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LOCAL POPULATION SIZE IN A FLIGHTLESS INSECT: IMPORTANCE OF PATCH STRUCTURE-DEPENDENT MORTALITY

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Abstract. In spatially heterogeneous systems, utilizing population models to integrate the effects of multiple population rates can yield powerful insights into the relative importance of the component rates. The relative importance of demographic rates and dispersal in shaping the distribution of the western tussock moth (*Orgyia vetusta*) among patches of its host plant was explored using stage-structured population models. Tussock moth dispersal occurs passively in first-instar larvae and is poor or absent in all other life stages. Spatial surveys suggested, however, that moth distribution is not well explained by passive dispersal; moth populations were greater on small patches and on isolated ones. Further analysis showed that several local demographic rates varied significantly with patch characteristics. Two mortality factors in particular may explain the observed patterns. First, crawler mortality both increased with patch size and was density-dependent. A single-patch difference equation model showed mortality related to patch size is strong enough to overcome the homogenizing effect of density dependence; greater equilibrium densities were predicted for smaller patches. Second, although three rates were found to vary with local patch density, only pupal parasitism by a chalcid wasp could potentially account for higher moth abundances on isolated patches. A spatially explicit simulation model of the multiple-patch system showed that spatial variation in pupal parasitism is indeed strong enough to generate such a pattern. These results demonstrate that habitat spatial structure can affect multiple population processes simultaneously, and even relatively low attack rates imposed on a reproductively valuable life stage of the host can have a dominant effect on population distribution among habitat patches.

Key words: image analysis; local patch density; logistic and Poisson regression; Orgyia vetusta; *patch size; spatially explicit simulation; stage-structured population models.*

INTRODUCTION

Population densities in patchy habitats exhibit spatial variation due to myriad factors, such as heterogeneity in patch quality (Stanton 1983), variability in mortality risk (Kareiva 1983), limited mobility (Hassell et al. 1991), and stochasticity in local interactions that arise from variable behaviors and phenotypes of individuals. Patch structure, such as patch size or isolation, can have major effects on population density within a patch by mediating the local impacts of those factors. For example, patch structure can play a direct role in dispersal by influencing movement behavior among patches, habitat selection, immigration rates, and dispersal mortality. Mediation of dispersal by patch structure is fundamental to metapopulation dynamics (Hanski and Simberloff 1997) and island biogeography (MacArthur and Wilson 1967), as well as conservation programs for species in fragmented habitats (Pulliam et al. 1992, Lamberson et al. 1994). Central to these concepts and applications is that isolated patches tend to receive few-

er immigrants and subsequently have low population sizes or patch occupancy rates, particularly when dispersal is poor relative to interpatch distances (Fahrig and Paloheimo 1988, Harrison et al. 1988, Hill et al. 1996, Matter 1996, Hertzberg et al. 2000, Roslin and Koivunen 2001). Understanding how large a role dispersal plays in a system and to what extent the configuration of the habitat affects population dynamics remain ongoing challenges for ecologists.

Patch structure can affect local demographics. Variation in habitat quality associated with patch structure can directly affect fecundity, survivorship, or growth rates and, subsequently, local population size of the organism (Thompson 1978, Bach 1988, Roland et al. 1997). Patch structure can also indirectly affect a population by mediating attack rates, such as when natural enemies impose mortality rates correlated with local patch density and/or patch size (Segarra-Carmona and Barbosa 1992, Lei and Hanski 1997, Roland et al. 1997, Doak 2000*b,* Hovel and Lipcius 2001, Williams et al. 2001, Cronin 2003). Natural enemies of herbivorous insects often cue into visual or olfactory characteristics of host plants to search for prey or use the host plants directly for resources such as nectar or shelter. If attack rates are correlated with natural enemy abundance or

visitation rate, herbivore population sizes may be reduced in areas of large or densely packed patches.

Local population size within a patch, therefore, can be affected by multiple factors associated with patch structure, and their effects may oppose or enhance one another. In a poorly mobile organism, for example, if dispersal mortality increased with interpatch distance, population abundance might be greatest in areas with high local patch density. However, if local death rates imposed by natural enemies were greater on densely packed patches, the joint effect of dispersal mortality and local mortality factors would be harder to predict. Understanding population distribution in patchy habitats thus requires assessment of whether and how local demographic rates vary with patch structure, as well as a method for quantifying the effects of multiple factors. Although patch structure effects have been examined in many population studies, relative effects of multiple factors have received far less attention (but see Pulliam et al. 1992).

In the present study, the density of the western tussock moth, *Orgyia vetusta* Boisduval (Lepidoptera: Lymantriidae), in the field was observed to vary greatly from patch to patch. A previous study at the site showed such variation cannot be attributed to differences in host plant quality (Harrison 1997). Studies of this moth have also shown that dispersal is poor. Movement between patches is limited to passively dispersing neonates. Adult females are flightless and do not disperse from their sites of eclosion.

Here, I ask: (1) can moth spatial distribution be explained by passive dispersal alone, or does local variation in demographic rates play a role? (2) If the latter, what factors, including mortality, combine with dispersal to explain the distributions? I answered these questions as follows.

First, I compared the distributions with two null expectations based solely on passive dispersal. The purpose of the null distributions was to understand the potential importance of local demographics in the system by first hypothesizing the role of dispersal alone. According to one null distribution, isolated patches would receive fewer immigrants, thus moth abundance would be greatest in areas of high local patch density (because such areas should "capture" more dispersing larvae) and lowest in isolated patches (because dispersal mortality increases with interpatch distance). Under the second null distribution, moth density would not vary with patch size, based on the assumption that immigration rate per unit of patch is independent of patch size for passive dispersers. This expectation assumes no relationship between patch size and local patch density.

Second, I investigated the potential effects of variation in local birth and death rates by developing two stage-structured population models to determine whether measured population rates are sufficient to generate the observed population distributions with re-

spect to two general patch characteristics, size and local density. The first is a nonspatial, single-patch model to explore the effect of patch size on moth distribution. This model excludes the effect of dispersal under the assumption that movement between patches is not correlated with patch size. The second is a spatially explicit simulation model that incorporates dispersal and the effects of patch density on demography to predict the distribution of moth abundances across a range of local patch densities.

METHODS

Study site and organism

This study was conducted on a population of the western tussock moth at Montaña de Oro State Park (MDO) in San Luis Obispo County, California, USA (35°18′ N, 120°52.5′ W). The field site was located on a 0.5 × 10 km sandspit that extends north-south and separates Morro Bay from the Pacific Ocean (Appendix A). Although the tussock moth is a generalist, it primarily inhabits the silver dune lupine, *Lupinus chamissonis* Eschsch (Fabaceae), at the site. The host plant is a woody perennial shrub distributed heterogeneously throughout the foredunes and backdunes.

The period from hatching to pupation is 2.5 mo. Neonates (instar I) are 2 mm in length and molt ~2 wk after hatch. The larvae have five (male) or six (female) total instars, during which they feed on leaves, stems, and fruit. Instars II–VI are henceforth referred to as "crawlers," to reflect the primary mode of locomotion on foliage. Pupae are found on stems or leaves of the plant and mature in 2 wk. Adult males fly, but females are sedentary and incapable of flight. A female oviposits her entire complement of eggs, in a single mass, onto her pupal exuvia. At MDO, the population has two or three generations per year.

Crawling dispersal between patches by larvae is negligible, i.e., only one out of 600 marked crawlers was recovered on a nonrelease patch compared with a 42% recovery rate on 11 release patches (Yoo 2002). The median crawling distance per generation even within a continuous blanket of the host plant is only 2 m (Harrison 1994). Of the moth developmental stages, neonates are the most capable of interpatch movement, although they disperse passively by wind and are unable to crawl effectively on the sandy interpatch substrate. Neonates are carried aerially a short distance before hitting the ground, at which point additional wind-propelled travel is possible. A three-day trapping study of marked neonates released onto a twig showed that wind-borne neonates typically hit the ground only 2 m from the release point (Yoo 2002). By comparison, the mean distance between nearest neighbor patches is 6.4 m.

A suite of natural enemies attack tussock moths at MDO. The three major parasitoids are endoparasitic and solitary. *Telenomus californicus* Ashmead (Hymenoptera; Scelionidae) attacks eggs. *Patelloa fusci-*

macula Aldrich & Webber (Diptera; Tachinidae) attacks larvae and emerges from pupae. *Brachymeria ovata* Say (Hymenoptera; Chalcididae) attacks and emerges from pupae. Other hymenopterans attack pupae, at very low rates (3%). Little is known about potential predators such as birds and rodents, but mice (especially *Peromyscus maniculatus*) are common at the site and known to feed on confamilial larvae and pupae (Grushecky et al. 1998).

Moth distribution among host plant patches

Two spatial surveys were conducted, in 1997 and 2000, to determine the distribution of moths with respect to patch size and local patch density. Patches were defined as one to several adjoining lupine shrubs whose foliage interdigitate and are separated from other patches by unsuitable habitat. Patch size was estimated by the volume of foliage contained within the patch. Local patch density was defined as the number of neighboring patches located within a given radius of the focal patch.

Moth density vs. patch size (1997).—Moth density (number per unit volume of foliage) was surveyed along a natural distribution of patch sizes. A total of 208 patches was selected on a 3.1-km section of the sandspit using an adaptive, multistage sampling design that consisted of three spatially nested grids (Appendix B). Foliage volume was estimated by measuring the key dimensions of the geometric shape(s) the patch most closely resembled, usually a hemi-ellipsoid minus a core of unfoliated branches. Two nonoverlapping 0.25-m² quadrats were placed haphazardly on top of each patch, and all stems intersecting the plane were counted.

On 4–6 August 1997, when crawlers were numerically dominant, visual counts of all moths were obtained on each patch and count durations were recorded. On 28–29 August and 2–4 September 1997, the majority of moths had pupated, and all patches that had contained moths, frass, or exuviae were surveyed for pupae. Counts were truncated at 20 (in 3% of surveyed patches); thus, only pupal counts of <20 were used in the analyses. Pupae were tagged in preparation for measurements of mortality.

Moth abundance vs. local patch density (2000).— The survey area was a 2.0-km section of the sandspit located within the extent of the previous survey. Aerial photos of the site taken in 1998 were used to target patches of average size (1 m radius) in very high patch density areas, as well as relatively isolated patches. Additional patches were also targeted in the foredunes and backdunes by systematic sampling at 140-m intervals along two respective transects drawn parallel to shore. If the target patch in an aerial photo could not be matched with one at the site, a patch within 10 m was selected, if present. If more than one such patch was available, the one appearing to have a higher density of moths was chosen; otherwise, patch selection was blind. Although this method slightly biased the survey toward higher moth densities, it was applied consistently to all patches. The final patch count was 50. For each patch, foliage volume was measured and the number of neighboring patches was counted; a patch was considered a neighbor if any part of its foliage fell within a 15 m radius of the center of the focal patch.

On 1–2 August 2000, when crawlers were numerically dominant, visual counts and count durations on each patch were recorded. On 6–7 September 2000, when pupae were abundant, the survey was repeated. On 6–7 September, 24–25 September, and 28 October 2000, all new egg masses were counted and tagged in preparation for measurements of egg mortality and fecundity.

Count corrections and analysis of patterns.—Prior to all analyses, visual counts of crawlers were corrected to represent absolute abundances, using the calibration method described in Yoo et al. (2003). These corrections were applied to improve accuracy of the quick, visual counts, which were likely to underestimate true counts. Crawler density on each patch was defined as the corrected abundance divided by foliage volume. Plots were generated for crawler density vs. patch size (1997) and crawler abundance vs. local patch density (2000) to test the null hypotheses that moth density is independent of patch size and that moth abundance increases with patch density. Patch size was regressed against local patch density within 15 m to test for independence of the two variables.

Local demographic rates

Crawler mortality (1997).—An index of crawler mortality, δ_C, was defined as the proportion of crawlers not accounted for on each patch as pupae, 22–30 d after the initial crawler count in 1997. The index of crawler mortality was potentially an overestimate, since a small number of crawlers may not have pupated during the interval. The underestimate, however, was unlikely to vary with patch characteristics.

Pupal predation and parasitism (1997).—On 10–11 and 15–17 September 1997, 13 d after the initial pupal count on each patch, all remaining tagged pupae and exuviae ($n = 510$) were collected and stored at room temperature until eclosion. Cadavers were dissected to determine causes of mortality, where possible. Pupal fates were classified as unparasitized, parasitized, or unknown. Emergences by the host and by *B. ovata* can be classified with certainty because they leave characteristic exit holes. *Patelloa fuscimacula*, however, does not leave a unique mark; therefore, identifications were made conservatively: pupal fates that could not be attributed with certainty to *P. fuscimacula* were classified as unknowns. Pupal predation rate, δ_{PR}, was estimated by the proportion of pupae not recovered 13 d after tagging. Parasitism by *B. ovata*, δ_{BO}, was the proportion of recovered pupae showing evidence of attack by the wasp. Parasitism by *P. fuscimacula*, δ_{PF}, was the

TABLE 1. Proportion of individuals dying due to each mortality factor.

Mortality factor	Abbreviation	Proportion dying
Egg mass predation	δ_{ER}	0.19
Egg parasitism by *Telenomus californicus*	δ_{TC}	0.36
Egg failure to hatch	δ_{FH}	0.12
Total egg mortality		0.58
Crawler disappearance	δ_{C}	0.93
Pupal predation	δ_{PR}	0.15
Pupal parasitism by *Patelloa fuscimacula*	δ_{PF}	0.23
Pupal parasitism by *Brachymeria ovata*	δ_{BO}	0.07
Pupal parasitism by other hymenoptera		0.03
Pupal parasitism by unidentified agents		0.33
Total pupal parasitism	δ_{PP}	0.66
Total pupal mortality		0.71

Notes: Parasitism rates were measured after predation on the same stage. This study was conducted on a population of the western tussock moth at Montaña de Oro State Park in San Luis Obispo County, California, USA.

proportion of recovered pupae whose fates were known that yielded evidence of attack by the fly.

Egg predation, egg parasitism, and fecundity (2000).—The egg masses tagged in 2000 were collected and stored at room temperature as hatching was completed. The masses ($n = 73$) were then dissected and inspected for emergence holes. Individual eggs were classified as having yielded the host or *T. californicus* or having failed to hatch. Three types of egg mortality were calculated as follows. Egg mass predation rate, δ_{ER}, was the proportion of tagged egg masses not recovered. Parasitism by *T. californicus*, δ_{TC}, was the proportion of eggs showing evidence of wasp emergence. Additional mortality was reported as the proportion of eggs failing to hatch, δ_{FH}. Fecundity was obtained from total egg count per mass, ε.

Analysis of mortality and fecundity data.—Mortality factor was defined as the mortality imposed on a moth stage by a predator, parasitoid, or unknown source. Multiple logistic regressions indicated whether each mortality factor was correlated with moth density, patch size, and/or local patch density. Model reduction was accomplished by minimizing Atkinson's Q, a generalized form of the Akaike Information Criterion (Atkinson 1981, McCullagh and Nelder 1989; Appendix C). Local patch density data for the 1997 survey patches were obtained from aerial photos taken in the spring of 1998. The number of neighboring patches within 5–50 m, in 5-m increments, of each survey patch was calculated in ArcView version 3.2 (ESRI 1999). See Appendix D for details on data collection and image analysis. To reduce the number of exploratory regressions for the various mortality factors, the effect of local patch density was only analyzed for the one neighborhood radius most likely to yield significant correlations. The radius selected for each factor was that yielding the smallest *P* value in simple logistic regressions of mortality vs. local patch density. The relationship between number of eggs per female and the three explanatory variables was explored by multiple Poisson regression analysis. Model reduction was

accomplished using the same method described for mortality (Appendix C). In a few of the regression analyses, where egg mass-specific data were clustered by patch and therefore not independent, the Generalized Estimating Equations (GEE) method was used (Liang and Zeger 1986; SAS 2001, PROC Genmod). Overdispersion was compensated for by correcting the standard errors and chi-square statistic using the Pearson chi-square (Allison 1999).

MODELS

The single-patch model—effect of patch size

The purpose of this model is to predict the dynamics, and hence the equilibrium abundance of moths, as a function of patch size, where fecundity and stage-specific mortality rates in relation to patch size were determined by the field studies described above. The model excludes the effect of dispersal because I assume that passive immigration has no effect on moth distribution with respect to patch size and that emigration rate is constant. The general form of the model is a difference equation that tracks adult female density, A_t, over time on a single patch:

$$A_{t+1} = A_t \times \varepsilon \times (1 - \delta_{ER})(1 - \delta_{TC} - \delta_{FH})$$
$$\times (1 - \delta_N) \times (1 - \mu\delta_C)$$
$$\times (1 - \delta_{PR})(1 - \delta_{PP}) \times f \quad (1)$$

where δ_N = the proportion of neonates dying, μ = a scaling constant for crawler mortality, δ_{PP} = the total proportion of pupae dying due to parasitism, f = the proportion of female adults = 0.5; the remaining variables are defined in *Methods: Local demographic rates* and Table 1. In a trapping study, one estimate for δ_N was 50% (*unpublished data*), but sampling was not sufficiently replicated. The proportion of neonates dying was therefore explored in the model across a range of reasonable values. In addition, δ_C was varied using a scaling constant, μ, to explore the range of effects

of crawler mortality on density, as the measured rates were possibly overestimates.

A probability function was substituted for proportion dying (or fecundity) wherever a significant relationship with moth density or patch size was found in the logistic (or Poisson) regression analyses of the field data. For example, if both explanatory variables were found to have significant effects on the probability of crawler death, p, the logistic regression for crawler death was first solved for p:

$$p = \frac{\exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2)}{1 + \exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2)}. \quad (2)$$

where $X_1 =$ crawler density and $X_2 =$ patch size. The probability of crawler death was then substituted for δ_C in Eq. 1. Otherwise, mortality estimates were obtained from field averages (Table 1).

Equilibrium crawler density, C^*, was calculated by setting $A_{t+1} = A_t$ in Eq. 1 and solving for X_1. The equilibria were compared for two patches, one in the first (small) and the other in the 99th (large) percentile of actual patch sizes measured in 1997. Parameter regions yielding extinction were determined by calculating A^*, adult female density at equilibrium. The extinction threshold was defined as <1 adult female per patch, i.e., $A^* < 1/X_2$.

The spatially explicit model—effect of local patch density

This model was developed to predict equilibrium moth distribution as a function of local patch density. It is a spatially explicit simulation model using actual patch configurations measured in the field and passive dispersal behavior. Moth fecundity and stage-specific mortality in a patch are determined by the relationships between these rates and patch density detected in the regression analysis of field data (see *Methods*). The model thus explores the joint effect of patch density-dependent rates in the field and limited, passive dispersal. In this section, the model's spatial structure, local demographics, and dispersal rules are first described, followed by the experimental design, method of analysis, and estimation of uncertain parameters. The simulation model was developed in an object-oriented programming environment (Swarm Development Group 2000).

Patch structure.—The simulation contained 850 circular patches with explicit, spatial locations. Their foci represented the actual configuration of patches within a 400 × 1600 m area of the dunes, obtained from aerial photos of the site (Appendix D). All patch radii were set at 1 m, the mean for 208 patches sampled in 1997.

Local demographics.—Population growth was discrete. Populations were stage-structured, with only neonates, crawlers, and pupae tracked explicitly per generation (Fig. 1). In each patch, transition probabilities were obtained directly from logistic (or Poisson) regression models of the mortality (or fecundity) data for
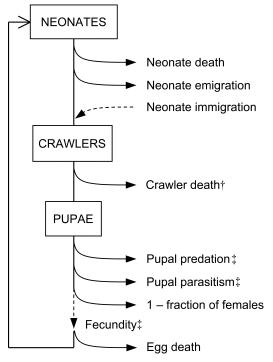

FIG. 1. Diagram of within-patch transitions between stages in the spatially explicit model. Rectangles contain stages explicitly tracked in the simulation. Solid arrows represent processes that reduce the number of individuals. Dashed arrows represent inputs to the patch through birth and immigration. Pupal parasitism is assumed to follow pupal predation. Rates are constant unless noted otherwise.

† Density-dependent probability.

‡ Probability that varies with local patch density.

which a significant relationship with moth density or local patch density had been found. Transition probabilities associated with all other mortality factors were fixed at the mean values obtained in the field (Table 1).

Dispersal rules.—A proportion, ϕ, of neonates in each patch dispersed synchronously following survival of within-patch neonate mortality, δ_N. Individuals dispersed independently of one another and according to the same set of rules. The predominant, onshore wind direction is perpendicular to the primary axis of patch distribution; thus, directionality is unlikely to be the main factor affecting moth distribution among patches along the axis. In the model, a locally dispersing neonate was therefore assigned a random direction, θ, a fixed aerial travel distance, α, and a random ground travel distance selected from the negative exponential distribution with mean, γ. $\tau = \alpha + \gamma$ was defined as the mean total dispersal distance assigned to the population. The total dispersal distance assigned randomly to a neonate, τ', was truncated to the maximum dispersal distance, τ_{max}, if τ' exceeded τ_{max}. If the neonate's trajectory crossed the area of any neighboring patches, it successfully immigrated into the closest patch along

TABLE 2. Default and range of values explored for parameters in the spatially explicit model.

Parameter	Abbreviation	Default value	Range
Neonate emigration	ϕ	0.25	0.1, 0.5, 0.8
Aerial travel (m)	α	5	1, 2, 5, 10, 20
Mean ground travel (m)	γ	20	10, 20, 45, 195
Maximum dispersal distance (m)	τ_{max}	100	30, 50, 100, 400†
Neonate predispersal death	δ_N	...	0.2–0.8, by 0.1
Crawler scaling constant	μ	...	0.65–1.00, by 0.01

† Actual value tested was 399.99.

that trajectory (Appendix E). If the trajectory crossed no other patches before reaching its endpoint, the neonate died. The default dispersal values are listed in Table 2. The northern and southern boundaries of the arena were periodic, while the east and west boundaries were absorbing to represent the natural water bodies at MDO. Crawling dispersal by the later instars was negligible in the field and is assumed to be zero in the model.

To evaluate the effect of localized dispersal, a global dispersal rule was developed for comparison. Following within-patch neonate death, all dispersers were assigned an equal probability of dying during dispersal. This probability was equal to the proportion of failed dispersers in the equivalent local dispersal case. For each successful disperser, a target patch was randomly selected from the entire set of 850 patches.

Experimental design and data analysis.—Four treatments were compared in a 2×2 experimental design to determine the independent and combined effects of dispersal and local demographic rates: global dispersal + fixed local rates (the control), local dispersal + fixed local rates, global dispersal + local patch density-dependent (LPDD) rates, and local dispersal + LPDD rates. In the treatments with fixed local rates, all transition probabilities, except for crawler disappearance rate, were fixed at their mean values. All treatments were assigned a density-dependent crawler disappearance rate based on the empirical data. Each treatment was run for 200 generations and replicated 15 times with different random seeds. Each patch was initially assigned 100 neonates.

When the combination of parameter values favored a positive growth rate, the simulations settled to a nonzero steady state (small fluctuations about a constant mean) within 80 or fewer generations, due to density dependence in the crawler stage. The duration before steady state was reached, or transient length, was calculated according to Welch's procedure (Welch 1983, Law and Kelton 2000). The crawler count for each patch, i, was averaged over time (at steady state) and over all runs and given the notation M_i^*. Plots of M_i^* against local patch density (15 m radius) were compared qualitatively across model treatments. To test for sensitivity of the results to dispersal parameter values, the following parameters were explored for the local dispersal + LPDD rates treatment: ϕ, α, γ, and τ_{max}

(Table 2). Because field data regarding neonate emigration behavior are unavailable, the potential effect of a density-dependent neonate emigration was examined in the model.

Estimation of parameter values for neonate (predispersal) and crawler mortality.—The proportion of neonates dying and $\mu\delta_C$ were explored in parameter space (Table 2) for the biologically realistic treatment (local dispersal + LPDD rates) to determine the combinations of values that result in predictions of M_i^* similar to mean crawler abundances in the field. Functionally, δ_N and $\mu\delta_C$ compensate for one another such that as one probability is raised, the other can be lowered to yield similar predictions of M_i^*. Four pairs of sliding parameter values that fit this criterion were identified and were subsequently run in four trials of the 2×2 simulation experiment. Since δ_N and $\mu\delta_C$ do not vary in the model with local patch density, however, their particular values were not expected to affect the relationship between M_i^* and local patch density.

FIELD RESULTS

Patterns of abundance and density

Crawler abundance varied from 0 to 1500 crawlers/ patch (62.4 ± 10.3 crawlers/patch [mean ± SE]; median 12.0 crawlers/patch; Appendix F). Both crawlers and pupae were denser in smaller patches (Fig. 2). Crawlers were more abundant in more isolated patches, and this pattern persisted through the pupal and egg stages (Fig. 3). There was no correlation between patch size and local patch density ($F = 0.96$, df = 1, 134, $P = 0.33$, $r^2 = 0.0071$).

Patterns of mortality and fecundity

The mortality imposed by natural enemies on various moth stages varied widely (Table 1). The greatest mortality, 93%, occurred during the crawler stage, although this is likely to be a slight overestimate, as explained in *Methods*. Crawler mortality increased significantly with both crawler density and patch size (Table 3, Fig. 4). No other rates were density- or patch size-dependent.

Three rates varied significantly with local patch density. Pupal predation rate decreased as local patch density within a radius of 45 m increased (Table 3, Fig. 5A). Pupal parasitism by *Brachymeria ovata* increased
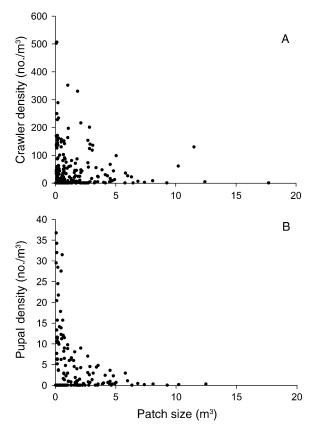
FIG. 2. Distribution of tussock moth densities across various patch sizes for the (A) crawler stage and (B) pupal stage. This study was conducted on a population of the western tussock moth at Montaña de Oro State Park in San Luis Obispo County, California, USA.

with local patch density within 15 m (Table 3, Fig. 5B). Fecundity increased with local patch density within 15 m (Table 3, Fig. 5C).

Model Results

The single-patch model—effect of patch size on equilibrium crawler density

This model, which excludes dispersal, was unable to predict stable, persistent local moth populations over much of the parameter range, but otherwise predicted that the measured variation in crawler mortality leads to greater moth density in small patches (Fig. 6). Predicted equilibria, C_{sm}^* and C_{lg}^*, were calculated for the representative small (0.1 m³) and large patches (11.5 m³), respectively (see Appendix G for equations). At high parameter values of neonate mortality, δ_N, and crawler mortality, $\mu\delta_C$, both populations went extinct, and at low joint death rates, both populations had an undefined equilibrium, i.e., showed accelerating growth (Fig. 6). Within the joint parameter space for which both patches had a positive equilibrium, C_{sm}^* had values 196–322 crawlers/m³ greater than those of C_{lg}^*. In a smaller region of parameter space, C_{lg}^* had a low,

positive equilibrium, but the moth population on the small patch was extinct throughout this region.

Comparison of field data and model results.—The two models were developed for exploring the mechanisms driving moth distribution rather than for precise prediction of local population densities; however, I compared model results with the field data quantita-
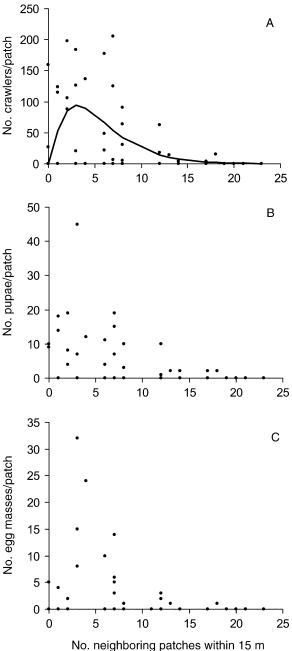

FIG. 3. Tussock moth (A) crawler, (B) pupal, and (C) egg mass abundance per patch at varying levels of local patch density. In panel (A), the solid line is a quasi-Weibull function, $f(x) = a_1 \times (x + 0.01)^{a_2} \times e^{a_3 x}$ fit to the crawler abundance data ($F = 12.78$, df = 3, 47, $P < 0.0001$).

TABLE 3. Results of logistic and Poisson regressions for effects of moth density (X_1), patch size (X_2), and local patch density (X_3, no. patches within 15 or 45 m) on fecundity (ε) and death rates (δ).

Moth stage	Rate	Pearson chi-square	df	Parameter	Estimate	SE	P
Eggs	ε†	777.66	71	intercept	4.9679	0.0359	<0.0001
				X_3 (15 m)	0.0387	0.0074	0.0348
	δ_{ER}	23.25	17	intercept	−1.4376	0.2985	<0.0001
	δ_{TC}†	1717.11	72	intercept	−0.6503	0.1223	<0.0001
	δ_{FH}†	1561.66	72	intercept	−1.9949	0.1113	<0.0001
Crawlers	δ_C	611.84	90	intercept	0.9153	0.3144	0.0036
				X_1 (crawlers)	0.0108	0.0026	<0.0001
				X_2	0.3050	0.0828	<0.0001
Pupae	δ_{PR}	111.18	69	intercept	−0.7024	0.3737	0.0602
				X_3 (45 m)	−0.0294	0.0105	0.0037
	δ_{PF}	107.50	66	intercept	−1.1945	0.2001	<0.0001
	δ_{BO}	60.44	75	intercept	−3.7537	0.3801	<0.0001
				X_3 (15 m)	0.1733	0.0424	<0.0001

Notes: Standard errors and type-3 P values were adjusted for overdispersion using Pearson chi-square. For explanations of variable abbreviations, see Table 1.

† The Generalized Estimating Equations method was used to account for clustering of egg mass-specific data by patch.

tively to gain insight into other potentially important processes in the system. In the parameter space where $C_{sm}^* > C_{lg}^*$ (Fig. 6), the two equilibrium density values at each location were used to predict slopes of a log-
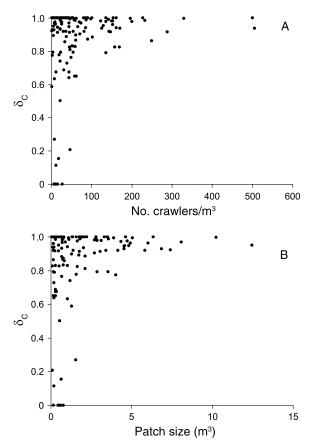

FIG. 4. Proportion of crawlers disappearing before pupation, δ_C, in relation to (A) crawler density and (B) patch size.

linearized relationship between crawler density and patch size. The minimum, median, and maximum predicted slopes within this region were −0.11, −0.31, and −0.77, respectively. The linearized slope of this relationship in the field data was estimated as −0.37, with 95% confidence limits of −0.20 and −0.53. The field estimate of the crawler density–patch size relationship thus falls well within the range of predicted values in the model.

The spatially explicit model—effect of local patch density on mean crawler abundance at steady state

First, the outcome of this model, which incorporated both dispersal and local dynamics in relation to patch density, was not sensitive to variation in the parameter values for which I had poor estimates: all four combinations of predispersal neonate mortality, δ_N, and crawler mortality, $\mu\delta_C$. The values (0.3, 0.93δ_C), (0.4, 0.90δ_C), (0.6, 0.81δ_C), and (0.7, 0.72δ_C) yielded distributions of mean predicted crawler abundances, M_i^*, that were qualitatively identical and similar to the field estimate. I therefore report results of the 2×2 model experiment for the $\delta_N = 0.4$, $\mu = 0.90$ case only.

I next show that the model predictions of moth abundance vs. patch density resembled the field pattern only when all processes as determined in the field were included in the model. In the control (global dispersal + fixed local rates), M_i^* was not correlated with local patch density (Fig. 7A; $F = 0.54$, df = 1, 848, $P = 0.46$, $r^2 = 0.0006$). When local dispersal was added to the model (local dispersal + fixed local rates), M_i^* was positively correlated with patch density (Fig. 7B; $F = 2847.36$, df = 1, 848, $P < 0.0001$, $r^2 = 0.77$). This result is consistent with the null hypothesis that moth abundance will increase with patch density if passive, local dispersal is the only spatially varying factor. When LPDD rates alone were introduced to the model
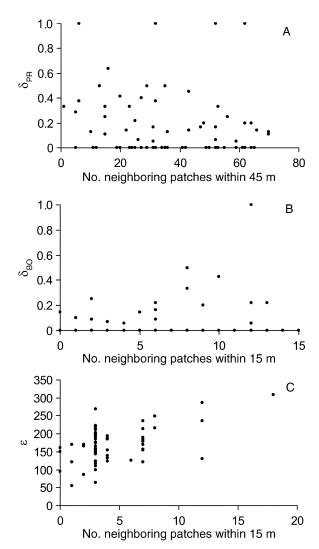
FIG. 5. (A) Proportion of pupae disappearing over a 13-day period, δ_{PR}, vs. local patch density at a radius of 45 m. The four observations at $\delta_{PR} = 1$ correspond with initial pupal counts of ≤ 3. (B) Proportion of pupae parasitized by *Brachymeria ovata*, δ_{BO}, vs. local patch density at a radius of 15 m. (C) Number of eggs per egg mass, ε, vs. local patch density at a radius of 15 m.

therefore, LPDD mortality was the major determinant of population distribution when the two factors were combined, and local dispersal had little effect on moth distribution among patches. Furthermore, parasitism (by *B. ovata*) was the only component of LPDD mortality that could account for suppression of moth population size in locally dense patches. Relatively high fecundity and low pupal predation would promote greater moth population size in densely packed patches, whereas only relatively high parasitism rates by *B. ovata* could suppress it.

Model sensitivity.—The humped distribution seen in the local dispersal + LPDD rates treatment varied minimally under a wide range of dispersal parameter values, thus the relative importance of LPDD rates over local dispersal was strongly robust against the choice of parameter values. The humped relationship between M_i^* and local patch density was persistent across a wide range of aerial travel distances for neonates (α; Appendix H, Fig. H1) and mean ground travel (γ) and maximum dispersal distance (τ_{max}; Appendix H, Fig. H2). The lack of a qualitative effect of α, γ, and τ_{max} implies that the ratio of τ_{max} to τ ($= \alpha + \gamma$) has no qualitative effect, therefore the joint effects of τ and emigration rate, ϕ, were explored for a fixed τ_{max}-to-τ ratio of 4:1 and $\alpha = 5$ m. There were no qualitative effects of either parameter, i.e., M_i^* peaked at intermediate levels of patch density and was lowest for the most crowded patches (Appendix H, Fig. H3). At the high emigration rate of $\phi = 0.8$, the distribution was less apparently hump-shaped due to high overall mortality, but patches in the intermediate ranges of local
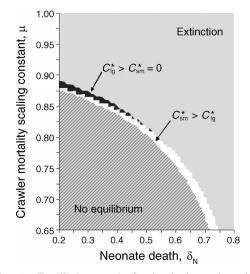

FIG. 6. Equilibrium results for the single-patch model. In the unshaded region, the equilibrium density in the small patch, C_{sm}^*, is greater than in the large patch, C_{lg}^*. In the darkly shaded region, the large patch maintains a low, positive equilibrium, but the small patch has gone extinct. In the lightly shaded region, both patches have gone extinct. In the hatched region, at least one patch has failed to reach equilibrium and exhibits accelerating growth over time.

(global dispersal + LPDD rates), the variability in local rates caused a hump-shaped relationship between M_i^* and local patch density, with a peak at a patch density of nine neighbors (Fig. 7C). Isolated patches have the lowest fecundity and highest pupal predation rates, while densely packed patches have the greatest pupal parasitism rates. The humped distribution resulted because patches with intermediate levels of isolation have relatively moderate birth and death rates and thus attain high M_i^*.

In the biologically realistic treatment (local dispersal + LPDD rates), the humped distribution was strongly retained, although the range of M_i^* was greater across all levels of patch density (Fig. 7D). Qualitatively,
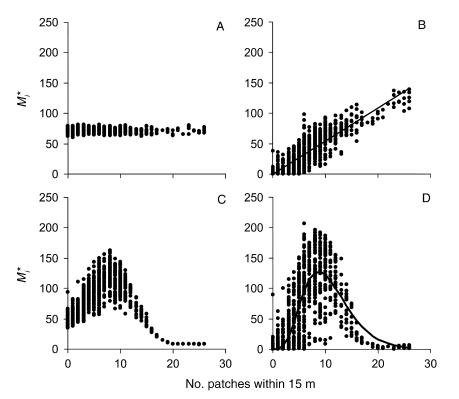
FIG. 7. Steady-state results for the spatially explicit model showing the independent and joint effects of dispersal and local demographic rates on the relationship between mean crawler abundance, M_i^*, and local patch density. (A) Global dispersal + fixed local rates, (B) local dispersal + fixed local rates, (C) global dispersal + local patch density-dependent (LPDD) rates, and (D) local dispersal + LPDD rates. In panel (B), the solid line is a least-squares simple regression line through the data. In panel (D), the solid line is a quasi-Weibull function fit to the data. Overall dispersal mortalities in the fixed local rates treatments and the LPDD rates treatments were 64% and 68%, respectively.

patch density still attained higher mean crawler abundances than did the most densely packed patches. In all cases, overall dispersal mortality decreased with increasing dispersal distance capability.

Both low and high levels of positive (direct) density-dependent neonate emigration generally led to a reduction in range of M_i^*, while negative (inverse) density dependence had the opposite effect (Appendix H, Fig. H4). Suppression of population size in crowded patches was again a persistent result. In general, higher emigration rates lead to higher overall levels of neonate mortality even though per capita dispersal mortality changes very little. Sensitivity of model results to density-dependent neonate emigration is low, in part because density dependence affects variance in the system without directly opposing the effects of patch structure-dependent mortality, but probably also because most LPDD processes occur in later life history stages.

Because the dominating influence of pupal parasitism on population distribution is somewhat unexpected given opposition by a significant number of other demographic processes, additional simulations explored whether the timing of LPDD mortality at the end of the immature moth stage is the key to its dominance.

In one case, LPDD parasitism was assigned prior to predation in the pupal stage (Fig. 8A). The results showed no qualitative differences from the local dispersal + LPDD rates treatment (Fig. 7D), indicating that timing of LPDD mortality *within* the pupal stage did not affect moth distribution. In another set of simulations, predispersal neonate mortality, δ_N, was replaced with the LPDD function for pupal parasitism (estimates in Table 3 for δ_{BO}), and pupal parasitism was fixed across all patches at its mean value. As a result, M_i^* increased monotonically with local patch density (Fig. 8B), indicating that the timing of LPDD mortality with respect to the life history of the moth is key to its impact on patterns of abundance.

Comparison of field data and model results.—I compared the distribution of field observations (Fig. 3A) and model output (Fig. 7D) by fitting a quasi-Weibull function, $f(x) = a_1 \times (x + 0.01)^{a_2} \times e^{a_3 x}$, to both data sets (Appendix I). As noted, the purpose of the models was to provide qualitative explanations, rather than accurate predictions, of the field patterns. Nevertheless, the model does a reasonable job of describing the data. In particular, it effectively captures the field decline in abundance as patch density increases. The function peaks at somewhat different levels (94 and 127 crawl-
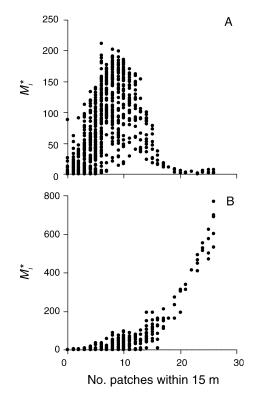
FIG. 8. Mean crawler abundance at steady state, M_i^*, vs. local patch density, for model manipulations in which the local patch density-dependent (LPDD) pupal parasitism function is assigned earlier in the simulation. In panel (A), LPDD mortality occurs prior to pupal predation. In panel (B), LPDD mortality occurs in the neonate stage prior to dispersal rather than during the pupal stage. Data represent 15 simulations run for 200 generations.

ers per patch, respectively) for the field and model data sets, although the value of the model's peak is not of particular interest since mortality rates (e.g., δ_N) can be adjusted slightly to modify M_i^*. The main difference is that the model distribution peaked at a higher local patch density (8.7) than did the field data (3.1). The model may simply be inaccurate, which is not unexpected since I did not have complete moth life tables. But the mismatch could result from comparing equilibria with a single snapshot. Temporal fluctuations in abundance are common in patches, and a handful of isolated survey patches may have been near peak, but temporary, levels at the time of survey. This explanation assumes that fluctuations tend to be greater in more isolated patches (see also Doak 2000a), perhaps due to greater stochasticity in immigration or death events.

DISCUSSION

Tussock moth populations were larger (and denser) on relatively isolated patches and small patches. Comparison of these moth distributions with the two null expectations for passive dispersal revealed that other processes must be at work; i.e., patch structure-depen-

dent demographic processes have a predominant effect on moth populations. Two mortality factors had the greatest potential impact on moth distribution. First, crawler mortality (most likely caused by small mammal or bird predation) increased with patch size. Although crawler mortality was also density-dependent, the single-patch model showed the effect of patch size to be strong enough to suppress crawler density on large patches under conditions that yield stable, persistent populations in both small and large patches. Second, parasitism by *Brachymeria ovata* was found to increase with local patch density. This effect was strong enough in the spatially explicit model to overcome the effects of three factors that, individually, would promote higher moth abundance in densely packed patches: dispersal mortality (Fig. 7B), fecundity, and pupal predation (also probably by small mammals or birds). The results were robust against a wide range of parameter estimates for dispersal and larval mortality. Thus, the measured rates of crawler disappearance and pupal parasitism by *B. ovata* were sufficient to explain greater moth densities in small and isolated patches, respectively.

The study was not intended to examine natural enemy behavior; however, the results suggest the wasp may be using host plant density as a direct visual or olfactory cue for finding host pupae or foraging less frequently in areas of sparse lupine density, where exposure to wind may be greater. Pupae are not generally known to release olfactory cues for foraging parasitoids, thus it would not be surprising if *B. ovata* cues in to the host's resource rather than to the host itself.

This study demonstrates that in plant–herbivore systems in spatially heterogeneous habitats, patch structure can have multiple indirect effects (e.g., parasitism and predation) on herbivore population distribution in addition to direct effects (e.g., dispersal). Several population rates varied with patch characteristics in opposite ways such that their joint effects were not intuitively predictable. The stage-structured models therefore used quantitative methods to make striking qualitative predictions about the relative importance of the stage-specific mortality factors.

Mortality in a late life history stage has a dominant effect on population distribution

The dominant effect of *B. ovata* on tussock moth population distribution is due partly to the rate of increase in its attack rate with local patch density, but also because it acts on a late life history stage in the moth. Differential pupal parasitism was unexpectedly influential given that overall parasitism by *B. ovata* was only 7%, a low percentage relative to pupal predation (15%) and simulated dispersal mortality (68%). The dominance of late pupal mortality reflects the relatively low number of individuals in that stage as well as the high reproductive value of individuals just reaching maturity (Stearns 1992). When LPDD mortality was removed from the pupal stage and simulated in neo-

nates, it could no longer override the opposing effects of dispersal mortality, fecundity, and pupal predation. In general, natural enemies attacking individuals of high reproductive value can have a great impact on local population size (Krebs 1994). In a study of 530 life tables of herbivorous insects, Cornell and Hawkins (1995) found the effect of natural enemies to be greatest in late stages of host or prey development.

Contrasts between two populations of tussock moths

Spatial patterning in another population of the western tussock moth on the northern California coast has been well-documented in the literature and provides complementary evidence for the importance of spatial structure in this species (Harrison 1994, Harrison and Wilcox 1995). At Bodega Marine Reserve (BMR), a tussock moth population formed a spatially restricted "outbreak" for over a decade (Harrison and Maron 1995), where an outbreak was defined by defoliation of the host plant (McCann et al. 2000). The mean abundance of larvae fell sharply outside the outbreak zone, decreasing as much as twofold within tens of meters (Harrison and Wilcox 1995, Brodmann et al. 1997). Formation of the spatially stable outbreak has been attributed to a phenomenon found in reaction-diffusion models; the leading edge of a slowly diffusing host is prevented from spreading by spillover of parasitoid or predator activity from within the outbreak, which generates high attack rates just ahead of the edge (Brodmann et al. 1997, Hastings et al. 1997, Maron and Harrison 1997). Endogenous spatial pattern formation requires interaction between a poorly dispersing host and a parasitoid or predator with greater relative mobility, as well as resource limitation within the outbreak (Wilson et al. 1999). McCann et al. (2000) showed that the phenomenon could also occur in a discrete space and time analogue of the reaction-diffusion model; stable, large amplitude patterning was obtained in a three-patch host–parasitoid model under similar biological conditions.

At BMR, 70% and 46% of bushes within the 100 × 400 m outbreak area had >100 larvae in 1993 and 1994, respectively, and larval densities were negligible outside this area (Harrison and Wilcox 1995). At MDO, in contrast, the tussock moth population is not characterized by spatially stable outbreaks. Only 16% of patches had >100 larvae based on the corrected count data, and these were scattered throughout almost the entire range of the 3000 × 500 m survey area (see also Appendix F). In addition, host plants were infrequently defoliated by tussock moth larvae at MDO, but when defoliation did occur, it happened on single or small groups of patches rather than on large clusters of patches (*personal observation*).

The spatial differences between the populations may be largely attributable to host plant distribution and natural enemies. In contrast to the heterogeneous distribution of *Lupinus chamissonis* patches at the MDO

study site (e.g., Appendix F), the main host plant at BMR, *L. arboreus*, is more closely packed, forming a continuous blanket of hundreds to thousands of bushes (Harrison 1994). While the reaction-diffusion framework and its discrete three-patch analogue assume a homogeneously distributed habitat and may be applicable to the system at BMR (Maron and Harrison 1997), they do not apply readily to the system at MDO, where variable patch spacing is likely to prevent constant or diffusive host dispersal. At BMR, nearest neighbor distances increased just beyond the edge of the outbreak in some areas (Brodmann et al. 1997), leaving the possibility that patch spacing may have contributed to low spread of the tussock moth population beyond the outbreak. Additionally, although some natural enemies are common to both sites, e.g., rodents and *Telenomus californicus*, some of the key parasitoids at BMR, i.e., *Tachinomyia similis* and *Protodejeania echinata* (Brodmann et al. 1997, Umbanhowar et al. 2003), were absent or rare at MDO. At the same time, the key pupal parasitoid at MDO, *B. ovata*, has not been reported in tussock moth studies at BMR and is presumed to be absent or rare there. Furthermore, although ants were thought to help prevent spread of the outbreak at BMR because of their poor mobility combined with local satiation (Harrison and Wilcox 1995), their distribution at MDO could not help to explain variability in moth abundance (Harrison 1997). Thus, while poor dispersal and spatial patterning in attack rates characterize both moth populations, their specific effects on moth distribution appear to differ between sites. At MDO, the spatial structure of patches plays a more direct role in moth distribution because the magnitude and variance of interpatch spacing are greater and can be limiting to both moth dispersal and to foraging by enemies (see also Maron et al. 2001). Indeed, even if the dispersal behaviors and interspecific interactions that permit endogenous spatial pattern formation are present in the MDO population, their effects may be masked or suppressed by the spatial complexity of the habitat.

LITERATURE CITED

Allison, P. D. 1999. Logistic regression using the SAS system: theory and application. SAS Institute, Cary, North Carolina, USA.

Atkinson, A. C. 1981. Likelihood ratios, posterior odds and information criteria. Journal of Econometrics **16**:15–20.

Bach, C. E. 1988. Effects of host plant patch size on herbivore density: patterns. Ecology **69**:1090–1102.

Brodmann, P. A., C. V. Wilcox, and S. Harrison. 1997. Mobile parasitoids may restrict the spatial spread of an insect outbreak. Journal of Animal Ecology **66**:65–72.

Cornell, H. V., and B. A. Hawkins. 1995. Survival patterns and mortality sources of herbivorous insects. American Naturalist **145**:563–593.

Cronin, J. T. 2003. Patch structure, oviposition behavior, and the distribution of parasitism risk. Ecological Monographs **73**:283–300.

Doak, P. 2000*a*. Habitat patchiness and the distribution, abundance, and population dynamics of an insect herbivore. Ecology **81**:1842–1857.

Doak, P. 2000*b*. The effects of plant dispersion and prey density on parasitism rates in a naturally patchy habitat. Oecologia **122**:556–567.

ESRI [Environmental Systems Research Institute]. 1999. ArcView. Version 3.2. ESRI, Redlands, California, USA.

Fahrig, L., and J. Paloheimo. 1988. Determinants of local population size in patchy habitats. Theoretical Population Biology **34**:194–213.

Grushecky, S. T., A. M. Liebhold, R. Greer, and R. L. Smith. 1998. Does forest thinning affect predation on gypsy moth (Lepidoptera: Lymantriidae) larvae and pupae? Environmental Entomology **27**:268–276.

Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 1–26 *in* I. A. Hanski and M. E. Gilpin, editors. Metapopulation biology: ecology, genetics, and evolution. Academic Press, New York, New York, USA.

Harrison, S. 1994. Resources and dispersal as factors limiting a population of the tussock moth (*Orgyia vetusta*), a flightless defoliator. Oecologia **99**:27–34.

Harrison, S. 1997. Persistent, localized outbreaks in the western tussock moth (*Orgyia vetusta*): the roles of resource quality, predation, and poor dispersal. Ecological Entomology **22**:158–166.

Harrison, S., and J. L. Maron. 1995. Impacts of defoliation by tussock moths (*Orgyia vetusta*) on the growth and reproduction of bush lupine (*Lupinus arboreus*). Ecological Entomology **20**:223–229.

Harrison, S., D. D. Murphy, and P. R. Ehrlich. 1988. Distribution of the bay checkerspot butterfly, *Euphydryas editha bayensis*: evidence for a metapopulation model. American Naturalist **132**:360–382.

Harrison, S., and C. Wilcox. 1995. Evidence that predator satiation may restrict the spatial spread of a tussock moth (*Orgyia vetusta*) outbreak. Oecologia **101**:309–316.

Hassell, M. P., H. N. Comins, and R. M. May. 1991. Spatial structure and chaos in insect population dynamics. Nature **353**:255–258.

Hastings, A., S. Harrison, and K. McCann. 1997. Unexpected spatial patterns in an insect outbreak match a predator diffusion model. Proceedings of the Royal Society of London B **264**:1837–1840.

Hertzberg, K., N. G. Yoccoz, R. A. Ims, and H. P. Leinaas. 2000. The effects of spatial habitat configuration on recruitment, growth and population structure in arctic *Collembola*. Oecologia **124**:381–390.

Hill, J. K., C. D. Thomas, and O. T. Lewis. 1996. Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. Journal of Animal Ecology **65**:725–735.

Hovel, K. A., and R. N. Lipcius. 2001. Habitat fragmentation in a seagrass landscape: patch size and complexity control blue crab survival. Ecology **82**:1814–1829.

Kareiva, P. 1983. Influence of vegetation texture on herbivore populations: resource concentration and herbivore movement. Pages 259–289 *in* R. F. Denno and M. S. McClure, editors. Variable plants and herbivores in natural and managed systems. Academic Press, San Diego, California, USA.

Krebs, C. J. 1994. Ecology: the experimental analysis of distribution and abundance. Fourth edition. Harper Collins, New York, New York, USA.

Lamberson, R. H., B. R. Noon, C. Voss, and K. S. McKelvey. 1994. Reserve design for territorial species: the effects of patch size and spacing on the viability of the northern spotted owl. Conservation Biology **8**:185–195.

Law, A. M., and W. D. Kelton. 2000. Simulation modeling and analysis. Third edition. McGraw-Hill, San Francisco, California, USA.

Lei, G.-C., and I. Hanski. 1997. Metapopulation structure of *Cotesia melitaearum*, a specialist parasitoid of the butterfly *Melitaea cinxia*. Oikos **78**:91–100.

Liang, K. Y., and S. L. Zeger. 1986. Longitudinal data analysis using generalized linear models. Biometrika **73**:13–22.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

Maron, J. L., and S. Harrison. 1997. Spatial pattern formation in an insect host–parasitoid system. Science **278**:1619–1621.

Maron, J. L., S. Harrison, and M. Greaves. 2001. Origin of an insect outbreak: escape in space or time from natural enemies? Oecologia **126**:595–602.

Matter, S. F. 1996. Interpatch movement of the red milkweed beetle, *Tetraopes tetraophthalmus*: individual responses to patch size and isolation. Oecologia **105**:447–453.

McCann, K., A. Hastings, S. Harrison, and W. Wilson. 2000. Population outbreaks in a discrete world. Theoretical Population Biology **57**:97–108.

McCullagh, P., and J. A. Nelder. 1989. Generalized linear models. Second edition. Chapman and Hall, New York, New York, USA.

Pulliam, H. R., J. B. Dunning, Jr., and J. Liu. 1992. Population dynamics in complex landscapes: a case study. Ecological Applications **2**:165–177.

Roland, J., P. Taylor, and B. Cooke. 1997. Forest structure and the spatial pattern of parasitoid attack. Pages 97–106 *in* A. D. Watt, N. E. Stork, and M. D. Hunter, editors. Forests and insects. Chapman and Hall, London, UK.

Roslin, T., and A. Koivunen. 2001. Distribution and abundance of dung beetles in fragmented landscapes. Oecologia **127**:69–77.

SAS Institute. 2001. The SAS system. Version 8. SAS Institute, Cary, North Carolina, USA.

Segarra-Carmona, A. E., and P. Barbosa. 1992. Host-plant patches as islands: effects of patch size, patch extinction and seasonality of a herbaceous tropical legume (*Crotalaria pallida* Ait.) on a pod borer (*Etiella zinckenella* (Treit.)) and its parasitoids. Insect Science and its Application **13**:709–718.

Stanton, M. L. 1983. Spatial patterns in the plant community and their effects upon insect search. Pages 125–157 *in* S. Ahmad, editor. Herbivorous insects: host-seeking behavior and mechanisms. Academic Press, San Diego, California, USA.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, New York, New York, USA.

Swarm Development Group. 2000. The Swarm simulation system. Version 2.1.1. Swarm Development Group, Santa Fe, New Mexico, USA.

Thompson, J. N. 1978. Within-patch structure and dynamics in *Pastinaca sativa* and resource availability to a specialized herbivore. Ecology **59**:443–448.

Umbanhowar, J., J. Maron, and S. Harrison. 2003. Density-dependent foraging behaviors in a parasitoid lead to density-dependent parasitism of its host. Oecologia **137**:123–130.

Welch, P. D. 1983. Simulation, implementation and evaluation of stochastic-models. Operations Research **31**:21.

Williams, I. S., T. H. Jones, and S. E. Hartley. 2001. The role of resources and natural enemies in determining the distribution of an insect herbivore population. Ecological Entomology **26**:204–211.

Wilson, W. G., S. P. Harrison, A. Hastings, and K. McCann. 1999. Exploring stable pattern formation in models of tussock moth populations. Journal of Animal Ecology **68**:94–107.

Yoo, H. J. S. 2002. The effects of patch configuration on spatial patterns of abundance of an herbivorous insect. Dissertation. University of California, Santa Barbara, California, USA.

Yoo, H. J. S., A. Stewart-Oaten, and W. W. Murdoch. 2003. Converting visual census data into absolute abundance estimates: a method for calibrating timed counts of a sedentary insect population. Ecological Entomology **28**:490–499.

APPENDIX A

A photograph of the field site (*Ecological Archives* E087-035-A1).

APPENDIX B

Details of the 1997 survey sampling design (*Ecological Archives* E087-035-A2).

APPENDIX C

Method of model selection for the logistic and Poisson regressions (*Ecological Archives* E087-035-A3).

APPENDIX D

A description of image analysis for patch spatial data (*Ecological Archives* E087-035-A4).

APPENDIX E

An illustration of the local dispersal rule for the spatially explicit model (*Ecological Archives* E087-035-A5).

APPENDIX F

A map of crawler abundances in the northern and southern halves of the 1997 survey area (*Ecological Archives* E087-035-A6).

APPENDIX G

Equilibrium density equations for the single-patch model (*Ecological Archives* E087-035-A7).

APPENDIX H

Figures showing sensitivity tests for the spatially explicit model (*Ecological Archives* E087-035-A8).

APPENDIX I

Comparison of field data with output of the spatially explicit model (*Ecological Archives* E087-035-A9).