper bound on egg dispersion by taking the average number of eggs laid per distance traveled (on a per move basis) and then assuming that females moved in a straight line (clearly an overestimate of average displacement) to give the relationship 7.72 eggs/m; this relationship is also shown in Fig. 7. These two types of estimates assume very different behaviors and thus describe different types of egg dispersion. The first assumes that eggs are dispersed within a circular radius of a given size, whereas the second assumes that they are laid along a linear path. Despite this difference, both estimates provide information about the maximum distance from a starting point over which eggs are expected to be laid.

**DISCUSSION**

*The scale of movement and oviposition*

*Caterpillar movement.*—Individual caterpillars on bare ground move less than pedicted by a correlated random walk. Given that areas occupied by Dryas are surrounded by vast areas of bare ground, river, and glacier, wandering away from Dryas could be risky. The large turning angles shown by caterpillars (Fig. 4c) are consistent with the behavior of area restricted search (Kareiva and Odell 1987), which will tend to keep caterpillars from leaving areas of host plants. Thus, it appears that most movement by caterpillars will lead to relatively small scale mixing between host plant patches.

Most movement by larvae involves later instars. This could result from an increased capacity for movement, behavioral changes, or increasing resource depletion at later instars. Movement by first instars dispersing from hatching sites to host plants, while not formally investigated, must occur in caterpillars hatching from eggs laid off of patches. I saw no evidence in the field or lab that this species balloons, and in the absence of ballooning, it is unlikely that first instar caterpillars move long distances in their search for host plants. Fifth instar caterpillars looking for puation sites will also contribute to movement, however these individuals will take the first suitable puation site found. I did not observe any long movements prior to puation.

![Figure 5](image5.png)  
*Fig. 5.* Results from the adult female immigration experiment showing the mean number of caterpillars found in each patch type. Patches are either surrounded or isolated and either open to adult walking or with a barrier. Means are back-transformed least-squares means (±1 SE) from an ANOVA.

![Figure 6](image6.png)  
*Fig. 6.* Adult female flight: (a) the frequency of flights by 63 females that flew during my observations and (b) the frequency of flight distances for 39 flights made by 19 females.
Given that 55% of the caterpillars reared from immigration patches were females and that a female caterpillar carries her full reproductive potential with her, much of this caterpillar movement will contribute to demographic mixing within sites, especially at high caterpillar densities. Rare incidents of long distance caterpillar movement may lead to larger scale mixing and colonization of new sites, but it appears unlikely that caterpillars move on a large enough scale to join neighboring sites into a single demographically (as opposed to genetically) intermixing population.

Adult female movement and oviposition.—Unlike caterpillars, all adult females move and contribute to population mixing through the spreading of eggs. Females mate at or near their site of emergence and then move as they lay eggs. Because Itame females do not feed or even search for places to drink, these behaviors do not lead to greater movement within or beyond the larval habitat.

Females lay eggs over a relatively short time and distance. Assuming a constant rate of oviposition, a female’s full egg complement, which ranges from 30–200 eggs (Doak 2000), can be laid in as little as 1.5–9 h (5.3 h for the mean load of 120 eggs). Furthermore, although eggs are clearly spread beyond the immediate area of emergence, they do not appear to be spread very far. Based on my estimates of movement and oviposition parameters, the mean radius of egg dispersion is between 5 and 15 m. These estimates are based on the assumptions that the rate of egg laying and the rate of movement do not change as females age and reduce their egg loads. However, I cannot rule out the possibility that behavior changes with decreasing egg numbers as is suggested for other species (Chew and Robbins 1984, Warren 1987, Rudd and McEvoy 1996). A change in behavior as egg load declines could lead to wider spreading of eggs, although it still appears that the majority of eggs will be laid near the emergence site.

Although flights could greatly increase the movement radius and thus the dispersion of eggs, I never witnessed females making long flights or even repeated short flights, nor did I observe females that had dispersed far from suitable larval habitat. Thus a separate behavioral phase of long distance dispersal appears unlikely. When in flight, females stayed close to the ground and always appeared clumsy and overladen. The fact that female immigration is significantly decreased by plastic barriers only 12 cm in height (Fig. 5) further indicates that flight is limited and that walking is the predominant mode of movement for these moths.

In sum, it appears that Itame females may commonly move on the order of tens of meters over their lifetime. Thus, the movement of Itame females is quite restricted compared to that seen in most Lepidoptera capable of flight. Although it would be most informative to compare Itame’s dispersal to taxonomically or ecologically similar species, the relevant data are not available. Other studies of Lepidoptera inhabiting subdivided systems find maximum generational movement distances on the order of hundreds of meters (Thomas and Harrison 1992, Warren 1987, Thomas et al. 1992, Hanski et al. 1994, Peterson 1994, Harrison et al. 1995, Rudd and McEvoy 1996, Sutcliffe et al. 1997) to several kilometers (Thomas et al. 1992, Harrison 1989, Neve et al. 1996). Dispersal is often deemed limited even for species capable of movements of 0.5–2.5 km (e.g., Thomas and Harrison 1992, Warren 1987, Thomas et al. 1992, Peterson 1994, Kuussaari et al. 1996). Although what constitutes limited dispersal will depend heavily on the spatial organization of habitat, it seems clear that Itame’s dispersal is very limited compared to many other Lepidoptera.

The scale of population processes and the role of different habitat types

Site scale.—Movement data suggest that fully intermixing populations are confined within sites. Demographic mixing between neighboring patches within sites is common for Itame and is largely due to the short distance movement of females. The movement of caterpillars also leads to mixing on this scale and will have a larger contribution at high population densities due to density-dependent emigration. In contrast, my data indicate that movement between sites separated by longer distances (e.g., >100 m) and obstacles to movement (e.g., other vegetation types, wide expanses of bare ground, gravel ridges) is likely rare. Sites probably are occupied by demographically (but not genet-
ically) distinct populations or perhaps subpopulations within a metapopulation.

The movement of adult males, although not studied in detail, is much more widespread and will almost certainly lead to genetic mixing on the larger, between-site scale (Doak 1997). Male movement will influence population dynamics when males are limiting or genetics are important (Ghilpin 1991, Hastings and Harrison 1994, Hedrick 1996). However, when inbreeding depression is not a concern, investigation of female movement alone will likely capture the important processes influencing spatial dynamics and population structure. Given the high mobility of male *Itame*, it is unlikely that inbreeding or male limitation are concerns in this system.

These findings are concordant with results of my studies of *Itame* population dynamics. I found that shifts in *Itame* densities on host plant patches within a site are highly synchronous over years while dynamics between sites are asynchronous (Doak 2000). Limited dispersal between asynchronously fluctuating sites may be important in maintaining metapopulations on a regional scale through colonization and extinction of sites or the input of colonists into low density or marginal sites.

**Patch scale.**—Although *Itame* movement links *Dryas* patches on a site-wide scale, small scale subdivision in the system still has the potential to influence patterns of *Itame* distribution and abundance. My earlier work (Doak 2000) suggests that regions of subdivided habitat may support more individuals than continuous habitats even though bare ground occupies a large part of subdivided habitats. Furthermore, most of the sites harboring *Itame* populations have at least some regions of subdivided habitat, whereas many areas covered by large carpets of *Dryas* appear to be totally unoccupied by *Itame* (personal observation). Thus the smaller patches which form subdivided habitats are likely disproportionally important in sustaining *Itame* populations. The current investigation of movement and oviposition patterns sheds more light on the possible mechanisms underlying these results.

My observations of adult female oviposition behavior indicated that most oviposition occurred on the ground than in *Dryas* patches. This pattern may lead to high caterpillar densities in smaller patches because caterpillars hatching in the proportionally large surrounding area of bare ground will move into these patches. Thus population densities may be highest in sites with subdivided habitat. These high density areas may further contribute to population dynamics through density-dependent caterpillar movement as seen in both the emigration and immigration experiments.

Isolated patches may also be important in providing dispersers through density dependent processes. Results of the female immigration experiment indicated that isolated patches had the highest caterpillar densities in the season following experimental manipulation (Fig. 5). This suggests that more oviposition took place in isolated patches. Although barriers were not replaced until just after first instars began to hatch, it is unlikely that immigration of first instars was responsible for the patterns seen. Patches with barriers to adult walking had significantly fewer caterpillars than patches without barriers which would not be expected if immigration of first instars was driving the pattern. While the result of higher densities in isolated patches is in contrast to the findings of my density surveys (Doak 2000), it is likely that they result from the high background *Itame* densities at the immigration experiment site. My earlier data also suggest that as densities get very high, isolated patches display disproportionally large increases in density (Doak 2000).

In summary, the results from both my observations of female oviposition and the female immigration experiment indicate that smaller patches and subdivided habitat are likely to have higher population densities and may contribute disproportionally to mixing and spread of populations through density-dependent caterpillar emigration. Poki (1981) finds a similar effect in a field vole metapopulation inhabiting an archipelago. In the *Dryas–Itame* system, smaller patches and subdivided habitat may be especially important in the dynamics of populations and metapopulations and may serve to maintain and to stabilize populations in less suitable sites.

**Regional scale.**—The absence of *Itame* from the vast majority of host plant habitat could be due to limited dispersal leading to limited colonization or to the fact that *Itame* is excluded from many sites. If long distance movement of females was common, I would expect to see more populations (even if transient ones) in the Kennicott River and McCarthy Creek valleys. The fact that only scattered populations exist along an ~3 km stretch of the east side of the Kennicott Glacier Valley and that no populations are found along the west side of the Kennicott Valley or any along the margins of McCarthy Creek, strongly suggests that new sites are seldom successfully colonized for even a single season. Occupied sites in the Kennicott Valley cannot be considered anomalous because a population of *Itame* exists at the foot of the Nizina Glacier, in similar habitat. Limited dispersal is further suggested by the fact that I have established persistent populations (≥5 yr) in previously unoccupied sites along McCarthy Creek and the Root Glacier (unpublished data). Populations may be excluded from some areas by biotic (e.g., predation by ants in later successional sites, secondary plant chemistry) or abiotic (e.g., periodic flooding) factors. Even so, if long distance dispersal was common, I would expect to find at least temporary populations of *Itame* at many more sites. In sum, my observations suggest that *Itame* is failing to colonize suitable sites where populations could persist.
Conclusions

Pattern of distribution and the dispersal capabilities of *Itame* are quite different from those of most Lepidoptera studied in the context of habitat patchiness. Most other studies find routine movement over much longer distances as well as more predictable occupation of habitat patches within a species’ dispersal range. *Itame*’s pattern of patchy occupation even within host plant patches most closely resembles that described by Harrison (1994) for a tussock moth with totally flightless females. She has shown that low dispersal is important in limiting the spread of this species (Harrison 1994). The resemblance of distribution patterns in my system to those described for a fully flightless species highlights the likely importance of limited dispersal in contributing to distribution patterns for *Itame*.

The limited movement of *Itame* coupled with the patchy nature of its habitat does appear to impact its patterns of abundance and distribution. In the *Itame–Dryas* system, restricted movement demographically isolates populations on a site scale. Limited between-site dispersal may link these populations into meta-populations and thereby contribute to regional persistence and stability. Preferential oviposition on bare ground as well as the accumulation of eggs on isolated patches under some conditions likely contributes to high *Itame* densities in subdivided habitats. Due to high population densities and density-dependent emigration of caterpillars, subdivided regions of *Dryas* will strongly contribute to population mixing within sites and occasional movement between sites. Thus areas of subdivided *Dryas* may act as sources in maintaining populations in marginal habitats or contributing colonists to new sites. Finally, low dispersal will contribute to determining *Itame*’s patchy distribution on a regional scale. Given *Itame*’s low dispersal abilities, historical occupation patterns are predicted to be important in determining current distribution with areas in close proximity to past populations being more likely to be colonized than areas isolated by even minor barriers. Thus, although both caterpillars and adult females move frequently and contribute to demographic mixing, this movement is not great enough to negate the impact of habitat patchiness on *Itame* populations.

Acknowledgments

This manuscript has benefited from the thoughtful comments of M. Geber, D. Doak, A. Power, R. Root, D. Winkler, S. Juliano, and four anonymous reviewers. D. Doak and B. Morris provided invaluable, on-the-spot advice in McCarthy. I especially thank M. Geber for her support and encouragement. Both Tully and Dan provided very helpful enthusiasm throughout this project. I thank C. McCulloch for his statistical advice. Funding was provided by a NSF Graduate Fellowship to P. Doak, a NSF Dissertation Improvement Grant 9311208 to M. Geber and P. Doak, Sigma Xi, and the Explorers Club.

Literature Cited


