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Effects of genetic structure of *Lupinus arboreus* and previous herbivory on *Platyprepia virginalis* caterpillars

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Abstract Two leaf-feeding caterpillars, western tussock moth (*Orgyia vetusta*) and ranchman's tiger moth (*Platyprepia virginalis*) are abundant on *Lupinus arboreus* along the California coast. Previous experiments and observations suggested that feeding caused by either of these two folivores could reduce the performance and possibly the abundance and distribution of the other species. Previous common garden experiments also indicated that genetically determined characteristics of the host plants were important for *O. vetusta*. Here we examined the effects of familial origin of the host plant, and previous damage caused by *O. vetusta* on the abundance of *P. virginalis*. Plants with parents from one of three locations had higher numbers of *P. virginalis* than plants with parents from the other two locations. However, this effect of plant origin depended on the statistical analysis and was not as strong as the effect of prior damage by *O. vetusta* on numbers of *P. virginalis*. Counter to our expectation, bushes that supported higher levels of damage by *O. vetusta* in the previous summer had more *P. virginalis* caterpillars. This strong effect could result by both moth species selecting bushes with the same traits or as the result of herbivory by *O. vetusta* enhancing the susceptibility of bushes for *P. virginalis*.

Key words Herbivory · Plant-insect interactions · *Lupinus arboreus* · Induced susceptibility · Plant origin

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Introduction

Many factors have been proposed to explain the abundance and distributions of herbivorous insects. Recently several authors have argued that plant traits are likely to play an important role (Whitham 1983; Hunter and Price 1992; Harrison and Cappuccino 1995). Variation in plant quality that affects herbivore populations may be genetically determined (reviewed by Karban 1992) or may change in response to herbivory (reviewed by Karban and Baldwin 1997). Prior herbivory may make plants more resistant or more susceptible to subsequent herbivory. Surprisingly few studies have considered both genetic and induced sources of plant variation simultaneously and attempted to evaluate their relative importance.

Plants in nature suffer attack from many different herbivore species. Some traits may provide generalized resistance against many species. For example, pressurized latex provides leaves of some plants with defenses that are effective generally against a wide variety of herbivore species (Dussourd and Denno 1994). Other plant traits may be repellent to some herbivores but attractive and/or nutritive to other herbivore species. For example, damage to squash leaves induces changes that make them more attractive and more susceptible to some beetles but less attractive and less susceptible to other beetle species (Carroll and Hoffmann 1980; Tallamy and McCloud 1991). Divergent effects of plant resistance traits on different herbivores have been hypothesized to explain the maintenance of plasticity in resistance traits (Adler and Karban 1994). Without such divergent effects, the most generally resistant plant phenotypes might be expected to exclude those that are less generally resistant. Therefore, it is of interest to determine how general plant resistance or susceptibility is. In other words, are plants that are resistant or less preferred by one herbivore likely to be resistant or less preferred by others?

The herbivores that feed on bush lupine, *Lupinus arboreus*, at the Bodega Marine Reserve (Sonoma

County, California) have been particularly well studied (Strong et al. 1995). Two leaf-feeding caterpillars occur in high numbers although they may not be as important to *L. arboreus* as below-ground herbivores and those that feed on reproductive tissues (Strong et al. 1995; Maron 1998).

The ranchman's tiger moth (*Platyprepia virginalis*) (Lepidoptera: Arctiidae) is univoltine at the study site, and elsewhere. Eggs hatch in late spring. The inconspicuous early instar caterpillars feed primarily on *L. arboreus* and perhaps several thistle species during the dry summer and autumn seasons when most other plants are dormant (R. Karban, personal observation). It is during this time that most mortality occurs for *P. virginalis*. Once the rains come in winter, many other plants leaf out and caterpillars grow rapidly, feeding on a variety of host plants, including *L. arboreus*. The success of later instar caterpillars is affected by their host plants and these caterpillars show considerable discrimination among host plant species (English-Loeb et al. 1993; Karban and English-Loeb 1997).

The western tussock moth (*Orgyia vetusta*) (Lepidoptera: Lymantriidae) forms persistent, localized outbreaks that completely defoliate bushes during the late spring and summer; sites of localized outbreaks have persisted for at least 10 years (Harrison 1995, 1997). Adults are flightless and caterpillars are restricted to feeding on *L. arboreus* at the study site. An early experiment indicated that tussock caterpillars forced to feed on branches that had been damaged earlier in the season by *P. virginalis* grew less rapidly, attained lower pupal weights, and produced fewer eggs than caterpillars reared on branches that had recieved no damage by *P. virginalis* (Harrison and Karban 1986). This suggested that populations of *O. vetusta* might be reduced by host-plant-mediated competition with *P. virginalis*, a hypothesis that was not supported by later work. Lupine quantity was found to limit populations of *O. vetusta* (Harrison 1994) although the persistence of high populations on bushes that had been repeatedly defoliated suggested that plant quality did not limit populations. Experimental manipulations of levels of defoliation in one year did not affect weights at pupation or rates of dispersal of *O. vetusta* in the following year (Harrison 1995).

In summary, early work showed that herbivory by *P. virginalis* affected caged caterpillars of *O. vetusta*. Field observations made it clear that such an effect was not important, as *P. virginalis* populations never reached levels at which they defoliated their host plants and *O. vetusta* outbreaks persisted on bushes that had been completely defoliated by previous generations of *O. vetusta*. However, the high levels of defoliation by *O. vetusta* and the apparent sensitivity of *P. virginalis* to host plant quality suggested that outbreaks of *O. vetusta* during the summer could reduce populations of early instars of *P. virginalis* which would become apparent during the following spring.

The hypothesis that resistance induced by *O. vetusta* could reduce populations of *P. virginalis* was supported by negative associations in the distributions of these two species at the Bodega Marine Reserve. During the summer of 1992, D.R. Strong scored and marked *L. arboreus* bushes depending upon whether they received low, medium, or high levels of defoliation by *O. vetusta*. We counted the number of *P. virginalis* caterpillars that were feeding on these same bushes on 30 March and 2 April 1993. Bushes which had higher levels of defoliation by *O. vetusta* supported fewer *P. virginalis* caterpillars (Table 1). While suggestive, these data are difficult to interpret because the three levels of defoliation were not interspersed (Hurlbert 1984). High defoliation occurred on the northernmost bushes, medium defoliation to the south, and the least defoliation on the southernmost bushes. Defoliation or some other factor which also followed a north-south gradient could have produced this distribution. A study in which the levels of defoliation were spatially interspersed is necessary to separate these hypotheses.

In this paper we report on a common garden study of the effects of plant origin and previous defoliation by *O. vetusta* on the populations of *P. virginalis* caterpillars. We attempt to answer the following questions:

1. Does the geographic origin of *L. arboreus* influence the number of caterpillars that it supports?
2. Since geographic origin may affect plant size, does plant size explain the relationship between origin and caterpillar abundance?
3. Is resistance general, such that those families that are resistant to *O. vetusta* are also resistant to *P. virginalis*?
4. Does previous defoliation by *O. vetusta* affect the number of *P. virginalis* caterpillars?

Materials and methods

Controlling plant genotype and measuring *O. vetusta* levels

Seedlings of *L. arboreus* were produced by controlled crosses and grown in a common garden from January 1996 to the present at the Bodega Marine Reserve. This plant is the dominant shrub in the grasslands at the study site (Barbour et al. 1973) although individuals seldom live for more than 8 years (Davidson and Barbour 1977; Maron 1998). Crosses were made with parents from three different origins (areas) on the reserve within 0.7 km of each other, which had three different historical herbivore regimes. Plants from Mussel Point were defoliated by *O. vetusta* every summer from at least 1983 to 1993 (Harrison 1995; R. Karban and P.M. Kittelson,

Table 1 Negative association between defoliation by *Orgyia vetusta* and numbers of *Platyprepia virginalis* at Bodega Marine Reserve

Level of defoliation by *O. vetusta*	Number of bushes	Mean number of *P. virginalis*	SE
Low	19	2.63	0.39
Medium	17	2.06	0.41
High	26	0.92	0.21

personal observations). Bushes from the Dunes site have not been defoliated during any summer from 1983 to the present. Plants from the Bayshore site had not been defoliated from 1983 to 1996 although they suffered varying levels of defoliation by *O. vetusta* during the 1997 season. Our common garden with all three seed origins represented was located at this Bayshore site.

Five maternal plants were crossed in spring 1995 with six paternal plants from each of the three sites. In our analyses these maternal and paternal lines are considered to be nested within the three sites. Each maternal × paternal combination was replicated six times and placed randomly in the common garden in February 1996 in three blocks. Plants in the common garden received relatively low levels of herbivory by *P. virginalis* and no herbivory by *O. vetusta* until the summer of 1997. During this summer, natural populations of *O. vetusta* became high in the garden and some bushes were defoliated. The extent of this population was evaluated on 18 August and bushes were categorized as having 0, 1–5, 6–10, 11–20, or >21 *O. vetusta* caterpillars on this date. An analysis of this outbreak of tussock moths is given elsewhere (Kittelson 1998).

The size of each plant was estimated in August 1997 by multiplying the height of each bush by two measures of width taken at right angles to each other.

Measuring herbivory by *P. virginalis*

By 25 February 1998, 334 of the original 540 seedlings were still alive in the common garden. At this time, *P. virginalis* caterpillars had not begun to feed and bask; they were still inconspicuous and none were observed on the lupine foliage. Caterpillars were first observed on lupine bushes on 13 March 1998. Populations were censused by examining the foliage of each bush on 9 dates between 13 March and 3 May 1998; by this later date the vast majority of caterpillars had pupated. Because the bushes were censused repeatedly, many caterpillars were counted more than once. The number of *P. virginalis* caterpillars from these censuses represents an estimate of the level of herbivory by this species that each bush recieved during the season rather than a true estimate of caterpillar population size.

Statistical analyses

Analyses were conducted to explain the variance in the number of *P. virginalis* caterpillars observed over the 1998 season. These analyses were conducted in several different ways because each method has unique advantages as well as limitations. We conducted a mixed model analysis of covariance (SAS Proc GLM) to determine the effects of geographic origin of lupine bushes (a fixed effect), and maternity and paternity (random effects) nested within geographic origin. Also included in this model was our index of the population of *O. vetusta* during the previous spring (a covariate), plant size (a second covariate) and location within the common garden (block). Since maternity and paternity and plant size were found not to influence numbers of *P. virginalis*, these variables were not considered in subsequent analyses. This parametric analysis is very powerful and allows us to consider several factors simultaneously (using type III sums of squares). However, this analysis assumes that our data are normally distributed, an assumption that our data did not fulfill and could not be made to fulfill by transformations.

One solution to this problem is to use multiway log likelihood ratio tests (*G*-tests) to determine relationships between variables; these tests make no assumptions about the distributions of the variables (Sokal and Rohlf 1969). These tests do not allow as many factors to be considered as the parametric test because observations should be lumped so that classes or cells used in *G*-tests have values greater than 5 (Sokal and Rohlf 1969, p. 565). We conducted two *G*-tests. The first considered the effects of geographic origin of plants and populations of *O. vetusta* in 1997 on presence or absence of *P. virginalis* in 1998. The second analysis considered the relationship between populations of *O. vetusta* in 1997 and numbers of *P. virginalis* in 1998. Because this later analysis did not include the effects of geographic origin of the bushes we were able to consider three levels of abundance of *P. virginalis* rather than merely presence/absence.

Results

The number of *P. virginalis* caterpillars per bush was influenced by the geographic origin of the *L. arboreus* host Fig. 1). This effect was marginally significant in the parametric analysis (Table 2) and highly significant in the non-parametric *G*-test that considered fewer factors (Table 3). The effect of origin of the host plant on *P. virginalis* was not affected by the level of herbivory by *O. vetusta* that the bushes received (interaction between origin and *O. vetusta* was not significant; $F_{2,242}=1.52$, $P=0.22$). Including this interaction in a saturated parametric analysis caused origin to become even less powerful as a predictor of numbers of *P. virginalis* (data not shown).

Shrubs derived from seeds that were originally from the Bayshore population supported more *P. virginalis* caterpillars in the common garden at the Bayshore site than plants derived from parents from the other two sites (Fig. 1). Plants with Bayshore parents also supported more *O. vetusta* caterpillars (Table 3). Although there was considerable variability in quality of the shrubs for *P. virginalis* depending upon the geographic origin of the parents, maternal and paternal parents within geographic sites varied little (Fig. 1, Table 2). In

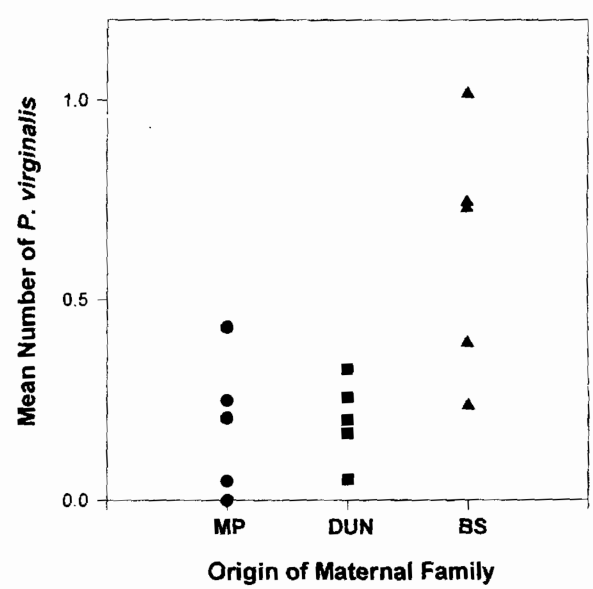

Fig. 1 Mean number of *Platyprepia virginalis* caterpillars on lupine bushes grown in a common garden from seed of three maternal origins: Mussel Point (*MP*), Dunes (*D*), and Bayshore (*BS*). Each *point* represents one maternal family originating at one of the three sites. Shrubs descended from Bayshore mothers supported more caterpillars than plants from the other two populations, although maternal lineages nested within sites explained relatively little variation in caterpillar abundance

addition, the size of the host plant was not a good predictor of the number of *P. virginalis* caterpillars that would be found over the 1998 season (Table 2).

Bushes that supported higher populations of *O. vetusta* caterpillars in 1997 also supported higher numbers of *P. virginalis* caterpillars in 1998. This positive association was statistically significant in all three analyses whether numbers of *P. virginalis* were analyzed in the parametric analysis (Table 2), presence or absence of *P. virginalis* was considered in a non-parametric *G*-test that also included geographic origin of the host bush (Table 3), or three abundance categories of *P. virginalis* were considered in a *G*-test with numbers of *O. vetusta* as the only other factor (Table 4).

Table 2 Analysis of covariance of the number of *P. virginalis* caterpillars observed in 1998

Source	*df*	MS	*F*	*P*
Origin	2	4.250	2.69	0.07
Block	2	0.175	0.11	0.90
Female (Origin)	12	0.937	0.91	0.54
Male (Origin)	15	0.577	0.57	0.89
Female × Male (Origin)	59	0.976	0.61	0.99
O. vetusta	1	16.356	10.27	0.002
Plant size	1	0.593	0.37	0.54
Error	242	1.592		

Discussion

Numbers of *P. virginalis* caterpillars were affected by the origin of the host *L. arboreus* bush. This effect was not strong and was only significant in the non-parametric analysis. Plants either of whose parents originated from the Bayshore location had higher numbers of caterpillars than bushes whose parents came from either of the other two locations (Fig. 1). Particular parents within a place of origin did not differ in the number of *P. virginalis* caterpillars that they supported. This result suggests that resistance is spatially structured; in other words that

Table 3 Log likelihood ratio test of independence between geographic origin of *Lupinus arboreus* bushes, number of *O. vetusta* in 1997, and presence/absence of *P. virginalis* in 1998

Origin	*P. virginalis*	*O. vetusta*					
		0	1–5	6–10	11–20	> 21	Total
Mussel Point	0	44	21	15	5	0	85
	≥1	1	5	3	1	2	12
	Total	45	26	18	6	2	97
Dunes	0	31	39	15	6	1	92
	≥1	2	3	1	1	2	9
	Total	33	42	16	7	3	101
Bayshore	0	13	41	21	13	8	96
	≥1	4	9	7	8	12	40
	Total	17	50	28	21	20	136
Total		95	118	62	34	25	334
All three origins	0	88	101	51	24	9	273
	≥1	7	17	11	10	16	61
	Total	95	118	62	34	25	334

Hypothesis tested	*df*	*G*	*P*
Origin × *P. virginalis* independence	2	19.466	< 0.001
Origin × *O. vetusta* independence	8	51.710	< 0.001
P. virginalis × *O. vetusta* independence	4	38.434	< 0.001
Origin × *P. virginalis* × *O. vetusta* interaction	8	−2.792	NS
Origin × *P. virginalis* × *O. vetusta* independence	22	106.818	< 0.001

Table 4 Log likelihood ratio test of independence between number of *O. vetusta* in 1997, and number of *P. virginalis* in 1998

P. virginalis	*O. vetusta*					
	0	1–5	6–10	11–20	> 21	Total
0	88 (93%)	101 (86%)	51 (82%)	24 (71%)	9 (36%)	273 (82%)
1	2 (2%)	9 (8%)	5 (8%)	3 (9%)	9 (36%)	28 (8%)
≥2	5 (5%)	8 (7%)	6 (10%)	7 (21%)	7 (28%)	33 (10%)
Total	95	118	62	34	25	334

$G = 41.396$, $df = 4$, $P < 0.001$.

neighboring plants may be more similar to each other in terms of their attractiveness or suitability to caterpillars than they are to conspecifics 1 km away. Several different factors may contribute to this effect of plant origin on numbers of *P. virginalis*. Plants from the same location may share similar evolutionary histories as well as similar short-term environments. Plants with parents that shared sites of origins also were similar in terms of traits such as growth and seed production when planted in several common gardens (Kittelson 1998).

The effect of origin on the number of *O. vetusta* caterpillars in 1997 was similar to that presented for *P. virginalis* in 1998 (Kittelson 1998). Plants with parents from the Bayshore population supported much higher numbers of *O. vetusta* than plants with parents from the other two locations.

In summary, the plants with the most caterpillars of both species were those whose parents came from the same location as that where the common garden was placed. One possible hypothesis to explain this pattern of greater caterpillar abundance on the local population of plants is that locally adapted plants were the largest (e.g., Schemske 1984; Rice et al. 1997). Although plants with Bayshore parents were larger than those with other parents (Kittelson 1998), this hypothesis was not supported. Plant size was not a good predictor of the number of *P. virginalis* caterpillars (Table 2).

Individual plants that supported more *O. vetusta* caterpillars were the same ones that supported more *P. virginalis* caterpillars. This positive association was opposite to our a priori expectation which had been based in part on the apparently negative spatial association between the two caterpillar species (Table 1). However, the negative spatial association could have been caused by unmeasured factors since all of the replicates of each level of defoliation by *O. vetusta* were clumped (Hurlbert 1984). The positive association between the number of *O. vetusta* caterpillars and the number of *P. virginalis* caterpillars that we observed in this study is unlikely to reflect spatial bias since the different levels of *O. vetusta* were well interspersed throughout the common garden. The positive association could have been caused by (1) bushes possessing genetically determined traits that made them resistant or susceptible to both herbivore species or (2) environmentally determined traits. One possible source of environmental variation is previous herbivory. In other words, bushes that were not originally attractive hosts for *P. virginalis* may have become so as a result of being fed upon by *O. vetusta*. There are numerous examples of induced susceptibility involving caterpillars and their woody host plants (Karban and Baldwin 1997). It is impossible to distinguish between these two hypotheses because levels of defoliation by *O. vetusta* were not randomly assigned to bushes.

L. arboreus at Bodega Bay has become a model system to study interactions between herbivore species and between herbivores and their host plants (e.g., Strong et al. 1995, and many others). We now have a clearer understanding of the interactions between the two abundant folivorous caterpillars in this system. *P. virginalis* induces resistance against *O. vetusta* (Harrison and Karban 1986) but this induced response has no effect on populations of *O. vetusta* (Harrison 1995, 1997). Previous damage by *O. vetusta* does not induce resistance and does not reduce populations of *P. virginalis* caterpillars on these bushes as we had originally hypothesized.

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