

COMMUNITY ORGANIZATION OF *ERIGERON GLAUCUS* FOLIVORES: EFFECTS OF COMPETITION, PREDATION, AND HOST PLANT¹

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Abstract. Experiments were conducted to determine the relative importance of inter-specific competition, predation, and host plant quality on the success of the common herbivores of *Erigeron glaucus*, the seaside daisy. Leaves of *E. glaucus* were attacked by spittlebugs (*Philaenus spumarius*), plume moth caterpillars (*Platyptilia williamsii*), and thrips (*Apterorhrips septicornis*).

Each species of herbivore was affected strongly by only one of the biotic factors examined. For spittlebugs, damage caused by caterpillars increased rates of desiccation and mortality of nymphs. This competitive effect probably caused the negative association between late-instar spittlebug nymphs and caterpillar damage wherever both species were encountered along the California coast. Plume moth caterpillars were most strongly affected by predator exclusion, at least during the late spring. Chicken-wire cages that excluded birds resulted in greater numbers of caterpillars on single rosettes and on whole clonal mats. *Passerculus sandwichensis*, Savannah Sparrows, were likely responsible for this effect which was only found during the season when adult birds were feeding insects to nestlings. On San Miguel Island, Savannah Sparrows were absent, densities of caterpillars were greater than on the mainland, and caging had no effect on caterpillar survival; these observations were all consistent with the hypothesis that Savannah Sparrows were important predators on the mainland.

The factor that was most important for each herbivore species did not interact with other biotic factors. The relative ranking of the factors for each species was similar among the 3 yr of the experiments, with only one exception. Observations suggested that experiments conducted at Bodega Bay were representative of this community at other locations in California where all of these species were present.

A scheme is proposed as a first step in predicting the importance of various biotic factors in herbivore community organization. If effects of predation, parasitism, or physical disturbance are very strong, host plant related competition and host quality are likely to be unimportant. If predation and disturbance are relatively less important, factors that reduce the choices available to an individual herbivore make host quality and interspecific competition more likely to play a significant role.

Key words: *California; community organization; field experiment; herbivores; host plant variation; interspecific competition; phytophagous insects; plant-insect interaction; plume moth; predation; spittlebugs; thrips.*

INTRODUCTION

For several decades ecologists have been arguing about the importance of various processes that can organize communities and determine population sizes. These arguments have been based on observations, experiments, and mathematical models. However, they share the characteristic of being concerned with only one primary factor, be it interspecific competition, predation, etc. Proponents of opposing positions have generally argued yes/no sorts of questions (e.g., either density-independent factors can affect populations over time or they cannot, either interspecific competition organizes communities or it does not).

In this study I have attempted a more inclusive ap-

proach to community organization. Rather than focusing on a single factor or trying to demonstrate the existence of any one process, I have sought to assess the relative importance of several different factors. I simultaneously examined the relative contributions of interspecific competition, predators and parasites, and host plant clonal variation upon the success of the common herbivores in one system. The system is simple enough for major components, including the clonal identity of the host plant, the density of herbivores, and the presence or absence of predators and parasites, to be experimentally manipulated in the field. Thus, I can treat the survival, growth rate, and mass at maturity of the herbivores as an analysis-of-variance problem and partition the effect of each factor upon these estimates of herbivore performance. Instead of yes/no questions, I have asked the question: how much variation is attributable to each factor?

¹ Manuscript received 1 August 1988; revised 3 October 1988; accepted 3 November 1988.

NATURAL HISTORY

The system includes the host plant, *Erigeron glaucus*, its three abundant herbivores, and their predators and parasites. *Erigeron glaucus*, the seaside daisy, is a native composite that grows on coastal headlands and dunes of the Pacific. It forms clumps of one to several hundred genetically similar rosettes that are connected at or just below ground level. *E. glaucus* remains green throughout the entire year, one of the few plants in the coastal prairie to do so. It produces most new leaves during spring and, to a lesser degree, during autumn. Single rosettes may be clipped and rooted during the rainy winter season.

Erigeron glaucus is abundant at the study site, south of Horseshoe Cove at the Bodega Natural Reserve, California. A detailed description of the geography, climate, and natural history of the study site was given by Barbour et al. (1973). The three common folivorous herbivores of *E. glaucus* at the study site were *Philaenus spumarius* (Homoptera: Cercopidae), the meadow spittlebug, *Platyptilia williamsii* (Lepidoptera: Pierophoridae), the calendula plume moth, and *Apterorthrips secticornis* (Thysanoptera: Thripidae). Less common folivores include *Friscanus friscanus* (Homoptera: Cicadellidae) and *Uroleucon erigeronensis* (Homoptera: Aphididae). Flowers and seeds are fed upon by *Tephritis ovatipennis* (Diptera: Tephritidae).

The experiments reported here have concentrated on factors affecting *P. spumarius* and *P. williamsii*. The two other homopterans were too rare to use in these experiments. The thrips were more common but were too small to manipulate and monitor as individuals. Factors that affected populations of thrips are described elsewhere (Karban 1987).

Both *P. spumarius* and *P. williamsii* were abundant at the study site each year from 1982 to 1987. Both feed on the foliage, particularly on the newly expanded buds. Both herbivores are relatively sessile, completing their entire immature development on a single rosette. Both are generalists over their geographic ranges, but at Bodega Bay the great majority of individuals of both species use *E. glaucus* as their most common host.

Spittlebugs are univoltine and first-instar nymphs hatch in early March from overwintering eggs. Spittlebug nymphs suck xylem fluid (Severin 1950, Wiegert 1964a, Horsfield 1978). Factors that affect populations of *P. spumarius* at several other locations have been relatively well studied. Desiccation is an important source of mortality for nymphs and climatic conditions correlate well with the distribution and density of *P. spumarius* (Weaver and King 1954). Shelters, which prevent desiccation, were shown to be an important, and potentially limiting, resource for nymphs in Oregon (McEvoy 1986). Survivorship of nymphal spittlebugs was significantly reduced on rosettes that either previously or concurrently hosted a plume moth caterpillar (Karban 1986). The probable mechanism re-

sponsible for this strong negative interaction was that caterpillar feeding made the new buds unavailable to spittlebug nymphs and new buds were where nymphs were best protected against desiccation (Karban 1986). Intraspecific competition probably does not occur for *P. spumarius* (McEvoy 1986) and several workers have observed that nymphal mortality is inversely density-dependent (Everly 1959, Wiegert 1964b, Whittaker 1973, Mangan and Wutz 1983). Nymphs in groups benefit from the spittle of conspecifics without suffering many other negative effects of crowding. Nymphs that fed on leaves with relatively high concentrations of amino acids in their xylem had higher survival than those fed on leaves with lower concentrations, suggesting the importance of host plant quality (Horsfield 1977). Spittlebug nymphs are attacked infrequently by predators and parasites in North America (Weaver and King 1954, Whittaker 1971), and I have observed few instances of predation and no parasitism at the study site.

Plume moths complete three or four overlapping generations without an extended dormant period at Bodega Bay (Lange 1950, R. Karban, *personal observation*). Larvae complete their development on a single healthy bud, often consuming it completely. Rarely were two early-instar caterpillars found on the same rosette in this study (of 385 rosettes with one caterpillar, 15 had two caterpillars). Because of the uncommonness of such co-occurrences, intraspecific competition is not likely to be an important source of mortality. Similarly, interspecific competition with spittlebugs and thrips was not found to reduce the survivorship of plume moth caterpillars in field experiments (Karban 1986).

Predators and parasites may play an important role in regulating populations of the plume moth. Several parasitic wasps have been reared from *P. williamsii*. *Diadegma chrysostictum* (Hymenoptera: Ichneumonidae) is the most common parasitoid of *P. williamsii* along the central California coast (Lange 1950, Bragg 1971, R. Karban, *personal observation*). It is a generalist with a world-wide distribution, attacking many other host species (Fisher 1959, 1961, 1962). At Bodega Bay, *D. chrysostictum* also attacks *Platyptilia carduidactyla* (Bragg 1971) but this moth is far less common than *P. williamsii* (R. Karban, *personal observation*). *D. chrysostictum* emerge from host prepupae to spin conspicuous silken grey cocoons; successful parasitism can thus be readily documented. Other generalist ichneumonid parasitoids have been reared from *P. williamsii*: *Diadegma acuta*, *Bracon hyslopi*, *Scambus pterophori*, and an undescribed *Phaeogenes* sp. (Bragg 1971). All of these latter species are rare at Bodega Bay. Several species of spiders are commonly associated with seaside daisy, and I have observed instances of spider predation on *P. williamsii* caterpillars. Song Sparrows (*Melospiza melodia*), Savannah Sparrows (*Passerculus sandwichensis*), and

White-crowned Sparrows (*Zonotrichia leucophrys*) are abundant year-round residents at Bodega Bay. Savannah Sparrows are more often found feeding in the shorter vegetation of the coastal prairie than the other two sparrows and I have observed Savannah Sparrows taking plume moth caterpillars. There is no record of any parasitic microorganism occurring in plume moth larvae, despite some attention given to potential pathogens of the economically important *P. caruidactyla* (Tanada and Reiner 1960).

METHODS

Simultaneous experiments were conducted to assess the relative importance of host clone, interspecific competition, and predators and parasites on the performance of spittlebugs and plume moth caterpillars.

Effects of host variability

Naturally-occurring variability in host plant quality can affect survival, growth rate, and fecundity of the herbivores feeding on that host. Effects of host clone were assessed by comparing the success of the herbivores on cuttings of three clones that were grown in a common garden in the field at Bodega Bay, where *Eriogon glaucus* and its associated herbivores occur naturally. In order to identify clones that were likely to vary in suitability to spittlebugs and plume moths, I censused herbivore densities on 10 clones during 1982 and 1983 in situ, where they grew naturally. I selected 3 of these 10 clones that had the greatest range in densities of the herbivores. The three clones grew within 500 m of one another and were described in detail elsewhere (Karban 1987). I transplanted cuttings (rosettes) from each of the three clones to a common garden that provided a relatively homogeneous environment. During December 1984 I transplanted 80 rosettes of each of the three clones (240 rosettes). Rosettes were planted, at 50 cm distances from one another in a randomly determined array, into the existing vegetation. Rosettes that failed to survive between December and March were replaced but rosettes that died after March were left and not replaced. During December, 1985 and 1986, I replaced any plants in the garden that had died during the preceding year. The performances of spittlebugs, from first instar to adult, and of caterpillars, from first instar to pupation, were measured on rosettes of these three host clones during March through May of 1985–1987.

Interspecific competition

Each rosette in the experimental garden was randomly assigned to one of the four competition treatments shown in Table 1. Five, first-instar spittlebugs were placed on each rosette slated for spittlebugs, when the insects became seasonally available (early March). This density is well within the range of densities encountered naturally (Karban 1986). One first- or second-instar plume moth larva was placed on each ro-

sette slated for caterpillars at the same time as the spittlebugs were introduced. Under natural conditions at Bodega Bay, I rarely found more than one caterpillar in a single rosette (see Introduction). Garden rosettes were kept free of other spittlebugs and caterpillars by hand removal at frequent intervals unless specified in the experimental design. The effects of interspecific competition were assessed by comparing the performances of the herbivores when they occurred with the other species to their performance when they occurred alone on a rosette.

Predators and parasites

The effects of predators and parasites were assessed by comparing performances of spittlebugs and caterpillars on open- and closed-caged rosettes. Each rosette was randomly assigned to one of the two cage treatments (Table 1) and was enclosed in a sleeve cage of white polyester organdy (wedding veil material, 24 cm long \times 24 cm in circumference). Each sleeve cage had Velcro along the top and bottom edges. Sleeve cages were fastened to the stem beneath each rosette of both treatments. Each closed cage also had the Velcro fastened above the rosette so that the plant and its herbivores were completely enclosed within the cage; the open cages were left unfastened on the top. Rosettes in open and closed cages differed in several ways including availability to predators and parasites, microclimate, possibility of dispersal by caterpillars, and spittlebug nymphs away from the rosette.

Herbivore performance

I monitored the success of spittlebug nymphs and plume moth caterpillars on rosettes that differed in clonal origin, interspecific competitors, and cage treatments. For spittlebugs, I recorded the number of days that each nymph remained alive on the rosette at 4-d intervals. This is an excellent estimate of survival because nymphs were unlikely to move away from their original rosette and even less likely to establish successfully on a new rosette (R. Karban, *personal observation*). Approximately one-half the nymphs that died were found dried up on the rosette, and I assume that most of those that were not recovered had desiccated and fallen off the rosette. Growth rates of spittlebugs were estimated by noting the instar of each nymph at 4-d intervals. The numbers of days required to reach various stages in development were then compared. Fecundity of spittlebugs was estimated by taking dry masses of male and female adults. In these experiments, the rosette was the appropriate sampling unit since the rosette was the unit that received the treatments. The five spittlebugs placed on each rosette were obviously not independent units. Therefore, a mean value for the five spittlebugs on each rosette for each performance variable (survival, growth, fecundity) was used in statistical analyses.

Estimates of plume moth caterpillar performance

TABLE 1. Experimental design to examine the effects of competitors, predators, and host clone on the success of spittlebug nymphs and plume moth caterpillars.

Competition treatments*		Predators, parasites*		Clones†		Replicates
1 caterpillar, 0 spittlebugs						
0 caterpillar, 5 spittlebugs	×	Enemies excluded	×	3 plant clones	×	10 replicates
1 caterpillar, 5 spittlebugs		Enemies have access				
0 caterpillar, 0 spittlebugs						
4 treatments	×	2 treatments	×	3 treatments	×	10 replicates = 240 rosettes

* Treatments are distributed randomly among rosettes within clones. Numbers of herbivores used in the treatments are explained in the text.

† Clones are distributed randomly in the garden.

were similar to those for spittlebugs. At 4-d intervals, the presence or absence of each caterpillar was determined. Growth rate was evaluated by determining the number of days that were required for each caterpillar to reach fourth instar and to pupate. Fecundity was estimated by measuring dry mass of pupae. Wet mass of pupae was found to correlate strongly with number of eggs at emergence ($r^2 = 0.72$, $n = 20$, $P < .001$).

Persistence of spittlebugs and plume moth caterpillars for each year's data were analyzed using SAS GLM procedure with host clone, cage, and competitors as main effects. Because sample sizes were reduced, growth rates of both herbivores, adult masses for spittlebugs and pupal masses for plume moths were combined for the 3 yr of the study and year was included along with host clone, cage, and competitors as main effects in the analyses. In these analyses clone, cage, and competitors are treated as fixed effects and year as a random effect.

Predation vs. other cage effects

Closed cages may have other effects besides excluding predators and parasites. They may, for example, prevent dispersal by caterpillars and alter microenvironmental factors. To test the effect of closed cages as a barrier to dispersal, I compared caterpillar persistence on open- and closed-caged rosettes in a greenhouse at Bodega Bay and on open- and closed-cage rosettes in the field outside the greenhouse. In the greenhouse, I had 10 rosettes enclosed in open cages and 10 in closed cages. All of the rosettes were cuttings from one clone. The rosettes were interspersed in one large fiberglass tray that was filled with soil from the study site. The spacing of plants was identical to that in the common garden described above. First-instar caterpillars were placed on each rosette on 15 March 1985 and censused at 4-d intervals. The number of days that caterpillars remained on the rosette before being found dead or disappearing was compared for the two cage treatments using a *t* test.

Another series of experiments to understand the mechanism of the cage effect was conducted in a field garden using three cage treatments. Rosettes in one treatment were enclosed in closed organdy cages. Rosettes in a second treatment were enclosed in a chicken-wire cage with 2.5-cm mesh. Rosettes in a third treatment were not enclosed in organdy or chicken wire.

One first-instar caterpillar was placed on each of 20 rosettes of each treatment on 7 June 1985, 30 March 1986, and 13 May 1986 and survival was assessed at 4-d intervals. A one-way analysis of variance of the persistence of caterpillars was conducted for each of these replicates of the experiment. This experiment allows me to separate other cage effects (dispersal, microenvironmental differences) from predation since rosettes in the chicken-wire cages are not accessible to birds but do not differ from rosettes without cages in most other ways.

Larger scale experiments

The experiments described above were all conducted on single rosettes. Results from small scale experiments may differ from trends that apply to larger patches over longer periods of time (Faeth and Simberloff 1981, Simon et al. 1981, Kareiva 1982). In addition, these experiments were conducted over only some incomplete portion of the insect's life cycle. Mortality that I measured may be compensated for and, as a result, may not affect future populations.

To resolve questions of scale and compensatory mortality, I have conducted (1) large scale experiments involving entire clonal mats to observe the effects of these manipulations on the current generation and upon the following generations of spittlebugs and plume moths, (2) experiments on San Miguel Island, California where Savannah Sparrows do not occur, and (3) analyses of association between the herbivores at several locations along the coast.

Experiments at the scale of entire clones and over more than one generation for the herbivores were only conducted for those interactions that were found to be important in the small scale experiments. Experiments that evaluated the role of interspecific competition on spittlebug populations were described elsewhere (Karban 1986). Since the small scale experiments indicated that predation was important for plume moth populations, I conducted enclosure experiments on the scale of entire clonal mats. Ten pairs of clonal mats of rosettes were selected such that the two mats of each pair were within 20 m of one another and were similar in size. One of the mats of each pair was randomly assigned to be enclosed in chicken wire (2.5-cm mesh) and the other mat served as the control. When the

experiment was begun on 16 March 1987, caterpillars were added or removed from each mat such that each had five early-instar caterpillars. On 30 March the number of these caterpillars that were still alive was recorded and densities were again adjusted so that each mat had five caterpillars. Number of caterpillars on each mat was recorded at monthly or bimonthly intervals for 15 mo. The mean number of caterpillars observed on each sampling date for the two cage treatments were compared with *t* tests.

Erigeron glaucus and *P. williamsii* are both abundant on San Miguel Island off the coast of California. However, Savannah Sparrows, presumed from earlier experiments to be important predators, are absent from this island (Diamond and Jones 1980). Twenty clonal mats were selected in Nidever Canyon on San Miguel such that pairs of mats were in close proximity to one another and were of similar size. Half of these mats were randomly assigned to be enclosed in chicken-wire cages (2.5-cm mesh) and the other mat of each pair served as an uncaged control. Five first-instar plume moth caterpillars were placed on each mat on 11 May 1987. Each mat was censused for caterpillars on 18 May and densities were again set at five caterpillars per mat. A final census of caterpillars was conducted on 26 June 1987 on the 20 clonal mats. The mean number of days that caterpillars persisted on rosettes with and without chicken-wire cages was compared using *t* tests.

Another method of assessing the generality of results from small scale experiments conducted in one single location is to examine patterns of species abundance and association over larger geographic areas. During late spring of 1988, when most spittlebug nymphs were late instars, 500 rosettes were examined at each of 13 locations for the presence or absence of the herbivore species. If competition with caterpillars results in a negative association between spittlebugs and caterpillar damage, this spatial pattern should be most pronounced when nymphs were late instars. Predators and parasites were not considered in these analyses because the rosette is not a meaningful censusing unit for these mobile species. Analyses of association were conducted for those sites in which both spittlebugs and plume moths were abundant.

RESULTS

Relative importance of factors for spittlebugs

The relative importance of factors on the success of spittlebugs was compared by examining performance on rosettes in the garden that were subjected to treatments specifying host clone, closed/open cage, and presence/absence of a caterpillar. The persistence, and hence survival, of spittlebug nymphs was not significantly influenced by the clonal identity of the host plant in the garden of experimental cuttings during any of the 3 yr (Table 2). Survival was greater inside of closed

organdy cages relative to open cages in 1985, but not in 1986 or 1987. Indeed, in 1985, the cage effect represented a twofold difference (mean \pm 1 SE time for nymphs in closed cages = 20.3 ± 1.6 d and in open cages = 10.5 ± 1.2 d) and accounted for more of the variance in persistence of nymphs than any of the other factors considered (Table 2). In all 3 yr the presence of a plume moth caterpillar resulted in a significant reduction in spittlebug persistence. Spittlebugs on rosettes without caterpillars survived ≈ 25 –33% longer than spittlebugs that co-occurred with caterpillars (Fig. 1). Although this interspecific competition was significant in all 3 yr, it accounted for little of the total variance in persistence for spittlebugs (Table 2). Of the possible pairwise and three-way interactions only the interaction between predation and competition was significant and only in 1985. This interaction was caused by caterpillars exerting a negative influence on spittlebugs in closed cages and no effect in open cages. In the absence of cages, caterpillar survival was reduced (see next section) and the caterpillars did relatively little damage to the host plant, and hence, had relatively little effect on spittlebugs.

The rate at which spittlebug nymphs reached maturity was not affected significantly by host clone, predation, or interspecific competition although it did vary from year to year (Table 3). Similarly the masses of adult spittlebugs were not affected by the experimental factors that I manipulated but did vary among years (Table 4). Several interactions were significant, however. For males in 1985 spittlebugs raised without competitors were heavier than those raised with caterpillars ($n = 8$). In 1986 and 1987, when sample sizes were greater ($n = 31$ in 1986 and $n = 37$ in 1987), male masses did not differ among competition treatments. For females, nymphs raised with caterpillars were heavier in 1985, lighter in 1986, and the same in 1987 as nymphs raised without moths. I do not attach much importance to these effects because of the overall lack of trend.

Relative importance of factors for plume moths

Plume moth caterpillars on rosettes in the experimental garden persisted longer on rosettes in completely closed organdy cages than on rosettes in organdy cages open at the top (Fig. 2). This cage effect was significant in all 3 yr and explained more of the variance in caterpillar persistence than the other factors considered (Table 5). The difference in persistence for caterpillars on rosettes in closed cages translated into large differences in the percent that survived to pupation (Fig. 2).

Additional experiments were conducted to examine the causes of the cage effect. In a greenhouse at Bodega Bay predators were not present although caterpillars were still free to disperse away from rosettes in open cages. Under these conditions, persistence was not significantly different for caterpillars in open and closed

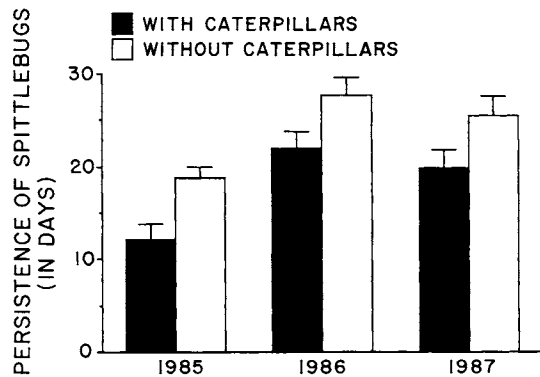


FIG. 1. Effects of caterpillars on the persistence of spittlebugs. Bars show the mean number of days + 1 SE. ANOVA results are in Table 2.

cages although the trend was for greater persistence in closed cages (Table 6). This suggests that dispersal was not responsible in the field for the difference in persistence of caterpillars repeatedly observed on open- vs. closed-cage rosettes. However, interpretation of this experiment is complicated because other factors besides predation are different between the greenhouse and the field.

An experiment was conducted in the field garden to consider persistence of caterpillars on rosettes in closed organdy cages, chicken-wire cages, and no cages. Persistence of caterpillars was higher on rosettes enclosed in either chicken-wire cages or closed organdy cages relative to uncaged moths in late spring of 1985 ($F_{2,57} = 5.7$, $P < .01$) and 1986 ($F_{2,57} = 9.7$, $P < .01$; Fig. 3). However, experiments in earlier spring of 1986 re-

TABLE 3. Analysis of variance of two estimates of the growth rate of spittlebugs.

Source of variation	ss	df	ms	F	P
Number of days to fifth instar					
Year	278	2	139	3.9	.02
Clone	88	2	44	1.3	.29
Predation (cage)	50	1	50	1.4	.24
Competition	49	1	49	1.4	.24
Interactions not significant					
Error	5370	152	35		
Total	6385	181			
Number of days to adult					
Year	471	2	236	9.9	.001
Clone	7	2	4	0.2	.86
Predation (cage)	4	1	4	0.2	.69
Competition	3	1	3	0.1	.73
Interactions not significant					
Error	2294	96	24		
Total	2865	115			

vealed no effects of cage treatments on caterpillar persistence ($F_{2,57} = 0.9$, $P = .43$; Fig. 3). These results suggest that during late spring, predators that were excluded by both chicken wire and closed organdy cages were responsible for the cage effect. These predators were not important during early spring. Savannah Sparrows are likely candidates as important predators of caterpillars during late spring at the study site.

Growth rates of caterpillars either to fourth instar or to pupation were not affected significantly by any of the treatments, either directly or through interactions

TABLE 2. Analysis of variance of the persistence time of spittlebugs for the 3 yr of the experiment.

Source of variation	ss	df	ms	F	P
1985					
Clone	256	2	128	1.3	.28
Predation (cage)	2907	1	2907	29.2	.0001
Competition	1367	1	1367	13.8	.0003
Clone × predation	55	2	27	0.3	.76
Clone × competition	366	2	183	1.8	.16
Predation × competition	481	1	481	4.8	.03
Clone × predation × competition	50	2	25	0.3	.78
Error	10 727	108	99		
Total	16 219	119			
1986					
Clone	347	2	173	0.8	.45
Predation (cage)	162	1	162	0.8	.39
Competition	978	1	978	4.5	.04
Interactions not significant					
Error	23 366	108	216		
Total	26 686	119			
1987					
Clone	1090	2	545	2.3	.10
Predation (cage)	36	1	36	0.2	.70
Competition	976	1	976	4.2	.04
Interactions not significant					
Error	25 250	108	234		
Total	29 505	119			

TABLE 4. Analysis of variance of the adult mass for spittlebugs during the 3 yr of the experiment.

Source of variation	ss	df	ms	F	P
Males					
Year	458	2	229	14.1	.001
Clone	9	2	5	0.3	.76
Competition	18	1	18	1.2	.55
Year \times clone	58	4	15	0.9	.47
Year \times competition	128	2	64	3.9	.03
Clone \times competition	49	2	24	1.5	.23
Error	993	61	16		
Total	1713	74			
Females					
Year	428	2	214	6.0	.004
Clone	196	2	98	1.8	.40
Competition	28	1	28	0.3	.77
Year \times clone	225	4	56	1.6	.19
Year \times competition	215	2	108	3.0	.06
Clone \times competition	221	2	110	3.1	.05
Error	2617	73	36		
Total	3930				

(results not presented). Similarly, masses of pupae were unrelated to my experimental manipulations.

Do results hold at larger spatial scales?

The herbivores associated with *E. glaucus* were surveyed at 13 sites along the California coast during April 1988 (Fig. 4). Densities of plume moth caterpillars were greater on the two Channel Islands visited than on the mainland. On San Miguel and Anacapa islands 63 and 57% of the rosettes had caterpillars or their damage. At the 11 mainland sites surveyed, 6–39% of the rosettes had caterpillars or their damage. I found very few thrips on the Channel Islands (only one isolated population on San Miguel). Thrips (*A. secticornis*) were present at all mainland sites examined although numbers varied greatly among clumps of rosettes within sites and among sites (Fig. 4). The meadow spittlebug (*P. spumarius*) was rare or completely absent along the coast of southern California. At several sites (San Simeon Creek, Point Lobos) another species of spittlebug, *Aphrophora permutata*, was found on *E. glaucus* and on many other host plants in the coastal prairie. At all four sites in northern California where both spittlebugs (*P. spumarius*) and plume moth caterpillars were found, they were strongly negatively associated (Table 7). Rosettes with caterpillars or their damage were less likely to have late-instar spittlebug nymphs than rosettes without caterpillar damage. Presumably, this negative association is the result of reduced survival of spittlebug nymphs on rosettes that have been pre-empted by caterpillars. None of the other pairwise associations between spittlebugs, caterpillars, and thrips were significantly different from random expectation. At several sites thrips and either spittlebugs or caterpillars were negatively associated but this was inconsistent among sites and probably results from the thrips having different microhabitat preferences than the other two herbivore species (Karban 1987).

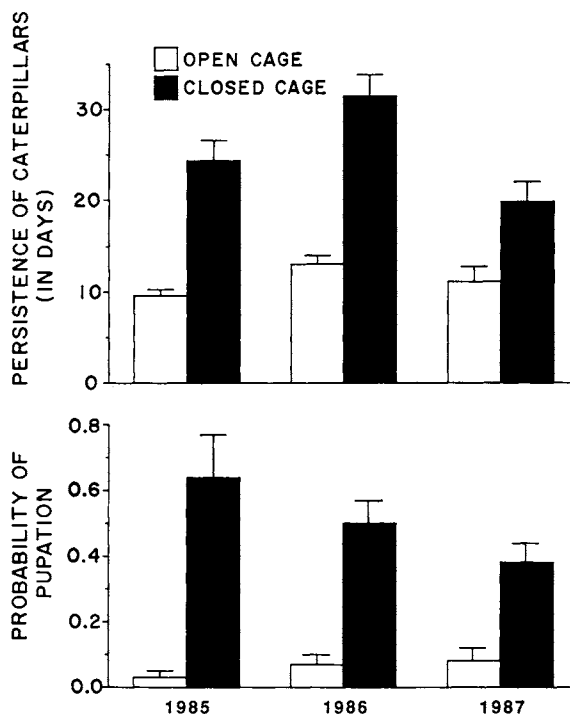


FIG. 2. Persistence and probability of pupation for caterpillars in open and closed organically cages. Bars show means and one standard error.

Prior experiments involving single rosettes at Bodega Bay during late spring demonstrated that caterpillar survival was greater on rosettes that were enclosed in chicken-wire cages (Fig. 3). An analogous experiment was established with 20 large mats of *E. glaucus* at Bodega Bay divided into two treatments: those with and without chicken wire around each mat. Five caterpillars were placed on each mat on 16 March 1987 (Fig. 5). By 30 March, the number of caterpillars remaining on the mats protected by the bird enclosure cages was significantly greater than on unprotected control mats (Fig. 5, $t = 5.15$, $df = 18$, $P < .01$). Caterpillars were again stocked such that each mat had five early-instar individuals. Numbers on the two treatments again diverged in late spring. Natural recruitment by ovipositing plume moths peaked during late April and late June. Following the April recruitment, mats enclosed in chicken wire had greater numbers of caterpillars than controls. However, following the recruitment of caterpillars that occurred in late June, numbers of caterpillars on mats of the two treatments were not different until the following spring. Another bout of caterpillar recruitment occurred in the spring of 1988. During late spring of 1988, numbers of caterpillars were greater on protected mats than on controls (Fig. 5; for May 1988, $t = 2.19$, $df = 18$, $P < .05$). These results are similar to those obtained from experiments on single rosettes. They are consistent with the hypothesis that during the late spring when sparrows are feeding young, avian

TABLE 5. Analysis of variance of the persistence of plume moth caterpillars for the 3 yr of the experiment (number of days before caterpillars were found dead or had disappeared).

Source of variation	ss	df	ms	F	P
1985					
Clone	4	2	2	0.0	.99
Predation (cage)	6599	1	6599	35.3	.0001
Competition	270	1	270	1.4	.23
Interactions not significant					
Error	20 201	108	187		
Total	27 709	119			
1986					
Clone	198	2	99	0.5	.60
Predation (cage)	10 175	1	10 175	52.0	.0001
Competition	10	1	10	0.1	.82
Interactions not significant					
Error	21 149	108	196		
Total	32 103	119			
1987					
Clone	938	2	469	2.1	.13
Predation (cage)	2262	1	2262	9.9	.002
Competition	78	1	78	0.3	.56
Interactions not significant					
Error	24 762	108	229		
Total	28 524	119			

predation is an important source of mortality for plume moth caterpillars. However, these experiments also suggest that the effects of predation may be short lived and that other factors more strongly affect plume moth numbers during other seasons.

An experiment to assess the role of Savannah Sparrows on survivorship of plume moth caterpillars was conducted on San Miguel Island. Savannah Sparrows do not breed on San Miguel, unlike the mainland. Plume moth caterpillars survived no better on rosettes protected by chicken-wire cages compared to rosettes without cages on San Miguel (Table 8). This was different from the results of caging experiments conducted at Bodega Bay, where Savannah Sparrows were abundant in the grassland and chicken-wire cages increased persistence for caterpillars (Figs. 3 and 5).

DISCUSSION

This and previous studies (Karban 1986, 1987) have considered the success of three folivorous insects on

TABLE 6. Persistence of caterpillars in the greenhouse where predators were absent but caterpillar dispersal was possible (number of days that caterpillars remained on the rosette before disappearing or being found dead).

Treatment	n	\bar{X}	SE	t	P
Open cage	10	22.8	4.2	1.03	NS
Closed cage	10	29.6	5.1		

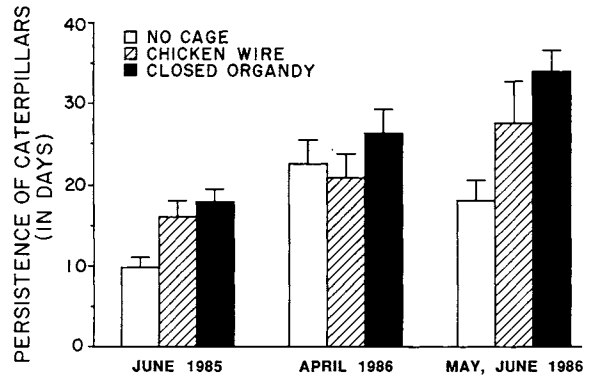


FIG. 3. Effects of chicken wire and closed organdy cages on the persistence of caterpillars at Bodega Bay. Bars show means + 1 SE.

Erigeron glaucus. For spittlebugs, asymmetrical inter-specific competition (amensalism) was a consistently important factor. Competition probably translates into differences in spittlebug population size from one year to the next (Karban 1986). This strong effect is caused by caterpillars pre-empting the habitat required by spittlebug nymphs to develop without desiccating. Spittlebugs and plume moth caterpillars are both abundant at the study site and interact frequently; spittlebugs often hatch on rosettes that have past caterpillar damage or are currently occupied by a caterpillar (Karban 1986). This interaction was not idiosyncratic to

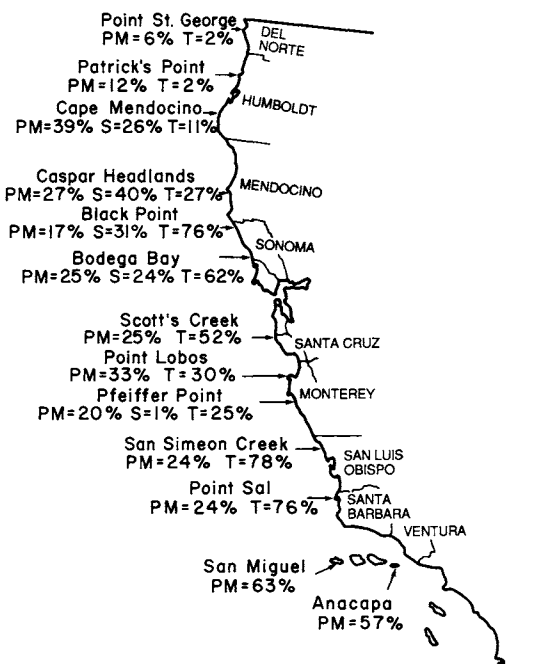


FIG. 4. Survey sites for the herbivores associated with *Erigeron glaucus*. The percentage of rosettes with plume moth caterpillars (PM), spittlebugs (S), and thrips (T) are shown. Sites where one or more of these symbols are missing had no individuals of that species.

TABLE 7. Association between spittlebug nymphs and caterpillar damage at several sites along the California coast where both species occurred.

Site	Rosettes with both	Rosettes with spittlebugs only	Rosettes with caterpillar damage only	Rosettes with neither	χ^2	P
Bodega Bay	8	114	119	259	30.2	.01
Black Point	10	143	74	273	16.6	.01
Caspar Headlands	35	163	100	202	14.5	.01
Cape Mendocino	15	116	181	188	57.4	.01

Bodega Bay. At all four sites surveyed where spittlebugs were common, they were negatively associated with caterpillar damage. However, spittlebugs were not common at many sites along the coast; several of the sites where spittlebugs were not found had relatively low densities of caterpillars at the time of the survey. Clearly, in geographical perspective, factors other than competition are also important for spittlebugs.

Predation was consistently the most important factor for plume moth caterpillars (at least during the spring generation). This result was consistent for caterpillars on single rosettes and on whole clonal mats of *Erigeron glaucus*. Savannah Sparrows are probably responsible for much of this predation. Of the birds present at Bodega Bay, only Savannah Sparrows commonly foraged on *Erigeron glaucus*. They are further implicated as important predators of plume moth caterpillars on the mainland by observations on San Miguel Island, where Savannah Sparrows are absent. On San Miguel, unlike Bodega Bay, protection by chicken-wire cages during spring did not result in increased survival for caterpillars, presumably because there were few avian predators on the island to exclude. At Bodega Bay, the chicken-wire cages produced differences in caterpillar numbers only during the spring (Figs. 3 and 5). This corresponds with the period when Savannah Sparrows are feeding nestlings and consequently are foraging ex-

tensively on insects (Johnston 1968); they are largely vegetarian during other times of the year. While avian predation probably affects densities of plume moths over much of their range, other unknown factors must be important as well. For example, at University of California Big Creek Natural Reserve, Monterey County, California, caterpillars were relatively rare (R. Karban, *personal observation*), although Savannah Sparrows were much too uncommon to be responsible (J. Smiley, *personal communication*).

For thrips, a third common herbivore on *Erigeron glaucus*, interspecific competition was found to have no detectable effect but host clonal variation was very important, as was weather to a lesser degree (Karbon 1987). Predation and parasitism were not considered in this study.

These same conclusions were reached in all 3 yr during which I ran the experiments for spittlebugs and plume moths. Indeed I was rather surprised by the lack of year-to-year variability in these results. Only for spittlebugs were the results different among the 3 yr. In 1985, but not the other 2 yr, there was a strong cage effect on spittlebug persistence. For plume moth caterpillars and thrips (Karbon 1987), yearly variability never reversed the importance rankings for the biological factors that were considered (interactions between year and other factors were not significant).

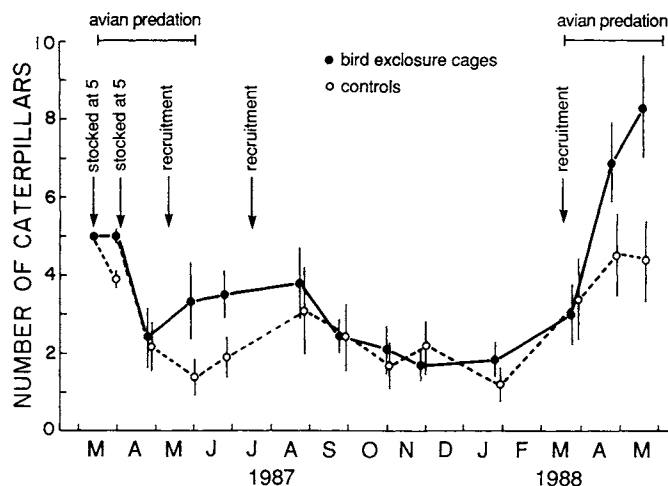


FIG. 5. Effects of wire enclosure cages around whole clonal mats of *Erigeron glaucus* upon the numbers of plume moth caterpillars. Each point shows the mean \pm 1 SE for caterpillars on 10 mats. Arrows show the dates when caterpillars were stocked and the approximate peaks of natural *Platyptilia* recruitment. Horizontal bars show that avian predation was most intense during late spring.

Variation among host plants was relatively unimportant for spittlebugs and plume moth caterpillars although it was important for thrips (Karban 1987). As with yearly variation discussed above, I was surprised by the lack of variation in the success of spittlebugs and plume moth caterpillars that could be attributed to their three different host clones. Many other workers have found that host variation was very important (e.g., Moran 1981, Service 1984) and this study supplies some of the few negative results that I am aware of. The more interesting question asks how important is clonal variation relative to other ecological factors and several workers who have tested multiple effects have reached differing conclusions (e.g., Ayres et al. 1987 and Maddox and Root 1987 find plant genotype to be less important whereas McCrea and Abrahamson 1987 and Fritz et al. 1986 find it more important than other factors).

In studying this plant-herbivore system, I attempted to understand the relative importance of several ecological factors in affecting population dynamics of the common folivorous insects. To achieve this end, most of my experiments followed cohorts of spittlebug nymphs or plume moth caterpillars through only a portion of one generation. I partitioned the variation in success of these cohorts into components causing different rates of mortality. However, the factors responsible for inflicting the greatest mortality may exert relatively little influence upon population dynamics. Indeed, understanding the relative importance of the effects of each factor upon populations demands more complex experiments conducted over more than one generation. In this system, I have reason to suspect that the factors which exert the greatest mortality also affect the population dynamics of these herbivores. Those plants which supported the greatest survivorship of spittlebug nymphs also had the greatest number of offspring during the following spring (Karban 1986). Those clones which were best for survival of thrips, consistently maintained the highest populations of thrips *in situ* and in common gardens (R. Karban 1987, and *personal observation*). However, for plume moths, the most mobile of the three herbivores, the caged plants, which had higher caterpillar survival in spring and also greater numbers of pupae, did not have more young caterpillars of the summer generation (Fig. 5). During seasons when bird predation was less intense than in the spring, factors other than predation more strongly influenced the dynamics of plume moth populations.

CONCLUSIONS

I had hoped that it would be possible to generalize about the relative importance of various factors for herbivorous insects from this and other, similar studies. Unfortunately, the results from the three folivores of *E. glaucus* and from other studies indicate that no single factor is likely to explain the success of all herbivores. Rather, the idiosyncrasies of each herbivore

TABLE 8. Persistence of caterpillars on San Miguel Island (mean number of days that caterpillars remained on the clump before disappearing or being found dead).

Treatment	<i>n</i>	\bar{X}	SE	<i>t</i>	<i>P</i>
11 May–18 May*					
No cage	10	1.5	0.5	0	NS
Chicken-wire cage	10	1.5	0.5		
19 May–26 June*					
No cage	10	3.0	1.1	0.2	NS
Chicken-wire cage	10	2.7	0.9		

* Caterpillars were added to or thinned from clumps to bring the density to five caterpillars per clump on 11 May and 19 May. Survival was assessed on 18 May and 26 June.

species appear to dictate which of several possible factors will be most important for that herbivore. To understand the organization of an assemblage of herbivores, I believe we must consider the details of the relationships of each of the individual herbivore species with its predators, competitors, and host plants. Nonetheless, several conclusions from these three herbivore species may be general observations.

In each case, a single factor was much more important than the others in explaining how well the herbivores performed. This was true even though the particular factor was different for each of the species. The factor that was important in each system, usually acted independently of other main effects. In marked contrast to much of the current excitement about indirect effects and interactions between main effects (e.g., Lawton and McNeill 1979, Price et al. 1980, Faeth 1987), these effects played almost no detectable role in this system. Using spittlebugs as an example, interspecific competition was important. The role of competition did not change across different host clones nor did it interact with predation.

Does the conclusion that no single factor is most important as an organizer of folivorous insect communities mean that no predictions or generalizations are possible? Generalities are possible but they must be made conditional upon a variety of life history, environmental, and community characteristics (see Schoener 1986 for an attempt to ordinate communities along a variety of axes). I propose that community processes be considered as a hierarchy. Parts of this scheme resemble those proposed by Hairston et al. (1960), Strong et al. (1984), and Lubchenco (1986), although this scheme emphasizes different factors.

If predation and parasitism are intense, host plant quality and interspecific competition are unlikely to affect populations of herbivores. This argument is supported by many studies. For example, rates of parasitism of leafminers on *Spartina alterniflora* were as high as 90% and improving plant quality was found to have little influence on their abundance (Stiling et al. 1982). Few studies have experimentally manipulated rates of predation or parasitism and examined effects

on the strength of competition or host plant quality. In one of the few studies that did consider several processes, Edson (1985) found that reducing rates of predation on aphids made them more sensitive to host plant differences and to interspecific competition. High levels of physical disturbance will also lessen the impact of host quality and competition on herbivore populations (e.g., McAuliffe 1984).

A herbivore will be affected by the quality of its host depending upon its sensitivity to variation in the host (by definition). To the extent that low vagility tends to make herbivores more sensitive (because they cannot leave), species with little ability to switch between host individuals are more likely to be affected by host quality and interspecific competition. Immobile leaf miners of oaks were more strongly affected by host quality than were mobile caterpillars that fed on the same hosts (West 1985). Interspecific competition was reduced when aphids were able to move between their goldenrod hosts (Edson 1985). The thrips on *E. glaucus* are wingless and move very little during their entire lives. To the extent that high plant density allows herbivores to move between plants, it should reduce competition. High density plantings of collards allowed herbivores to move in response to quality (competitive release) which lessened the potential impact of competition (Kareiva 1982). Adult hispine beetles constantly change hosts (Strong 1982); in retrospect, perhaps, they are not very likely candidates for interspecific competition.

To the extent that host specialization may reduce a herbivore's choices, I expect that specialists are more likely than generalists to be affected by host quality and interspecific competition. Many of the best examples of interspecific competition (or amensalism) involve an herbivore which is specialized on a single, limited host species. Blakley and Dingle (1978) described intense competition between monarch butterflies and milkweed bugs. The monarchs used two milkweed species on Barbados, the milkweed bug was restricted to only a single species. The monarchs found and destroyed most individuals of the host plant of the bugs. Gibson and Visser (1982) found that competition between two species of bugs was reduced when an alternate host species for one of the bugs was present. The spittlebugs described in the present study were affected by changes in host quality caused by caterpillar feeding. At least at Bodega Bay, where they were found to be affected by competition, they are dependent upon *Erigeron glaucus*.

It has often been assumed that intraspecific competition is a necessary prerequisite for interspecific competition (e.g., Strong et al. 1984:121). This is not the case since conspecifics can improve host quality for one another (at field densities) but individuals of other species may decrease quality. In this present study, spittlebugs benefited from conspecifics but suffered from the presence of plume moth caterpillars.

The conditions mentioned above may increase the

likelihood that host plant quality and competition will be important but they are certainly not sufficient for this outcome. At best, they may provide some increased power of prediction.

This is not a novel attempt to understand the relative importance of several factors that affect communities of herbivores. Attempts to find generalities have become increasingly conditional. Earlier workers hypothesized that knowledge of trophic position was sufficient to provide intuition about the importance of competition and predation (Hairston et al. 1960, Menge and Sutherland 1976). More recent syntheses have included information about the taxa, habitat, and body size of the species involved (Connell 1983, Schoener 1983, Sih et al. 1985). Here I argue that biological details are as important as the broader characteristics in determining the relative strengths of competition, host plant effects, and predation. Factors such as the rate of disturbance, the extent of movement possible to the herbivore, and the ability of the herbivore to choose its host may strongly affect the relative importance of competition, predation, and host plant variation.

ACKNOWLEDGMENTS

I thank Liam Davis, Greg English-Loeb, Karen English-Loeb, Susan Harrison, Lisa Serafini, Kevin Uhlinger, and Carol Wolin for field assistance and Greg English-Loeb, Larry Harshman, Tom Schoener, Dave Spiller, Peter Stiling, Sharon Strauss, and Don Strong for improving the manuscript. I also benefited from discussions with many people about this work. The work at Bodega Bay was conducted at the UC Bodega Marine Reserve and the staff there was extraordinarily helpful. I thank Brian Arnold, Charles Droste, and Frank Ugolini for assistance and permission to work at Channel Islands National Park. This work was supported by NSF grants BSF-86 14528 and BSR-87 06425 and special UC Intercampus travel funds.

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