

HOST PLANT PHENOLOGY AND BUTTERFLY DISPERSAL: CAUSES AND CONSEQUENCES OF UPHILL MOVEMENT

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Abstract. In the Wenatchee Mountains of central Washington State, populations of the lycaenid butterfly *Euphilotes enoptes* occur patchily with their sole host plant, *Eriogonum compositum* (Polygonaceae). Nearly all courtship and adult feeding occur on the inflorescences of this long-lived perennial. Furthermore, because females oviposit on inflorescences and larvae feed only on flowers and developing seeds, the window of opportunity for exploiting this resource is narrow. I demonstrated that inflorescence phenology varied according to the aspect and elevation of plant patches, and butterflies were most likely to occur in patches nearing full bloom. A mark–release–recapture study revealed that individual butterflies can disperse far enough to sample from a wide range of patch phenologies, and the movements of females are apparently influenced by those phenologies. In particular, an uphill bias in female movement appeared to be the result of greater emigration from senescing low-elevation patches than from phenologically delayed, high-elevation patches. Males showed no such uphill movement. The apparent result of the uphill movement by females was that larval densities increased fourfold over a 300-m elevational gradient in each of two years. Differential mortality is an unlikely explanation for this variation in larval density, as both parasitism rates and frequency of visitation by ants, which tend larvae, did not vary with elevation.

To demonstrate the influence of host plant phenology on adult behavior, I manipulated flowering phenology in an artificially established grid of small host plant patches and observed the encounters of adult butterflies with those patches. Inflorescences in patches that were nearing full bloom received disproportionately many visits by females, indicating that patches in this phenological state were more attractive to females. Small sample sizes prevented me from determining if this result was due to increased entry into those patches by females, an increased number of inflorescence visitations per female, or both. The frequency with which inflorescences in the different patches were visited by males did not vary with patch phenology. These results suggest that the uphill bias in dispersal by females is indeed a response to host plant phenology. Thus, in this system, among-patch variation in host plant phenology apparently influences the relative densities of larvae in different host plant patches by altering patterns of dispersal among those patches.

Key words: dispersal; *Eriogonum compositum*; *Euphilotes enoptes*; flowering phenology; Lycaenidae; population density; topography.

INTRODUCTION

Herbivorous insects often face substantial phenological variation both within and among patches of their host plants (e.g., Breedlove and Ehrlich 1968, Weiss et al. 1988, Jordano et al. 1990, Floate et al. 1993, Rodríguez et al. 1994, Mopper and Simberloff 1995, Peterson 1995a). For insects that specialize on ephemeral plant parts, this phenological variation increases the chance of phenological mismatches with host plants, and such mismatches may bring dire consequences to these insects (e.g., Varley and Gradwell 1968, Thompson and Price 1977, Raupp and Denno 1983, Dobkin et al. 1987, Meyer and Montgomery 1987, Hunter 1992, Quiring 1993, but see Crawley and

Akhteruzzaman 1988, Watt and McFarlane 1991, Hunter 1993). As a result of heightened plant defenses (e.g., Feeny 1970, 1976, Mooney et al. 1980), early leaf abscission and other factors which accompany host plant senescence (e.g., Singer 1972, Faeth et al. 1981, Cappuccino and Kareiva 1985, Connor et al. 1994), phytophagous insects may suffer increased mortality or reduced fecundity if the timing of their development does not match that of their host plant.

Given the importance of assuring a proper phenological match with host plants, it is not surprising that a number of herbivorous insects can discriminate among phenologically varying plants within a patch (Breedlove and Ehrlich 1968, Ramachandran 1987, Floate et al. 1993, Mopper and Simberloff 1995), and that this behavior influences the relative densities of herbivores on different plants in a patch (Breedlove and Ehrlich 1968, Floate et al. 1993, Mopper and Simberloff 1995). However, to date it has not been demonstrated that the same

Manuscript received 29 January 1996; revised 22 April 1996; accepted 23 April 1996; final version received 6 May 1996.

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process can influence among-patch variation in herbivore densities. To test the hypothesis that patch-to-patch variation in host plant phenology can influence the densities of herbivorous insects occupying those patches, I determined: (1) whether among-patch dispersal by the flower- and seed-feeding butterfly *Euphilotes enoptes* (Boisduval) (Lepidoptera: Lycaenidae) is influenced by the flowering phenology of its host plant, *Eriogonum compositum* Dougl. (Polygonaceae), and (2) whether among-patch variation in larval densities along a phenological gradient can be explained by phenologically biased dispersal.

Euphilotes enoptes is an ideal organism with which to address this question because of its intimate association with host plant inflorescences. In central Washington State, the widespread *E. enoptes columbiana* (Mattoni) feeds only on *E. compositum* (Peterson 1995a). Like all members of the genus, adult *E. enoptes* feed, court, and mate almost exclusively on the host inflorescences (Langston and Comstock 1966, Shields 1975), and females lay single eggs only on buds and newly opened flowers (Shields 1975, Pratt 1988). Torpid males and females commonly use host inflorescences as overnight roosting sites (M. A. Peterson, *personal observations*). There is no evidence that females avoid laying eggs on inflorescences that already harbor other eggs; I have seen over 20 *E. enoptes* eggs on a single inflorescence (M. A. Peterson, *personal observations*), and multiple larvae often share an inflorescence (Peterson 1995b). The use of host plant inflorescences varies among the sexes of this species (M. A. Peterson, *personal observations*). Females are encountered nearly always on host plant inflorescences, where they intersperse bouts of feeding and oviposition. Males typically fly among inflorescences in search of potential mates, and settle on inflorescences only long enough to drink nectar. Males also visit mud outside of host plant patches. This species does not use "hilltopping" behavior (*sensu* Shields 1967) to locate mates; all matings occur within host plant patches (M. A. Peterson, *personal observations*). In fact, adult *E. enoptes* are fairly sedentary; they typically disperse <500 m, and only 20% of adults have been found to move among the host plant patches within a small area (2.3 ha) of habitat (Arnold 1983a,b). These observations of limited dispersal are supported by the fact that genetic neighborhoods in this species are small (<40 individuals) (Peterson, *in press*). Thus, in this paper, I use the term population to indicate all of the individuals occupying a patch of *E. compositum*.

Early-instar larvae of *E. enoptes* feed on pollen, and begin feeding on developing seeds as those become available (Pratt 1994). The duration of the larval period is typically ≈ 3 wk (Pratt 1988). Because the period from the beginning of flowering to the setting of seeds takes ≈ 6 wk for patches of most *Eriogonum* species (including *E. compositum*, M. A. Peterson, *personal observations*), there is roughly a 3-wk window of op-

portunity in which females can exploit a given host plant patch (Pratt 1994). This window of opportunity would be even narrower if not for within-patch variation in flowering phenology both among plants and among inflorescences within a plant (M. A. Peterson, *unpublished data*). *E. enoptes* adults are most frequently encountered in host plant patches that are nearing full bloom (Langston 1963, Langston and Comstock 1966, Shields 1975), but it remains unclear whether dispersal plays a role in this correspondence, because the timing of adult emergence is correlated with the flowering phenology of the *Eriogonum* host of a given population (Pratt and Ballmer 1993). However, since emergence within a population can occur over a period exceeding one month (Pratt and Ballmer 1993, Peterson 1995a), it seems likely that movement into phenologically suitable patches also plays a role in establishing a close match between adult presence and host plant phenology.

I used a combination of experimental and observational approaches to establish that variation in the densities of *E. enoptes* occupying different host plant patches is due in part to an ability to discriminate among host plant patches based on their phenology. To do this, I documented the extent of naturally occurring phenological variation within an archipelago of host plant patches occupied by *E. enoptes*, and performed a mark-release-recapture study to assess whether patterns of dispersal among those patches reflect variation in flowering phenology. Second, I examined larval densities along a phenological gradient to determine if variation in those densities could be explained by phenologically biased dispersal. To explore the possibility that variation among patches in larval density was due to differential mortality, I examined variation in parasitism and ant attendance along phenological gradients. Finally, to verify experimentally that adults discriminate among host plant patches that differ in phenology, I manipulated flowering phenology in an artificially created grid of host plant patches and observed adult behaviors in those patches.

METHODS

Patterns of host plant phenology and butterfly dispersal

Variation in patch phenology and the timing of patch occupancy.—To determine if the occurrence of adults in host plant patches is synchronous with patch phenology, I documented variation in host plant phenology in a montane archipelago of host plant patches and assessed the range of inflorescence phenologies in patches occupied by adult butterflies. The study site was an archipelago of 25 patches of *E. compositum* occurring within a 5 km² area near Tarpiscan Creek, in the Wenatchee Mountains (Kittitas County, Washington). This site straddles two ridges, and contains patches along gradients of both elevation and aspect (Fig.

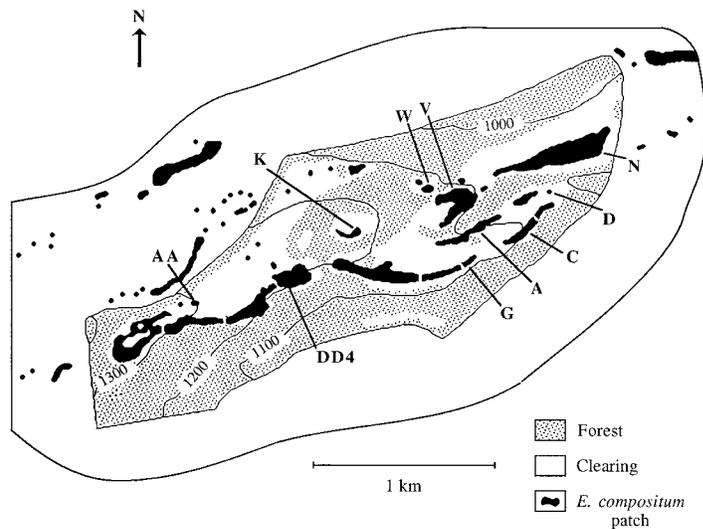


FIG. 1. The Tarpiscan Creek study site and surrounding area, showing the locations of all patches of *E. compositum*. The flowering phenology of all patches within the site was monitored in 1992. Labeled patches are the 10 focal patches for the 1991 mark–release–recapture study. Contour lines show elevation in meters.

1). To monitor flowering phenology, I visited the archipelago on five occasions: 14–15 May, 29–30 May, 6 June, 19 June, and 26–28 June 1992. During all but the first of these visits, I determined the flowering phenology of each of the 25 patches in the archipelago; on the first visit, I examined only 17 patches. In large patches (>100 inflorescences), I haphazardly selected 100 inflorescences and assigned each to one of four phenological categories (in order of development): red bud, yellow bud, in bloom, and past bloom. An inflorescence was designated “red bud” if at least half of the flower buds in the inflorescence had either a red or green hue. More than half of the flower buds on “yellow bud” inflorescences had a yellow hue, but none were yet open. Inflorescences with at least one open flower were classified as “in bloom,” and inflorescences which no longer had any open flowers were called “past bloom.” Typically, females oviposit on inflorescences that are at either the “yellow bud” or “in bloom” stage of development, and feeding by both sexes is restricted to “in bloom” inflorescences (Langston and Comstock 1966, Shields 1975, Pratt 1994; M. A. Peterson, *personal observations*). In patches with <100 inflorescences, I classified all inflorescences. In all patches, I noted the presence of any adult *E. enoptes* I encountered to determine the relationship between patch phenology and adult presence or absence.

From the flowering phenology data, I determined a “phenology score” for each patch on each of the five dates. This score was based on the percentage of inflorescences in each phenological category as follows: one point for each percentage of inflorescences in “red bud,” two points for those in “yellow bud,” three points for those “in bloom,” and four points for “past bloom” inflorescences. Thus, the patch score could range from 100 (all inflorescences in the “red bud” stage) to 400 (all inflorescences “past bloom”). I performed repeated-measures analysis of variance (SAS

1990) to determine the effects of elevation, aspect, date, and their interactions on patch phenology score, using the Greenhouse–Geisser adjustment for significance levels. For this analysis, I scaled the phenology scores to range from zero to one, and subjected them to angular transformation (Sokal and Rohlf 1981). Because I did not sample seven patches on the first date, I performed this analysis without data from those patches. In addition, I reran the analysis excluding the first date to allow the inclusion of data from all 25 patches.

Patch phenology and butterfly dispersal.—To determine the degree to which host plant patch phenology influences patterns of dispersal by *E. enoptes* at Tarpiscan Creek, I compared the above observations of phenological variation among patches with the results of a mark–release–recapture study in 1991. In this study, I had focused on 10 of the 25 patches at the site (Fig. 1) so that I could maximize my effort in each patch. The 10 focal patches were scattered throughout the study site, and were representative of high- and low-elevation patches with both north- and south-facing aspects, such that the entire spectrum of patch phenologies was included. At the beginning of this study (8 June), host plant patches at low elevations were approaching full bloom and inflorescences in higher elevation patches were not yet in bloom. By the end of the study (28 June), most of the inflorescences at low elevations were past bloom, and those at higher elevations were at full bloom. On 9 d during this period (8–10, 12–16, 28 June), I netted as many butterflies as possible, noted their location (patch and approximate location in a patch) and sex, marked each with a unique mark, and released them immediately at their points of capture. If the butterflies were already marked, I noted their location and identity, and released them immediately. The length of marking efforts in each patch was roughly proportional to the size of the patch so

that effort per unit area was approximately equal across all patches. To mark butterflies, I used a fine-point permanent marker, placing small dots on the ventral surfaces of all wings in a code modified from Ehrlich and Davidson (1960). Using this scheme, I marked as many as 151 butterflies with a single color of pen. Butterflies were handled as briefly and carefully as possible to avoid injury. On the first marking day and part of the 2nd d, I anaesthetized butterflies in the net with CO₂ to minimize struggling (after Mattoni and Seiger 1963). This technique proved to be time consuming and I found that removing butterflies from the net in a plastic tube was just as effective in reducing their struggles. Once their wings were grasped in forceps, butterflies exerted themselves only minimally.

Because the north-facing slopes (AA, A, K, W) were not sufficiently phenologically advanced to support adult butterflies at the onset of this study (based on observations in 1989 and 1990), I visited only the six south-facing patches (patches C, D, G, N, V, and DD4, spanning a broad elevational range) on all marking days. I visited the four north-facing patches every few days to determine if flowering phenology had progressed sufficiently to warrant daily visits. These occasional visits confirmed that the north-facing patches remained unsuitable for adult butterflies until at least 16 June, at which point I began marking adult *E. enoptes* in those patches. By reducing my efforts in north-facing patches that could not yet support adult butterflies, I was able to increase the number of individuals marked and recaptured in south-facing patches. As part of ongoing studies on the population biology of *E. enoptes*, I also made infrequent visits to other patches in the site, during which I looked for marked butterflies.

From the mark–release–recapture data, I calculated proportion recaptured, the distance travelled per individual (straight-line distance between release point and maximum observed displacement from that point, obtained from a topographic map), and the proportion of individuals moving to a new patch (number of recaptured butterflies found in patch other than original patch/number of individuals recaptured anywhere). To compare overall recapture rates for females and males, I used a *G* test of independence (Sokal and Rohlf 1981). In addition, for each sex, I determined if recapture rates varied with elevation by regressing the angular-transformed proportion of butterflies recaptured at least once against the elevation of the patch in which they were originally captured. I restricted this analysis to populations in which at least eight individuals of a sex had been marked. I also used *G* tests to compare the proportion of recaptured males and females that had moved to a new patch, and the frequency with which males and females had moved uphill. To test the hypothesis that emigration rates were greater from the declining low-elevation patches than from the improving high-elevation patches, I regressed the angular-transformed proportion of recaptured butterflies emi-

grating from a patch against patch elevation (Sokal and Rohlf 1981). The small number of butterflies recaptured in some patches required that I pool data from the sexes for this analysis. A significant negative slope would indicate that butterflies left the declining low-elevation patches more readily than the improving high-elevation patches.

Patch phenology and larval density.—To determine if within-patch densities of *E. enoptes* larvae at Tarpiscan Creek were correlated with phenological variation among those patches, I analyzed data on the relationship between larval densities (number per inflorescence) and elevation for the nine south-facing patches at this site in both 1990 and 1991. The number of larvae per inflorescence is the appropriate measure of density for this species because inflorescences, rather than individual plants, are the resource around which adult behavior and larval feeding revolve. To assess larval density in the six largest patches in 1990, I determined the number of larvae on all inflorescences in each of seven randomly located 100-m² quadrats. In the three smallest patches, I walked through the patch, haphazardly selected roughly one-third to one-fourth of the inflorescences, and examined these for larvae. In 1990, the number of inflorescences sampled in the patches ranged from 30 to 426 (mean = 139.2). In 1991, I haphazardly sampled inflorescences while walking a transect through each patch (range 20–150 inflorescences per patch, mean = 97.0). Typically, larval densities were assessed when most larvae were in the third instar (penultimate instar), to ensure that differences could be attributed to actual differences in density, rather than sampling of different developmental stages. I performed linear regression to determine the relationship between larval density (number per inflorescence) and elevation in both years. If butterflies move uphill through the flight period and tend to lay more eggs at high elevations as a result of this movement, one would predict an increase in larval density with elevation.

To be sure that any elevational differences in larval density were not due to the responses of adults to variation in the density of inflorescences in different patches, I also determined the relationship between inflorescence density (number per square meter) and elevation for both 1990 and 1991. To establish this relationship in 1990, I determined the number of inflorescences in seven randomly located 100-m² quadrats in each of six south-facing patches. In 1991, I assessed inflorescence density in 25 randomly located 25-m² quadrats in each of eight south-facing patches. To determine the relationship between elevation and inflorescence density (number per square meter, averaged across all plots within a patch) in both years, I performed linear regression.

Because elevational patterns in larval density could also be attributed to elevational patterns in mortality, I examined the relationship between elevation and both larval parasitism and ant attendance. Although the ben-

efits of ant attendance to larval *E. enoptes* are not known, other lepidopteran larvae are known to enjoy protection from natural enemies as a result of their association with ants (Atsatt 1981, Pierce and Eastal 1986, Pierce et al. 1987, DeVries 1991). During three field seasons (1990–1992), I assessed the proportion of larvae tended by ants in each of the *E. compositum* patches at Tarpiscan Creek (methods described in detail in Peterson 1995b). Because the proportion of larvae tended by ants varies with larval instar (Peterson 1995b), I used only the data for fourth-instar larvae to determine the relationship between ant attendance and elevation. In some patches, I observed few or no fourth-instar larvae, so I only included data from patches in which I encountered at least 14 fourth-instar larvae (1990: $n = 3$ patches, mean = 24.3 larvae/patch; 1991: $n = 7$ patches, mean = 43.7 larvae/patch; 1992: $n = 12$ patches, mean = 30.8 larvae/patch). I performed linear regression of the angular-transformed proportion of larvae tended by ants against patch elevation (I did not perform this analysis for the 1990 data because I had data for only three patches) (Sokal and Rohlf 1981).

I have never witnessed a predator attack an *E. enoptes* larva, but I have documented that larvae are attacked by a suite of parasitoids in central Washington State (including *Apanteles* sp. (Braconidae), *Tetrastichus* sp. (Eulophidae), *Anisobus coloradensis* (Ichneumonidae), and an unidentified tachinid fly) (Peterson 1994). To determine if parasitism rates vary with elevation, I collected larvae in 1989 from eight populations in central Washington at sites ranging from 450 m elevation to 1288 m elevation. Five of these populations were located in the Entiat Mountains, ≈ 30 km north-northwest of the Tarpiscan Creek site. The remaining three populations were in the Wenatchee Mountains. I reared larvae (see Peterson 1995a for description of rearing procedure) to either the eclosion of adults or the emergence of parasitoids (parasitoids emerge from either last instar larvae or pupae). From these data, I calculated parasitism rates (the proportion of individuals parasitized) for each population in which I had data for at least 14 larvae. Larvae or pupae that died of unknown causes were not included in the calculation of parasitism rates. The relationship between angular-transformed parasitism rates and elevation was determined using linear regression (Sokal and Rohlf 1981).

Flowering phenology and local butterfly movement

To test the hypothesis that differences in flowering phenology influence the attractiveness of patches of *Eriogonum compositum* to adult *E. enoptes*, I manipulated the phenology of host plant patches and observed the encounters of individual butterflies with those patches. For this experiment, I selected a large, dense stand of *E. compositum* on a hillside near Red Top Mountain, Kittitas County, Washington, and di-

vided a section of this stand into an array of 15 10×10 m square patches, with 5 m between adjacent patches. The scale of this experiment was selected to allow butterflies to choose from patches based solely on their phenology and not on their accessibility. The small distances among patches were necessary to achieve this purpose. Furthermore, the size of plots is representative of many small patches of *E. compositum* found in nature (M. A. Peterson, unpublished data), in addition to being a size which enabled me to observe the activities of all butterflies entering a patch.

I removed all host plant inflorescences from areas between patches, as well as within a 5 m buffer zone around the edges of the outermost patches. I divided the 15 patches into five blocks, with one block at the highest elevation and two each at the middle and low elevations on the hillside. The reason for this stratified design was that the inflorescence phenology was more advanced at the bottom of the hill than at the hilltop. Within a block, I randomly assigned each patch to one of three phenological categories: “delayed,” “normal,” and “advanced.” In four of the “delayed” patches, I removed all inflorescences except the 25 inflorescences that were least advanced in development. In the fifth “delayed” patch there were only 14 inflorescences to start with, all of which were delayed in development. Consequently, I removed none of these inflorescences. In all five “advanced” patches, I removed all but the 25 most phenologically advanced inflorescences. In four of the “normal” patches, I haphazardly selected 25 inflorescences to save and removed all others, producing a patch with a flowering phenology that was representative of the phenology of the entire stand. The fifth “normal” patch had only 20 inflorescences, so I removed none. In nearly all patches after the establishment of treatments, no more than two inflorescences were intact on a single plant, and in all patches, these intact inflorescences were scattered among many plants.

I performed all removals on 31 May and 1 June 1992, shortly after the beginning of the adult flight period at this site. To assess the effectiveness of the different treatments, I assigned each inflorescence in each plot to one of the four phenological categories (red bud, yellow bud, in bloom, past bloom) on both 4 and 18 June. In setting up the array of host plant patches, I discovered that host plant density varied among blocks. In blocks with high densities, selective removals of all but 25 inflorescences in each plot created dramatic differences among the three treatments, whereas in blocks covering low-density areas, I could not produce such dramatic differences. Nonetheless, the selective removal of inflorescences did produce the desired result when all plots within each treatment were combined; inflorescences in “advanced” plots were indeed the most advanced phenologically, and those in “delayed” plots were the least advanced ($G = 46.5$, $df = 4$, $P < 0.001$, Fig. 2A). At the onset of this experiment, inflo-

rescences in the "advanced" plots were typically in bloom or nearly so, whereas most inflorescences in "delayed" plots were not very close to blooming (Fig. 2A). By 18 June, the phenological difference among the treatments had disappeared, because nearly all inflorescences in all treatments were in bloom ($G = 5.0$, $df = 4$, $P > 0.15$, Fig. 2B).

I returned to the site on four occasions through the flight period: 3–4 June, 10–11 June, 17–18 June, and 23 June to monitor butterfly activity. On each of these days, I observed butterflies in each patch for 20 min, with observations typically beginning between 1020 and 1220 PDT, and ending between 1640 and 1800 PDT. All observations were made on clear, warm (20°–27°C) days, when winds were calm. The order in which I observed both blocks and patches within blocks was determined randomly each day to avoid biases from changes in adult behavior with time of day. During the 20-min observation periods, I noted the number of individuals of each sex landing in a patch (sexes are easily distinguished in flight because males are bright blue dorsally, whereas females are brown) and the total number of times each of those individuals alighted on inflorescences of *E. compositum*. Small patch size and high visibility of butterflies enabled me to observe all butterflies entering and leaving a patch.

To determine whether butterfly responses to the three treatments varied through the season, I conducted G tests of independence (Sokal and Rohlf 1981) on the counts combined across all five patches of each phenology treatment over each 2-d period (200 min of observation per patch type per period). Small sample sizes for each sex required combining data across all patches of a given type, thus necessitating contingency analyses. A significant pattern of statistical nonindependence would indicate that patch attractiveness (either in terms of number of individuals entering and landing in patches, or number of times individuals alighted on inflorescences in patches) did not vary equally with date for the three treatments. If butterflies prefer either patches or individual plants near full bloom, we would expect a decline in the relative attractiveness of "advanced" patches and an increase in the relative attractiveness of "delayed" patches.

RESULTS

Patterns of host plant phenology and butterfly dispersal

Variation in patch phenology and the timing of patch occupancy.—Observations at Tarpiscan Creek showed that throughout the flight period of *E. noptes* (through 19 June 1992), *Eriogonum compositum* flowering phenology varied over short distances due to the combined effects of elevation and aspect (Fig. 3). By 26–28 June, all patches were past bloom and adult *E. noptes* were not present, so I did not analyze phenological variation for this date. On all of the remaining dates, patches

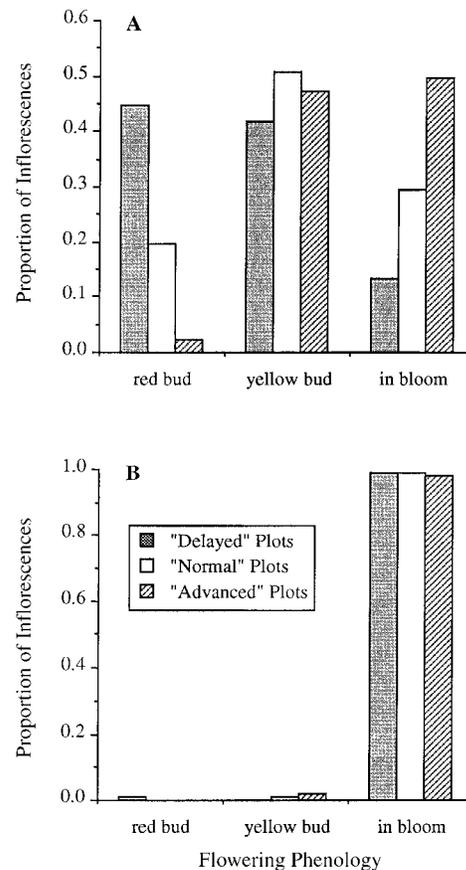


FIG. 2. The flowering phenology of inflorescences in the field experiment during (A) the first observation period, 4 June 1992, and (B) the last observation period, 18 June 1992. Inflorescences were combined across all plots ($n = 5$) of a given treatment. The proportions of inflorescences in the different stages of development varied across treatment type on 4 June ($G = 46.5$, $df = 4$, $P < 0.001$), but not on 18 June ($G = 5.0$, $df = 4$, $P > 0.15$).

were less phenologically advanced at higher elevations and in north-facing patches (Table 1). Both the non-significant interaction between elevation and aspect and the nonsignificant three-way interaction were removed from this analysis to determine the significance of the main effects and other interactions. With two exceptions, the results from the analysis including the data from 14–15 May were equivalent to those obtained when the 14–15 May data were excluded (allowing inclusion of data from all 25 patches). In the latter analysis, the date by elevation interaction had a highly significant effect ($F_{2,44} = 6.51$, $P < 0.005$), and the date by aspect interaction had a significant effect ($F_{2,44} = 5.86$, $P < 0.01$).

Butterfly presence tracked flowering phenology (Fig. 3) as the season progressed. On 14–15 May, adult *E. noptes* were only found in three south-facing, phenologically advanced patches. Two weeks later, all of the south-facing patches contained adult butterflies, as

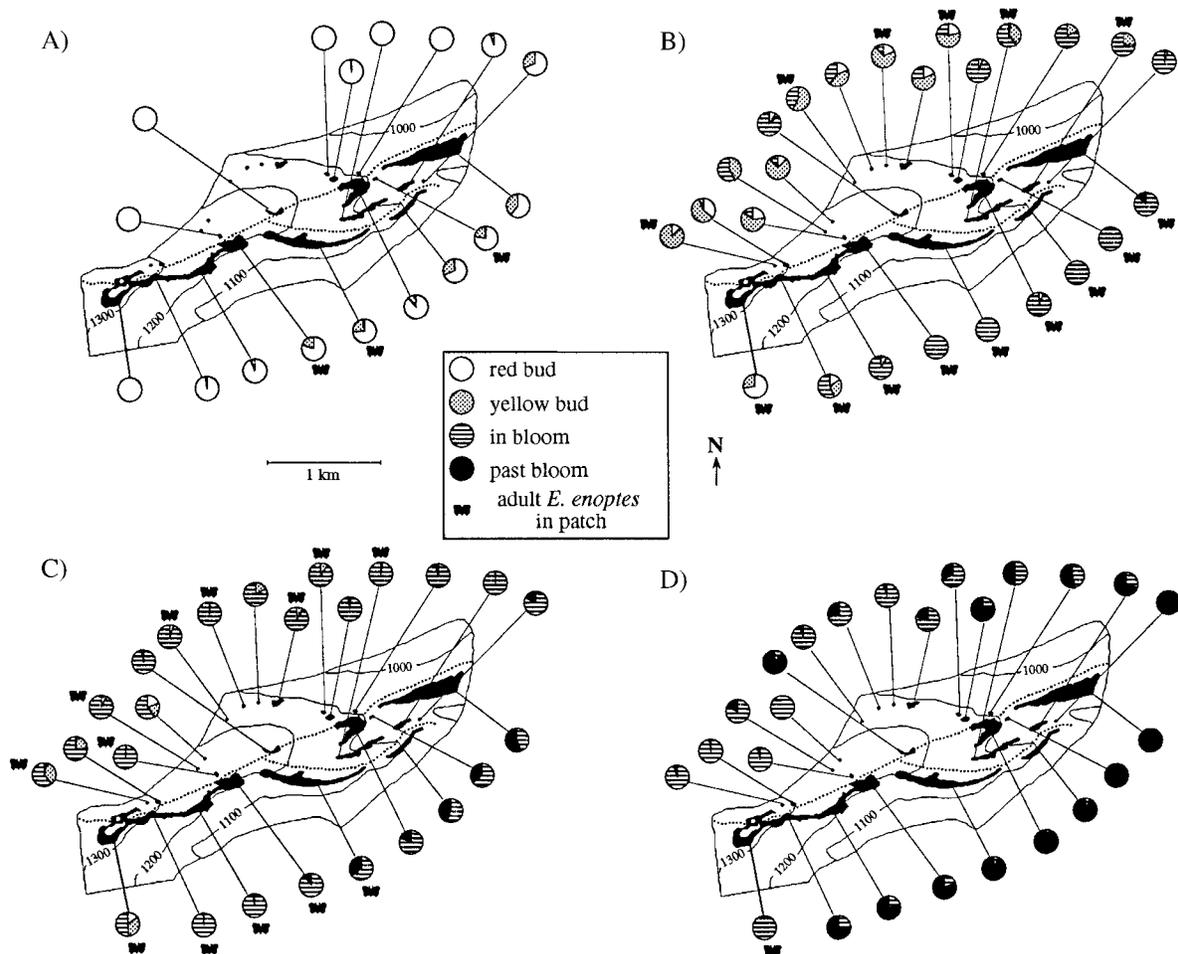


FIG. 3. Flowering phenology of *E. compositum* patches at Tarpiscan Creek (A) 14–15 May 1992, (B) 29–30 May 1992, (C) 6 June 1992, and (D) 19 June 1992. Dotted lines show the location of ridgelines. Pies above the map represent north-facing patches, and pies below the map represent south-facing patches. Pies are arranged from right to left, according to increasing elevation. Patches in which adult *E. enoptes* were seen are indicated with a butterfly.

did several of the north-facing patches. By 6 June, butterflies were no longer found in the most phenologically advanced patches, but were found in many of the less advanced, north-facing patches. On 19 June, only the highest elevation stand of *E. compositum* supported adult *E. enoptes*. Finally, by the last observation period, 26–28 June, all patches were past bloom, and none harbored adult butterflies. The range of phenology scores for the occupied patches was rather narrow (260.9 ± 10.9 [mean \pm 1 SE]), and corresponded to a patch that was nearly at peak bloom.

Patch phenology and butterfly dispersal.—I marked 295 adult *E. enoptes* at the Tarpiscan Creek site, of which I later recaptured 114 (38.6%) at least once. Of 178 marked females, I recaptured 84 (47.2%) at least once, whereas I recaptured only 30 (25.6%) of the 117 marked males. The lower recapture rate for males ($G = 14.1$, $df = 1$, $P < 0.001$) was probably because males, which are often caught on the wing, are more

TABLE 1. Effects of elevation, aspect, date, and their interactions on the flowering phenology of *Eriogonum compositum* patches at Tarpiscan Creek in 1992. Each patch was assigned a phenology score as described in the methods, and the scores were rescaled from 0 to 1. Results are from repeated-measures ANOVA of angular-transformed, rescaled scores. The nonsignificant interaction between elevation and aspect and the nonsignificant three-way interaction were excluded from this analysis.

Source	df	F	P
Elevation	1, 14	36.38	<0.001
Aspect	1, 14	20.54	<0.001
Date	3, 42	8.44	<0.005
Date \times elevation	3, 42	3.23	0.053
Date \times aspect	3, 42	1.57	>0.20

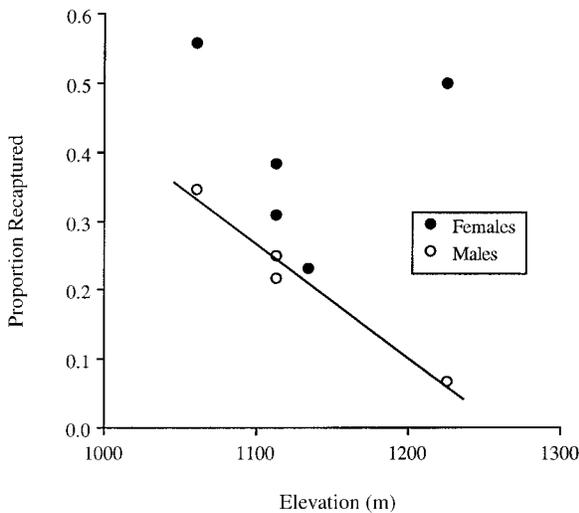


FIG. 4. The relationship between the proportion of individuals recaptured and the elevation of their patch of original capture. There was no relationship between the angular-transformed proportion of individuals recaptured and elevation for females ($P > 0.9$), but males were significantly less likely to be recaptured if they were first caught in high-elevation patches ($y = -0.002x + 2.978$, adjusted $r^2 = 0.98$, $P < 0.01$). Only the significant regression for males is plotted.

difficult to capture than the relatively sedentary females. Crab spider predation undoubtedly claimed a significant portion of the butterflies that were never recaptured; I encountered several butterflies (including one marked butterfly) in the grasp of crab spiders on *E. compositum* inflorescences. Although males were more likely to be recaptured if they were originally caught in a low-elevation patch ($P < 0.01$, $r^2 = 0.981$), recapture rates did not vary with elevation for females ($P > 0.9$, $r^2 = 0.000$) (Fig. 4). Recaptured males and females were equally likely to have moved to a new patch; 6 of 30 recaptured males (20%) and 16 of 84 females (19%) moved among patches ($G = 0.01$, $df = 1$, $P > 0.9$) (Fig. 5A,B). No butterflies were ever encountered in more than two patches. *E. enoptes* adults were rather sedentary at this site; few moved > 500 m, and none were seen to move the maximum observable distance (Figs. 5A,B and 6).

The dispersal behavior of butterflies at this site indicated that the movement of females, unlike males, was biased in an uphill direction, consistent with the hypothesis that females followed the uphill progression of suitable patches. All of the 16 females that relocated did so to a higher patch, whereas only four of the six males that moved among patches moved uphill ($G = 5.39$, $df = 1$, $P < 0.025$) (Fig. 5A,B). Nearly all of the females that moved uphill moved from the large, low-elevation patch N, in which I originally captured over half of all marked females. Although 13 females left this patch for the uphill patch V, none were seen to move downhill from patch V to patch N, in spite of

the large number of recaptured individuals that originated from patch V (Fig. 5A). The small number of males that moved among patches appeared to do so independent of elevation (Fig. 5B). The uphill bias in female dispersal at this site appears to have resulted from increased emigration from low-elevation patches (sexes combined: $P = 0.056$, adjusted $r^2 = 0.67$, Fig. 7). Although small sample sizes necessitated combining data for the sexes in this analysis, the data for three patches with a sufficient number of females showed the same pattern (Fig. 7). This result is consistent with the

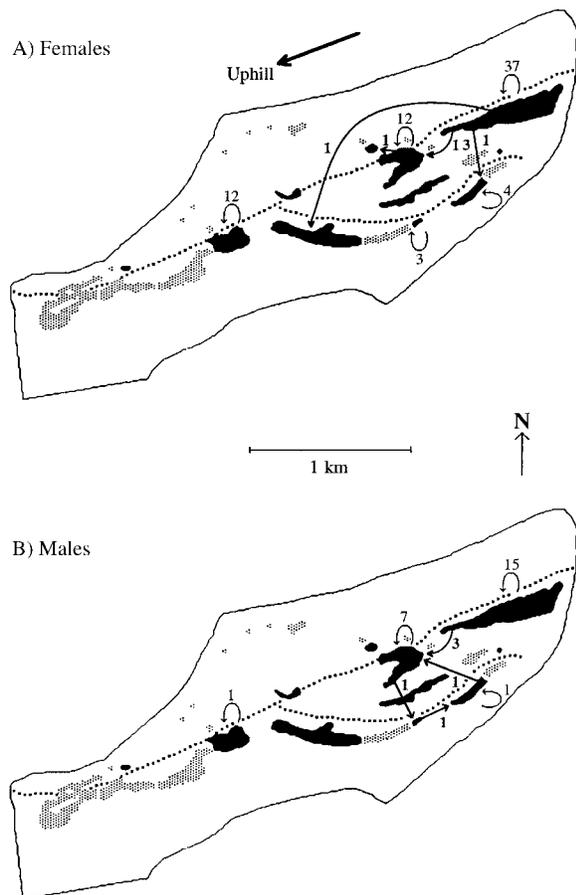


FIG. 5. Movement patterns of the 114 recaptured *E. enoptes* females (A) and males (B) at Tarpiscan Creek. Dark patches represent the 10 focal mark-release-recapture patches plus any additional patches in which marked butterflies were found. (See Fig. 1 for identities of patches.) Shaded patches represent all other host plant patches in the study area. Dotted lines show the location of ridgelines. Arrows indicate the direction of movement, and the number next to each arrow shows the number of individuals making a particular move. Arrows that return to the starting patch indicate individuals that did not move to a new patch. Each data point represents the maximum movement of butterflies since their first capture. No individuals were observed to transfer patches more than once. The large arrow above the figure indicates an approximation of the overall slope of the site.

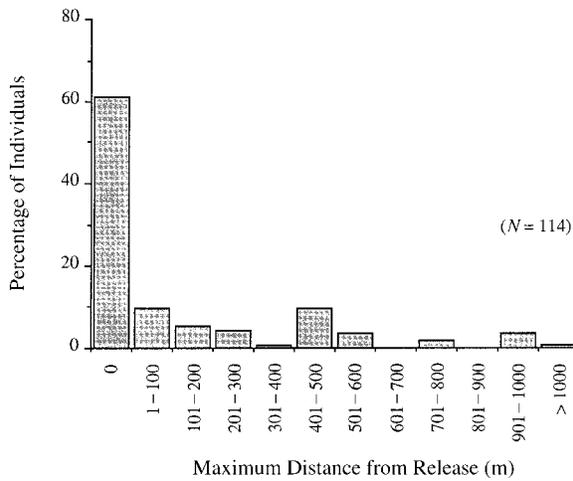


FIG. 6. Maximum observed distances moved from original release point by adult *E. enoptes* at Tarpiscan Creek. Distances were determined for movements both among patches and within patches.

hypothesis that as patches senesce, they retain female *E. enoptes* less well.

Patch phenology and larval density.—At Tarpiscan Creek in both 1990 and 1991, there was a significant increase in larval density (number per inflorescence) with elevation, consistent with the hypothesis that uphill movement leads to increased oviposition at higher elevations (Fig. 8A). In both years, there was an approximately fourfold increase in larval density over a 300-m elevational gradient, and over a distance of < 3 km [1990: density = 0.001(elevation) - 1.285, adjusted $r^2 = 0.64$, $P < 0.01$; 1991: density = 0.002(elevation) - 1.860, adjusted $r^2 = 0.46$, $P < 0.05$]. This

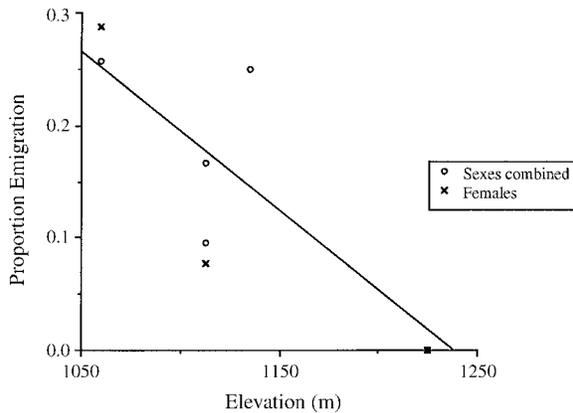


FIG. 7. The relationship between emigration rates and elevation of the patch in which butterflies were first marked. The angular-transformed proportion of recaptured individuals that had moved to a new patch decreased with elevation (sexes combined: $y = -0.003x + 3.943$, adjusted $r^2 = 0.67$, $P = 0.056$). Although the regression was not performed for the data on female dispersal, the pattern was the same as for the combined data set, for which the regression is plotted.

pattern was not the result of variation in inflorescence density across the elevational gradient, since inflorescence density (number per square meter) did not vary predictably with elevation (Fig. 8B; 1990: $P > 0.4$; 1991: $P > 0.3$). Furthermore, in 1991 and 1992, the proportion of fourth-instar larvae that were tended by ants did not vary with elevation (Fig. 9; 1991: $P > 0.9$; 1992: $P > 0.3$), suggesting that larval mortality also did not vary with elevation. Although there were too few populations sampled in 1990 to allow regression, ant attendance in those three patches similarly showed no obvious relationship with elevation (Fig. 9). Parasitism rates varied widely among populations in 1989, but also did not vary with elevation (Fig. 10; $P > 0.3$).

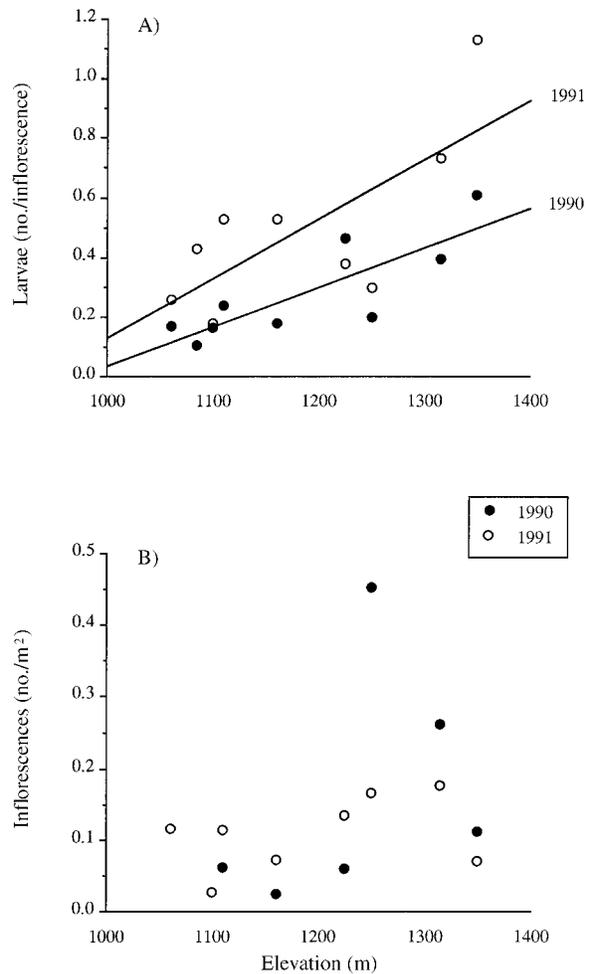


FIG. 8. The relationship between (A) larval density (no. larvae/no. inflorescences) and (B) inflorescence density (no./m²) and elevation, for the south-facing host plant patches at Tarpiscan Creek in 1990 and 1991. Larval density increased significantly with elevation in both years (1990: $y = 0.001x - 1.285$, adjusted $r^2 = 0.64$, $P < 0.01$; 1991: $y = 0.002x - 1.860$, adjusted $r^2 = 0.46$, $P < 0.05$), but inflorescence density showed no consistent relationship with elevation in either year (1990: $P > 0.4$; 1991: $P > 0.3$).

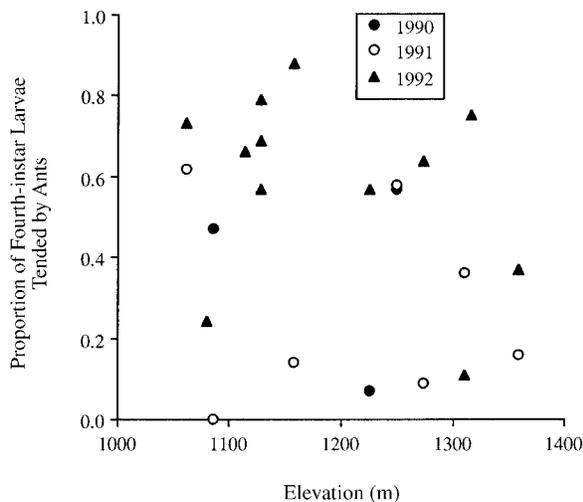


FIG. 9. Variation in the proportion of fourth-instar larvae that were tended by ants along an elevational gradient at Tarpiscan Creek in 1990, 1991, and 1992. Ant attendance (angular-transformed proportion of larvae that were tended) did not vary with elevation in the two years (1991, 1992) in which there were sufficient data to allow regression (1991: $P > 0.9$; 1992: $P > 0.3$). Variation among the three populations surveyed in 1990 also suggested no relationship between ant attendance and elevation.

Flowering phenology and local butterfly movement

I predicted that if butterflies have a preference for patches that are nearing full bloom, "advanced" plots in the experimental grid would be the most attractive to butterflies early in the flight period because these patches were approaching full bloom at this time, whereas inflorescences in "delayed" patches were mostly either "red bud" or "yellow bud" (Fig. 2A). I further predicted that this relative preference for "advanced" plots over "delayed" plots would decline through the experiment as inflorescences in the "delayed" plots matured. Because males are less tightly constrained by inflorescence phenology than are ovipositing females, I predicted that females would show a stronger response to patch phenology than males.

The number of times females alighted on inflorescences in "advanced" patches declined through the experiment, while the alightings on inflorescences in "delayed" patches increased during this same time ($G = 18.2$, $df = 4$, $P < 0.005$, Fig. 11A). The number of alightings on inflorescences in the different treatments converged by the last observation period (Fig. 11A), at which time nearly all of the inflorescences in all three treatments were in bloom (Fig. 2B).

Although there was a suggestion that more females entered "advanced" patches early in the study and "delayed" patches late in the study, this pattern was not statistically significant, perhaps because of the small number of females observed during this study ($G = 4.9$, $df = 4$, $P > 0.30$, Fig. 11B). Thus, it remains

unclear whether females can assess flowering phenology before entering a patch. Nonetheless, their attraction to inflorescences of a particular phenology caused them to disproportionately visit inflorescences in patches that were either near or at full bloom. This behavior resulted in more alightings on inflorescences in the "advanced" patches early in the experiment and a similar frequency of alightings in all three treatments at the end of the experiment.

Males, on the other hand, showed no ability to discriminate among patches based on their phenology, as evidenced by the fact that the relative numbers of alightings by males on inflorescences in phenologically differing patches did not change through the flight period ($G = 6.5$, $df = 4$, $P > 0.25$, Fig. 12A). In addition, the relative numbers of males entering those patches also did not shift in the predicted direction during this study ($G = 3.7$, $df = 4$, $P > 0.40$, Fig. 12B).

DISCUSSION

Host plant phenology and herbivore movement

The results of this study show that the presence of adult *Euphilotes enoptes* follows the uphill march of the peak flowering period of *Eriogonum compositum* in lockstep fashion (see also Peterson 1995a). For this butterfly, there is a narrow window of opportunity to exploit the inflorescences of its host plant (Pratt 1994), so it is critical that individuals utilize patches of a particular phenology. One means by which this is ensured is through a match between the timing of adult emergence and host plant flowering (Pratt and Ballmer

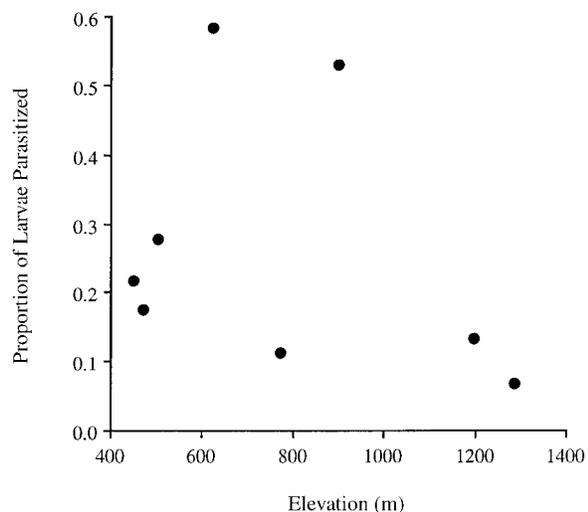


FIG. 10. The relationship between parasitism rates and elevation in eight populations of *E. enoptes* in central Washington State, 1989. Although parasitism rates varied considerably among populations, there was no relationship between the frequency of parasitoid attack (angular-transformed proportion of larvae attacked by parasitoids) and elevation ($P > 0.3$).

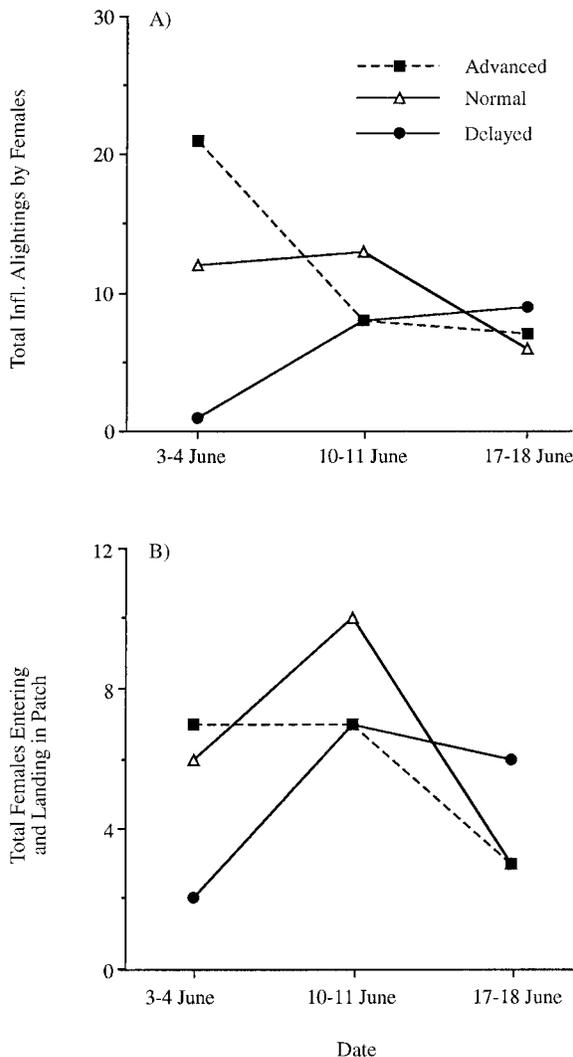


FIG. 11. Combined data on female behavior in the experimental grid. (A) The total number of alightings on inflorescences by females in patches of each type during three observation periods in the experimental grid. The proportions of alightings on inflorescences in the different patches varied over the three dates ($G = 18.21$, $df = 4$, $P < 0.005$). (B) The total number of females entering and landing in patches of each type during three observation periods in the experimental grid. The proportions of females landing in the different patches did not vary across the three dates ($G = 4.90$, $df = 4$, $P > 0.3$).

1993). Indeed, central Washington populations of *E. enoptes* from high elevations emerge later under laboratory conditions than their low-elevation counterparts (Peterson 1995a), and delayed emergence in high-elevation patches undoubtedly facilitates a phenological match between butterfly and plant. However, even under laboratory conditions, the range in adult emergence dates within a population can exceed a month (Pratt and Ballmer 1993, Peterson 1995a), and there is

considerable overlap in emergence dates among populations in the elevation range studied at Tarpiscan Creek (Peterson 1995a). Thus, emergence alone cannot explain the precision of the match between adult presence and patch phenology. The study herein shows that dispersal also helps ensure the occupation and exploitation of patches that can potentially support offspring. Although several authors have examined the hypothesis that among-patch dispersal by an herbivorous insect can be influenced by host plant phenology (Singer and Ehrlich 1979, Jordano et al. 1990, Rodríguez et al. 1994), to my knowledge, this study represents the first case in which such effects have been demonstrated.

Observational support of the hypothesis that host plant phenology influences among-patch dispersal by *E. enoptes* was provided by the detailed studies of host plant phenology and dispersal at Tarpiscan Creek. At the onset of a mark-release-recapture study at this site, inflorescences in low-elevation patches were near full bloom, but for most of the 3-wk period they were senescing. High-elevation patches, on the other hand, reached full bloom only at the last sampling date. Female *E. enoptes*, unlike males, apparently responded to this phenological variation by moving uphill, tracking the progression of flowering *E. compositum*. The recapture data suggested that this uphill movement was the result of relatively greater emigration from declining low-elevation patches than from improving high-elevation patches.

Support of this influence of flowering phenology on butterfly behavior was provided by the field experiment. In this experiment, small sample sizes made it difficult to determine if either sex can assess patch phenology before entering a patch, but the results clearly indicated that inflorescences in patches of a particular phenology received a disproportionately great number of visits by females. Most significantly, females frequently visited inflorescences in the most phenologically advanced patches early in the season, but later in the season, when the inflorescences in both the "advanced" and "delayed" patches were in bloom, they visited inflorescences equally in the different treatments. It is important to note that this result may be due to either slightly greater visitation of patches in bloom or increased frequency of inflorescence visitation by females upon entering, or both. As predicted from their relatively reduced need for a phenological match with host plants, males were less affected by flowering phenology than females. In fact, males showed no switch in preference from "advanced" to "delayed" patches through the season, indicating that movement patterns of males are probably not influenced by patch phenology. The increased visitation of inflorescences by females in patches nearing full bloom suggests that reduced emigration rates at higher elevations at Tarpiscan Creek were due to the greater attractiveness of high-elevation patches as they came into bloom while the low-elevation patches senesced.

In addition to phenologically biased dispersal, one might argue that the apparent pattern is an artifact of sampling rather than a true bias in movement. This would be a problem particularly if the relative effort spent in low- and high-elevation patches shifted from greater effort at low elevations in the beginning of the study to greater effort at high elevations toward the end of the study. This was not the case. Throughout the mark–release–recapture study, the recapture effort in each patch was roughly proportional to the area of the patch. A second source of sampling bias may result from the fact that, on average, individuals were captured at a slightly earlier date in low-elevation patches than in high-elevation patches, and so individuals from low elevations could have had a greater length of time for recapture. However, since the length of the mark–release–recapture study was long relative to the average life-span ($\approx 3\text{--}4$ d) of *E. enoptes* adults (Arnold 1983a), individuals captured in both low- and high-elevation patches had effectively equal amounts of time in which they could be recaptured (in fact $< 10\%$ of individuals were recaptured more than six days after their original capture).

Phenologically biased movement and population density

In an uneven landscape like that found at Tarpiscan Creek, female *E. enoptes* respond to the phenologically shifting mosaic of host plant patches by moving uphill as low-elevation patches senesce. Does this uphill bias in dispersal influence the relative density of this species in patches that differ in phenology? Without experimentally manipulating levels of dispersal among patches, this question is difficult to answer with certainty, but examination of the data on larval density suggests that it does. Over a 300-m gradient at Tarpiscan Creek in two separate years, larval density increased roughly fourfold. Apparently, the uphill movement of females at this site leads to increased oviposition at higher elevations. These individuals have a limited opportunity for dispersing to even higher elevations since the number and size of *E. compositum* patches decline rapidly above the upper reaches of this site (M. A. Peterson, *personal observations*). This may explain why females apparently accumulate and lay many eggs in the high-elevation patches at the Tarpiscan Creek study site rather than continuing farther uphill.

Alternative explanations for the increase in larval density with elevation include variation in host density, plant quality, and rates of attack by natural enemies, but each of these seems unlikely. There was no evidence that the density of inflorescences in a patch varied with elevation at this site in either of the years in which larval densities were assessed. Furthermore, inflorescences were not noticeably larger or better pollinated in high- compared to low-elevation patches. Finally, neither the frequency of ant attendance nor rates of parasitism varied with elevation, suggesting that dif-

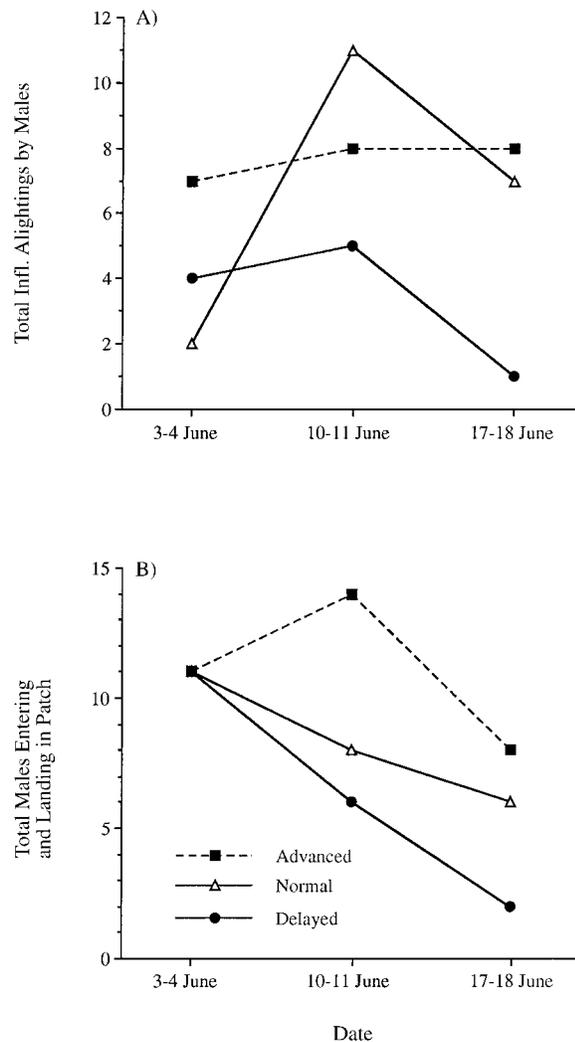


FIG. 12. Combined data on male behavior in the experimental grid. (A) The total number of alightings on inflorescences by males in patches of each type during three observation periods in the experimental grid. The proportions of alightings on inflorescences in the different patches did not change over the three dates ($G = 6.52$, $df = 4$, $P > 0.25$). (B) The total number of males entering and landing in patches of each type during three observation periods in the experimental grid. The proportions of males landing in the different patches did not change over the three dates ($G = 3.72$, $df = 4$, $P > 0.4$).

ferential pressure from natural enemies does not adequately explain the elevational variation in larval density. Thus, it appears that uphill dispersal by butterflies tracking phenological variation among host plant patches is the most compelling explanation for the elevational increase in larval density in *E. enoptes*.

In addition to its impact on among-patch variation in larval density, the relationship between patch phenology and butterfly dispersal has important evolutionary implications. In this species, there is consid-

erable gene flow among low- and high-elevation populations, even when there is no overlap between their flight periods (Peterson 1995a, *in press*). The steady uphill march of females documented in this study offers a plausible explanation for these observed high levels of gene flow, since it allows genes to flow in stepping-stone fashion from low to high elevations. Such a directional bias in gene flow may constrain populations at high elevations from adapting to the cooler local conditions they face, because gene flow from populations occupying low-elevation sites may overcome any selective differences along these elevational gradients.

ACKNOWLEDGMENTS

I am indebted to J. Pelham for stimulating my interest in *Euphilotes*. A. Peterson, R. Root, and C. Yoon assisted with fieldwork, for which I am grateful. The Brannon family provided much-needed logistical support in the field, bailing me out of at least a couple of jams. Many of the ideas in this paper were formed during discussions with the Root lab members and the Insect Movement discussion group at Cornell, and with P. Kareiva. This manuscript benefitted from the thoughtful comments of E. Connor, R. Denno, G. Eickwort, R. Harrison, S. Harrison, P. Marks, F. Messina, R. Root, C. Wicklund, C. Yoon, and anonymous reviewers. M. Eubanks assisted with statistical analyses and G. Eickwort identified the parasitoids, for which I am grateful. Financial support for this project was provided by NSF (a graduate fellowship and grants BSR-8817961 (to R. B. Root) and BSR-9100860 (to R.B.R. and M.A.P.)), the Graduate School of Cornell University, the Rabinowitz/Whittaker Memorial Fund of the Section of Ecology and Systematics at Cornell University, the Theodore Roosevelt Memorial Fund of the American Museum of Natural History, and Sigma Xi. Completion of the manuscript was supported by the Maryland Agricultural Experiment Station (Competitive Grant ENTO 95-10 to M.A.P. and R. F. Denno). This paper is dedicated to the memory of George Eickwort, who encouraged me to study the behavioral ecology of *E. enoptes*.

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