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The importance of host plant limitation for caterpillars of an arctiid moth (*Platyprepia virginalis*) varies spatially

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Abstract. Spatial dynamic theories such as source–sink models frequently describe habitat-specific demographies, yet there are surprisingly few field studies that have examined how and why interacting species vary in their dynamics across multiple habitat types. We studied the spatial pattern of interaction between a chewing herbivore and its primary larval host plant in two habitat types. We found that the interaction between an arctiid caterpillar (*Platyprepia virginalis*) and its host (*Lupinus arboreus*) differed in wet vs. upland dry habitats, as did yearly population dynamics for the caterpillar. In upland sites, there was a strong positive relationship between lupine cover and the abundance of caterpillars although this relationship was not apparent in wet sites. Additionally, in wet sites, caterpillar populations were larger and less variable across years. Caterpillars appeared to exhibit source–sink dynamics, with the time-averaged finite growth rate $\lambda > 1$ in wet sites (sources), $\lambda < 1$ in upland dry sites (sinks), and predominant source-to-sink movement of late-instar caterpillars. Populations in upland dry sites also went locally extinct in years of low regional abundance. Emigration from wet sites could potentially explain the lack of coupling of herbivore and host plant dynamics in these sites. These results indicate that movement and other factors affecting demography are habitat-specific and have important implications for trophic control. Acknowledging such complexity makes simple models of trophic control seem overly general but may allow us to formulate more broadly applicable ecological models.

Key words: Bodega Marine Reserve, California, USA; bottom-up control; lambda; Lupinus arboreus; metapopulation; movement; Platyprepia virginalis; *population dynamics; source–sink; trophic interaction.*

INTRODUCTION

For almost as long as ecology has been a self-identified discipline, ecologists have argued about the factors that control populations of herbivorous insects. The relative importance of predators, parasites, and diseases (top-down control) vs. limited resource quality and quantity (bottom-up control) has been at the center of the controversy (Elton 1927, Hairston et al. 1960, Hunter and Price 1992, Shurin et al. 2002, Borer et al. 2006, Denno and Kaplan 2007). Although most ecologists now acknowledge that both top-down and bottom-up controls can be important, many other important issues are still poorly understood. For instance, we need to more fully understand the conditions favoring top-down or bottom-up factors, interrelationships among the factors, the scale at which they operate, and the role of non-trophic interactions.

More recently, ecologists have come to appreciate that most populations are not arrayed randomly or uniformly over the landscape but are instead structured in heterogeneous patches over space and time. The subset of species that are present at a particular patch greatly influences the possible interactions that can potentially occur (MacArthur and Wilson 1967, Levins 1969, Hanski and Gilpin 1991, Holyoak et al. 2005). Because accounting for spatial dynamics is relatively new, there has been little synthesis of the spatial arrangement of limiting factors with herbivore population regulation (Denno et al. 2005, Gripenberg and Roslin 2007). In addition, most empirical studies of population limitation have focused on one single habitat or field site. This has been dictated by practical constraints and attempts to reduce unexplained environmental variation, but it precludes a consideration of the spatial arrangement of limiting factors. Gripenberg and Roslin (2007) argued that ecologists must include a spatial approach when considering population limitation of herbivores because: (1) habitats are patchy and vary greatly in abiotic and biotic conditions that affect herbivores, (2) herbivore populations are themselves variable across space, and (3) other important interactions vary over space. The study of how spatial dynamics influences species interactions is difficult and the number of such studies in the literature is limited (e.g., Holyoak et al. 2005).

Ecologists have described many populations that are scattered over heterogeneous landscapes using variants

on source–sink models (Pulliam 1988). These models are based on two key ideas. (1) High-quality "source" patches support populations with finite growth rates λ > 1, whereas low-quality "sink" patches have λ < 1 in the absence of immigration. (2) Repeated movement of individuals from sources to sinks maintains small populations in the sink patches by preventing them from declining to extinction. Most source–sink models assume consistent unidirectional movement from sources to sinks (Diffendorfer 1998) and that patches have fixed finite rates of growth. However in reality, some species might move back and forth between patches depending on resource availability (Diffendorfer 1998), density dependence may alter λ (e.g., pseudosinks, sensu Watkinson and Sutherland [1995]), or patches may undergo either directional (source–sink inversions; Dias 1996), or less predictable change in quality through time (e.g., Boughton 1999, Virgl and Messier 2000, Johnson 2004, Hodgson et al. 2009).

Most empirical studies of populations with source–sink structure have generally not considered movement of immature life stages between patches, perhaps because most studies of source–sink dynamics have involved vertebrates (reviewed by Kawecki 2004). Moreover, studies of birds and amphibians have often examined only breeding individuals and ignored other life stages and nonbreeding adults (e.g., De Bruijn 1994, Dias et al. 1994, Vierling 2000, Gamble et al. 2007, Martinez-Solano and Gonzalez 2008). For organisms with multiple life stages, focusing on only adults may provide an incomplete picture of how spatial variation in habitat quality influences population growth. One danger is that carryover effects can be missed, where conditions in one habitat influence the demography of individuals in subsequent habitats (e.g., Benard and McCauley 2008). Furthermore, habitats may switch as sources and sinks over the season as cohorts of individuals change life stages. For example, salt marsh habitats for adult planthoppers early in the season became suboptimal for nymphs later in the season (Gratton and Denno 2003). Overall, there is a paucity of information on how movement relates to local population dynamics in species that use different habitats in different life stages. Our study examined spatial variation in the role of host plant limitation on an herbivore. Host plant abundance and quality can critically influence spatial and temporal variation in the abundance of herbivorous insects (e.g., Murdoch 1966, Root 1973, White 1993). Because host plants provide habitat for herbivorous insects, plant structure may affect herbivore distributions (Jones et al. 1994) and plant structure is capable of interacting with nutritional quality in complex ways (e.g., Thomas et al. 2009). Despite these potential roles for host plant abundance and quality as drivers of population processes, most studies that have attempted to understand the conditionality of limiting factors have concentrated on conditions that affect top-down effects, particularly trophic cascades (e.g., Schmitz et al. 2000, Shurin et al. 2002, Borer et al. 2006). Our study of the relationship between lupine cover and caterpillar abundance across the landscape along with caterpillar movement integrates the habitat (emphasizing local processes) and spatial dynamic (emphasizing movement) paradigms (sensu Armstrong 2005).

Study system

This study investigated spatial and temporal variability in a polyphagous caterpillar, *Platyprepia virginalis* (Lepidoptera: Arctiidae; see Plate 1) across the landscape at the Bodega Marine Reserve in northern California, USA. Annual variation in population numbers collected since 1985 at the study site varied by three orders of magnitude and was not driven by a locally specialized and abundant tachinid parasitoid nor by variation in weather (Karban and de Valpine 2010).

This moth species completes a single generation each year at the study site. Caterpillars pupate in spring (April–June) and adults live for several weeks. Eggs hatch in early summer (May–July) and early-instar caterpillars feed through summer, autumn, and early winter on the litter and leaves of *Lupinus arboreus*, and to a lesser extent other decaying and living plants (English-Loeb et al. 1993, Karban and English-Loeb 1997). In spring, later instars become increasingly mobile and increasingly polyphagous (Karban et al. 2010). At the study site, late instars preferentially feed on lupine (*L. arboreus*; see Plate 1), poison hemlock (*Conium maculatum*), fiddleneck (*Amsinckia menziesii*), and thistles (six spp.). *L. arboreus* is the dominant woody vegetation in the two dry upland habitats on the reserve, grasslands, and dunes (Barbour et al. 1973). Individual lupine bushes are short-lived and lupine cover at marked plots varied among years from close to zero to >60% (Davidson and Barbour 1977, Strong et al. 1995).

P. virginalis caterpillars never completely defoliate adult lupine bushes. While absolute shortages of food seem unlikely for mobile later instars, it is possible that less mobile early instars can experience food limitation in areas where lupine dies back or if food quality rather than absolute shortage becomes limiting. Common garden experiments suggested that the quality of lupine bushes affects the success of *P. virginalis* caterpillars (Karban and Kittelson 1999). Caterpillars beneath bushes that were supplemented with additional litter either experimentally or as the result of feeding by tussock moth caterpillars (*Orgyia vetusta*) supported greater numbers of *P. virginalis* (Karban et al. 2012). *L. arboreus* contains quinolizidine alkaloids (Seigler 1998, Adler and Wink 2001, Adler and Kittelson 2004), although we found no evidence that *P. virginalis* caterpillars were deterred by the alkaloids nor sequestered them (Karban et al. 2010). Rather, they appear to make the alkaloids nonreactive while the food is passing through their guts.

Preliminary observations of the abundance and distribution of caterpillars at the study site suggested that the habitat can be divided into two categories: favorable wet marshy areas and less favorable drier upland prairie and dunes (hereafter "wet" and "dry"). *L. arboreus* grows in both habitat types although wet areas have primarily *Juncus* spp. rushes and poison hemlock, *Conium maculatum*, in the matrix between lupine bushes, while upland areas have a diversity of grasses and forbs filling the matrix (Barbour et al. 1973). Preliminary observations also suggested that wet areas supported some caterpillars even in low caterpillar density years but that upland areas failed to support caterpillars in some years. In this study we attempted to characterize the relationship between caterpillars and lupine across the landscape. We addressed the following questions: (1) Are *P. virginalis* populations more variable over time and space in dry than in wet habitats? (2) Are wet sites sources ($\lambda > 1$) and dry sites sinks ($\lambda < 1$)? (3) Is there movement between habitat types and is it biased from wet to dry sites? (4) Is the net relationship between caterpillar abundance and the abundance of their primary host, *L. arboreus*, different in the two kinds of habitats?

METHODS

Caterpillar abundance, variability, and finite growth rates across the landscape

We estimated the number of *P. virginalis* caterpillars at 13 sites at the Bodega Marine Reserve, California, USA (Fig. 1) annually from 2007 to 2011. The sites were selected to span the range of densities of caterpillars encountered at the reserve. All of the sites except one have consistently supported stands of *L. arboreus* plants and densities of this plant did not vary consistently among these sites. Caterpillars are conspicuous from February until pupation from April onward, so sites were sampled repeatedly during this period (two to four times per year) because censuses before February miss inconspicuous caterpillars. For each site and year the maximum number of caterpillars observed on 10 haphazardly selected healthy *L. arboreus* bushes was used as the measure of caterpillar abundance. Maximum numbers summed for the 10 bushes at each site were used rather than the average over the season to allow for variation in the timing of peak numbers from site to site. The short lifespan of *L. arboreus* meant that the identity of bushes included at each site shifted through time as some bushes died and similarly sized additional ones were included. At one of the sites, *L. arboreus* was rare or absent and the number of caterpillars observed over an area equivalent to the surface area of 10 mature lupine bushes (144 m^2) was used as an estimate of abundance.

We refer to our sampling units as sites because they were not discrete habitat patches separated by inhospitable matrix. Our system clearly exhibited patchiness although it was not possible to formally define patches vs. matrix. Source–sink theory does not require strictly

defined patches and also applies to a spatial continuum. Sites were categorized as either being seasonally wet or dry upland using two criteria: wet sites support *Juncus* spp. rushes or poison hemlock and flood in wet years and dry sites do not. These two criteria gave consistent site descriptions. Of the 13 sites, five sites were categorized as wet and eight sites as dry (Fig. 1). Sites were far enough apart to be independent and represent a subset of available sites within the landscape.

We characterized the variability over the five census years (2007–2011) at each site using Taylor's (1961) power law relationships for the maximum number of caterpillars per 10 lupine bushes. Specifically, we compared the ln (variance) vs. ln (mean) of peak numbers of caterpillars per site over the five years for wet vs. dry upland sites (Fig. 2). We used a general linear model in R version 2.13.1 (R Development Core Team 2011) using function "lm" with ln (variance) as the dependent variable, habitat (wet/dry) as a factor, and ln (mean) as a continuous variable (covariate). Because this analysis necessarily used only mean abundances per site, rather than all years of data, we also compared ln (numbers) of caterpillars between wet and dry sites with a repeated-measures ANOVA across all five years.

To determine source vs. sink status of wet and dry habitat areas we calculated values of finite growth rate for each site as $\lambda = N_{t+1}/N_t$, where N_t is peak abundance in year t, and $\lambda > 1$ indicates putative sources and $\lambda < 1$ indicates putative sinks. Calculations used all possible pairs of years where $N_t > 0$ and $N_{t+1} > 0$. A linear mixed-effects model in R (procedure lmer in library lme4; R Development Core Team 2011) was used to compare ln (λ) values across years and habitats (wet/dry) as fixed factors. Site was included as a random factor and repeated measures across years were allowed for in the error structure; a habitat by year interaction could not be fitted because of simultaneous extinctions in dry habitats in some years. Values of λ were ln-transformed to meet assumptions of normality. We also used a similar linear mixed-effects model to determine if λ values were density dependent by regressing ln (λ) against ln (N_t) in a model that included repeated measures in the error structure. (Given the limited number of sites we did not attempt to test for differences in density dependence across sites or habitats.)

Caterpillar and lupine abundance in dry, upland sites

We examined the relationship between lupine cover and caterpillar numbers by taking advantage of an existing experiment in the upland sites to ask whether the abundances of these two were positively correlated. In 1998, Maron established 48 experimental plots, each 9×9 m in dry, upland habitats (Maron and Kauffman 2006). Eight plots were placed in each of six locations, at the north end of the reserve, in the middle and at the south end, in each of the two dry habitats: grassland and dune (8 plots $\times$ 3 locations $\times$ 2 habitats). Following a die-off of lupine in 1998, dead and a few live lupine

FIG. 1. Map of the Bodega Marine Reserve, California, USA, showing the location of the 13 sites from Table 1 (A, artemisia; AL, across from lab; E, edge of marsh; F, fire marsh; H, hemlock; ND, north dune; D, draw; DM, dorm marsh 1; M, Mussel point; NS, north of S-curve; R, rabbit valley; SS, south of S-curve; T, top of hill) and the distribution of upland and wet habitats. Sites marked with red circles are located in dry upland habitat, and those marked with blue circles are located in wet habitat. Blue dashed-line polygons indicate the spatial extent of wet habitat and sites outside of the blue polygons are dry upland.

bushes were removed from the plots and 69 seedlings were transplanted into each plot.

We counted the number of *P. virginalis* caterpillars in each plot yearly in late March 2007, 2008, and 2009. The percentage of ground covered by *L. arboreus* at each plot was estimated during censuses. We used a linear mixed-effects model to fit the relationship between caterpillar abundance and lupine cover using plot identity as a random factor nested within year number. The analysis was performed in R using the LME function in the NLME package (R Development Core Team 2011). Fitting the model either with a Poisson error distribution or normal errors did not produce much difference in the results, and for simplicity we report the latter. We also used percent cover of lupine as either an untransformed variable or as arcsine square-root transformed and report the untransformed analyses because the residual deviance was lower. In broad terms this analysis resembles an analysis of covariance with year as a factor and repeated measures of caterpillar abundance and lupine cover.

Caterpillar and lupine abundance in wet habitat

We tested the correlation between the abundance of caterpillars and lupine cover using annual caterpillar censuses conducted in one wet site ("hemlock" in Fig. 1) from 1997 to 2011. Each year we selected five different transects (10 × 4 m) parallel to the ridge. For each transect, we estimated the number of caterpillars per square meter and the percent cover of *L. arboreus* and other host plants. We conducted an ANCOVA (Fit Model command in JMP 9.0; SAS Institute, Cary,

North Carolina, USA) to compare the relationship between lupine cover as a predictor of the number of caterpillars per square meter with year as a blocking variable. Because different transects were used each year, a repeated-measures analysis was not appropriate and year as a blocking variable accounts for between-year variation. We also conducted a second ANOVA on the number of caterpillars per square meter, detrended by the annual variation in caterpillar numbers (using
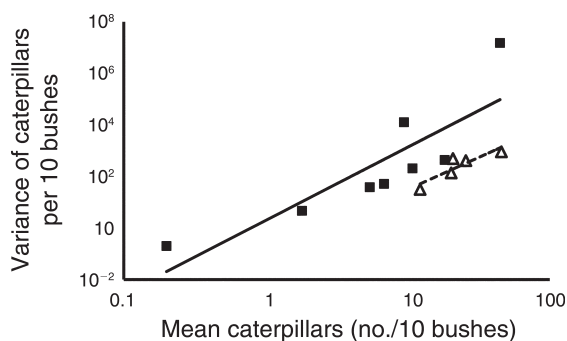

FIG. 2. Variance vs. mean plots for caterpillar populations at dry sites (solid squares and solid line) and wet sites (open triangles and dashed line) from 2007 to 2011. Lines are the result of a general linear model with ln (variance) as the dependent variable, habitat (wet/dry) as a factor, and ln (mean) as a continuous variable (a covariate). Equations for lines are: for dry sites, ln (variance) = 0.712 + 2.82 × ln (mean), and for wet sites, ln (variance) = −3.303 + 2.82 × ln (mean). The interaction between slope and habitat was not significant ($t = 0.13$, df = 1, $P = 0.9$). The difference in intercepts was significant ($t = −2.55$, df = 1, $P = 0.03$).

TABLE 1. Maximum numbers of caterpillars of the arctiid moth *Platyprepia virginalis* observed on 10 lupine (*Lupinus arboreus*) bushes at each site during spring 2007–2011 in the Bodega Marine Reserve, California, USA.

Site	Habitat	2007	2008	2009	2010	2011	Mean	CV
North S curve	dry	3	28	0	1	15	9.4	12.01
South S curve	dry	51	15	0	1	24	18.2	1.15
Draw	dry	200	21	0	1	1	44.6	87.32
Top of hill	dry	15	7	0	0	5	5.4	1.15
Mussel point	dry	15	14	1	0	4	6.8	1.06
Artemisia	dry	31	21	1	0	1	10.8	1.33
North dune	dry	3	5	1	0	0	1.8	1.2
Across from lab	wet	51	40	9	3	25	25.6	0.79
Hemlock	wet	30	30	2	16	23	20.2	0.58
Dorm marsh 1	wet	1	17	12	15	59	20.8	1.07
Edge of marsh	wet	7	19	6	13	16	12.2	0.46
Fire marsh	wet	50	90	50	10	28	45.6	0.66

the residuals of the model caterpillars density equals year), to test whether transects with more lupine in each year supported more caterpillars. Percent lupine cover was transformed using the arcsine transformation in both analyses to satisfy the assumptions of ANOVA. We tested for correlations between the cover of all preferred host plants (*L. arboreus*, *C. maculatum*, *A. menziesii*, and thistles) together and separately in each transect with the abundance of caterpillars from 1997 to 2011 as described earlier in this paragraph for lupine cover.

Movement of caterpillars from wet to dry habitats

We conducted two experiments, informed by an observational study to determine if the direction of movement of caterpillars was biased with respect to habitat type. We observed caterpillars that crossed the reserve road that separated the wet habitat on the northeast side of the road from the dry habitat on the southwest side of the road (near the site "across from lab" in Fig. 1). We recorded caterpillars crossing the road on 10 dates from 19 March and 30 April 2008. The number of caterpillars that started on one side of the road and moved to the other was recorded. Caterpillars that started on one side, crossed the median line, and ultimately headed back to the side from which they originated were included as moving to the side they ultimately chose, although caterpillars that did not cross the median line but moved parallel to the side of the road were not included. The number of caterpillars that moved from wet to dry and dry to wet were compared to a null expectation that movement was equal across the moisture gradient (50% of caterpillars moved in each direction) using the binomial exact test.

We conducted an experiment that followed the movements of individuals across ecotones of wet and dry habitat to corroborate results from our observations. Twenty cohorts of five caterpillars (penultimate and ultimate instar) were marked with a dot of acrylic paint and released at 10:00 hours on 24 and 25 April 2010. Caterpillars were recaptured at 14:00 on the same day they were released and the direction of their movement over the 4 h (toward wet or dry habitat) recorded. One-half of the release points were oriented with wet habitat to the northeast and one-half with wet habitat to the southwest (using the marshes and upland in the northeast corner of Fig. 1). Cohorts rather than individual caterpillars were considered independent replicates. The number of caterpillars (cohorts) that moved toward wet or dry habitat was compared to the null expectation that movement was not biased along the moisture gradient (50% of caterpillars moved in each direction) using a binomial exact test.

We conducted a second experiment to determine if caterpillar density per bush influences the likelihood that a caterpillar will emigrate from that bush. We selected 24 bushes and randomly assigned them to have three, six, or nine caterpillars. The mean number of caterpillars per bush in wet sites in 2011 was three caterpillars, so these densities represent 1×, 2×, and 3× the mean although they were all well within the range of naturally observed densities. Cohorts of caterpillars (penultimate and ultimate instars) were collected, marked with a dot of acrylic paint, and released at 10:00 hours on 6 April 2011. Marked caterpillars were recaptured at 14:00 and their location (release bush or a different substrate) at the time of recapture was recorded.

We fitted generalized linear models to the data in R to test the effect of density on emigration using the mle2 function implemented in the bbmle package (R Development Core Team 2011). Because our data were overdispersed, the analyses were carried out with a negative binomial distribution of sampling error and a logit link function. We used a likelihood ratio test to compare AIC values resulting from a model with density as an explanatory variable and a null model where the proportion of caterpillars emigrating increased linearly with density.

RESULTS

Caterpillar abundance and variability across the landscape

Sites differed greatly in the number of caterpillars that they supported (Table 1). Wet sites had approximately twice as many caterpillars (mean = 24.9) as dry, upland

sites (mean = 12.2; repeated-measures ANOVA $F_{1,11}$ = 20.4, $P = 0.001$). In addition, dry upland sites showed far more variance in caterpillar abundance through time than wet sites: the best-fitting linear mixed-effects model relating variance to mean abundance showed a significantly greater intercept for dry compared to wet habitats (Fig. 2; difference in intercepts for wet vs. dry, Student's $t = -2.55$, $P = 0.02$), and a common slope that was significantly different from 0 (Student's $t = 5.14$, $P < 0.001$; the difference in slopes for habitats was not significant; Student's $t = -0.129$, $P = 0.9$). The coefficient of variation of abundance for dry sites was $18\times$ greater than that for wet sites. Populations went locally extinct at all eight upland (dry) sites in either 2009 and/or 2010, while all of the wet sites had caterpillars in all years (Table 1).

Finite growth rates, λ, from one year to the next showed that on average wet sites were sources, with mean $\lambda = 1.06$. Conversely, on average, dry upland sites were sinks, with mean $\lambda = 0.66$. However both kinds of habitat showed considerable variation from year to year (Fig. 3A). In particular, 2008–2009 had lower λ values for both wet and dry sites than other years (Fig. 3A; Student's t from lmer = 2.20, $P = 0.03$). In 2010–2011 for dry sites, estimates of λ came from just three sites and each of these had very low caterpillar densities in 2010 so that the mean λ value for these sites had a very large confidence interval (see legend to Fig. 3A). Overall, the effect of habitat type was significant and $\ln(\lambda)$ was lower for dry habitats than wet habitats (Fig. 3A; Student's t from lmer = 2.87, $P = 0.01$). We could not investigate the full interaction between years and habitat types because there were too many zero abundance values (due to local extinctions) to be able to calculate λ values. Caterpillar abundances were also strongly density dependent, such that finite growth rates were lower in years when the abundance was initially higher (Fig. 3B and statistics in legend to Fig. 3). This compensatory response to high densities might be due to mortality, reduced recruitment, or emigration.

Caterpillar and lupine abundance in dry, upland sites

Upland plots with more lupine cover had more caterpillars and this result was consistent across all three years of the study (Fig. 4). Lupine cover and caterpillar abundance were positively related such that in 2007 number of caterpillars = 0.122 × percent lupine cover (SE of slope = 0.041, $P = 0.0035$), and the intercept was not significantly different from zero ($P = 0.76$) in any year. For 2008 the slope was 0.32× greater than in 2007 (SE difference = 0.050, $P < 0.0001$), and for 2009 the slope was slightly lower than 2007 (difference = −0.095, SE difference = 0.046, $P = 0.04$). Hence, while there were differences in the slope of the relationship between caterpillar abundance and lupine cover, the slope was significant and positive in all years.
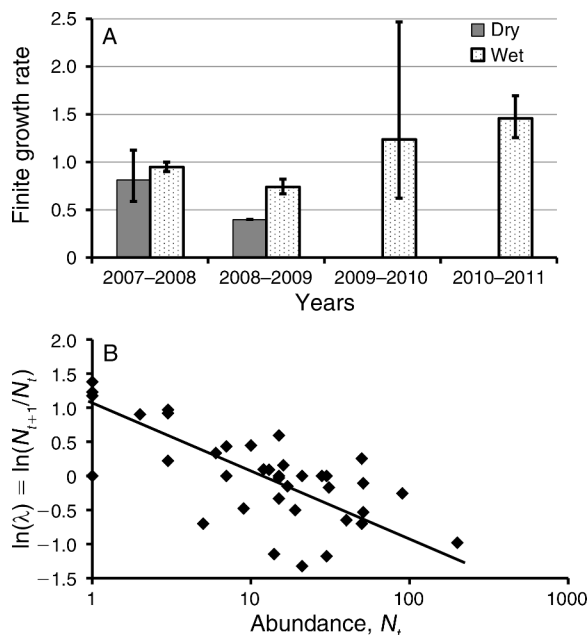

FIG. 3. Linear model estimates of finite growth rates, λ, shown (A) for years and habitat types and (B) as a density-dependent function of population size (N_t). In panel (A), values are back-converted from ln values, making the error bars asymmetric. Shown are means ± SE. The λ value for dry sites in 2010–2011 was deliberately omitted from the chart because it came from just three sites, and each had only one caterpillar/site in 2010 (Table 1), creating very large confidence intervals for the λ value; mean λ for 2010–2011 in dry sites was 7.11 (95% confidence interval 1.02–49.6). In panel (B) the linear regression line is illustrative only: the actual equation is $\ln(\lambda) = 0.63 - 0.275(\ln N_t)$ with a standard error of the slope of 0.108 (Student's $t = 2.55$, $P = 0.01$) from a linear mixed-effects model fitted in R using lmer with year as a random repeated-measures variable to account for temporal autocorrelation.

Caterpillar and lupine abundance in wet habitat

Abundance of lupine varied considerably among transects and especially among years although we found little relationship between lupine abundance and caterpillar numbers in transects through wet habitat. Lupine cover explained little of the variation (Fig. 5A; $F_{1,59}$ = 1.85, $P = 0.18$), although considerable variation was explained by annual differences caused by other factors (year: $F_{14,59}$ = 11.34, $P = 0.0001$). When estimates of caterpillar numbers for each transect were detrended for yearly fluctuations, lupine was still a poor predictor of caterpillars (Fig. 5B; $F_{1,73}$ = 1.06, $P = 0.31$). If only data from 2007 to 2009 were considered (similar to analyses in the upland habitat), lupine cover again failed to explain variation in caterpillar numbers ($F_{1,11}$ = 0.31, $P = 0.59$).

If the combined cover for all of the preferred hosts for caterpillars in each transect through wet habitat was included in the model, we still failed to explain significant variation in caterpillar numbers ($F_{1,59}$ = 0.04, $P = 0.85$). Considering individual host species, in
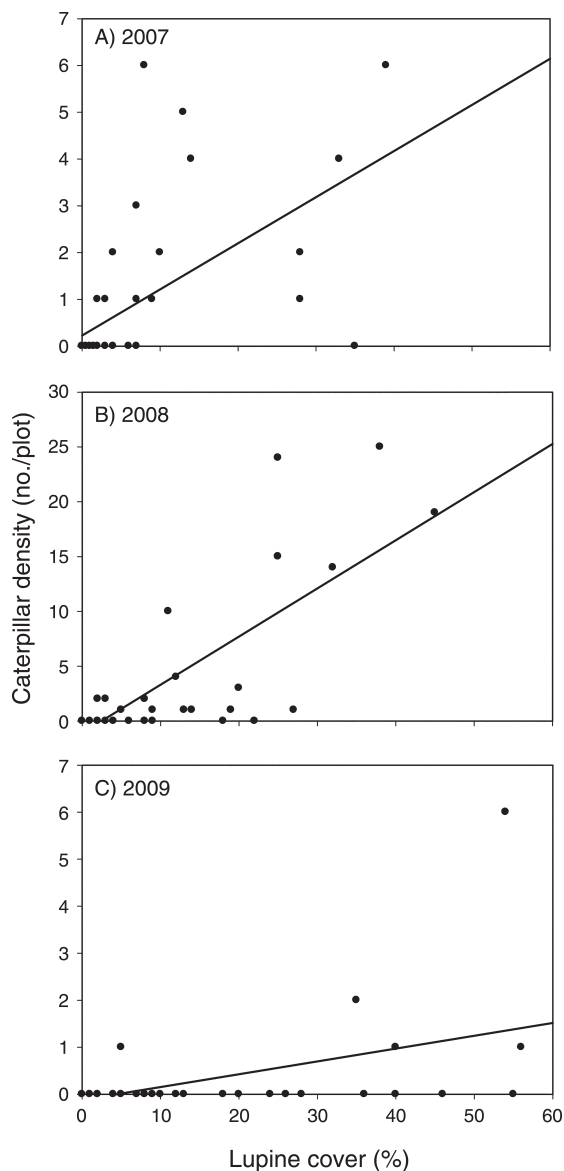
FIG. 4. The relationship between the number of *P. virginalis* caterpillars per plot and lupine cover (percentage of total area) for upland plots in 2007–2009. Lines represent best-fit regressions.

addition to *L. arboreus*, separately also provided no better predictors (data not shown).

Movement of caterpillars from wet to dry habitats

Caterpillars only started to cross the road as late instars (penultimate and ultimate instars accounted for 73 of 76 individuals). Most caterpillars (59/76 individuals) moved from the wet habitat to the dry habitat. Movement did not occur randomly but was strongly biased along the moisture gradient toward dry habitat (binomial exact test $P < 0.01$).

Marked caterpillars that were released at ecotones between wet and dry habitat patches were more likely to

move toward dry habitat (16/20 cohorts moved toward dry, binomial exact test $P = 0.012$).

Marked caterpillars were more likely to leave a bush that they were released on if that bush supported more conspecific caterpillars (likelihood ratio test $\chi^2 = 4.41$, df $= 1$, $P = 0.036$). Overall, the probability of leaving a bush was 46% if the bush had three caterpillars, 38% if the bush had six caterpillars, and 60% if the bush had nine caterpillars.

DISCUSSION

On average, wet areas acted as sources and dry habitat acted as sinks for this species. Populations in wet sites sometimes increased ($\lambda > 1$) and sometimes decreased slightly (λ slightly < 1) from year to year, but with mean $\lambda > 1$ (Fig. 3A). Dry sites acted as sinks with $\lambda < 1$ in most years and populations went extinct at all eight dry sites during the course of the study (Fig. 3A, Table 1). We cannot rule out the possibility that some dry sites were pseudosinks (sites with $\lambda < 1$ because of density-dependent immigration; Watkinson and Sutherland 1995, Boughton 1999) because we did not manipulate movement and were unable to precisely measure movement rate. Population growth was nega-
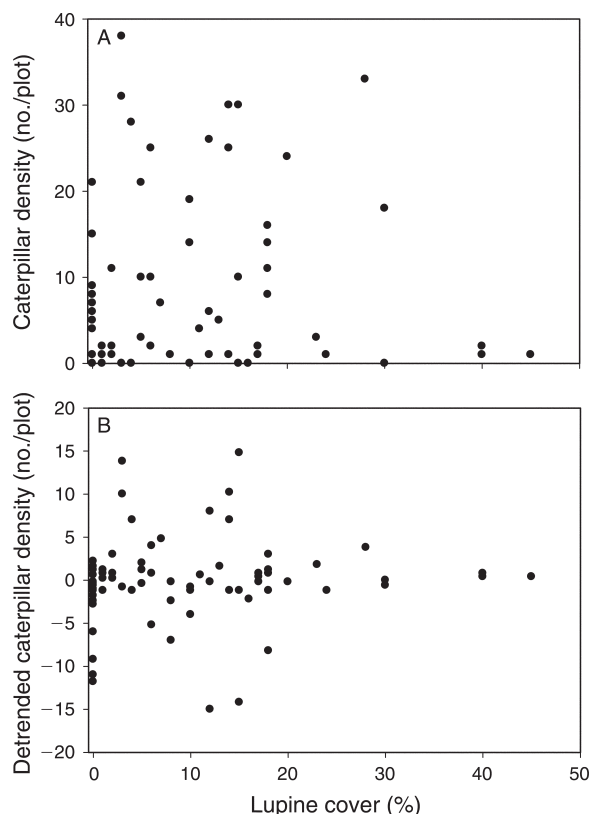

FIG. 5. The relationship between the number of *P. virginalis* caterpillars and lupine cover (percentage of total area) for wet plots in 1997–2011. (A) Number of caterpillars per plot. (B) Number of caterpillars per plot detrended by the average annual density for each year.

PLATE 1. A late-instar *Platyprepia virginalis* caterpillar feeds on a leaf of *Lupinus arboreus*. Early-instar caterpillars at our study site overwinter in the litter beneath this host plant and crawl up into the canopy to feed as they mature. Photo credit: R. Karban.

tively density dependent overall in both habitats, with λ becoming more negative as population size increased (Fig. 3B). While there are many possible explanations, density-dependent emigration may be responsible for the overall density dependence observed in λ values. The three studies of movement all suggest that late-instar caterpillars move away from bushes in wet habitats that have high densities of conspecifics. Emigration from wet habitats to dry habitats is likely to allow caterpillars to repopulate dry sites that fail to support early-instar caterpillars in many years. Wet sites may be more favorable for caterpillars because of reduced desiccation, more varied food, and/or reduced risk of predation (Karban et al. 2010; R. Karban, P. Grof-Tisza, and M. Holyoak, *unpublished data*).

The relationship between *P. virginalis* caterpillar abundance and lupine abundance varied across the landscape. In upland habitats, including both grasslands and dunes, more caterpillars were found in plots with more lupine cover (Fig. 4). These results were stronger and explained more of the variation (55% in 2007, 76% in 2008, 28% in 2009) than most statistical models from ecological studies, which generally explain <7% of the variance (Moller and Jennions 2002). However, in wet

habitats, we detected no relationship between lupine cover and caterpillar abundance (Fig. 5). These results suggest that lupine may possibly limit caterpillar numbers in less favorable upland habitats but not in wet ones.

There are also other possible explanations for these patterns that should be considered. We conducted different experiments in the two habitats, for different periods of time, at different spatial scales. However, the differences in results appear to be robust to these considerations. First, we consistently observed a relationship between lupine and caterpillars in upland sites in all three years. We failed to observe the relationship in any of those three years in the wet habitat or over other time frames from 1997 to 2011. Whenever experiments produce negative results, as we found relating lupine cover with caterpillar abundance in wet habitats, it is important to determine whether those negative results were likely caused by a lack of statistical power or an actual absence of a relationship (Cohen 1988). Because the model effects were so large in the upland sites, we can be quite confident that we were not overlooking effects of this magnitude in the wet habitat ($R^2 = 0.55$ in 2007, 0.76 in 2008, 0.28 in 2009 in the upland, $\alpha = 0.05$, $n = 59$ once degrees of freedom for years are removed,

power > 0.99 in all three years to detect effects of this magnitude in wet sites). The small effect sizes in the wet site ($R^2 = 0.02$ and $R^2 = 0.01$ in Fig. 5A, B) also suggest that lack of statistical power was not the primary cause of the negative results relating lupine abundance and caterpillars in the wet habitat.

The relationship between caterpillars and their primary host plant varied over the landscape with a positive association in upland areas but no such relationship in wet locations. Other population characteristics also varied over this spatial scale. Abundances of caterpillars were on average about twice as great in wet areas compared to dry ones and they were far less variable (Fig. 2). Since 1985 we have observed some caterpillars every spring in wet sites (Karban and de Valpine 2010), but they become locally extinct at dry sites in years of low regional abundance. Although we recorded the number of caterpillars on only 10 bushes per site, we failed to find any caterpillars on any bushes over several (3–4) census dates at our dry sites and feel confident that they were locally extinct in some years. However, as in other metapopulation studies, using negative census data to conclude that a species has gone extinct always lacks certainty.

This system appears to be characterized by source–sink dynamics where wet habitats are sources for early-instar caterpillars that move to dry, upland sites as late instars and adults, while dry sites later occasionally exhibit local population extinctions. We found that late-instar caterpillars were more likely to move from wet habitats to dry ones than the reverse in several sets of observations and experiments. The bias for the caterpillars crossing the road may have been driven by greater numbers of early-instar caterpillars originating in wet habitats because we also found that caterpillar movement was density dependent; however, it is the net flux of individuals between sources and sinks that matters for supporting sink populations (Diffendorfer 1998). Nonetheless it is interesting to also consider whether movement was biased between habitat types. For caterpillars that were marked and released at ecotones between wet and dry habitat, the bias in movement that we observed was probably not caused by differences in the size or density of the source populations but probably reflected a habitat preference of late-instar caterpillars. Habitat-specific movement, coupled with differences in λ and local extinctions suggest that population dynamics in wet sites influence those in dry sites. Individuals recolonizing dry sites likely come from adjacent wet habitats because very few caterpillars were found except in wet sites. Moths, not caterpillars, may recolonize locally extinct sites although they probably originate from wet sites. As this example illustrates, the consequences of adult movement by these moths may be important, and spatial dynamics in species with multi-stage life histories deserve more investigation in general.

We found that finite growth rates varied across years, both in wet and dry sites (Fig. 3A). This kind of variation

is typical of other source and sink studies (e.g., Dias 1996, Boughton 1999, Johnson 2004). While part of this variation is likely due to measurement error, especially when abundances become low, it also represents a mismatch between an equilibrium concept (source–sink models as originally described by Pulliam 1988) and dynamics in response to abiotic and biotic conditions in nature. Some source–sink models have included ideas about variation in population size. Indeed, our finding that temporal population variability was substantially lower in wet habitats than in dry upland habitats (Fig. 2) is consistent with predictions from source–sink models (Howe et al. 1991). There are few published tests of this prediction that sources will be less variable than sinks. Another prediction is that emigration from a source population could obscure the relationship between resources and consumer population levels in a source–sink model. For instance, Pulliam (1988:659) warned that "autecological studies of populations in sink habitats may yield little information on the factors regulating population size if population size is determined largely by the size and proximity of sources." The converse should also be true: emigration of all individuals above the carrying capacity from a source population can produce a relatively invariant source population. Such a source population would then show no relationship to resource fluctuations if carrying capacity is determined by something other than resources. For example, planthopper herbivores dispersed more from patches with high spider predator densities such that planthopper population levels showed no relationship with resource quality or quantity (Cronin et al. 2004).

These results suggest that different factors may be controlling populations in the different types of habitat patches and that source–sink dynamics are involved. In dry, upland sites populations may be limited by the availability of lupine hosts but lupine does not limit populations in more favorable wet sites. It is not clear at this point what does limit populations at favorable wet sites although we can also exclude tachinid parasitoids despite high rates of parasitism (Karban and de Valpine 2010), diseases including entomophagous nematodes (Karban et al. 2011), and vertebrate predators (R. Karban, P. Grof-Tisza, and M. Holyoak, *unpublished data*). We have preliminary evidence that predation by ants and resource quality may be involved although a complete understanding of the relative importance of various factors over development in different habitats is still lacking.

Other studies have considered trophic interactions in spatially extended systems that include multiple habitats (Rosenheim 2001, France and Duffy 2006, Howeth and Leibold 2008). They differ from our study in that the form of spatial dynamics in other systems was frequently unknown and local extinctions were not seen to occur. In contrast, in our system, we probably observed source–sink dynamics with populations from dry sink habitats going locally extinct and consistent directional movement among habitats with caterpillars moving

from wet habitats (sources) to dry habitats (sinks). Most previous work on spatially extended systems has involved trophic cascades. For example, fish predators varied in different habitat types and this factor controlled the ability of herbivores to move and colonize patches, ultimately affecting plant biomass (Howeth and Leibold 2008). Under conditions where herbivores could move freely, movement had a strong effect on plant–herbivore coupling (Howeth and Leibold 2008). Consistent with this, we observed movement from wet to dry habitats and saw a strong plant–herbivore coupling in the dry sites. In seagrass ecosystems, increased mobility of herbivore grazers reduced the effect that those grazers had on plant biomass (France and Duffy 2006). Habitat selection by mobile grazers prevented them from overexploiting their food plants. It is less clear in our study whether density-dependent emigration from wet habitats averted strong effects of consumers on their resources. Movement has been found in other terrestrial plant–insect systems to play a critical role. For example, the ability of lacewing predators and aphid prey to move freely affected the strength of predation and the herbivore–plant relationship (Rosenheim 2001).

In conclusion, the evidence argues that populations of *P. virginalis* are affected by different factors at different kinds of habitat patches. Differences among habitats are consistent with source–sink dynamics, which could possibly explain reduced coupling in wet (source) sites. Recognizing that there is no single factor that controls herbivore populations in all places is certainly more complicated and less elegant than more universal simple hypotheses (e.g., Hairston et al. 1960); paradoxically a realization of the complexity may allow ecologists to work toward an explanation that will apply more generally. A broader consideration of the role of movement may provide an important context-dependent factor that could help explain the variation in plant–herbivore relationships that continue to puzzle and fascinate ecologists.

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