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Nectar and hostplant scarcity limit populations of an endangered Oregon butterfly

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Abstract As grassland habitats become degraded, declines in juvenile and adult food resources may limit populations of rare insects. Fender's blue butterfly (*Icaricia icarioides fenderi*), a species proposed for listing as endangered under the US Endangered Species Act, survives in remnants of upland prairie in western Oregon. We investigated the effects of limited larval hostplants and adult nectar sources on butterfly population size at four sites that encompass a range of resource densities. We used coarse and detailed estimates of resource abundance to test hypotheses relating resource quantity to population size. Coarse estimates of resources (percent cover of hostplant and density of nectar flowers) suggest that butterfly population size is not associated with resource availability. However, more detailed estimates of resources (density of hostplant leaves and quantity of nectar from native nectar sources) suggest that butterfly population size is strongly associated with resource availability. The results of this study suggest that restoring degraded habitat by augmenting adult and larval resources will play an important role in managing populations of this rare butterfly.

Key words Fender's blue butterfly · Habitat degradation · Kincaid's lupine · Nectar quantity · Resource dependence

Introduction

Resources limit population size. This simple observation motivated a decade of heated debate in the 1950s (e.g. Andrewartha and Birch 1954; Lack 1954; Nicholson 1957). After numerous studies, ecologists concluded that in many cases (largely vertebrates species) resources limit population size but that in others (largely insect species) unpredictable abiotic factors such as weather often drive population trends (see Begon et al. 1996 for further discussion). Although the debate was largely abandoned, the issues continue to emerge today, often in the context of rare species management. If scarce resources limit populations of endangered species, then we can improve their chances for survival by enhancing key resources.

Habitat degradation reduces resources and threatens numerous butterfly species (Sibatani 1990; Thomas 1991; Warren 1992). In many grasslands, invasion by non-native plants and the cessation of natural disturbance regimes contribute to habitat deterioration (Agee 1996). For butterflies, this degradation often takes the form of fewer larval hostplants and fewer adult nectar sources (Warren 1992; Zaremba and Pickering 1994). In this study, we investigate whether scarce juvenile and adult resources influence populations of Fender's blue butterfly (*Icaricia icarioides fenderi*), a species proposed for listing as endangered under the US Endangered Species Act (Anonymous 1998).

For specialist butterflies, scientists and amateur lepidopterists have long recognized that the distribution of larval hostplants, a butterfly's juvenile resource, often define its distribution (Brues 1920; Ehrlich and Raven 1965). Butterfly guides often suggest places to find butterflies based on the distributions of their hostplants (Pyle 1990; Tilden and Smith 1986). If hostplant abundance drops, butterfly populations may fall. For example, researchers believe that populations of the endangered Karner blue butterfly (*Lycaeides melissa samuelis*) plummet when its hostplant, the wild blue lupine (*Lupinus perennis*) declines (Savignano 1994).

Nectar sources, a butterfly's adult resource, are also critical to maintaining butterfly populations (Hill 1992). Floral nectar provides water, sugar, and amino acids for adult butterflies (Boggs 1987). As nectar availability increases, butterflies live longer and lay more eggs (Boggs

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and Ross 1993; Hill 1992; Murphy et al. 1983). For example, Hill and Pierce (1989) found that the imperial common blue, *Jalmenus evagoras*, lays three times more eggs when nectar is plentiful. They observed that females compensate for insufficient nectar by spending more time feeding, which leaves less time to oviposit. In addition, butterflies often leave sites that have abundant hostplants but inadequate nectar. Grossmueller and Lederhouse (1987) observed that eggs of the tiger swallowtail, *Papilio glaucus*, were concentrated in areas of dense nectar plants rather than in areas with more vigorous hostplants. In some species, low nectar species diversity may also limit butterfly populations. Britten and Riley (1994) found that sites with higher nectar source diversity were more likely to support populations of the endangered Uncomphrage fritillary (*Bolaria acrocnema*). Similarly, Williams (1988) observed that butterfly population size in *Euphydryas gillettii* increased as nectar diversity increased.

We investigate the roles of juvenile and adult resources in limiting populations of the Fender's blue. Fender's blue butterflies are only found at sites that maintain at least one of its larval hostplants, either Kincaid's lupine (*L. sulphureus kincaidii*) or spur lupine (*L. laxiflorus*). However, our previous casual observations suggested that Fender's blue butterflies seemed rare at sites with abundant hostplants and abundant non-native nectar sources but few native nectar sources. Therefore we tested the following hypotheses: (1) butterfly population size is higher at sites with higher hostplant abundance, (2) butterfly population size is higher at sites with higher total nectar abundance, and (3) butterfly population size is higher at sites with higher native nectar abundance. In each case, we examined resource abundance at coarse and fine scales in order to assess whether measurement methods influence the predicted relationships. Coarse-grain approaches, if sufficient, allow more rapid assessment of habitat conditions but, if insufficient, may lead to faulty conclusions.

Methods

Study species and sites

The Fender's blue is a rare Oregon butterfly found only in Willamette Valley prairies that support either Kincaid's lupine (*L. sulphureus kincaidii*) or spur lupine (*L. laxiflorus*). Both the butterfly and Kincaid's lupine are extremely rare. Less than 4000 butterflies survive in 12 isolated prairie remnants (Hammond 1998; Schultz 1998). Among these, 7 sites have less than 100 butterflies, 2 sites have 100–300 butterflies, and 3 sites have more than 300 butterflies. Prairie patches are rare because agriculture, urbanization, and the cessation of annual fires have resulted in the loss of more than 99% of Willamette Valley prairies over the last 150 years (Agee 1996; Alverson 1993). Remaining patches are quickly being invaded by non-indigenous plants (Hammond and Wilson 1993). At some sites, these weeds have reduced the diversity and abundance of nectar flowers available to Fender's blue butterfly (Wilson et al. 1997).

The Fender's blue is a "spring" species. Adults emerge in May, mate, and females oviposit on the underside of Kincaid's lupine leaves. Eggs hatch a few weeks later and the larvae eat hostplant leaves for a few weeks until the lupines senesce. Larvae then enter an extended diapause that lasts until the following March. Larvae emerge from the soil litter when lupines resurface and eat young lupines until they pupate in mid-April. Most of their larval growth occurs in March and April. To test hypotheses about resource limitations, we estimated butterfly population size in 1997, adult resources in 1996, and larval resources in 1997. We compared adult resources with population size a year later because we expect adult resource density to influence oviposition rates and thus population size in the following year. We assessed larval resources in the same year as population size because we expect resource density in March and April to influence population size in May.

We studied Fender's blue butterflies and their juvenile and adult resources at four populations in Lane County, Oregon, the southern end of the butterfly's range. These include two populations at The Nature Conservancy Willow Creek Natural area (44°N, 123°W) a population near Fir Butte Road (44°N, 123°W), and a population along Coburg Ridge (44°N, 123°W). We refer to the Willow Creek populations as "Willow Creek" and "Bailey Hill". These four sites were chosen because they encompass a range of nectar source diversities and butterfly densities. Kincaid's lupine is the sole larval hostplant at Willow Creek, Bailey Hill, and Fir Butte. At Coburg, spur lupine is the only hostplant in the study area, but Kincaid's lupine serves as a larval hostplant at nearby areas on Coburg Ridge. At each site except Coburg, 60 12×12 m grid cells were established for butterfly and vegetation sampling. For consistency with other studies at Coburg, cells at this site were 12.5×12.5 m. These areas represent the habitat with the highest Fender's blue density at each site.

Butterfly census

We used aspects of two common methods of estimating butterfly population size to estimate the density of Fender's blue. The mark-release-recapture (MRR) technique is commonly used to estimate butterfly longevity and population size (Begon 1979; Warren 1992). MRR is considered quantitatively precise, but may harm fragile butterflies due to repeated handling. In addition, recapturing enough individuals to get accurate estimates often requires frequent visits to the site and results in trampling of sensitive plants. We employed a limited MRR experiment in 1994 to estimate Fender's blue longevity. The second common method is a walking transect, a technique developed by the British Butterfly Monitoring Scheme (BBMS; Pollard and Yates 1993). BBMS has less impact on both butterflies and habitat than MRR, but it is less precise. BBMS provides an index of the number of butterflies, not an absolute count or density estimate. We adapted BBMS techniques to assess the number of Fender's blue each week during its flight period.

We used the following protocol to estimate the number of Fender's blue butterflies each week. We surveyed each site every 7–10 days during the flight period, noting the number of blue butterflies in each grid cell. Censuses were conducted on calm, sunny days. Fender's blue males are blue and showy whereas the females are brown and inconspicuous. Therefore butterfly counts included Fender's blue males only and did not include females. In addition, several morphologically confusing species of blue butterflies live in these lupine areas. To account for this, we assessed the relative proportion of Fender's blues versus other blues at each census. After each census, 20 blue butterflies were netted and identified. In cases where fewer than 40 butterflies were counted, 50% of the observed butterflies were netted for identification. We assumed there were equal numbers of males and females and estimated the number of Fender's blue butterflies in census i as:

$$n_i = 2 \times (\mathrm{FB}_i/\mathrm{TB}_i) \times \mathrm{BB}_i$$

where FB_i = the number of Fender's blue butterflies counted in each net sample i, TB_i = the total number of butterflies identified by hand, and BB_i = the number of blue butterflies counted in the census.

To estimate butterfly longevity, we conducted a limited MRR trial. We marked about 15% of the population at Willow Creek in 1994. These data suggest that Fender's blue butterflies live, on average, 9.5 days (95% CI: 7.2–13.8 days; see Schultz 1995 for details).

To calculate the density of butterflies, N, at each site, we modified the BBMS by combining weekly census numbers with longevity in the following manner:

$$N = \frac{1}{r}\sum_{i=1}^{w} n_i t_i \quad \text{where} \quad t_i = (d_{i+1} - d_{i-1})/2$$

where r = residence time for Fender's blue (9.5 days), n_i = the number of Fender's blue butterflies in census i, t_i = the time interval represented by census i, d_i = Julian date of census i, and w = the number of census counts.

Vegetation survey

To survey vegetation, we randomly selected 15 cells at Bailey Hill and Fir Butte and 25 cells at Willow Creek and Coburg Ridge. In each selected cell, we randomly chose a 0.25 × 12 m strip in which to measure lupine and flower abundance. Thus the total area sampled was about 0.5–1.0% of the study area.

We used two methods to assess the abundance of lupine: percent cover and leaf density. We used percent cover to investigate whether butterfly densities are low in areas with abundant lupine, as we had casually observed in previous observations. We estimated percent cover using a line-intercept method. We noted whether lupine fell under the meter tape at each 10-cm interval along the 12-m sampling strip. We used density of lupine leaves as an alternative index of hostplant abundance because leaves are the resource used by juvenile butterflies. We assessed the density of lupine leaves using a quadrat sampling method. We counted the number of lupine leaves in three 0.25 × 0.5 m quadrats randomly placed along each 12-m sampling strip. Willow Creek, Bailey Hill, and Fir Butte were sampled in 1997. Due to constraints in the field, Coburg was not measured in 1997. Instead, we averaged estimates from years in which lupine was sampled: 1994 and 1996. Because individuals of both spur and Kincaid's lupine often live for decades (Kuykendall and Kaye 1993), estimates from recent years are unlikely to differ significantly from 1997. For example, at Willow Creek in 1994, 1995, and 1996, estimates for Kincaid's lupine leaf density (number/m^2) were 57.0, 61.0, and 63.5, respectively (C. Schultz, unpublished data).

To estimate nectar flower density, we counted all inflorescences of all nectar flowers used by Fender's blues in a 0.25 × 12 m strip-quadrat along each randomly placed strip. For the vetches *Vicia hirsuta*, *V. sativa*, and *V. villosa*, we counted branches of each plant in place of inflorescences due to the prolific nature of the plants. To estimate the density of flowers too rare to appear in the sampling strips, we counted all flowers of each rare species at each site. Next, to assess the number of flowers per sampling unit, we counted the number of flowers per inflorescence (e.g., number of florets per head on a composite like *Chrysanthemum leucanthemum*) at the end of the butterfly flight season. In each of 25 randomly chosen cells, three inflorescences (or branches) from each species were selected for counting. Open and wilted flowers, fruits, and scars of abscised flowers were counted on each inflorescence (or branch). Finally, we estimated the number of days each flower produced nectar. For all flowers that stay open more than 1 day, buds of 15 flowers were marked. Buds were checked daily until all flowers had opened and flowers were checked daily until all closed.

Quantifying nectar

We sampled nectar three times within the gridded areas at each site during the extent of the 1996 flight season. During each sampling period, 15 flowers were selected haphazardly. These flowers were bagged to prevent visitation for 24 h before sampling. Flowers that both produced nectar for multiple days and produced significant quantities of nectar were drained with filter paper wicks prior to bagging. These flowers included *Camassia quamash*, *Sidalcea virgata*, and *Calochortus tolmiei*.

After the 24-h period, we removed the bags from the flowers and sampled the nectar. We used small wicks of Whatman no. 1 filter paper to extract the nectar from each flower/floret. We allowed the wicks to air dry before freezing them for analysis. Later, we analyzed nectar samples for total sugar content using the anthrone method described by McKenna and Thomson (1988) and used by Holl (1995) in a similar study of nectar abundance. This method allows analysis of total grams of sugar per flower. We did not estimate nectar volume and sugar concentration with a pocket refractometer, a more common technique for estimating nectar (Jones and Little 1983), because nectar volumes in 14 of 18 species we sampled were too small to be drawn into capillary tubes. In addition, although water is a critical limiting resource for some butterflies (Shreeve 1992), it is unlikely that it is a limiting resource for Fender's blue butterfly given the amount of rain during a typical western Oregon spring.

Nectar data analysis

We used the estimates of sugar content and flower density to estimate the total amount of sugar each flower species produced at each site. We used the following conversion to estimate the total sugar each species produced each year at each site:

$$\mathrm{TS}_i = S_i \times D_i \times F_i \times U_i$$

where TS_i = total sugar/m^2 from species i, S_i = daily sugar (mg) from each flower of species i, D_i = number of days each flower of species i produces nectar, F_i = number of flowers per sampling unit for species i, and U_i = sampling units/m^2 for species i.

Quantifying butterfly foraging

To estimate the relative amount of time butterflies seek and feed on nectar, we conducted behavioral observations at Fir Butte and Willow Creek. These sites were chosen because Fir Butte had the lowest butterfly density and appeared most limited in its nectar resources whereas Willow Creek had the highest butterfly density and appeared to have substantially more available nectar. We quantified daily activity patterns by conducting fifteen 2-min behavioral observations each hour from 0800 to 1900 hours on two sunny days. In each case, we located a butterfly, recorded its behaviors for 2 min, then walked in a random direction and searched for another butterfly. These behaviors included fly, perch, bask, nectar, oviposit, and chase. At each nectar observation, we noted the flower species the butterfly was using. The behaviors were entered into a hand-held computer that recorded the time at which each activity was initiated. We used these data to estimate the percent time butterflies spent nectaring at each site on sunny days.

Results

Butterfly population density

At the four censused sites, Fender's blue butterfly densities varied widely (butterflies/ha = 44 at Fir Butte, 36 at Bailey Hill, 96 at Coburg, and 690 at Willow Creek). These densities reflect differences between sites. For example, Willow Creek and Bailey Hill differ greatly in butterfly density although they are less than 0.5 km apart. The total population size at Willow Creek was more than 1000 butterflies across 2.3 ha whereas at Bailey Hill there were only 41 butterflies across 1.9 ha (Schultz 1998).

Lupine and nectar quantities

Lupine cover varied from just under 2% at Bailey Hill to almost 10% at Willow Creek (Table 1). Leaf densities varied almost fourfold from 15.8 leaves/m^2 at Bailey Hill to 54.7 leaves/m^2 at Willow Creek.

Nearly 200 nectar samples were collected at each site. Eight to 46 random samples from each species were analyzed for total sugar content (Table 2). The sugar content ranged from 0.031 mg/day from flowers of *Myosotis discolor* to 0.577 mg/day from flowers of *S. virgata*. The sugar content per flower of native species was significantly higher than the sugar content of non-native species (unpaired *t*-test, $n = 18$ species in Table 2, $P = 0.05$). Based on measured nectar flower densities and estimated total sugar per vegetation unit, we calculated total mg sugar/m^2 (Table 3).

Table 1 Kincaid's lupine density at Bailey Hill, Fir Butte, and Willow Creek. Spur lupine density at Coburg

Site	Year	Leaves/m^2		Percent cover	
		Mean	SD	Mean	SD
Bailey Hill	1997	15.8	26.5	1.9	1.5
Coburg	1994	27.2	26.2	1.8	1.5
	1996	18.5	19.2	2.4	1.6
	Average	22.8		2.1	
Fir Butte	1997	24.2	30.0	5.5	5.2
Willow Creek	1997	54.7	34.5	9.5	5.7

Nectaring behavior

Fender's blue butterfly activities were quantified by monitoring butterfly behavior throughout the day near the peak of the flight period. (peak census counts in 1996 at Willow Creek on 1 June and at Fir Butte on 2 June. Behavioral observations at Willow Creek on 27 May and 5 June, and at Fir Butte on 1 June and 6 June). Percent of time nectaring was similar at Fir Butte and Willow Creek (17.3% of time nectaring in 430 min of observation at Fir Butte, 16.2% of time nectaring in 138 min of observation at Willow Creek). At Willow Creek, 81% of 89 nectar observations were on native flowers although native flowers accounted for only 9% of those available. At Fir Butte, 0 of 95 observations were on native flowers and native flowers accounted for 2% of those available.

Associations between butterfly numbers and limiting factors

Butterfly densities were not associated with percent cover of lupine but were significantly associated with lupine leaf densities (linear regressions, Fig. 1a,b). Butterfly densities were also not associated with total flower density, native flower density or total sugar density (Fig. 1c–e). However, butterfly densities were highly associated with native sugar densities (Fig. 1f).

As additional support for these associations, resources from 1996 (nectar sources) and 1997 (hostplant sources) were correlated with other years in which butterfly densities were assessed at these sites (see Schultz 1998 for census data). Since all hostplant and most nectar resources are perennial plants, resource abundance is likely to be similar from year to year. Linear regressions were used to assess relationships between resources in 1996/1997 and butterfly densities in 1994, 1995,

Table 2 Nectar quantities averaged across all sites (*N* number of samples analyzed, *S* sugar per flower (mg), *SD* standard deviation of sugar, *D* number of days individual flower was open, *U* sampling unit, *F*/*U* flowers per sampling unit, and *S*/*U* sugar per sampling unit (mg)

Species	N	S	SD	D	U	F/U	S/U	Native?
Allium amplectens	15	0.196	0.192	7.00	Head	16.7	22.90	Yes
Anthemis arvensis	13	0.033	0.034	1.00	Head	88.0	2.88	No
Bellis perennis	17	0.032	0.033	1.00	Head	35.9	1.15	No
Calochortus tolmiei	14	0.506	0.507	3.00	Flower	1.0	1.52	Yes
Camassia quamash	26	0.352	0.516	2.13	Stalk	6.6	4.96	Yes
Chrysanthemum leucanthemum	34	0.040	0.074	1.00	Head	226.0	9.08	No
Cryptantha intermedia	13	0.046	0.047	1.00	Flower	16.1	0.74	Yes
Eriophyllum lanatum	37	0.057	0.056	1.00	Head	67.8	3.87	Yes
Hypochaeris radicata	42	0.052	0.052	1.00	Head	68.5	3.53	No
Lathyrus sphaericus	21	0.061	0.074	1.00	Flower	3.5	0.21	No
Linum angustifolium	9	0.092	0.149	1.00	Plant	1.4	0.13	No
Lupinus laxiflorus	34	0.057	0.107	2.29	Stalk	16.7	2.16	Yes
Lupinus sulphureus spp. *kincadii*	35	0.073	0.220	2.29	Stalk	61.8	10.28	Yes
Myosotis discolor	46	0.031	0.034	1.00	Stalk	14.8	0.47	No
Sidalcea virgata	45	0.577	0.432	2.81	Stalk	15.5	25.12	Yes
Vicia hirsuta	26	0.072	0.203	1.00	Branch	27.6	1.98	No
Vicia sativa	28	0.127	0.175	1.00	Branch	6.1	0.77	No
Vivia villosa	21	0.200	0.178	1.00	Branch	85.0	17.01	No

Table 3 Flower and nectar density by site [– species not present at the site, *U* sampled units (see Table 2), *TS* total sugar (mg)]

Species	Willow Creek		Coburg		Fir Butte		Bailey Hill	
	U/m^2	TS/m^2	U/m^2	TS/m^2	U/m^2	TS/m^2	U/m^2	TS/m^2
Allium amplectens	0.76	17.41	–	–	–	–	0.22	5.09
Anthemis arvensis	–	–	–	–	0.13	0.38	–	–
Bellis perennis	0.00	0.0	0.00	0.00	–	–	–	–
Calochortus tolmiei	–	–	0.19	0.29	–	–	–	–
Camassia quamash	0.12	0.58	0.00	0.00	0.00	0.01	0.04	0.22
Chrysanthemum leucanthemum	11.24	102.04	0.99	8.95	–	–	10.73	97.44
Cryptantha intermedia	–	–	0.32	0.24	–	–	–	–
Eriophyllum lanatum	0.29	1.14	0.20	0.79	0.02	0.07	0.03	0.10
Hypochaeris radicata	–	–	0.87	3.07	2.60	9.17	–	–
Lathyrus sphaericus	–	–	–	–	0.33	0.07	–	–
Linum angustifolium	4.88	0.63	10.87	1.40	0.20	0.03	–	–
Lupinus laxiflorus	–	–	0.31	0.66	–	–	–	–
Lupinus sulphureus spp. *kincadii*	0.79	8.09	–	–	0.44	4.57	0.20	2.06
Myosotis discolor	0.09	0.04	0.06	0.03	0.36	0.17	0.42	0.20
Sidalcea virgata	0.08	2.01	0.24	6.11	0.02	0.56	–	–
Vicia hirsuta	3.01	5.98	–	–	6.33	12.56	3.09	6.13
Vicia sativa	0.40	0.31	–	–	10.67	8.21	4.42	3.41
Vivia villosa	0.52	8.84	–	–	0.89	15.12	–	–
Total flower density	22.18		14.06		21.99		19.16	
Total native flower density	2.04		1.27		0.49		0.49	
Total nectar density		147.06		21.55		50.92		114.64
Total native nectar density		29.22		8.10		5.20		7.47

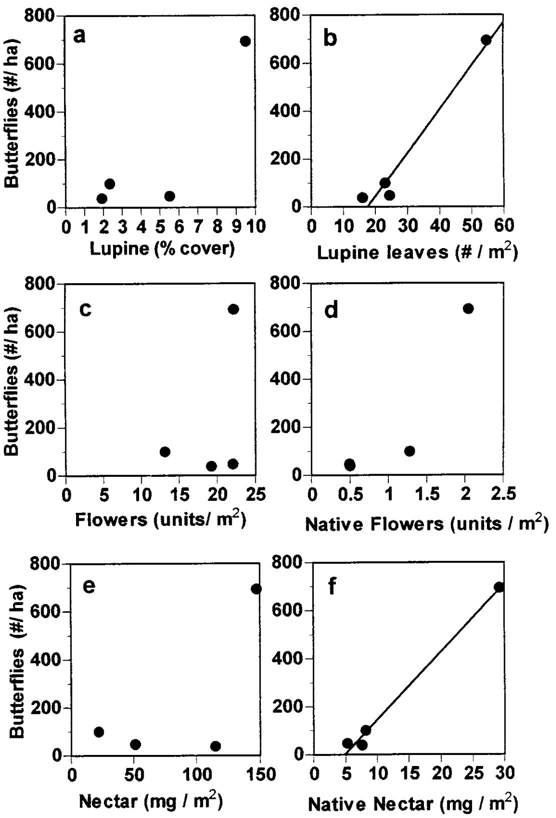

Fig. 1 Relationship between resources and Fender's blue population density in 1997: percent cover of lupine (**a**), density of lupine leaves (linear regression, $r^2 = 0.95$, $P = 0.018$) (**b**), flower abundance for all available flowers (**c**), native flowers (**d**), all available nectar (**e**), and all native nectar (linear regression: $r^2 = 0.99$, $P = 0.004$) (**f**). Where not shown, linear regressions were not statistically significant. Note, hostplant abundance is from 1997 except at Coburg, as indicated in Table 1

and 1996. Trends evident in the initial analyses were similarly striking in other years despite wide fluctuations in butterfly densities. Fender's blue densities were significantly associated with lupine leaf densities ($P < 0.01$ in all years) but not associated with percent cover ($P > 0.1$ in all years). Similarly, butterfly densities were not associated with total flower density ($P > 0.6$ in all years), native flower density ($P > 0.1$ in all years) or total sugar density ($P > 0.2$ in all years), but were significantly associated with native sugar density ($P < 0.02$ in all years).

Discussion

The abundance of both juvenile and adult resources influences Fender's blue population size. However, quick assessments of habitat may not reveal these associations. Two aspects of juvenile resources and four aspects of adult resources were examined in this study. In each case, factors that were seemingly appropriate (lupine percent cover, total nectar density, and total and native flower density) did not uncover relationships between resources and butterfly numbers while more detailed assessments of resource availability (lupine leaf density and native nectar density) revealed significant relationships (Fig. 1).

In terms of juvenile resources, we examined percent cover of hostplant lupines and density of lupine leaves. Percent cover is often useful in assessing overall plant abundance at a coarse level. However, lupine leaves, not lupine cover, are the key resource for larval Fender's blue. Although lupine cover is correlated with lupine leaf density (Kendall's tau, $P = 0.04$), the relationship is not tight enough for lupine cover to be a viable index of leaf density. Fender's blue density was associated with leaf density but not with cover in any year (Fig. 1a,b). The need to assess leaf density, not just cover, may stem from the structure of lupine plants in which some plants are more "layered" than others. A more layered plant would not increase the percent cover but would increase the amount of food available to larval butterflies. We note two additional caveats. First, lupine cover and lupine leaf densities were estimated using different field methods: line-intercept for cover and quadrat sampling for leaf density. Methodological differences, rather than the biology, may contribute to the conclusion that leaf density, and not percent cover, is associated with butterfly density. However, the more detailed method, quadrat sampling, resulted in a positive association between butterfly numbers and resource availability. This suggests that, even if our results are partially an artifact of the sampling method, fine-scale measures may be required when investigating resource limitations. The second caveat is that we cannot determine the shape of the relationship between resource availability and population size with these data. For example, the relationship between lupine cover and butterfly population density is suggestive of a threshold effect, whereby the Fender's blue requires a minimum percent of lupine cover to support a high population density (Fig. 1a), but the number of sites sampled was not sufficient to statistically evaluate this observation. However, regardless of the shape of the association, the data strongly indicate a response of butterfly population density to hostplant availability.

We assessed availability of adult resources in four ways: abundance of all nectar flowers, abundance of native flowers, total nectar from all flowers and total nectar from native nectar flowers. Flower abundance is the easiest factor to measure. It requires sampling all flowering plants on which the butterflies have been observed nectaring. However, since all flowers are not equal in their nectar content, estimating resource availability simply from flower numbers can lead to serious errors – as happened here. Overall, flower abundance does not predict butterfly abundance and native flower abundance is only weakly associated with butterfly abundance (Fig. 1c,d). Quantifying nectar, the aspect of the resource that the butterflies use, is a far more complex and labor-intensive task. When we quantified nectar, we uncovered significant associations. Although the abundance of nectar from all species does not predict butterfly numbers, the abundance of nectar from all native species is significantly associated with butterfly numbers (Fig. 1e,f).

The association between Fender's blue density and native nectar density is not surprising given the preference of Fender's blue for native flowers. Fender's blue butterflies are more often observed nectaring on native flowers than non-native flowers (Results; Wilson et al. 1997). Observations in 1994 by Schultz are consistent with those in our current study. Of 315 nectar observations at Willow Creek in 1994, 244 were on native flowers even though native flowers accounted for only 5% of the available flowers in that year. In particular, 34% of the observed nectar visits were to one native flower, *S. virgata*, while one exotic flower, *C. leucanthemum*, accounted for more than 80% of the available flowers. The results speak to a need to incorporate peculiarities of a species' behavior into resource assessments. For example, Fender's blues do not seem opportunistic in terms of trying new flowers. In the course of this study, we attempted to add nectar experimentally to a site using artificial nectar and flowers. In about 12 h of observations, only one Fender's blue briefly investigated our flowers while other local butterfly species came and sipped nectar from the artificial flowers. These species included ringlets (*Coenonympha ampelos*) and anise swallowails (*Papilio zelicaon*). In addition, in this study, although 2% of available flowers at Fir Butte were native, none of our nectar observations were at native nectar sources. Native nectar sources at Fir Butte are few and are often not intermixed with the hostplants. Thus it is possible that Fender's blues are not finding the native nectar at Fir Butte.

This study is unusual in jointly considering the effect of both larval and adult resources on population size. Surprisingly, few studies have investigated the shared contribution of adult and larval resources to population size. In five studies, biologists observed that adult resources affect butterfly life history traits and/or population size, but did not consider larval resources (Boggs and Ross 1993; Hill 1992; Hill and Pierce 1989; May 1993; Murphy et al. 1983). In another four studies, biologists investigated correlations between nectar source distribution, hostplant distribution and butterfly life history traits, but did not look at the effect of these factors on population size (Grossmueller and Lederhouse 1987; Murphy 1983; Murphy et al. 1984; Rodrigues et al. 1993). In addition, while five of these nine studies investigated resource limitation in the field, none of them considered the effect of both nectar and hostplant densities across a number of sites.

Assessing food resources is one of the most basic requirements in considering management for an endangered species. Although many species decline due to outright habitat loss, an increasing number are suffering from habitat degradation. These changes may include loss of key food resources, as is certainly the case for the Fender's blue. For example, Fir Butte was lightly plowed in the early 1980s. Kincaid's lupine survived relatively intact because its deep roots allowed it to lie dormant for a few years and reemerge after the disturbance. However, most of the native wildflowers were lost. Butterflies at this site, with fewer than 100 butterflies in 4 of the last 5 years (Schultz 1998), hover on the brink of extinction and might be rehabilitated by augmenting native nectar flowers.

Finally, resource availability is often a critical factor in determining the distribution and abundance of species. At a broad scale, both the Fender's blue and the Kincaid's lupine are only found in the Willamette Valley in Oregon (Hammond and Wilson 1993; Wilson et al. 1997). Within this area, the lupines persist only in the upland prairies of the valley. The Fender's blue cannot survive in the absence of its larval hostplants and thus the butterflies are found exclusively in or near lupine patches. Further limiting is the need for high densities of native nectar sources. Associations such as this are important in determining a species' distribution and abundance across the landscape. As resource distributions change, due to large-scale geologic events such as ice ages or shorter-scale changes such as those resulting from global climate change, the distribution and abundance of species such as the Fender's blue will also change. How they will do so in the coming years is still unknown, but studies investigating the manner in which resources influence species distributions will aid in our understanding of ecological communities in the coming century.

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