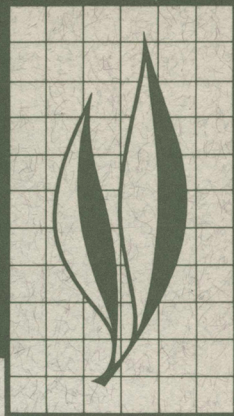


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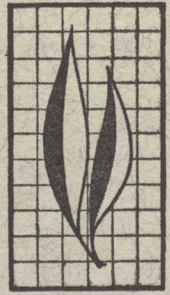
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Predation on Aphids in California's Alfalfa Fields

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Alfalfa fields in two climatically different regions were sampled for aphids and their natural enemies throughout 3 years (1957–1959). The fields were under an integrated control program and therefore received minimum amounts of insecticides. The four imported parasites of the spotted alfalfa aphid and the pea aphid were not yet important in the study area, so predators were mainly responsible for the high degree of naturally occurring biological control. By pooling the data of entire regions, it was possible to follow changes in populations of these mobile predators more accurately than is possible from surveys of single fields because short-distance migration resulting from harvesting practices as well as uneven distribution could be neglected.

Coccinellids and hemerobiids, two oligophagous groups, were closely linked in a density-dependent fashion to the aphid populations. This is a good indication that these predators (especially the lady beetles) are able to control the aphids. The more polyphagous predators, the chrysopidae and Hemiptera, become important in the control of the aphids only when the dominant coccinellids are inactive because of diapause or when lack of aphids for reproduction prompts the beetles to leave the fields. When aphid development exceeds the lady beetles' momentary capacity for increase, however, syrphids are able to take a large toll. Furthermore, several species having similar biologies were found to replace each other throughout the year. Finally, the phenologies of the species could be explained by their biologies (diapause, temperature thresholds, ovipositional behavior).

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Predation on Aphids in California's Alfalfa Fields²

INTRODUCTION

THE PRESENT HIGH DEGREE of naturally occurring biological control in alfalfa in California (reviewed in Hagen *et al.*, 1971) can be preserved if an integrated control approach such as that developed by Stern *et al.* (1959), Stern and van den Bosch (1959), and Smith and Hagen (1959) is used.

In the late 1950's the main pests in alfalfa were two exotic invaders: the spotted alfalfa aphid, *Therioaphis trifolii* (Monell), and the pea aphid, *Acyrtosiphon pisum* (Harris). The most important biotic mortality agents of the two aphids were native coccinellids (Dickson *et al.*, 1955; van den Bosch *et al.*, 1959; Smith and Hagen, 1959 and 1966 for California; Goodarzy and Davis, 1958, for Utah; Simpson and Burkhardt, 1960, for Kansas; Nielson and Currie, 1960 for Arizona). In some investigations, however, other predators were found to be more important, e.g., syrphids in eastern Washington-Oregon (Cooke, 1963) or nabids in Utah (Taylor, 1949). More recently four imported parasites have become very important for the regulation of the spotted alfalfa aphid and the pea aphid. Although the ecology of the imported parasites (van den Bosch *et al.*, 1964) and of the coccinellids (Smith and Hagen, 1966) is well known, little information is avail-

able as to the relationship between other predators and these aphids.

Because of the widespread use of resistant alfalfa varieties during the 1960's the spotted alfalfa aphid virtually disappeared as a pest. Along the coast the pea aphid was controlled most of the time by an introduced parasite. In the great Central Valley (which includes the San Joaquin Valley and the Sacramento Valley) the pea aphid at times attained damaging levels during summer time, probably because of changes in harvesting practices (Hagen *et al.*, 1971). But, on the whole, aphid outbreaks were infrequent and occurred mostly as a consequence of insecticide sprays applied against caterpillars.

The spread of the Egyptian alfalfa weevil (*Hypera brunneipennis* (Boehman)) through most of California's alfalfa-growing area in the 1970's (van den Bosch, 1971), threatened the whole industry. To control this new key pest, broad spectrum insecticides are applied frequently to alfalfa (Smith and Huffaker, 1973). The result has been a serious upsetting of the ecology of the rather stable system achieved by the former integrated-control program. Aphid outbreaks, for example, are occurring with almost predictable frequency (J. H. Black, personal communication).

¹ The work of this author has been made possible by a grant from the Swiss National Foundation.

² Submitted for publication January 10, 1974.

This recent turn of events strengthens the need for a thorough ecological assessment of a relatively undisturbed situation.

We therefore investigated the phenology of all major predators in alfalfa from old data covering almost 3 years, from January, 1957, until October, 1959. Much of the earlier difficulty in assessing population changes in these predators stemmed from the great mobility of most predators and the resulting huge fluctuations in individual fields (Smith and Hagen, 1966). To overcome this problem, data of entire regions were pooled, thus averaging effects of (a) migration caused by harvesting practices or local overexploitation of the aphids by the predators and (b) of uneven distribution of the species.

These data were gathered by Smith and Hagen prior to the establishment of the newly introduced hymenopterous parasites and prior to the introduction of aphid-resistant alfalfa varieties.

These mostly unpublished data thus offer a unique opportunity to analyze natural biological control by predators alone in an agroecosystem subject to virtually no insecticide sprayings—a situation which does not exist today. The purpose of this paper is to present new basic knowledge on the phenologies of the main predators in California alfalfa, to explain these phenologies as far as possible by using biological information from the literature, and to describe interactions between different predators and their common prey, the aphids. The general impact of the predators on the aphid populations is estimated. It is hoped that this study will help all concerned to appreciate the role of naturally occurring biological control in a new integrated-control program against the alfalfa weevil, as well as to appreciate the importance of conservation of the general predators for an entire region.

MATERIALS AND METHODS

Methods pertaining only to specific sections are described in the appropriate places.

Fields. The fields for this study were located in two areas (fig. 1), one in the middle coastal region designated as "coast," the other in the San Joaquin Valley hereafter called "valley." The number of fields in this survey from January, 1957 until October, 1959, ranged from 2 to 6 in January to 5 to 8 in July in each region (exception: coast 1959 in summer, with only three fields). This difference in field numbers is due to adverse weather in the winter, which often precluded sampling in a field over an entire month, and/or to some fields being plowed under in late fall.

Alfalfa culture. Alfalfa is one of the main crops in both regions; average field sizes are about 100 acres (approx. 40 hectares) in the valley and about half

that on the coast. All fields were planted with alfalfa varieties susceptible to both aphids. Alfalfa was harvested 4 to 6 times per year from the beginning of April until the beginning of November. The cuttings of all fields of every region were spread out evenly over the entire growing season, so the effects of harvesting on mobile predators when pooling the data can be neglected.

At the time of data accumulation the height of the stubble immediately following the harvest was uniformly about 7.5 cm. Today it varies between 7.5 cm and 15 cm, thus apparently allowing the aphids to continue development after harvest (Hagen *et al.*, 1971).

After each cutting the fields were irrigated. No insecticides were applied in the coastal region fields during the period of the study. In the valley, a total of only 11 insecticide sprays over the 3-

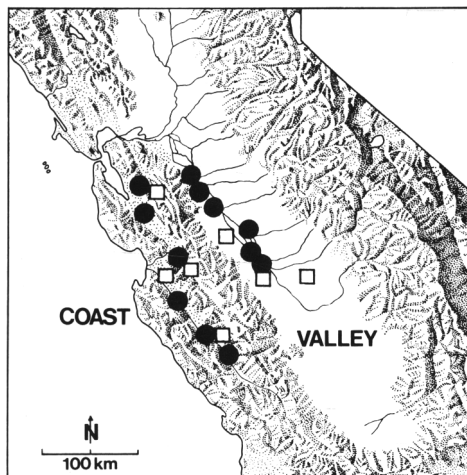


Fig. 1. Location of the fields in central California. Black circles represent groups of alfalfa fields with a weather station in the field. Data on rainfall were taken from U. S. Weather Bureau Stations represented by white squares. Alfalfa is grown to the north and south of the study areas. (Map courtesy of California Insect Survey, University of California, Berkeley.)

year period were applied in August with 2 ounces of Systox® per acre (8 fields, one of them twice) or 6 ounces of malathion (1 field twice). This is much less than in 1956 (prior to the use of an integrated-control program) when up to 15 treatments with organophosphates per year were applied to a single field. Now the situation for the predators is again worsened due to the intensity of the spray program against the alfalfa weevil. In 1973, e.g., one or two treatments with the broad spectrum insecticides Furadan®, a carbamide, and Imidan®, a phosphate, were applied in 75 per cent of all fields in spring and, because of resurgence, losses of alfalfa hay were as high as in 1956 (van den Bosch, personal communication.)

Meteorological data. Temperatures and relative humidities were recorded in each field by hygrothermographs (Smith and Hagen, 1966) and the data pooled for each region as shown in figure 2. Rainfall data were gathered from the U. S. Department of Commerce "Climatological Data" for the stations shown in figure 1. Mean minima temperatures in January in the fields were above freezing, namely 3.3°C for the coast and 0.6°C in the valley (the long-term means from "Climatological Data" for the stations shown in figure 1 are 9.1°C and 7.2°C respectively). Mean maxima in July were 29.4°C on the coast and 33.3°C in the valley (with peak temperatures of 43°C) (long-term means are 19.6°C and 27.8°C). Mean total annual rainfall on the coast was 33.5 cm but only 21.8 cm in the valley, with most of the rain falling in winter.

Thus the coastal region, which is separated from the valley by the Coast Range (up to 1247 meters in height) enjoys cooler summers and warmer and more humid winters than does the valley (about 93 m above sea level for the study area).

Comparing the data for the 3 years of the study shows that 1958 had a wet and cold spring: 11.7 cm rain above the long-term average on the coast, +14.2 cm in the valley, and a warm December (+2°C), whereas 1959 was rather dry (-6.9 cm on the coast, -5.6 cm in the valley).

Sampling and analysis of data. Sampling of predators was done with the normal 38-cm diameter sweep net with 10 × 10 sweeps per sampling date. Numbers of live aphids were determined by using the canister method (Gray and Schuh, 1941) with usually 100 stems per sampling date; diseased and parasitized aphids were counted from the same stems (Smith and Hagen, 1959). During winter, samples were taken semi-monthly; from spring to fall, weekly. Samples were not taken when it rained nor when the field was being mowed.

All phenologies are therefore based on counts totaling 200 to 800 sweeps and the same number of stems for January, and 2,000 to 3,900 sweeps and stems

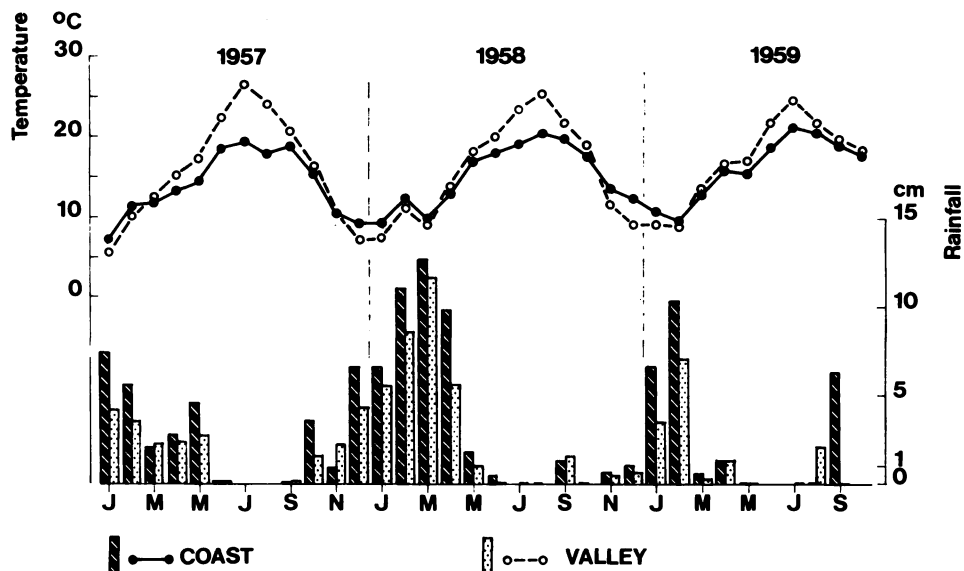


Fig. 2. Climate in the two regions: Black circles (coast) and white circles (valley) show monthly mean temperatures as recorded from the fields; bars indicate monthly mean rainfall (from U. S. Department of Commerce *Climatological Data*) for stations shown in figure 1. Every other month is marked on the baseline.

(1300 on the coast in 1959) for July. The values represent monthly means for

each area. A sweep samples approximately .46 square meters.

RESULTS AND DISCUSSION

I. Aphids and Predators

In each of the subsequent sections we will first discuss the species involved and their relative abundance in the samples and then the phenology (figs. 3 and 4) taking into account feeding habits, thresholds for development, and diapause. A description of these major predators in alfalfa can be found in Smith and Hagen (1956).

Aphids. The two introduced species, the pea aphid (PA), *Acyrtosiphon pisum* (Harris), and the spotted alfalfa aphid (SAA), *Therioaphis trifolii* (Monell), are by far the most common and abundant aphids in alfalfa in the western United States. The PA, introduced prior to 1883, has been considered a pest since 1889 (Chittenden, 1909; Campbell, 1926). The SAA reached southern

California in 1954 and infested all areas in middle California by June, 1956, threatening the whole alfalfa industry especially in the valley (Dickson *et al.*, 1955; van den Bosch *et al.*, 1959; Smith, 1959).

The relative abundances of the aphids in the two regions over the three year period are shown in figures 3 and 4. The aphids are expressed as biomass per one stem (including leaves). Only live aphids were used to derive the biomass, with the SAA biomass being equated to the PA's, (4 SAA = 1 PA) assuming all PA and SAA to be of medium size (Hagen and Sluss, 1966).

The phenology of these aphids in both regions shows a decline of the population in each year from January to Feb-

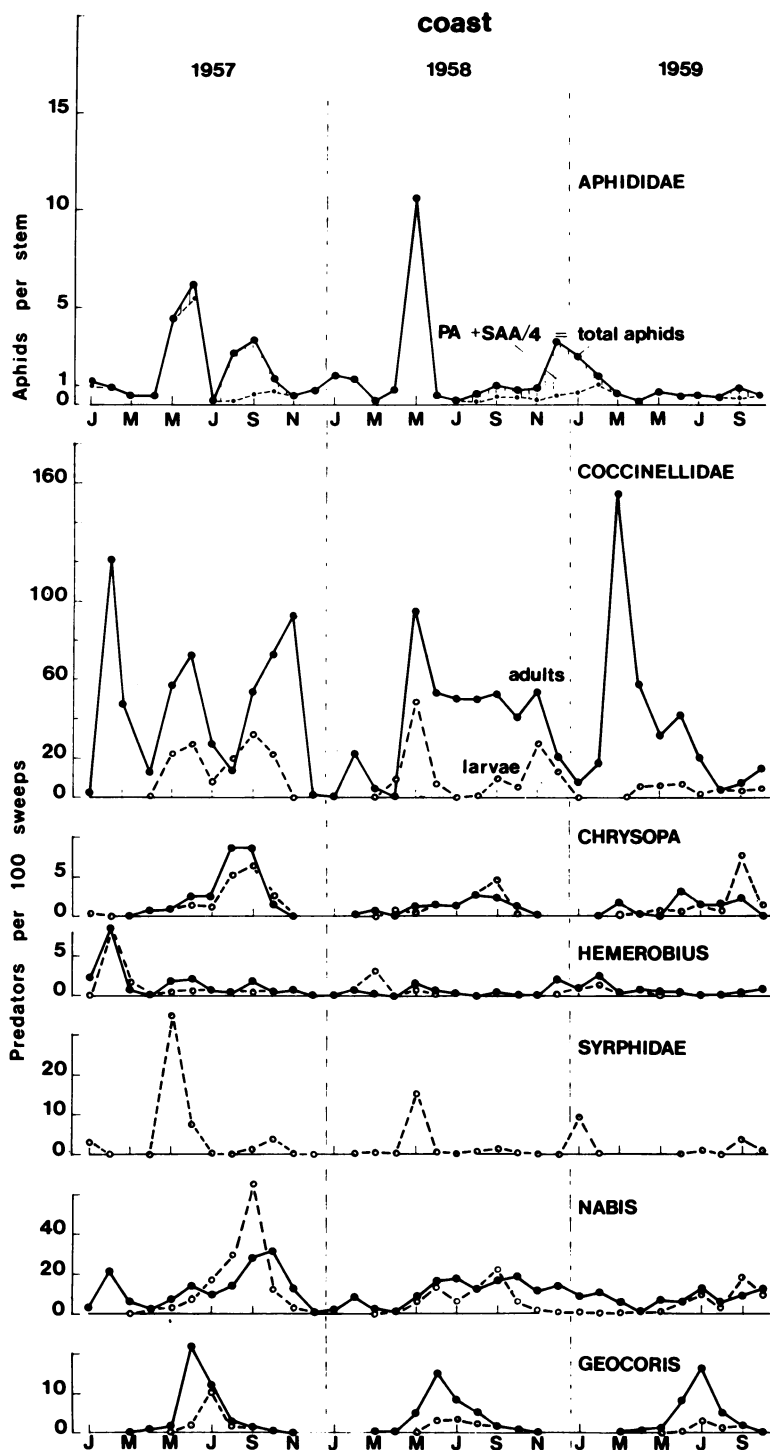


Fig. 3. Phenologies of aphids and their predators on the coast. Black circles represent adults (except for *Chrysopa*, where only gravid females are shown). White circles indicate immature stages. Number of aphids is expressed in terms of biomass units ($4 \text{ SAA} = 1 \text{ PA}$).

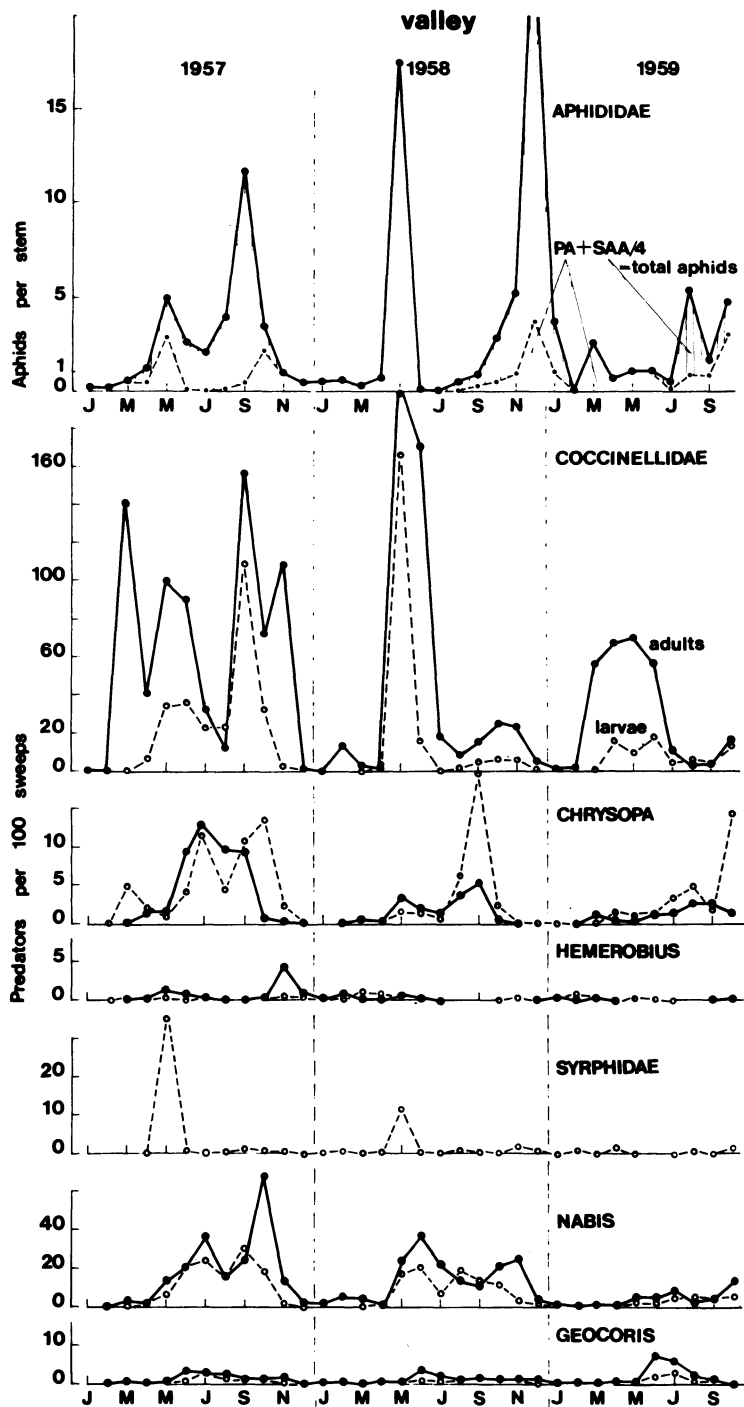


Fig. 4. Phenologies of aphids and their predators in the valley. (Same as figure 3.)

ruary–March; a maximum peak in May–June is followed by a crash to a minimum in June–July and a slow recovery leading to a second peak in the fall. In the valley the fluctuations are much more violent as a result of higher SAA populations. A special feature in this annual pattern is given by the aphid outbreak in December 1958, which was induced by the unusually high temperatures at that time.

This phenology reflects the fact that both aphids reproduce parthenogenetically throughout the year on alfalfa in the study area. However, in the state of Washington for example overwintering of PA occurs in the egg stage (Cooke, 1963). SAA prefers warmer conditions, as shown by its greater abundance in the valley. This is also reflected by the reproductive temperature threshold for the two aphids: PA 5.2°C (Campbell *et al.*, 1974) and SAA 8.5°C (from Graham, 1959). Every monthly mean, both in the valley and on the coast, was higher than the PA threshold, thus allowing continuous growth and reproduction. The SAA threshold, on the other hand, was not reached by the December and January mean temperatures in the valley, thus the SAA could not reproduce there during this time.

Coccinellidae: Species composition and phenologies. The common lady beetles in California alfalfa fields are native to North America and all belong to the predominantly aphid-feeding tribe Coccinellini (Sasaji, 1968).

Table 1 shows the percentages of the mean annual catch of the six most common species. Obviously, *Hippodamia convergens* and *H. quinquesignata*, each varying greatly in abundance, together account for a rather stable four-fifths of all lady beetles in alfalfa. Figure 5 shows the seasonal abundance of these two species. (Records of especially interesting single fields are shown in Smith and Hagen [1966] and Hagen

TABLE 1
RELATIVE ABUNDANCE OF DIFFERENT COCCINELLID ADULTS IN ALFALFA, 1956–1959

Species	Location and abundance*	
	Coast	Valley
<i>Hippodamia convergens</i>		
Guérin-Ménéville	19–65%	20–73%
<i>H. quinquesignata</i> Kirby.....	11–54%	26–71%
The above two species together in any one year.....	65–84%	84–92%
<i>H. sinuata</i> Mulsant	4–26%	1–8%
<i>H. parenthesis</i> (Say)	1–9%	0–2%
<i>Coccinella novemnotata franciscana</i> Mulsant	0–0.8%	0–15%
<i>C. californica</i> Mannerheim.....	4–5%	0%
Others	0–5%†	2–10%

* Spread of the four annual means (from weighted monthly means throughout the years); 100% = all coccinellids sampled in every year.

† With a constant increase of *C. trifasciata* Mulsant on the coast from 0% in 1956 to 4% in 1959.

[1974, fig. 2]). *H. convergens* shows a peak in abundance in every other early spring, a second major peak occurred only in the fall of 1957 in the valley. This coincided with an aphid peak in October, 1957. Figure 5 also shows that the proportion of *H. quinquesignata* over *H. convergens* increases throughout the year.

Migration and diapause. These phenologies reflect the early spring migration of *H. convergens* from their montane overwintering sites into the alfalfa fields where they reproduce. When aphids are abundant, as in the fall of 1957, the beetles of this species produce a facultative second generation and enter winter diapause in the fields at temperatures below 18.3°C (Hagen, unpublished results). If there are not sufficient aphids in June for a second generation, the beetles leave the fields and enter an estival-hibernal diapause in the mountains (Hagen, 1962). *H. quinquesignata*, on the other hand, spends its facultative summer diapause as well as its winter diapause at the edges of the fields. Because it does not migrate long distances it can easily respond to new increases in aphid numbers by producing summer and fall generations (Hagen, 1962). This explains its in-

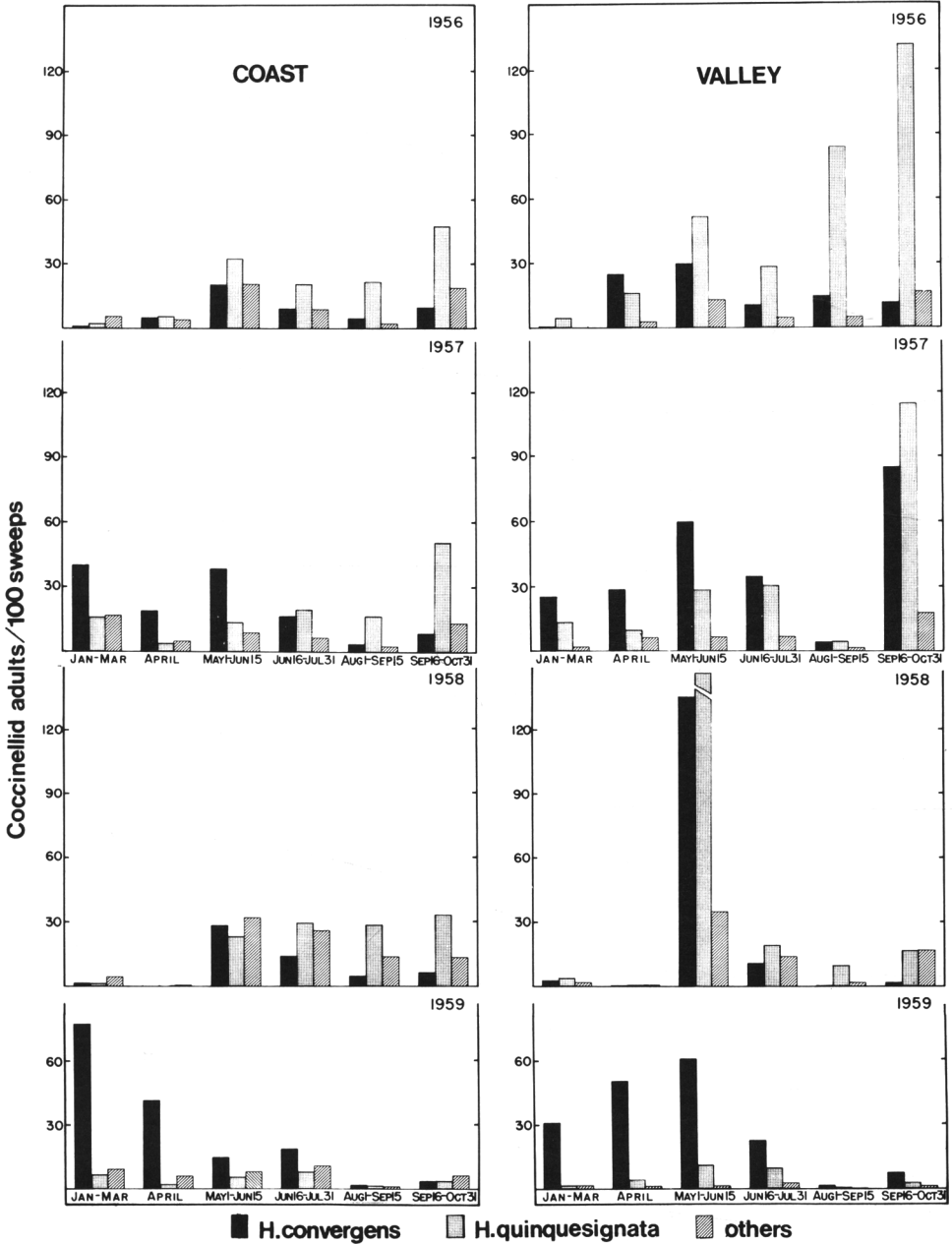


Fig. 5. Seasonal abundance of *Hippodamia convergens*, *H. quinquesignata*, and other aphidophagous coccinellid species in coast and valley alfalfa fields.

creasing importance in autumn.

Relation to aphid population. Figures 3 and 4, in which all coccinellid species are pooled, show that there are

three major peaks, namely in February–March, in May, and in October–November. From April until October, the numbers of lady beetle adults are made up

mainly of *H. convergens* and *H. quinquesignata* in varying proportions and are positively correlated to the aphid population (r_1^2 , the explained variance = 0.593, $p < 1$ per cent; for regression equations, see Appendix). The correlation of the lady beetle larvae with the aphid populations from April until October is even closer than that found with the adults ($r_2^2 = 0.865$, $p < 1$ per cent). These are the first records of a long-term positive correlation between aphids and lady beetles. The size of the new beetle generation is dependent upon the number of immigrating beetles as follows. Based on single field records (except for the single extended peak in 1959 in the valley) the numbers of beetles in the first peak, although not statistically significant, seems to be negatively correlated to the numbers of beetles in the May peak. There is also a slight indication that the first larval peaks and the first adult peaks are negatively correlated ($r_3^2 = 0.137$, 5 per cent $< p < 10$ per cent).

These findings are easily explained by the following observations: adult lady beetles entering the fields in the early spring (mainly *H. convergens*) prey heavily on the aphids, and from January until March they drive the aphid population down despite improving weather and plant conditions for the aphids. The greater the number of immigrating beetles, the fewer the number of eggs that can be produced from the limited food supply, thus explaining the negative correlation between the first adult and first larval peak. These larvae in turn give rise to the second peak of adults which occurs in May–June. Unless there is a second generation between late summer and fall, these adults form the diapausing generation of *H. convergens* in the mountains. They are thus largely responsible for the number of beetles immigrating back to the valley in the following spring. This may explain alternating high-low numbers of immi-

grating adults to the valley. These data showing a 2-year cycle of aphidophagous coccinellids in California support the same findings by European workers (Blattny, 1925; Broadbent and Heathcote, 1961; Behrendt, 1966; Meier, 1966; Müller, 1966). Whereas these European workers dealt mainly with the impact of univoltine coccinellids on aphid populations, the California picture is more complicated. The facultative summer and fall coccinellid generations further amplify the 2-year fluctuations by reducing the number of aphids available to make up the overwintering aphid populations and by adding to the number of immigrating adult coccinellids in the next spring.

Temperature thresholds. The deposition of the first coccinellid eggs in spring is determined both by the availability of aphids and by temperature. It involves the beetles leaving the hibernation quarters, migrating to the fields (Hagen, 1962), and consuming about 300 aphids during the preoviposition period (Hagen and Sluss, 1966). The ovipositional temperature threshold has yet to be determined. The eggs have a rather high temperature threshold of 11.7°C (Butler and Dickerson, 1972). This ensures a good start of the aphid population which has a lower temperature threshold for development. *H. convergens* larvae indeed were not found in the fields in spring before the monthly mean exceeded 12°C. The threshold for larval development, however, is much lower (8.9°C according to Butler and Dickerson, 1972). The larvae are always able to develop in the valley except during December–January, when temperatures are below this threshold. This adaptation may be of some importance in the fall, when it allows a late generation to complete development at the low temperature found during this time of year.

H. quinquesignata, though usually in close proximity to the fields, starts egg

deposition later than *H. convergens*. In any one field the first larvae of *H. convergens* were caught on the average 7.2 days before the first of *H. quinquesignata* (Wilcoxon's Signed Rank Test $p < 1$ per cent). This behavior is also reflected in *H. quinquesignata*'s higher larval temperature threshold for development (13.3°C calculated from Kadou, 1960).

Chrysopidae. *Chrysopa carnea* Stephens is by far the most common lacewing species in California alfalfa. Other species are encountered, but they are rare. The larvae of green lacewings are rather general predators (Balduf, 1939) and they can utilize a wide variety of prey in alfalfa. It has been found, however, in a choice experiment, that *C. oculata* Say larvae prefer aphids over alfalfa weevil larvae, leafhoppers or plant bugs (Lavalley and Shaw, 1969). Adult *C. carnea*, on the other hand, are not predaceous but feed on pollen (Sheldon and MacLeod, 1971) or honeydew (review in Hagen et al., 1970a).

The number of larvae increases from April until a peak is reached in September (figs. 3 and 4). The last larvae are observed in late November and the beginning of December. Higher numbers were recorded from the valley as compared to the coast. The phenology of gravid females exhibits a pattern similar to that of the larvae, but the decline in autumn is usually 1 month earlier. The number of all adults (only gravid females are shown in figures 3 and 4) including males and non-gravid females reveals a tremendous build-up, particularly in the valley, with a peak in November of 50 adults per 100 sweeps. By December these mostly reddish-brown-colored adults had almost completely disappeared from sweep-net samples though they were still recovered from the litter by suction machine sampling.

The late start in spring despite relatively low thresholds of 8.3°C for larval and 7.8°C for egg development (Butler

and Ritchie, 1970) is explained by the ovipositional behavior of the females. For one thing they require honeydew as a nutrient for egg production, and this becomes available in sufficient amounts only with high aphid populations. Furthermore pollen as an alternate food is not generally available in alfalfa.

The fluctuations in numbers of gravid lacewing females and larvae are similar and often do not exhibit a density-dependent relationship to changes in aphid abundance. The larvae can bridge a period of aphid scarcity by using alternate food sources such as moth eggs (Butler and May, 1971; Hafez and Abdel-Hamid, 1965) and mites (Fleschner, 1950), and the females can rely on old honeydew accumulation on the leaves. The phenology shows three population peaks in the valley and two on the coast. These peaks probably represent several overlapping generations. Toschi (1965), reports three to five generations of *C. carnea* in the San Francisco Bay Area, Ickert (1968) two in Germany, and Neumark (1952) eight in Israel.

In autumn the reddish-colored adults are in diapause (review in Tauber and Tauber, 1973). Most of them leave the fields by December and seek sheltered places (Zelený, 1965; Sheldon and MacLeod, 1971), making occasional foraging flights and re-entering the alfalfa in the spring.

Hemerobiidae. The brown lacewings are predaceous in both the adult and the larval stages. The larvae are mainly aphid feeders and seem to have less alternate food sources than do the chrysopids (Killington, 1936; Balduf, 1939). In central California only two species are regularly encountered in alfalfa: *Hemerobius ovalis* Carpenter, which makes up about 80 per cent of the coastal population and essentially 100 per cent of the valley population, and *H. pacificus* Banks, which accounts for about 20 per cent on the coast and is rare in the valley. In alfalfa, hemerobiids in

general are much rarer than chrysopids.

Figure 3 shows that on the coast the number of brown lacewing adults is strongly correlated with the number of aphids from March until December ($r_4^2 = 0.504$, $p < 1$ per cent), while the relative number of adults is higher in January and February. Gravid females account for approximately half of the catch throughout the year. Larvae are abundant only in early spring and again late in the fall. In the valley, the adults (fig. 4) responded to the May peak of the aphids and later in the season 1957 to the declining September peak exhibiting no significant year round correlation to aphid numbers ($r^2 = 0.001$). In July 1958 and 1959 the hemerobiids apparently were eliminated by high temperatures and hardly recovered in the winter of 1958–1959.

The continuous occurrence of brown lacewings in small numbers throughout the year on the coast reflects the fact that they do not have a winter diapause in this climate (Wegenek, 1950)^a and that they have an extremely low threshold of 4.1°C for larval and $+0.4^\circ\text{C}$ for egg development (Neuenschwander, unpublished results). Since they are mainly predaceous on aphids as adults, and need not rely on honeydew for egg production, they can produce and deposit their eggs at lower aphid densities than do the chrysopids. They also show a stronger dependence on aphids as a food source than do the green lacewings. This explains the strong correlation between brown lacewings and aphids in the cool coastal areas. In the valley, however, brown lacewing eggs, larvae, and pupae suffer heavy mortality under higher temperatures occurring from July through September—adults do not estivate, and barely survive high summer temperatures (Neuenschwander, unpublished results). Thus the popula-

tion is disassociated from the aphids until winter when new adults invade favorable fields. Because they have extremely low developmental thresholds they can again increase abundantly in winter.

Comparing phenologies of *Hemerobius* in the two areas, it is apparent that the coastal alfalfa fields constitute a stable zone of permanent occupancy (Huffaker and Messenger, 1964). Here *Hemerobius* adults exhibit a rather high degree of density-dependence in relation to the aphids, though it is not known why they do not exploit this food source to a greater extent. In the valley alfalfa fields, however, physical conditions are rigorous and often unfavorable; this habitat lies within the marginal zone of permanent occupancy.

The phenomena of larvae of hemerobiids occurring in early spring and late fall and larvae of chrysopids during summer in the coastal area are not based on direct competition. This is shown by the fact that high populations of *Hemerobius* and *Chrysopa* may well occur in the same field at the same time and that there is no negative correlation between the monthly means of the two neuropterans in single fields. However, this exclusion is an expression of the different temperature requirements of the species of the two families, which is also shown in their differential occurrence in the two regions.

Syrphidae (Syrphinae). Larvae of the following hover flies, which are all strictly aphid feeders (Schneider, 1969), were collected from alfalfa: *Scaeva pyrastris* (L.), *Metasyrphus mcadai* (Jones), *Syrphus opinator* Osten Sacken, *Metasyrphus subsimus* Fluke, and *M. venabilesi* (Curran), the latter two being rare. The larvae of several other syrphids, whose adults were fre-

^a Wegenek, E. G. 1950. Studies of the brown lacewings of California, with special emphasis on the genus *Hemerobius* Linnaeus (Order Neuroptera, Family Hemerobiidae). Ph.D. thesis Univ. of Calif., Berkeley. 168 pp.

TABLE 2
RELATIVE SEASONAL ABUNDANCE OF DIFFERENT SYRPHID LARVAE
IN ALFALFA, 1957-1959

Location, season and annual mean	Type of larvae				Total numbers of larvae
	<i>Scaeva</i>	<i>Metasyrphus</i>	<i>Syrphus</i>	Others	
Coast:					
May peak.....	70%	22%	7%	1%	1424
Autumn peak....	15%	44%	10%	30%	79
Annual mean....	67%	23%	8%	2%	1503
Valley:					
May peak.....	42%	54%	1%	2%	1009
Autumn peak....	15%	81%	1%	1%	80
Annual mean....	40%	56%	1%	2%	1089

quently swept, were found in extremely small numbers.

Table 2 shows that *Scaeva* and *Metasyrphus* together account for over 90 per cent of all syrphid larvae, but are not equally distributed in the two areas (Karl Pearson Chi square test of independence with $p < 1$ per cent. The strength of association, $\Phi = \sqrt{X^2/N}$, was 0.325, which suggests a weak-to-moderate association). It is concluded that *Scaeva* is more abundant on the coast and during springtime than is *Metasyrphus*.

Figures 3 and 4 indicate that syrphid larvae occur only at the time of aphid peaks and that each aphid peak gives rise to a syrphid peak. In the valley the number of syrphid larvae is lower despite larger aphid populations. In both regions the winter syrphid peak of 1958-1959 consisted entirely of *Metasyrphus* larvae.

These phenologies reflect the fact that the females in all three genera lay their eggs mainly in or near aphid colonies which they normally discover visually, though odor may help in host finding (Volk, 1964). Older females may also lay eggs remote from colonies (Chandler, 1967). Because of this ovipositional behavior, syrphids in general only work at high aphid densities.

Scaeva hibernates as an adult (Schneider, 1948) and it did not respond to the aphid peak in winter 1958-

1959, which indicates that it has a true diapause in the Californian climate. The other syrphids overwinter as larvae. *Metasyrphus* seems to be able to respond to aphids throughout the year and does not show any diapause. *Scaeva* and *Metasyrphus* are reported to prefer the cooler months (Campbell and Davidson, 1924; Knowlton et al., 1938), which is also reflected in the higher syrphid populations on the coast.

Hemiptera. Hemipteran predators of three different families were commonly collected: The damsel bugs, *Nabis americanoferus* Carayon and perhaps *N. alternatus* Parshley (Nabidae); the big-eyed bugs, *Geocoris pallens* Stål, *G. atricolor* Montandon, and *G. punctipes* (Say) (Lygaeidae); and the minute pirate bug, *Orius tristicolor* (White) (Anthracoridae). *Orius* usually occurred in minute numbers and seemed to be associated mainly with thrips populations (Hagen, unpublished results), and therefore we shall not further consider this species here. *G. atricolor* and *G. punctipes* were found only in the valley, where each accounted for 10 per cent of the big-eyed bugs, *G. pallens* being by far the most abundant species. *Nabis* and *Geocoris* are both general predators with no special preference for aphids. Their feeding habits and especially their ability to also feed on plants will be discussed later.

Nabis adults (figs. 3 and 4) show a

small peak in February and higher peaks in June–July and October. Adults can be collected in small numbers the year round, while no nymphs are found before April. Subsequently, their numbers build up to two peaks in June–July and August–September. *Geocoris* adults (figs. 3 and 4) are absent in sweep net samples on the coast before April; they reach peak numbers in June–July and disappear from the samples by November. In the valley, adults can be swept throughout the year but they never attain high numbers. In both areas nymphs are less numerous than adults throughout the year. They do not occur before June.

These phenologies suggest that both *Nabis* and *Geocoris* overwinter as adults. In suction-machine samples taken in January adults were recovered in small numbers from the leaf litter, where net sweeping would not normally reach them. This overwintering near the ground probably largely explains the absence of *Geocoris* in the winter sweep net samples from coastal fields.

Population changes in these two hemipterans do not reflect changes in aphid abundance. This phenomenon was already discussed for *Chrysopa* and

seems to be typical for the general predators. In contrast to *Chrysopa*, however, *Nabis* is also able to subsist on plant juices in the absence of insect food (Stoner, 1972), though alfalfa may not be suitable (Taylor, 1949). With *Geocoris* some plant feeding is essential (Stoner, 1970; Tamaki and Weeks, 1972) and both hemipterans are therefore directly susceptible to poisoning by systemic insecticides (Ridgway *et al.*, 1967).

In our fields, nymphs of *Geocoris* first occurred in June when the monthly mean temperature surpassed the relatively high threshold for nymphal development (16.5°C according to Butler [1966], 14.0°C–19.8°C according to species from Dunbar and Bacon [1972]) or for egg development (15.9°C–17.5°C calculated from Dunbar and Bacon [1972]). Using data from Tamaki and Weeks (1972), who reported the same phenology of *Geocoris* and found two generations per year, we calculated developmental temperature thresholds of 6.7°C–9.4°C. These lower thresholds may be an adaptation to the cooler climate in Washington and Oregon where their studies were conducted.

II. Impact and Interactions

In this second part we will discuss the interactions between predators and aphids and between different predator groups. The purpose is to examine the general magnitude of predator impact, not to estimate it precisely from these data. However, the data are, with some additional assumptions, useful for such a general evaluation.

Number of aphids destroyed by predators

We will first try to estimate the number of aphids killed by each predator group. This number was estimated from laboratory data cited in table 3. In order

to attribute a fair amount of aphids consumed by an average larva which has not yet completed its development, half of the cited number of aphids needed until pupation was arbitrarily chosen. For each predatory adult the mean number of aphids eaten in 10 days, which is considered a fair average lifetime, was calculated. The mean size of a pea aphid was taken as a unit, and data from the literature (table 3) were accordingly adjusted.

By using laboratory data to estimate the predation in the field, it is assumed that food consumption of these predators is similar in the laboratory and the

TABLE 3
NUMBER OF APHIDS KILLED BY EACH PREDATOR
(PER 100 SWEEPS = PER 500 SQUARE FEET)

Taxa	Aphids eaten in the lab	Sampling factor*	Aphids destroyed per predator caught	Citation for voracity data
	A	B	C = A × B	
<i>Coccinellidae</i> adult.....	450	12.5†	5625	Clausen, 1916; Knowlton <i>et al.</i> , 1938; Goodarzy and Davis, 1958; Simpson and Burkhardt, 1960; Kaddou, 1960; Hagen and Sluss, 1966.
larva.....	175	7.4	1295	
<i>Chrysopa</i> larva.....	75	48.9	3668	Withycombe, 1923; Wildermuth, 1916; Hafez, 1965; Ickert, 1968.
<i>Hemerobius</i> adult.....	100	12.5‡	1250	Moznette, 1915; Wegenek, 1950.
larva.....	110	48.9§	5379	
<i>Syrphidae</i> larva.....	150	7.4	1110	Campbell, 1926; Knowlton <i>et al.</i> , 1938; Lal and Haque, 1955; Simpson and Burkhardt, 1960; Hughes, 1963; Sundby, 1966; Schneider, 1969.

* From Dietrick *et al.* (1960) values × 0.5 (see text).

† From Dickson *et al.* (1955) we calculated a factor of 10.

‡ From Dietrick *et al.* (1960) we took the data for coccinellids because data for adult Neurotera are lacking.

§ From Dietrick *et al.* (1960) for *Chrysopa* larvae.

|| See footnote 3, page 63.

field. All data used in table 3 come from experiments where surplus food was offered and practically no searching was involved. But energy-consuming extensive searching at lower prey densities in the field may well require more food. Or, on the contrary, some insects may show a functional response and devour more prey at the high densities (Holling, 1966; Shands and Simpson, 1972) offered in the laboratory. In hunger experiments syrphid larvae, for example, can develop on about half their normal food requirement and produce undersized but fertile adults (Campbell and Davidson, 1924; Bombosch, 1962). *Chrysopa*, too, is able to complete development on a minimum amount of food of only 72 aphids (Sundby, 1966). But laboratory experiments may also induce a negative functional response because too much food was offered (Kuchlein, 1966). Furthermore, temperature (Gurney and Hussey, 1970) and its changes, humidity, and light also play a role as discussed in Hodek *et al.* (1972) and Schneider (1969). Last but not least the aphid population in the

field can react actively to predation by alarm reactions (Dixon, 1958; Klingauf, 1967; Brown, 1972; Nault *et al.*, 1973; Arzet, 1973), which help disperse a colony and may eventually result in a stimulation of aphid reproduction (Niku, 1972).

It is evident that our methods of determining the number of aphids destroyed by predators in the field give only a rough estimate of the real situation, because many factors are involved which could not be accounted for.

Population estimate from field samples

All predators were sampled with a sweep net. This method proved to be highly reproducible but does not give a direct measurement. The problem therefore arose how to estimate the total predator populations from sweep-net samples. An almost total sample including leaves and litter of a square foot can be taken by using a suction machine as described by Dietrick *et al.* (1960). These authors also present a comparison of sweep-net and suction-machine

catches which allows calibration of the faster sweep-net sampling relative to the tedious machine procedure. From these data conversion or sampling factors (machine counts over net counts of insects adjusted for the same area) were calculated. These conversion factors depend much on the height of alfalfa sampled. In low alfalfa a higher percentage of all predators present is taken by the sweep net than in high alfalfa, where only the upper part of the plants can be sampled effectively. Since Dietrick *et al.* (1960) made the comparison of the two sampling techniques in alfalfa of more than average height, namely 37.5 cm, the conversion factors for predators calculated from their data are too big for this study. In order to make sure that the predator populations were not overestimated, these sampling factors were therefore divided by two (table 3). Thus the conversion factor presented by Dickson *et al.* (1955) for coccinellids was approached. In essence these conversion factors correct the sweep-net counts for the predators which were present but not caught in the sample area.

The aphids, on the other hand, were sampled by the canister method (Gray and Schuh, 1941). By this direct method the number of aphids per 100 stems was determined quite accurately. It was then possible to compare aphid per 100 stems with predators per 100 sweeps by assuming that predators from 300 stems were collected per one sweep (Hagen, unpublished results). Thus in figures 6 and 7 aphid as well as predator numbers are based on 100 sweeps, which cover approximately 500 square feet ($= 46.4\text{m}^2$).

Impact of predaceous insects on seasonal abundance of aphids in alfalfa

In order to estimate the impact of the predators on the aphids, each month the numbers of aphids present in an

area covered by 100 sweeps (approximately 500 square feet) will be compared with the numbers of aphids killed by the predators present in the same area ($=$ number of predators caught \times value in table 3). By adding the number of aphids killed to the number of live aphids (figs. 6 and 7) the potential number of the aphids is estimated in the absence of biotic mortality factors as used by Hughes (1963), who includes losses by emigration. This phenomenon does not play a role in our data, which cover a large area. (See also Hodek *et al.*, 1972.) We think that our estimate of the toll taken by predators is, in general, conservative except for June–July, when the aphids are at low densities and *H. convergens* particularly does not remain in the alfalfa fields for the assumed 10 days. Instead, these beetles usually move to their estival hibernial quarters in the Sierra Nevada and Coast Range, and for this reason the estimate for predation is probably too high for this period. But this overestimate may not be too great because we do not include estimates for *Nabis* and *Geocoris*, which are active during the time *H. convergens* starts leaving.

It appears from this study that the whole predator complex was able to keep the aphid populations which have a potential for considerable damage below the economic threshold for PA and SAA (University of California Alfalfa Hay Recommendations for Pest and Disease Control Program, 1973). Two exceptions occurred in the valley when average SAA levels exceeded the thresholds, although damage happened for only a short time and the mostly untreated aphid populations crashed completely. In the September peak in 1957, the crash can be safely attributed to predator action. In the crash in January, 1959, weather—and especially rainfall following the dry and relatively warm December, 1958—seems to be a more likely explanation. Local migration accounting for a change in aphid

abundance in individual fields as found by Stary (1971) cannot be an explanation, since in this study data for an entire region were pooled.

If the impact of the different biotic mortality agents in figures 6 and 7 is compared, it becomes clear that predation by adult coccinellids removes most aphids. The negative correlation ($r_s^2 = 0.194$, $p < 5$ per cent for single fields) between the number of lady beetles flying in from their hibernation quarters (peak in February or March) and the aphid peak in May is a strong indication that early season predation on the slowly developing aphid population is of great importance. But when the aphid populations explode in May, the predators have difficulties in checking them. As mentioned, however, the high number of predators produced on these aphids play an important role in the fall and during the next year. Another example of the importance of predation in the early phases of an aphid build-up is provided by the data obtained in summer 1958 on the coast. The high number of beetles remaining in the fields during summer and fall permitted only a small aphid peak in the warm December of 1958. By contrast in the valley, lady beetles usually disappeared in the hot summer and the developing aphid populations were unchecked in fall; thus resulting in a tremendous aphid outbreak in December of 1958. It is important to notice that most coccinellids are inactive in December as they are diapausing; their impact in our example is mostly restricted to the slowly developing aphid populations in fall. In a similar case involving *Chrysopa*, Hagen *et al.* (1970b) attributed the reduction of aphid peaks in plots sprayed with artificial honeydew (a food and attractant for *Chrysopa*) to the action of predaceous larvae in an early phase of the

build-up of the aphid populations.

The high correlation between aphids and coccinellid larvae as also demonstrated in laboratory experiments (Rautapää, 1972) shows that reproductively the lady beetle adults act in a density-dependent manner and exhibit a clear numerical response, which is a good indication of their ability to control aphid populations (Huffaker and Messenger, 1964). When only single fields are observed, this fact is often obscured due to the discontinuity evoked by the harvesting practices on both the aphid and beetle populations.

Another though indirect measurement of the impact of lady beetles is given by comparing biomasses of aphids and lady beetle adults. The average biomass of the coccinellid adults in May is 27.5 per cent⁴ to 71.3 per cent of the aphid biomass. After the aphid crash the coccinellids represent up to 88 times the biomass of the remaining aphids, whereupon the beetles leave the fields. This change in the ratio of biomasses also demonstrates the usual delay in the predator activity.

The pooled data presented in figures 6 and 7 show that all the predaceous larvae together do not destroy many aphids. Judging by the mere numbers of aphids killed one could conclude that the predaceous larvae are not important, apart from providing predaceous adults for the next generation. If, however, we look at what is happening in single fields different conclusions are drawn. Because larvae cannot leave a field after cutting, they also prey on aphids in the stubble and can drive the aphid population down to lower levels than adults usually do.

We concluded that the coccinellid larvae were primarily responsible for the aphid crash in May–June while the freshly emerged adults usually do not

⁴ These data were calculated from the monthly means for May, 1957 and 1958 from both regions with 1 aphid = 0.3 mg and 1 lady beetle = 25 mg. These values include the correction factor for sampling coccinellid adults.

remain long in the field. Where coccinellid larvae are scarce as in summer, *Chrysopa* larvae may fill their niche (fig. 6b and 7b). And in February and March, *Hemerobius* larvae, though not numerous, are the only larval predators which may help delay the aphid build-up especially in situations where adult coccinellids are absent or inactive.

Syrphid larvae were not important in these years in the two regions, as compared to records from other crops and from Europe (Bombosch, 1963; Tamaki *et al.*, 1967; Hagen and van den Bosch, 1968). The rather poor performance of syrphids in the study fields may be attributed to the size and uniformity of the fields, which have little attraction to the pollen-feeding syrphid flies (Fluke, 1929; Banks, 1959; Bombosch, 1966; Gafecka, 1966).

Nabis and *Geocoris*, which need not rely on aphids, peak at times when other predators are rare and the aphid populations are low (Benedict and Cothran, 1974). Their killing of a few aphids may therefore help delay a new build-up and the two Hemiptera may be more important than the feeding records indicate.

In addition to their role in the alfalfa community some of the minor and rather polyphagous predators are also of importance to adjoining crops. This was shown, for example, for *Geocoris*, which in spring can move to orchards (Tamaki and Weeks, 1972) or along with *Nabis* to cotton (van den Bosch and Hagen, 1966; Eveleens *et al.*, 1973), or for *Chrysopa*, which can be attracted to cotton (Hagen *et al.*, 1971; Hagen, 1975). These findings confirm the role

of alfalfa as an "insectary" of beneficial insects for the entire region.

The role of parasites and pathogens

Our samples were taken shortly before the introduced parasites spread through central California. Thus in the 3 years parasites were of very little importance in the two regions studied. Over-all parasitization of the two aphid species never reached more than three aphids per 100 stems or 2.4 per cent as a monthly mean. By contrast, van den Bosch *et al.* (1964) report SAA parasitization rates of up to 65 per cent by the recently introduced *Trioxys complanatus* Quilis, *Praon exsoletum palitans* Muesebeck (both Aphidiidae), and *Aphelinus asychis* Walker (Eulophidae, Aphelininae) only 120 miles south of our fields. *Aphidius smithi* Sharma and Rao (Aphidiidae) which was released against the PA from 1958 onward (Hagen and Schlenger, 1960), reached parasitization rates of 40 to 60 per cent in the early 60's, exhibiting a clearly density-dependent response (van den Bosch *et al.*, 1966, 1967). These Hymenoptera were found only in low numbers in our fields.

Fungus diseases occurred irregularly, more often in the valley than on the coast. In the pooled data (figs. 6 and 7) no distinct correlation to the rain pattern could be observed. On a regional basis fungal diseases never attained major importance, though they could be devastating at times in single fields (Hall and Dunn, 1957). This rather small impact of fungi on aphid populations is to be expected in the Mediterranean-like climate of our study area (Voronina, 1971).

CONCLUSION

New insights into the ecology of highly mobile predators were gained by sampling entire areas over several seasons, a procedure which also proved to be successful in the investigation of the vari-

ous aphidiid parasites of the PA (Stary, 1972). The coccinellids elicit a good density-dependent response to the aphid populations. Since it could be demonstrated that the lady beetles influenced

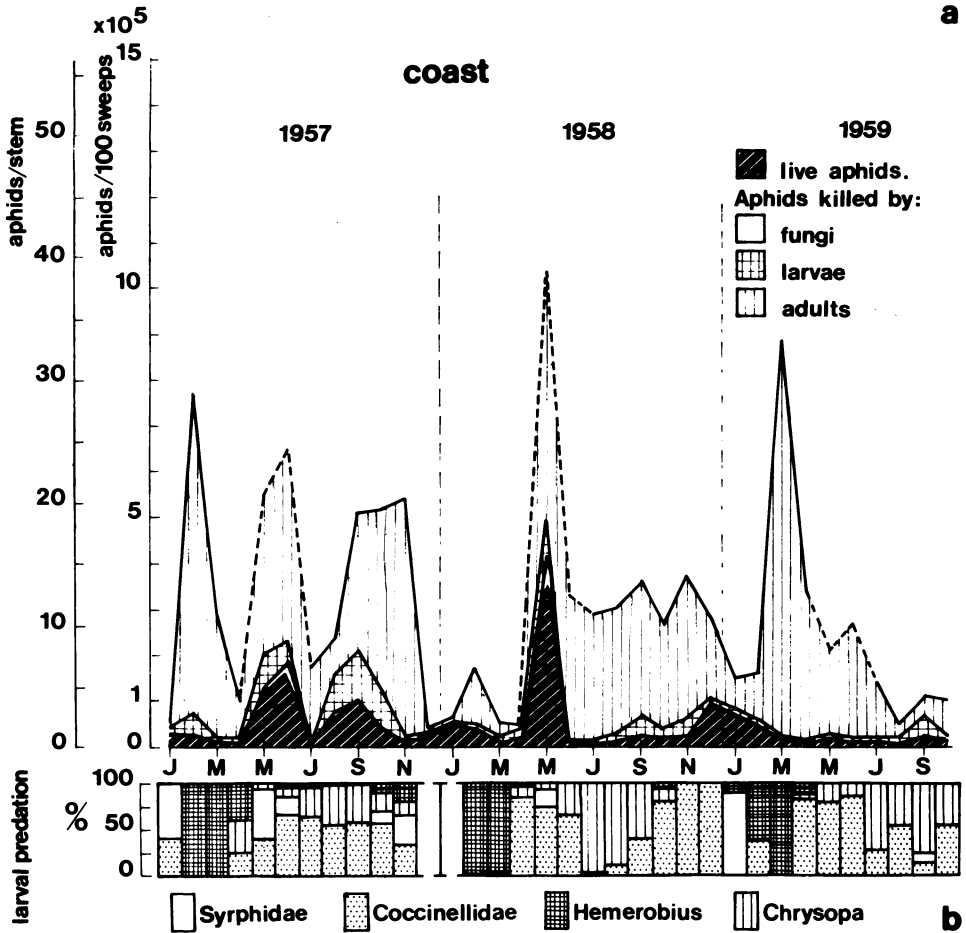


Fig. 6. Potential aphid abundance in coastal California alfalfa fields. a. Number of aphids killed by various biological mortality agents (pathogenic fungi, predaceous larvae and adults) is here added to the actual number of live aphids. (Broken lines indicate a possible overestimate of the potential aphid number.) b. Percentage of total number of aphids destroyed monthly by larvae of each group of predators.

the abundance of the aphids, it is concluded that this density-dependence is of a reciprocal nature. It is interesting to note that two major coccinellid species which replace each other throughout the season are responsible for this relationship.

Hemerobius adults show a density-dependent response to the aphid populations in the milder middle coastal areas too. However, their predation is of no importance for the aphids. Addition-

ally, a mutual exclusion of *Hemerobius* and *Chrysopa* larvae over the year was found, with *Hemerobius* larvae occurring in spring and late fall and *Chrysopa* in summer. This exclusion is due to different temperature thresholds and not to direct competition for food.

Summing up the findings on the interactions of the different predators, it can be stated that coccinellids are dominant and all the other predators become important only when lady beetles are

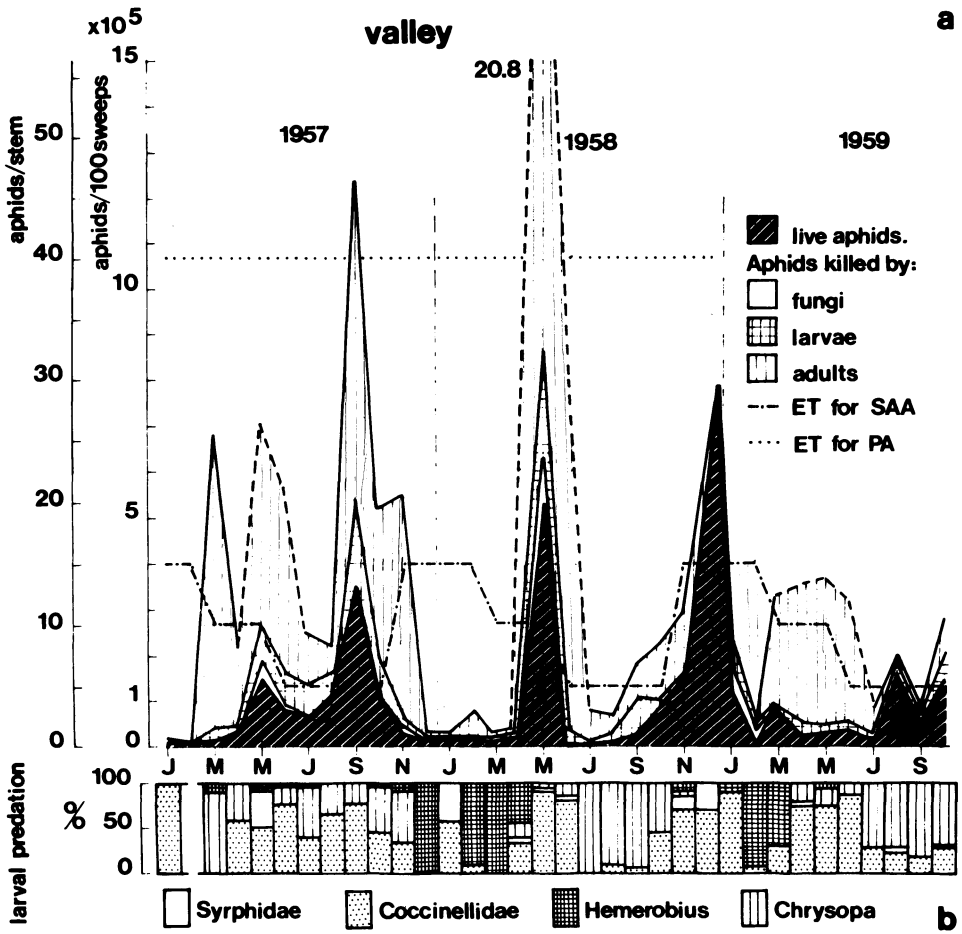


Fig. 7. Potential aphid abundance in San Joaquin Valley alfalfa fields. (Same as figure 6.) The economic threshold (= ET) expressed in biomass aphids per stem (4 SAA = 1 PA) was surpassed only in September, 1957, and December, 1958, in the average alfalfa field. For further information see pages 67-68.

scarce. For example, *Chrysopa* becomes important in some summers when lady beetles leave the fields because of diapause induction; *Hemerobius* thrives early in the season, before lady beetles

become active; syrphids enter the picture throughout the year whenever aphid levels are high; and predaceous Hemiptera are active during the hot summer at low aphid populations.

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APPENDIX
REGRESSION EQUATIONS

r^2 in text	Y	\bar{X}	N	a	b	r	Based on:
r^2_1 .	Coccinellid adults/100 sweeps	Aphids per 100 stems	42	0.10	0.17	0.77	Monthly means of each area
r^2_2 .	Coccinellid larvae/100 sweeps	Aphids per 100 stems	42	0.00	0.08	0.93	Monthly means of each area
r^2_3 .	Coccinellids: 1st adult peak	First larval peak	25	95.61	-0.33	-0.37	Maximum monthly means of each field
r^2_4 .	<i>Hemerobius</i> adults/100 sweeps	Aphids per 100 stems	28	0.50	0.01	0.71	Monthly means for the coast
r^2_5 .	Aphids May peak	Coccinellid adults first peak	25	128.71	-4.25	-0.44	Maximum monthly means of each field

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