

Ecology of Insect Host-Parasitoid Communities

Competition may be the most vital factor in the
structure and function of these systems.

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"Ecology" is a remarkable word. In recent years it has come to denote a startling variety of things to a variety of people. We keep hearing that our very survival as human beings depends on how well we understand our ecology and what we are willing to do for it. Apparently the essence of this plea is: How can we stop polluting our environment, overpopulating our earth, and overusing our resources? But the term ecology was first used with somewhat simpler and purer connotations. Ecological studies originally dealt with natural history, and with the tolerances of plants and animals (excluding human beings) to physical conditions in their environments. Attempts were made to determine the effects of temperature, humidity, and other physical factors on various organisms and their distribution. In later studies, the trend was toward more nebulous things—such as finding out the effects of competition, trophic structure, or species diversity on organisms and their organization. We were trying to understand how natural environmental factors affect the distribution and abundance of species, other than man, on this earth. Perhaps this form of the science should be called "classical ecology" to distinguish it from the newer, more human-oriented form.

Over the past two decades, classical ecologists have become more interested in studying number dynamics in groups of single species and in the puzzling and entertaining things that happen when groups of several species attempt to live together. Such studies, known

as population and community ecology, have attracted a surprisingly large number of investigators, possibly because the data that can be collected are often so complex as to be almost overwhelmingly difficult to analyze, and thus they present an irresistible challenge. In any event, the endeavors of these investigators have provided the basis for some of the most profound and heated controversies science has ever known.

Not long ago, population ecologists spent much time arguing whether "density dependent" or "density independent" factors regulate natural population numbers. Fortunately, after several years the controversy somewhat subsided when a close scrutiny of the various positions showed that frequently the opponents were saying very much the same thing only in a different way. Some ecologists, with perhaps more insight than others, concluded that there were often no valid means of differentiating density dependent from independent factors. Nevertheless, the debate was thought-provoking and allowed time for the gathering of more evidence which, after some analysis, began to indicate what probably should have been realized from the beginning—that no two populations are necessarily regulated or even influenced by the same kinds of factors. Colinvaux (1) has written a lucid and penetrating account of this position.

There have been other hotly debated issues in population and community ecology; issues that may be a long time in their resolving. Reasons for the regular cycling in numbers of some animal species have never been agreed upon. Indeed, there is still con-

troversy over the question of whether the cycles are real or not. The importance of predators, weather, and diseases in population dynamics is still largely undetermined. Why are some species in a community relatively rare and others common? Is it a fact that populations are more stable in tropical than in temperate areas, and if so, why? There are even some issues that have been considered closed, but that could benefit from reinvestigation; ecological succession is one such issue (2). All in all, it is apparent that there are many mysteries in classical ecology yet to be solved. It is also apparent that these mysteries will not be solved entirely by simulated computer studies nor from long-winded debate. The issues will be resolved ultimately from long-term, in-depth studies of natural populations and communities under both field and laboratory conditions. This task will not be easily nor quickly accomplished.

Since 1966, I have been studying an aggregate of insect species that I prefer to call a community. Others might like to call it a segment of a community, a species complex, or something else, and this attitude is understandable according to various definitions of a community. This particular community consists of a tiny midge *Rhopalomyia californica* Felt (Diptera: Cecidomyiidae) that forms galls on the plant *Baccharis pilularis* De Candolle (coyote brush), and a number of parasitic wasp species (parasitoids) (Hymenoptera) that attack the midge, each other, or both (3). All members of this community are endemic to the northern and central coastal region of California and extend inland to the Sierra Nevada foothills in limited areas. There are both primary parasitoids (attacking only the host insect, the midge) and facultative hyperparasitoids (attacking either the midge or another parasitoid) present in the community. *Rhopalomyia* has altogether perhaps a dozen species of parasitoids, some of which are very common and appear in most samples, and others which occur sporadically and even very infrequently. I have studied intensively the six species that are most consistent in their presence within the coastal area observed; the other species seem to be so sporadic in occurrence that they must have much less effect on the community.

Although very few of them have

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been looked at intensively, endemic host-parasitoid communities make ideal ecological systems in which to study a great variety of ecological factors. They are particularly interesting when one is studying competition because very frequently they contain a large number of parasitoid species interacting with a host and each other, and this interaction normally brings about a great deal of rivalry for resources. It is not uncommon for an endemic host insect to have as many as 30 or 40 species of parasitoids attacking it—often more. It seems remarkable that so many species can coexist using the same resource.

So much has been written about competition in ecological systems that one can easily become apprehensive when contemplating anything so immense as an inclusive survey of the literature. And yet, curiously, so few facts are known about the effects of competition among all but a few organisms that the subject is still largely in a state of confusion. It is impossible at times to be certain that competitive factors rather than other kinds of factors are responsible for normal population and community phenomena. Although a number of studies in the laboratory have shown clearly and conclusively the impact of competition among the individuals of a species or between two or more species, only a very few studies in the field have been able to do so. Connell (4) conducted a classic study in which he was able to observe directly that competition between two animal species in a natural situation resulted in one of the species being driven out of the community. The trouble with being uncertain about how competition affects the structure of relations among organisms is that so many fundamental concepts in ecology are dependent upon a thorough

understanding of the process. Ecological succession, speciation, population regulation and dispersion, and community stability are but a few of the concepts that suffer from the paucity of incontestable data on competition. Part of the problem may be that competitive mechanisms appear to differ among different kinds of organisms. We have been looking for ways in common that plants and vertebrate and invertebrate animals struggle with one another for survival, and perhaps there are none. Each organism, or at least each type of organism, seems to have its own special way of handling the situation.

Besides being of interest in elucidating general concepts of population and community ecology, the study of natural host-parasitoid systems has a more practical aspect. Parasitoids are used in the practice of biological control, a form of pest control that has been revitalized recently because of the environmental problems caused by chemical insecticides. In spite of the fact that biological control has been practiced throughout the world for the past 80 or 90 years, relatively little basic information is available about the ecology of endemic host-parasitoid communities. This particular study was undertaken in an attempt to learn as much as possible about the interactions among the various parasitoid species in the *Rhopalomyia* community, to discover whether parasitoid competition plays a key role in the dynamics of this system, and to learn whether other factors, such as weather, play an important part in its functioning. I here summarize the results of studies reported elsewhere (5, 6) and relate new findings which, I hope, will provide broader insights into ecological communities in general and host-parasitoid communities in particular.

Results of Laboratory Experiments

In order to be effective in finding and utilizing their host insects, parasitoids are thought to be dependent upon certain basic characteristics. Biological control authorities have usually considered the following to be among the most important: (i) searching ability—the ability to find their hosts readily; (ii) reproductive potential—the higher the better; and (iii) physiological tolerances similar to those of the host. In addition to these basic attributes, parasitoids often possess other complex and diverse characteristics, not all of which need to be discussed here. But among the parasitoids attacking *Rhopalomyia* were found (i) those that lay their eggs in the egg stage of the host, others that lay their eggs on or in the larval or pupal stage; (ii) those that live and feed (after hatching) inside the body of the host larva, others that feed from an external position; and (iii) those inclined toward superparasitism, multiparasitism, hyperparasitism, various combinations of these, or with no such inclinations (7). These diverse habits provide unique opportunities for competition, both intra- and interspecifically. Table 1 gives the names and various data for each of the six species of parasitoids studied. These data were gathered from tests conducted in small laboratory cages under controlled conditions (5). It will be necessary to discuss the habits of these insects at some length during the course of this article.

If one were to attempt a classification of these six parasitoids from the most competitive interspecifically to the least (Fig. 1), many of the attributes in Table 1 would have to be considered. The two facultative hyperparasitoids, *Zatropis* and *Amblymerus* would have to head the list since both

Table 1. Certain attributes of six species of parasitoids that attack *Rhopalomyia californica*. The statistic r_e is the approximate calculation of the innate capacity for increase by the formula $\log_e(R_0)/T$, where R_0 is the net reproduction rate and T is the approximate generation time [see (24)]. The innate capacity for increase was not calculated for *Amblymerus* or *Zatropis* because these species attack a variety of hosts (other parasitoids), each of which may affect this statistic differently.

Species	r_e	Type of larval feeding	Adults feed on (kill) hosts	Superparasitism	Multi-parasitism	Hyperparasitism
<i>Platygaster californica</i>	.092	Internal	Possibly	Never	Not possible	Not possible
<i>Torymus koebelei</i>	.090	External	Sparingly	Common	Varies	Occasional
<i>T. baccharicidis</i>	.080	External	Commonly	Common	Varies	Occasional
<i>Tetrastichus</i> sp.	.200	Internal	Never	Uncommon	High restraint	Never
<i>Zatropis</i> sp.		External	Extensively	Common		Extensive
<i>Amblymerus</i> sp.		External	Commonly	Common		Extensive

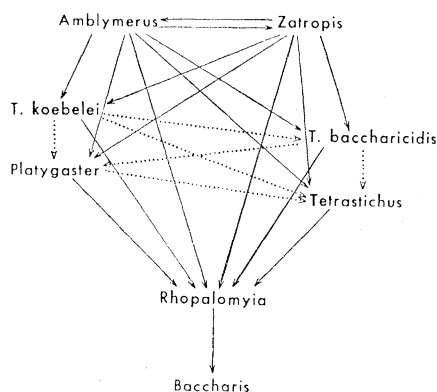


Fig. 1. Trophic structure of the *Rhopalomyia*-parasitoid community. The four trophic levels of the community are shown diagrammatically: (i) producer (*Baccharis*); (ii) primary consumer (*Rhopalomyia*); (iii) secondary consumers (*T. koebelei*, *T. baccharicidis*, *Platygaster*, *Tetrastichus*); and (iv) tertiary consumers (*Amblymerus*, *Zatropis*). Solid arrows denote direct attack and feeding on one organism by another. Dotted arrows indicate some other form of attack or inhibition leading to death of the attacked or curtailment of reproduction. The six species of parasitoids are progressively poorer competitors as one reads downward from the top of the diagram. The number of arrows pointing to each species indicates how many other species affect its survival.

successfully attack either *Rhopalomyia* or other parasitoids, although the latter are attacked with some discrimination according to species. *Tetrastichus*, for example, is parasitized more often by *Zatropis* than would be expected on the basis of random host selection, and both species of *Torymus* are attacked less often by both *Zatropis* and *Amblymerus* than would be expected. Then too, all the primary parasitoids are completely inhibited from attacking hosts already parasitized by either *Zatropis* or *Amblymerus*, although these last two species readily attack each other. This discriminatory behavior is common among parasitoids (8). *Zatropis* adults feed extensively (*Amblymerus* to a lesser extent) on *Rhopalomyia* larvae, thereby killing them and any other parasitoid larvae that happen to be feeding there at the time. In this manner, *Zatropis* acts more like a true predator than a parasitoid.

Next on the list of competitors would have to come *Torymus koebelei*, followed by *T. baccharicidis*. *T. koebelei* has a somewhat higher capacity for increase than the other which would be an advantage. It also readily multiparasitizes hosts already attacked by

the other primary parasitoids and frequently kills the latter in the process. *T. baccharicidis* also freely multiparasitizes hosts with one exception; it never attacks hosts already parasitized by *T. koebelei*. Next on the list would appear *Platygaster* and then *Tetrastichus*. *Platygaster* adults parasitize the eggs (instead of larvae) of *Rhopalomyia* and, therefore, multiparasitism and hyperparasitism by this species are not possible because it always attacks the host at an earlier stage of development than do the other species. *Platygaster* larvae feed internally on the host larvae, which is a distinct disadvantage because most internal parasitoids appear to be readily killed by external parasitoids in cases of multiparasitism, and *Platygaster* is no exception. *Tetrastichus* has a very high innate capacity for increase which would appear to give it an advantage. However, it is what might be called a very sensitive parasitoid; that is, its increase is very restrained by the presence and activities of other species. It will rarely attack hosts already parasitized by other species but, being an internal feeder, it is frequently killed by external parasitoids that attack hosts in which it is already present. *Tetrastichus* is also attacked more readily by the two facultative hyperparasitoids than are the other primaries.

Results of Glasshouse Experiments

From the data compiled in Table 1 and discussed in the preceding section, one should be able to predict with some accuracy the relative degree of parasitization each species of parasitoid by itself is able to effect on a host population, and also something about the outcome of similar studies where different combinations of species are introduced to the host. Studies of this type were undertaken in cages (Fig. 2) under partly controlled conditions in a glasshouse (5). Figures 3 and 4 show the results of these studies of parasitization. As might be expected, the factor that correlates best with the ability of each species by itself to infect the host population is its innate capacity for increase (see Table 1). *Tetrastichus*, having by far the greatest capacity for increase of the four primary parasitoids, produces 100 percent parasitization in about 100 days. The other three primaries (*Platygaster*, *Torymus koebelei*, and *T. baccharicidis*)



Fig. 2. Type of cage in which *Rhopalomyia* parasitization studies were conducted under glasshouse conditions. The tests were initiated to examine the effectiveness of each parasitoid species by itself and in combination with other species.

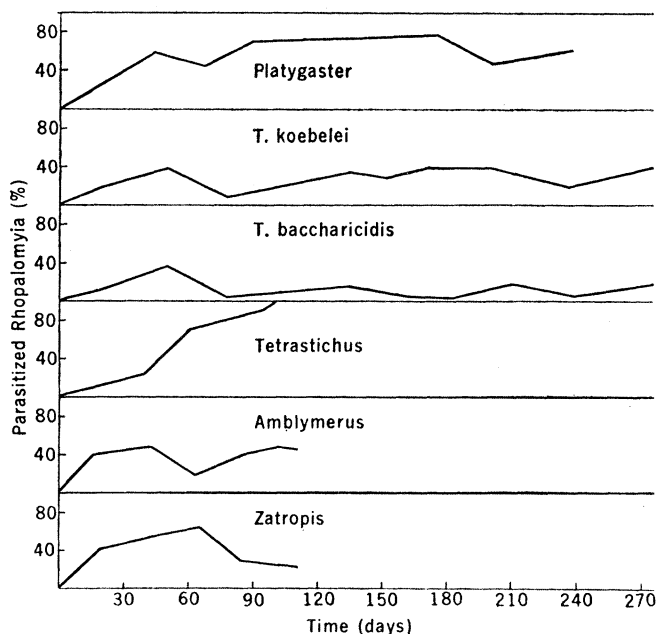
do not have reproductive rates high enough to bring about total infection of the host, but the degree of parasitization is in each species directly related to its capacity for increase. This statistic was not calculated for either of the two hyperparasitoids (*Zatropis* and *Amblymerus*), but can be estimated from Fig. 3. The average number of hosts parasitized by *Amblymerus* appears to be about 35 to 40 percent; the average for *Zatropis* is somewhat higher, but the *Zatropis* adults' habit of feeding on and killing host larvae, many of which are already parasitized, brings about a reduction in parasitism later in the experiment.

In studies of mixed species, other factors take precedence over a parasitoid's capacity for increase, and direct correlations between this statistic and the degree of parasitization by a particular species no longer necessarily exist. Figure 4 shows the results of several different species combination studies. These tests were continued for only about 100 days, the amount of time taken for *Tetrastichus* by itself to parasitize the entire host population. The effect of competition between species is clearly recognizable in most cases. When the two *Torymus* species and *Tetrastichus* are put together (Fig. 4a), *Tetrastichus* becomes gradually more dominant as the test progresses. This result is probably because of the high capacity of *Tetrastichus* for increase; the increase is slow because of inhibition by the other two species, but these others leave so many hosts unparasitized that *Tetrastichus* is able to

increase continually in spite of them. Total parasitization at the end of the test is less than 80 percent, however, whereas *Tetrastichus* by itself is capable of 100 percent parasitization (Fig. 3) in the same amount of time. When *Platygaster* is combined with the three species just discussed (Fig. 4b) both it and *Tetrastichus* are affected by the presence of the two *Torymus* species. *Tetrastichus* again improves its position as the test continues, but *Platygaster* apparently cannot compete under these conditions and dies out completely. Total parasitization reaches about 90 percent.

Field studies that I describe later have shown that *Platygaster*, *Torymus koebelei*, and *T. baccharicidis* are the three dominant parasitoids under most natural conditions (Fig. 5). Therefore, tests combining these three species were conducted (Fig. 4c). Once more, the least competitive (*Platygaster*) is dominated by the others and eventually becomes nearly extinct. Even more interesting is the low degree of total parasitization by these three species that are dominant under field conditions—only about 60 percent at the peak; *Platygaster* does somewhat better than this in tests by itself (Fig. 3). One of the most surprising facts learned from field studies of this community is that *Tetrastichus*, in spite of its high reproductive rate, is invariably the least dominant of all the species studied under natural conditions. Perhaps this enigma can be explained by what happens when *Zatropis* and *Amblymerus* are added to the experiments, combining all six species in one test (Fig. 4d). *Platygaster* is for the most part dominated by the other species as in previous tests but, surprisingly, so is *Tetrastichus*. In fact the latter is never responsible for more than about 5 percent of the total parasitization, and most of the time only 1 to 3 percent. Apparently the addition of *Zatropis* and *Amblymerus* has a profound effect on *Tetrastichus*, a conclusion which is reinforced by looking at the results of tests combining only *Zatropis* and *Tetrastichus* (Fig. 4e). *Zatropis* completely dominates the other, probably because *Zatropis* prefers to hyperparasitize *Tetrastichus* rather than to lay its eggs on *Rhopalomyia* larvae. Another surprising result (not shown in Fig. 4d) of studies containing all six species is that *Torymus baccharicidis* is responsible for a higher degree of parasitization than *T. koebelei*,

Fig. 3. Parasitization of *Rhopalomyia* by each of six species of parasitoids under cage conditions. The data for *Amblymerus* and *Zatropis* are shown for only about 110 days because the sex ratios decline of these species after this period of time.



lei, a reversal of what might be expected based on a comparison of their attributes. This outcome can perhaps be explained by the behavior of *Amblymerus*, which is restrained about 50 percent of the time from hyperparasitizing *T. baccharicidis*, but is not so restrained in the case of *T. koebelei*.

I believe at least two important points can now be deduced from these experiments. The first is that these particular parasitoids, and probably many other organisms, have subtle and complex behavioral characteristics which may greatly affect their normal competitive interactions, and that these characteristics can often be demonstrated under laboratory conditions, at least in the case of small animals such as insects. This is not to say that behavior is never changed under artificial conditions—it undoubtedly is. I suspect, for example, that *Tetrastichus* is even more sensitive to other parasitoids under field conditions than in the crowded confines of the laboratory, and that *Platygaster* must be less affected by other species in the field than laboratory tests indicate or it would not be so common in field samples. Nevertheless, there are many observations made

possible by laboratory studies that could never be gathered from field studies alone. The second point is something that is of great importance to biological control specialists and has often been discussed and debated by them; namely, does interspecific competition among parasitoids reduce their capability of controlling the host insect? Under the conditions of these studies it did. The parasitoid with the highest reproductive potential and poor-

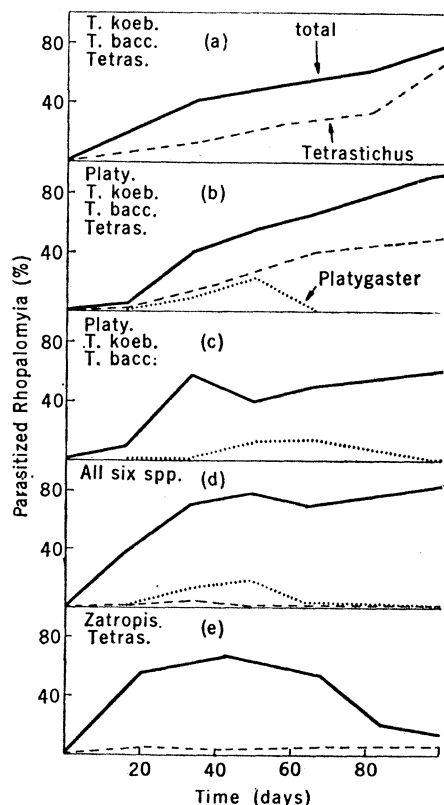


Fig. 4. Parasitization of *Rhopalomyia* by cultures of various mixed species of parasitoids under cage conditions. Parasitization by the poorest competitors, *Platygaster* (dotted lines) and *Tetrastichus* (dashed lines), is shown individually along with the total percentage for all species (solid lines) in order to emphasize how these two species are affected by the others.

est competitive abilities (*Tetrastichus*) was capable in pure culture of a higher degree of parasitization than were any of the mixed cultures.

Results of Field Studies

The ditypic plant *Baccharis pilularis* is endemic to California; the subspecies *pilularis* forms prostrate spreading mats perhaps 15 centimeters (6 inches) high, and the subspecies *consanguinea* is an erect form that may grow to a height of 3.7 meters (12 feet). Both subspecies prefer maritime habitats, *pilularis* being limited to a narrow coastal belt extending about 160 kilometers (100 miles) north and 160 km south of San Francisco Bay. The subspecies *consanguinea*, on the other hand, can be found along the coast the entire length of California and grows sporadically inland for some distance, as far as the Sierra foothills in the Sacramento area. *Baccharis* is an evergreen plant and continues to grow throughout the year if sufficient moisture is available. Because of California's Mediterranean-like climate, moisture is often deficient during the summer and early autumn, especially in the inland areas, and *Baccharis* is frequently inhibited from putting out new growth. On the coast, however, with persistent fog to provide moisture and cool temperatures, growth usually continues through the summer. The plant often forms a dense scrubby cover almost like chaparral and is considered detrimental to pasture development. Apparently, the life span of *Baccharis* is about 10 years (9).

The midge *Rhopalomyia californica* is restricted to *Baccharis pilularis*. The female midge deposits her bright red eggs in clusters on the terminal growing stems of the plant, where the midge larvae work their way into the buds and new leaf axils. The feeding of the larvae appears to stimulate the plant into producing multichambered galls, each chamber housing one larva. Large galls may contain 50 or 60 larvae. Pupation occurs inside the gall and then the adult males and females emerge and mate. The midges may be attacked by parasitoids in the egg, larval, or pupal stages. Doutt (10), who studied this host-parasitoid community in some detail, reported that the midge is never found south of Santa Barbara even though the host plant is common in those areas; I have

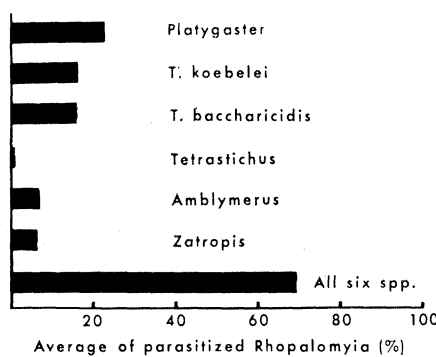


Fig. 5. Average proportion of field-collected *Rhopalomyia* parasitized during a 6-year period by six species of parasitoids, separately and collectively. Several other species of parasitoids that occur only sporadically add slightly to the total number of hosts parasitized.

observed this phenomenon also and have no explanation for it.

The field sampling procedure consisted of my gathering galls for a 30-minute period at each collecting site. Galls are obvious on the plant and are therefore easily collected. Eleven sites on or very near the coast were selected from Bodega Bay, 80 km north of San Francisco, south to Pismo Beach, a total distance of nearly 480 km. Because of the distances, these sites were visited only once every 2 or 3 months. Galls were picked and placed in plastic bags, and the parasitoids and their host insects were collected and counted for as long as they emerged from the galls.

Figure 5 indicates the relative frequency of each parasitoid species during the 6-year study period. *Platygaster* is the most common, followed closely by the two *Torymus* species at similar frequencies. The two facultative hyperparasitoids, *Amblymerus* and *Zatropis*, are somewhat less frequent; and *Tetrastichus*, which has such a high capacity for increase but poor competitive abilities, is least frequent. The six species collectively parasitize an average of a little under 70 percent of *Rhopalomyia*. One might ask why *Platygaster*, a rather poor competitor, is the most common species. Since the other species are all larval and pupal parasitoids, *Platygaster*, an egg parasitoid, has no competition when ovipositing and is capable of parasitizing a comparatively large percent of the host egg population. Dissections of host material have often shown 70 to 80 percent of the eggs to be parasitized by *Platygaster*. The other parasitoids attack the hosts at a later stage of development whether they have been parasitized earlier by

Platygaster or not (except *Tetrastichus*, which avoids hosts containing *Platygaster*). However, because of their limited reproductive capabilities and mutual competitive problems, these other parasitoids are not always capable of becoming numerous enough to parasitize a very large proportion of the hosts; thus *Platygaster* may remain the most abundant species in the community even though a considerable portion of its population has been destroyed by multiparasitism. During those times when the other species (particularly *Torymus*) do become really abundant, *Platygaster* may nearly disappear.

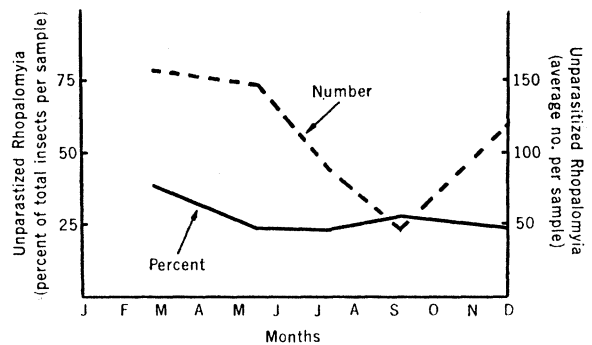
Figure 6 is an index of the relative seasonal changes that occur in the *Rhopalomyia* population. The most interesting conclusion to be drawn from these data is that the relative proportion of unparasitized *Rhopalomyia* remains very stable throughout the year despite the considerable change in average numbers. Or to put it another way, the degree of parasitization changes very little with season, although the number of hosts and parasitoids does. The reduction in number of *Rhopalomyia* during the summer and early autumn is probably due to the weather—the decrease in moisture results in somewhat poorer growing conditions for *Baccharis* plants and hence less successful gall formation by the insect. Since the degree of parasitization remains about the same, a reduction in the numbers of *Rhopalomyia* means that parasitoids are also reduced in numbers by about the same factor. But averages are misleading and it is often more useful to disregard them and observe other data.

There has evolved among ecologists an unproved but intellectually satisfying hypothesis which, simply stated, says that more complex ecosystems are more stable. In other words, the more species and interactions that occur among them, the more stable (with number fluctuations being more predictable and of a lesser magnitude) each population of a community should be. This concept is appealing because it makes good common sense and agrees with physical laws that indicate greater equilibrium in certain operations when there are a greater variety of feedback factors affecting the system. The hypothesis is also amenable to mathematical manipulation, and MacArthur (11) has suggested by the information-theory approach that sys-

tems with more species should be more stable. However, May (12) appears to have come to just the opposite conclusion regarding the hypothesis as a generality, but agrees that there may be certain types of complexity that lead to stability. It is necessary to realize, however, that the concept involves both interspecific relationships at any particular trophic level, and relationships between the various trophic levels of a community. Watt (13) concluded that stability should be enhanced when there is a large number of species at the same trophic level competing for a single host species at the next lower trophic level. On the other hand, a single species feeding on a large number of host species at a lower trophic level should lead to instability. If this analysis is correct, parasitoid communities where there are many parasitoid species feeding on a single host species should be comparatively stable systems. Hence, the *Rhopalomyia*-parasitoid community ought to show considerable stability.

There is another reason for suspecting that *Rhopalomyia* and its parasitoids might show stability, at least in those areas I have investigated; that is the mildness of the climate. The sites that I sampled are situated on or very near the coast where there are no great fluctuations in temperature or humidity throughout the year, although there is a summer period relatively free of rain. The conditions would have to be considered largely subtropical, with no perturbations that would cause excessive insect mortality or other numerical fluctuations. All the insects are multivoltine, reproducing throughout the year, with the exception of one parasitoid, *Torymus koebelei*, a sizeable proportion of which appears to undergo diapause for a short period during the winter. The interactions of these diverse species throughout the year should act to buffer any great fluctuations in the amount of parasitization and in the numbers of hosts and the various species of parasitoids, according to the stability hypothesis. In Fig. 7 I show the proportion of parasitized *Rhopalomyia* found at six different collecting sites over a 6-year period. The degree of parasitization is comparatively high much of the time, as might be expected of an endemic host species having a number of parasitoids, but there is little indication of stability. The fluctuations are of considerable magnitude and they do not

Fig. 6. Relative seasonal changes in *Rhopalomyia* field populations over a 6-year period. Data are for samples from all collecting sites. The graph shows both the average number of *Rhopalomyia* adults that emerged unparasitized per sample, and the number of unparasitized *Rhopalomyia* expressed as a percentage of the total number of insects (seven species). Data for January and February are omitted because of the small number of samples taken during these months. All points on the graph represent mean values.

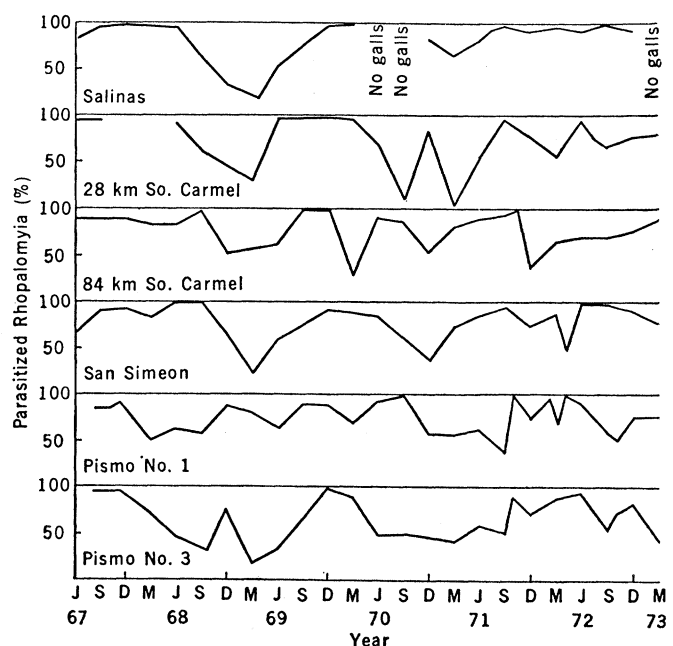


seem to follow any kind of a regular pattern other than a general dip in early 1969 at five of the locations. Each collecting site appears to have its own program of events. Even at the Pismo sites 1 and 3, which are only 4.8 km apart, there is little similarity in pattern.

From the standpoint of great and irregular fluctuations, the data on population numbers shown for three collecting sites in Fig. 8 are even more interesting. Actually, because of the type of sampling procedure used, the number fluctuations shown in this figure are greatly dwarfed in magnitude compared to what they were in the field. This problem of graphic misrepresentation arises because the samples consisted of galls that could be collected in a certain period of time—30 minutes in this case—instead of galls contained in a certain measured area. The latter method, which would

have given a true index of numbers, was impractical for technical reasons. With the 30-minute collecting procedure, the size of the collecting area differed at each location depending on the relative abundance of galls; when galls were scarce a much larger area could be collected than when they were numerous. That some of the fluctuations in numbers of insects per hectare, for example, must have been enormous is indicated by occasions on which galls were so scarce that only one or two (or none) might be found, even though the ground was covered with *Baccharis*; on other occasions nearly every growing tip of every plant would contain a gall. The differences in magnitude, if the data had been expressed as insects per fixed area, would have been in the tens of thousands or even hundreds of thousands. Therefore, Fig. 8 does not indicate anything about the precise magnitude of fluctuations, but

Fig. 7. Proportion of parasitized *Rhopalomyia* at six collecting sites on the coast of central California over a 6-year period. On three occasions no *Rhopalomyia* galls were found at the Salinas site.



There is no doubt that the temporal oscillations of frequencies of *Rhopalomyia* and its parasitoids are correlated, in the way that host-parasitoid systems usually are (Fig. 8). Each host change is usually followed, after the necessary time interval, by a parasitoid change in the best Lotka-Volterra tradition (14); and being a believer in the power of natural enemies to do such things, I assume the parasitoids are responsible for the host changes. The alternative explanation would be that some other factor is responsible for the oscillations of *Rhopalomyia* and the parasitoids are simply following the same pattern dictated by the number of hosts available for parasitization at various

Watt (15) suggested that excessive interspecific competition within the trophic level of a parasitoid complex attacking a common host may stabilize that complex so that it cannot respond quickly to host number fluctuations (16). Zwölfer (17) provided evidence that this may be true. It seems very possible that in cases such as *Rhopalomyia*, one or two of the most effective parasitoids would by themselves bring about greater control of the host, including perhaps, though not necessarily, a more stable system, than the

Figure 9 depicts the relative amount of parasitization by each of the six species at one collecting site (San Simeon) over a 6-year period. Several observations can be made. *Torymus koebelei* is obviously more effective during the summer months, and the reason for this is undoubtedly that a large proportion of these insects appear to undergo diapause for perhaps 2 months during the winter. Because

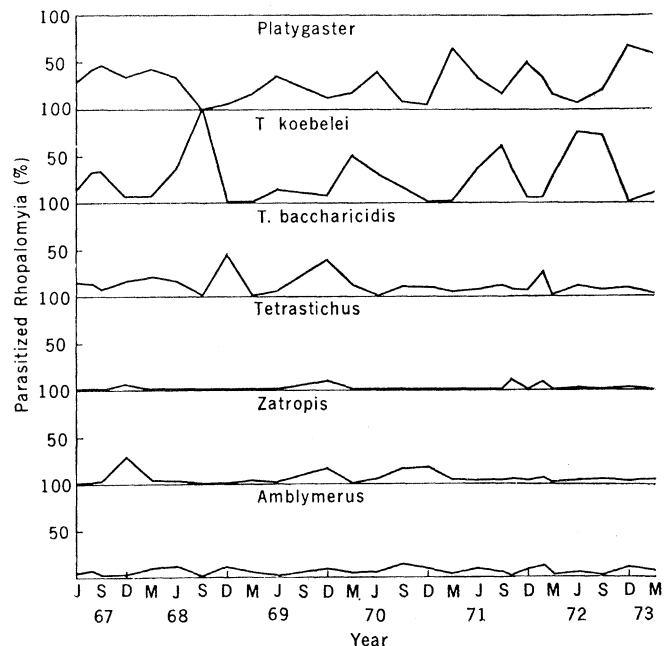


Fig. 8 (left). Numbers of hosts (*Rhopalomyia*) and parasitoids that emerged from samples of galls collected at three different sites over a 6-year period. The numbers indicate only relative variations of magnitude for reasons explained in the text. Fig. 9 (right). Proportion of *Rhopalomyia* individuals parasitized by each of six species of parasitoids at the San Simeon collecting site over a 6-year period.

of its relatively more effective competitive traits, during the summer *T. koebelei* tends to dominate *T. baccharicidis*, which is more effective in the cooler months according to the data. *Platygaster* is less effective than both of the others and therefore tends to fill in the unoccupied gaps when neither of the others is very effective. And *Tetrastichus*, of course, is overwhelmingly dominated by all of the other species. The reasons for the relatively subdued status of the hyperparasitoids (*Zatropis* and *Amblymerus*) are not very clear. Parasitization of *Rhopalomyia* by *Amblymerus* tends to peak during the cooler months; this may have something to do with temperature preferences or host availability during that period. Perhaps neither hyperparasitoid species is very effective in finding hosts and this tends to keep their numbers down. One might be tempted to suggest, after studying Fig. 9, that each species fits very nicely into its own niche; that each is a more effective parasitoid than any of the others in that particular niche because of its specialized traits or tolerances.

Parasitoids are considered by many people to be narrow specialists, and therefore a number of different species are required to control a host population over a variety of physical conditions. Two of my students have been working on the climatic tolerances of the four primary parasitoids of *Rhopalomyia*. They find that *Tetrastichus* and *Torymus koebelei* are very tolerant of high temperatures, and that *Platygaster* and *T. baccharicidis* are considerably less tolerant. On the other hand, *T. baccharicidis* is the most tolerant of low temperatures. These data might help to explain why *T. koebelei* is more abundant in summer and *T. baccharicidis* in winter, even if one disregarded the winter diapause of the former. However, they do not explain those occasions when summer collections have shown *T. koebelei* to be low in number and *T. baccharicidis* invariably high at the same time. Nor do they explain why *Tetrastichus*, since it is the most heat tolerant of the four species, is not more dominant in summer and particularly in the hot inland areas where all of these insects are found; nor why *Platygaster*, with its poor heat tolerance, is one of the dominant species in the inland areas (10). These observations must be explained in some other way, and I be-

lieve that competition, or lack thereof as the case may be, is responsible in many instances. I am particularly convinced of this since I have found, in dissecting field-collected galls, a high incidence of multiparasitism. Obviously, competition is occurring.

Parasitoids as "r" and "K" Strategists

The subject of *r* (reproduction rate) and *K* (carrying capacity) selection (18) has become a popular one. Numerous articles have appeared on its various aspects, probably because the concept is appealing and effective in explaining away some of the tougher problems that population and community ecologists encounter. Species known as *r* strategists tend to occupy unpredictable environments, have high capacities for population increase (high *r* values), and are poor competitors; *K* strategists tend to exist in more constant environments, have relatively low capacities for increase, and are good competitors. I have discussed previously (6) the fact that the four primary parasitoids (also discussed here) of *Rhopalomyia* appear to have reproductive capacities inversely related to their competitive abilities, and that, therefore, they form a sequential series of *r* to *K* strategists, one to another. It seems possible that many, if not all, endemic parasitoid complexes have evolved as sequential series of *r* to *K* strategists (19), and it is not improbable that many other kinds of endemic communities have also. Goulden (20), Slobodkin and Sanders (21), and others have suggested mechanisms for this general kind of community development.

An endemic host-parasitoid community could evolve as follows. The early environment might be one of large and irregular natural perturbations of various sorts or an area disturbed by man. If one assumes that the host insect is able to adapt to this situation, any parasitoid that could successfully attack the host under these conditions would have to have physiological tolerances enabling it to survive the environmental perturbations, or a high rate of increase enabling it to build up its numbers between disturbances, or both. In other words it could not be a narrow specialist; it would have to be an opportunist or *r* strategist. Under normal ecological succession, the physical ecosystem in time is likely to become less stringent,

allowing the invasion and establishment of parasitoid species which are less tolerant physiologically and less fecund, but more competitive, that is, the *K* strategists. A whole series of invasions might ensue over a long period of time, each new species using superior competitive mechanisms to usurp part of what was the niche of an earlier arrival. This would explain the great number of different species found in endemic host-parasitoid communities. Thus, there develops a series of *r* to *K* strategists, but the *r* strategists become dominated because of limited competitive abilities by the more *K*-selected species, and the former eventually become scarce in the community. They survive best at the outer range limits of the host where physical factors may be more stringent, or in more central areas when the environment is periodically disturbed in some manner, thereby decimating the *K* strategists at least temporarily. I have evidence that a disturbance altered the parasitoid complex of *Rhopalomyia* at the Salinas collecting site in 1971. Most of the *Baccharis* plants at the site were cut low to the ground or removed, disturbing the distribution and abundance of plants and host insects. By the next collecting date, parasitization of *Rhopalomyia* by *Tetrastichus* had increased from 1 to 46 percent, and total parasitization of *Rhopalomyia* increased from 81 to 97 percent. *Tetrastichus*, of course, because of its high reproductive capacity and feeble competitive abilities, has to be considered the most *r*-selected parasitoid in the complex. Gradually over the next few months, as the plant growth returned, *Tetrastichus* became progressively less common and finally regressed to its normal status while the more *K*-selected species resurged.

The problem of having *K* strategists as the dominant members of a community (particularly where a pest organism is present) is that they may bring about instability. This is possible because of their low reproductive potential and hence slow response to fluctuations in numbers of other organisms in the community. The delay in response is therefore greater than it would be with *r* strategists and allows larger fluctuations to occur. Biological control specialists can tell us that some of the best controlled and most stable pest insect populations have only one or two natural enemies attacking them; the cottony-cushion scale that is at-

tacked by the vedalia beetle, is only one example of a number that could be cited. These same specialists, whose job it is to import natural enemies into areas where pest insects have invaded, might benefit in being more selective in the organisms they import to control the pests. This advice has been offered before (22), but apparently has been largely ignored. Generally, the natural enemies chosen for importation are those most conspicuous in the endemic community of the pest, and the most conspicuous organisms in an endemic community are likely to be *K* strategists. The distressing fact about *K* strategists is that they have neither the characteristics of good colonizers nor of good biological control organisms, which must be (i) tough and adaptive organisms to survive unfavorable conditions, (ii) fast reproducers to take advantage of ephemerally favorable circumstances, and (iii) good dispersers and host searchers to find needed resources. These are the qualities found in *r* strategists. It is little wonder that the record of establishment of natural enemies in new areas by biological control workers has been rather dismal; only about 22 percent of the colonization attempts have succeeded according to Carter (23). And a large proportion of those that have become established have not been successful in containing their pestiferous hosts. Where and how does one find the *r* strategists in an endemic community? They are possibly among the least dominant species except in disturbed and marginal conditions where they should be much more common.

Conclusions

Although conclusive evidence is lacking for its establishment, the thesis that complexity adds stability to communities is probably accepted by the majority of ecologists. I believe this attitude found its origins in the indisputable fact that there are latitudinal and altitudinal changes in community complexity. As one progresses northward or southward from the equator, or higher in altitude in most parts of the world, one cannot help but notice that communities tend to become simpler, that is, there are fewer species per community. At the same time, these communities appear to be-

come less stable. But perhaps this change in stability is in appearance only; they appear to be less stable because of the relatively greater number of individuals comprising each species population in temperate areas. Each population, because of its greater numbers, is therefore conspicuous, and changes in these numbers are noticed. We are particularly aware of such changes because populations in these areas of the world have been comparatively well studied. Many of the most studied populations include species of economic importance where changes in population numbers are vital to agricultural or forestry practices. Equatorial populations, on the other hand, contain smaller numbers of individuals of each species because of the greater number of species present. Number changes are simply not as noticeable because the population itself is not as obvious among the other populations. It may be that when (if ever) we have as much data on equatorial populations as we have on those of temperate climates, we will find fluctuations of equal relative magnitude (but not of equal numbers, of course). If, on the other hand, we really do find a correlation between complexity and stability, the suggestion by May (12) that stability *permits* complexity may be well worth investigating.

Because of its organization and physical setting, the *Rhopalomyia* community I have studied might be expected to have considerable stability. In fact, however, it does not. Each of the populations in the community fluctuates greatly and irregularly in both percentages and numbers, and these populations apparently become locally extinct occasionally, because they sometimes cannot be found even in extensive collections. After studying several of the more important parasitoid species, it is evident to me that there is little or nothing about their interactions that might induce greater community stability. Each species seems to have evolved into the community with no higher purpose than simply to usurp what it can from some other member, and it does this by concentrating its energies on better competitive mechanisms rather than higher reproductive capacities. There are never empty niches to be filled by organisms having the "correct specifications" because new niches are cre-

ated out of parts of older, broader niches which were occupied by other, more *r*-selected organisms.

Thus, perhaps we have read too much into community organization. Perhaps the "filling of niches" is essentially nothing more than the haphazard result of competitive jostling among species; and that as communities develop, they are not necessarily programmed for such things as greater stability or better energy utilization—the species merely become more closely packed.

References and Notes

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