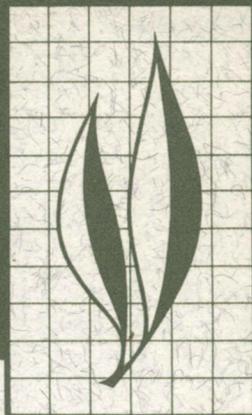




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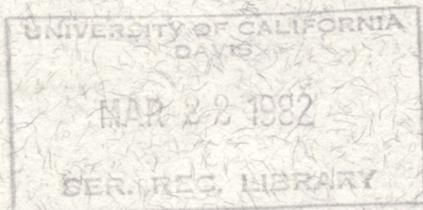
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Ecology of *Rhopalomyia californica* Felt (Diptera: Cecidomyiidae) and Its Parasites in an Urban Environment

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The ecology of an endemic gall midge, *Rhopalomyia californica* Felt, and its larval parasites was studied over a 3-year period in the city of Davis, California. Six species of parasites were associated with larvae of the midge: *Torymus koebelei* (Huber), *T. baccharidis* (Huber), *Platygaster californica* (Ashmead), *Zatropis capitis* Burks, *Mesopolobus* sp., and *Tetrastichus* sp. However, the midge was from four to ten times more abundant in Davis than in the endemic environment. In Davis, neither parasitization by any given species nor by the aggregate of species was a consistent regulating factor. These results suggest that, whereas parasite guilds in urban environments may be structurally similar to their non-urban counterparts, adequate or comparable levels of natural biological control of the host will not necessarily result. Thus, the use of native plants in urban environments may not always minimize attendant pest problems. The data obtained provide some empirical support for multiple-species introductions in classical biological control and illustrate the utility of facultative secondary parasites. A method for assessing competitive interactions among parasites before introduction is described, and the relevance of the theory of r- and K-selection to biological control is assessed.

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Ecology of *Rhopalomyia californica* Felt (Diptera: Cecidomyiidae) and Its Parasites in an Urban Environment¹

INTRODUCTION

NUMEROUS CALIFORNIA NATIVE PLANTS are available for use as ornamentals in urban environments. Coyote brush, *Baccharis pilularis* DC, is a case in point. Dwarf coyote brush, subspecies *pilularis*, is a popular ground cover in certain areas and is also planted along some freeway margins. Insect fauna of coyote brush in natural or endemic environments (primarily coastal California) has been studied extensively; however, knowledge of the associated fauna in urban areas is virtually nonexistent. In 1977, I initiated a long-term study of certain insects associated with dwarf coyote brush in the city of Davis, California. The insects are a cecidomyiid midge (*Rhopalomyia californica* Felt), which induces multichambered galls on coyote brush, and the hymenopterous parasites (parasitoids) associated with its larval stages. A major purpose of the present paper is to summarize the first 3 years of these investigations.

The data obtained are relevant to several questions in modern biological control, especially those pertaining to the use of native plants in urban environments: *viz.*, (1) Is the parasite guild associated with the midge in the urban environment structurally similar to its non-urban counterpart? (2) Given some degree of structural similarity, are adequate or comparable levels of biological control found in the two environments? This study is also relevant to certain aspects of classical biological control—*viz.*, interspecific competition among parasites and its relevance to multiple-species introductions, assessing competitive interactions among parasites before introduction, utility of facultative secondary parasites, and the applicability of the theory of r- and K-selection to biological control.

Host Plant, the Midge, and Its Parasites

Host plant

Two subspecies of *Baccharis pilularis* DC occur in California (Munz and Keck, 1959). Subspecies *pilularis* (= *typica*) is a prostrate shrub which forms dense mats 10 to 15 cm high and 1 to 4 m across. It occurs along windswept dunes and headlands along the northern California coast from the Russian River in Sonoma County south to Point Sur in Monterey County. Subspecies *consanguinea* is an erect or rounded shrub 1 to 4 m high. It is common on hillsides and canyons, particularly below 600 m; it is found especially along the coast ranges from San Diego County in California northward to Tillamook County in Oregon. This subspecies also occurs on the Channel Islands and in certain portions of the Sierran foothills of central California.

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Subspecies *pilularis* has been used as a ground cover in urban areas for several years. Cultivars of this form (which are essentially commercial clones derived from wild types) are available; Twin Peaks cultivar is the commonest one used in urban areas. A major horticultural advantage of ssp. *pilularis* is its relative adaptedness to the environment in many areas of California—e.g., it is able to derive sufficient water for maintenance and growth during the mild wet winters and can survive the hot, dry summers without any irrigation. It is thus well adapted to the Mediterranean climate which characterizes much of California.

The midge

Over 220 species of insects are associated with *Baccharis pilularis* in California (Tilden, 1951a). Of these, *Rhopalomyia californica* Felt is one of the more conspicuous. Detailed biological studies of this cecidomyiid midge were conducted by Tilden (1951b) and Doult (1961). The midge is host specific and lays its eggs on the actively growing terminals; larvae hatch and enter the plant between bud scales. Gall formation begins after larvae enter the plant. Galls are multichambered (one midge larva per chamber) and contain from as few as one or two larvae per gall to as many as 100. Larvae pupate inside the gall. Both male and female adults are short-lived (e.g., a day or two) and have vestigial mouthparts.

According to Doult (1961), the maximum rate of development from egg to pupa is about 30 days. Whereas all plants are susceptible to gall formation, physiology of the plant can determine rapidity of gall formation and development of larvae. The midge is multivoltine and generations will develop year round so long as temperature and host plant are favorable. There is no known diapause. The midge occurs from Del Norte County to Santa Barbara, but not south of Santa Barbara—even though the host plant occurs as far south as San Diego (Doult, 1961; Force, 1974).

Parasites of the midge

Over 10 species of parasitic Hymenoptera have been reared from *R. californica* in California. Virtually all available information on these species is contained in the works of Doult (1961), Force (1970, 1972, 1974, 1975), Ehler (1979a, 1979b), and Hopper (1981).

Torymidae. At least two—possibly three—torymid species have been reared from the midge: *Torymus koebelei* (Huber), *T. baccharidis* (Huber), and an undescribed species of *Torymus*. However, only the former two occur in Davis and will be considered here. The undescribed "species" may well be a form of the polytypic *T. koebelei* (D.C. Force, personal communication).

Torymus koebelei is a solitary ectoparasite of midge larvae and is an arrhenotokous, obligate primary parasite (Doult, 1961; Force, 1974). It has been reared from cecidomyiid galls collected in Arizona, California, Idaho, Montana, Nevada, New Mexico, Texas, Utah, Washington, Wyoming, and central Mexico (Grissell, 1976; 1979). As the midge host is not known to occur in most of these areas (Felt, 1912; Pritchard, 1953; Stone *et al.*, 1965), *T. koebelei* must not be host specific. However, the identity of any additional hosts has yet to be established.

According to Doult (1961), *T. koebelei* is coextensive with the midge in California,

and he regarded it as the dominant species in the parasite guild. Force (1974) also reported *T. koebelei* to be among the dominant parasites, although not necessarily the dominant species. In Davis, I have collected *T. koebelei* at numerous locations, and it is clearly one of the dominant species. I have also collected it at two natural sites near Davis—Putah Creek, about 32 km to the west, and Newcastle, about 64 km to the east.

Force (1974) stated that *T. koebelei* was very tolerant of high temperatures and was an effective parasite especially during the summer months. In Davis, *T. koebelei* is especially abundant in late spring (April to June) and in the fall. During winter, it is relatively rare. Many, if not most, of the larvae apparently undergo diapause during winter (cf. Force, 1974), although this hypothesis has yet to be fully verified experimentally.

The second torymid, *T. baccharidis*, is also a solitary ectoparasite of larvae and an obligate primary parasite (Doutt, 1961; Force, 1974). Both Doutt and Force referred to this species as *T. baccharicidis*, which, according to Grissell (1976), is an erroneous spelling. Also, *T. pilularidis* Huber, listed by Doutt (1961) as a parasite of *R. californica*, is a synonym of *T. baccharidis* (Grissell, 1976). This parasite is apparently host specific to the midge and known only from California (Grissell, 1976; 1979). The following information was determined by Force (1970) for *T. baccharidis* under laboratory conditions: mean total fecundity, 94.2 ± 45.3 ; gross reproduction rate, 56.3; net reproduction rate (R_0), 53.9; capacity for increase (r_c), 0.080; generation time (days), 49.8; sex ratio, $0.8 \sigma : 1 \text{ } \varnothing$; and sex determination, arrhenotoky.

Doutt (1961) stated that *T. baccharidis* was not necessarily coextensive with the midge; he noted that it was more "active" and abundant near the coast rather than inland or at the fringe of the midge's range. However, it is often among the dominant members of the parasite guild in the field (Doutt, 1961; Force, 1974). I have collected *T. baccharidis* at various locations in the city of Davis and at the Putah Creek and Newcastle sites mentioned earlier.

Force (1974) observed that *T. baccharidis* was more effective during the cooler part of the year and was less tolerant of high temperatures. My observations in Davis tend to support the conjectures with respect to temperature tolerance; however, this species has been comparatively rare in Davis, even during the cooler months of the year.

Platygastridae. Three platygastrid species have been reared from *R. californica*: *Platygaster californica* (Ashmead), *P. lampronota* Fouts and an undescribed species of *Platygaster* (Doutt, 1961). The latter two species are not known to occur in Davis and will not be dealt with here.

Platygaster californica is a solitary, egg-larval, endoparasite of the midge and is an obligate primary parasite (Doutt, 1961; Force, 1974). It is known only from galls on *Baccharis* in California and Idaho (Muesebeck, 1979) and is apparently host specific to *R. californica*. Force (1970) determined the following data for this species under laboratory conditions: mean total fecundity, 194.8 ± 124.6 ; gross reproduction rate, 80.2; net reproduction rate (R_0), 74.2; capacity for increase (r_c), 0.092; generation time (days), 46.8; sex ratio, $1.4 \sigma : 1 \text{ } \varnothing$; and sex determination, arrhenotoky.

According to Doutt (1961), *P. californica* is coextensive with the midge in California and second to *Torymus koebelei* in dominance under field conditions. Force (1974) also found this species to be among the dominant members of the parasite guild in the field. In Davis, *P. californica* occurs wherever the midge occurs and is clearly one of the dominant parasites. I have also collected it at the Putah Creek and Newcastle sites.

Force (1974) noted that *P. californica* was less tolerant of high temperatures, particularly in comparison with *Torymus koebelei*. I have observed a similar phenomenon in Davis—i.e., *P. californica* is particularly abundant during winter and early spring and

comparatively rare during summer and fall. Whether or not a summer diapause exists is not known.

Pteromalidae. Two pteromalid species are associated with *R. californica* in the natural environment. These are *Zatropis capitis* Burks and an undescribed species of *Mesopolobus*. Both occur in Davis.

Zatropis capitis is a solitary ectoparasite; however, it is a facultative secondary parasite (Force, 1974). That is, it can parasitize either a primary parasite or the midge larva. It was apparently listed as *Meraporus* sp. by Doutt (1961) and was referred to as *Zatropis* sp. by Force (1970, 1974). *Zatropis capitis* occurs in California, Nevada, Oregon, and Utah (Peck, 1963; Burks, 1979); no information on host specificity is available. This species is apparently coextensive with the midge in California and is common in Davis. In Davis, *Z. capitis* shows no clear seasonality pattern compared to *Torymus koebelei* and *P. californica*. I have also collected it at the Putah Creek and Newcastle sites.

Mesopolobus sp. is a solitary ectoparasite and is also a facultative secondary parasite (Force, 1974). Both Doutt and Force referred to this species as *Amblymerus*. According to Doutt (1961), it is particularly "active" along the coast, although it is apparently coextensive with the midge in California. It occurs in Davis but is very rare. I have also collected it at the Putah Creek and Newcastle sites.

Eulophidae. The only eulophid characteristically associated with *R. californica* is an undescribed species of *Tetrastichus*. It is a solitary endoparasite of midge larvae and is an obligate primary parasite (Doutt, 1961; Force, 1974). As this *Tetrastichus* is undescribed, its geographic distribution and host range cannot be stated with any degree of confidence. However, Force (1970) did provide the following data for this species: mean total fecundity, 117.5 ± 47.9 ; gross reproduction rate, 117.5; net reproduction rate (R_0), 98.2; capacity for increase (r_c), 0.200; generation time (days), 34.4; sex ratio, 0 ♂ : 1 ♀; and sex determination, thelytoky. Although *Tetrastichus* sp. is considered thelytokous, males do occur, (but rarely); whether or not these males are functional has not been established.

Tetrastichus sp. occurs throughout the midge's range but is generally a very rare species (Force, 1974). Force (1974) observed that this species was very tolerant of high temperatures and was perhaps the most tolerant among the members of the parasite guild. My observations in Davis are generally consistent with these conclusions—i.e., *Tetrastichus* sp. occurs at most (if not all) sites infested by the midge, is comparatively rare and does not appear to be adversely affected by intense heat during summer months. I have also collected it at the Putah creek site west of Davis.

Other species. There are still other species of parasites associated with larvae of *R. californica* in the state, but none occurs in Davis. These include: (1) *Eupelmus inyoensis* Girault (Eupelmidae), a highly polyphagous, facultative secondary parasite (Peck, 1963); and (2) *Eupelmus* sp., a primary ectoparasite of midge larvae which is found only along the coast (Doutt, 1961; Force, 1974). Still others have been found in association with the midge and their precise relationships to the host are the subject of ongoing investigations.

MATERIALS AND METHODS

Study sites

The study site consisted of a 46-m strip along the north side of the 1600 block of Colusa Avenue in Davis, California. It contained the following (from east to west) approximate areas of plant material: 8.9 m² mixed planting of ice plant (later replaced by oleander) and ornamental ceanothus; 13 m² solid patch of coyote brush (site 1, 1617 Colusa Avenue); 6 m² mixed planting of ice plant, California poppy, and various annual flowers; 15 m² solid patch of coyote brush with an almond tree in the center (site 2, 1615 Colusa Avenue); a 9.1-m wide cement driveway; 5 m² mixed planting of ornamental ceanothus, rosemary, and an almond tree; 18 m² solid patch of coyote brush with an almond tree at the western edge (site 3, 1611 Colusa Avenue); and, finally, an abandoned yard.

The coyote brush at each site was established during early summer of 1975, shortly after dwellings were constructed. During the study, plants were neither fertilized nor regularly watered; also, no chemical pesticides were used by the owners. The only cultural practice employed was periodic trimming of the edges of the plants.

Sampling procedures

Sites were first sampled in December, 1977, again in April, 1978, and bimonthly thereafter. Generally, 50 galls were collected at random per site per sample date; fewer were taken when galls were scarce. A population index was devised to measure midge abundance. The index is simply the product of (1) the average number of chambers per gall and (2) the number of galls collected per minute of search. The index thus represents the total number of "chambers" collected per minute of search time. This index was used primarily so that the data from Davis would be comparable to those obtained by Force in the endemic environment.

Galls were transferred to the laboratory, placed individually in capped 30-cc plastic cups, and held in a rearing room maintained at about 26°C and 16 hr photoperiod. Midges and parasites which emerged were collected daily and preserved in 70 percent ethanol. After about 2 months, galls were moistened with ethanol and dissected to determine number of chambers per gall. This figure represents the number of midge larvae which originally formed the gall and was therefore used in calculating midge survival and percent parasitization.

Partial life tables

Mortality factors associated with midge larvae and pupae were summarized in life-table form. However, as mortalities for eggs and young larvae were not tabulated, the life tables are only partial ones. That is, they show the survival and mortality of midges from gall formation through pupal eclosion.

Age interval is designated in the x column. Three intervals were used—larva, pupa, and adult. "Larva" represents the time from gall formation to pupation rather than the entire larval period. Apparently, numerous larvae die before and independent of gall

formation (Tilden, 1951*b*); thus, data on mortality of larvae in the present case should be interpreted in this context.

Mortality factors associated with larvae and pupae inside the gall are listed in the dxF column. These were classified as either parasites or residual. The parasites were *T. koebelei*, *T. baccharidis*, *Z. capitis*, *P. californica*, *Mesopolobus* sp., and *Tetrastichus* sp. In some cases, it was not clear as to which of the above species an individual belonged (parasite larva, mutilated adult or the like), and these were assigned to the "undetermined" category. However, this category does not represent species other than the six listed above. The residual is essentially the mortality which could not be assigned to parasites and likely has several components, including death of larvae or pupae due to other causes plus death due to host feeding and/or ovipositional probing by the adult parasites. According to Force (1970, 1974), *T. koebelei*, *T. baccharidis*, *Z. capitis*, and *Mesopolobus* host feed; also, the first two may kill host larvae simply by probing with the ovipositor.

Number of individuals entering stage x is given in the lx column. The lx for the larval stage is the total number of chambers tabulated for the 50 or so galls collected per sample date. The lx for the adult stage is the number of adults (males + females) which emerged from a set of galls. The lx value for the pupal stage was determined by deduction. The number of galls used for each life table is given in the appropriate table.

Numbers of midge larvae and pupae estimated to have died are given in the dx column, and each is associated with a particular factor in the dxF column. As all of the parasites are solitary (i.e., one parasite/host individual), dx for each species was simply the number of individuals of that species which emerged from the set of galls. (In some cases, dissection revealed additional individuals of certain species and dx values were adjusted accordingly.) Residual for the larval stage was determined by deduction, whereas that for the pupal stage was the number of dead pupae either inside the gall or on the floor of the container. The dx column is additive, and the attendant total is an estimate of the total number which died from the time the gall was formed until adults emerged.

Percent mortality associated with each item in the dxF and dx columns is given in the 100rx column. This mortality is based on the lx value for larvae and thus represents "apparent mortality" of larvae and a modified form of "real mortality" for pupae. Percentages in this column are additive, and the attendant total represents the total percent mortality during the period from gall formation to adult eclosion—i.e., $\Sigma dx \div lx$ for larvae.

Competitive interactions

Galls of *R. californica* are multichambered. Thus, a given gall contains either non-parasitized hosts, parasitized hosts, or both. Galls containing parasitized hosts can contain various combinations of parasite species—e.g., *T. koebelei* alone, *T. koebelei* + *P. californica*, *T. koebelei* + *Z. capitis*, *T. koebelei* + *P. californica* + *Z. capitis*, and the like. Because of this, percent parasitization could be calculated (on a per gall basis) for whichever combinations of species were present in a given set of 150 galls. Such an analysis was done for a given species when the species occurred alone plus with at least one other species in a sufficient number (usually ≤ 10) of galls. Thus interspecific competition could be detected when the average percent parasitization by a given species was higher when it occurred alone compared to when it occurred with other species. Such competition would presumably represent "intrinsic" competition between larvae of parasites for the same host individual. Interspecific competition among adults would

not necessarily be detected by this particular approach. The lsd test was used to detect significant differences among three or more means whereas a t-test was employed in cases involving two means.

RESULTS AND DISCUSSION

Midge population trends

Although the coyote brush plantings were established in early summer of 1975, the midge did not effectively colonize the habitat until late summer of 1977. A few isolated galls were observed at that time, and into the fall months. By November, a gall "outbreak" was evident, and the first samples were taken the following month. The two-year interval between habitat establishment and midge colonization may be typical of this species. Another study site in Davis was over one year old before it was effectively colonized by the midge. Furthermore, one would not expect an insect associated with such a durationally stable (i.e., long-lived) plant to necessarily be a superior colonizer.

The dynamics of the midge population from December, 1977, through December, 1980, are illustrated in figure 1. The points represent mean values of the population index derived from the three sites. In general, the midge population was highest during late winter and early spring and lowest during summer and early fall. This dynamic pattern generally corresponds to the rainfall pattern of the Mediterranean climate typical of this region of California. Following an abundance of winter rainfall, climatic conditions become favorable for plant growth in early spring. Virtually all of the new growth occurs at this time, and the plant is apparently favorable for development of midge populations. During the hot, dry summer and early fall months, little development of either the plant or midge population occurs.

Analysis of life-table data

The first set of galls was collected in December, 1977 (table 1). Only two parasites (*Z. capitis* and *P. californica*) were collected at sites 1 and 2, whereas only *Z. capitis* was taken at site 3. Total parasitization averaged only 7.7 percent. Survival of midges was comparatively high (avg. = 58.1%), and this would seem typical for the early stages of such a colonization episode. By April, 1978, the population had increased (fig. 1), and two additional species of parasites (*T. koebelei* and *T. baccharidis*) had colonized the sites (table 2). Total parasitization was considerably higher than in December, 1977 (avg. = 22.9%), and among the four species of parasites, *P. californica* was the dominant one. However, midge survival remained comparatively high (avg. = 62%). By June, 1978, the midge population had declined to a level comparable to that observed in December, 1977 (Fig. 1), and an additional species of parasite (*Mesopolobus* sp.) was detected (table 3). Total parasitization was the highest recorded thus far (avg. = 58.3%), and among the five species of parasites present, *T. koebelei* was clearly dominant. Midge survival was now comparatively low (avg. = 5.6%). At this point, the midge population appeared to be under considerable natural control and further declined to relatively low levels in August (Fig. 1). On August 24, 149 galls were collected (887 chambers), and these yielded 56 *T. koebelei*, three *Z. capitis*, five *P. californica*, two *Mesopolobus* sp., and nine adult midges (5 ♂♂ : 4 ♀♀). The population index was 19.3, 25.8 and 30.9 for sites

1, 2, and 3, respectively. Whereas total parasitization was low (avg. = 7.4%), midge survival was also low (avg. = 1%). Thus, the first clear population cycle of the midge had ended, and there was evidence that the parasites—particularly *T. koebelei*—were exerting some degree of control.

TABLE 1
PARTIAL LIFE TABLES FOR COHORTS OF *RHOPALOMYIA CALIFORNICA* COLLECTED ON DECEMBER 18, 1977

Age interval (x)*	dxF	Site 1 (46 galls)			Site 2 (48 galls)			Site 3 (45 galls)			Mean			
		lx	dx	100rx	lx	dx	100rx	lx	dx	100rx	lx	dx	100rx	
Parasites		606			744			492			614			
Larva†														
	<i>T. koebelei</i>		0	0		0	0		0	0		0	0	
	<i>T. baccharidis</i>		0	0		0	0		0	0		0	0	
	<i>Z. capitis</i>		27	4.5		21	2.8		47	9.6		31.7	5.2	
	<i>P. californica</i>		34	5.6		12	1.6		0	0		15.3	2.5	
	<i>Mesopolobus</i> sp.		0	0		0	0		0	0		0	0	
	<i>Tetrastichus</i> sp.		0	0		0	0		0	0		0	0	
	Undetermined		0	0		0	0		0	0		0	0	
	Total		61	10.1		33	4.4		47	9.6		47	7.7	
	Residual		176	29		216	29		143	29		178.3	29	
Pupa	Residual		369	25	4.1	495	44	5.9	302	27	5.5	388.7	32	5.2
Adult‡	Not assessed		Σ=	Σ=		Σ=	Σ=		Σ=	Σ=		Σ=	Σ=	
			344	262	43.2	451	293	39.4	275	217	44.1	356.7	257.3	41.9

* Key to symbols: x = age interval; dxF = mortality factor; lx = number of individuals entering stage x; dx = number of individuals dying during stage x; 100rx = dx as a % of lx for larvae.

† Population index = 63.2, 76 and 54.5, for sites 1, 2, and 3, respectively.

‡ Sex ratio (♀ : ♂) = 1.9:1, 2.5:1, and 2.6:1 for sites 1, 2, and 3, respectively.

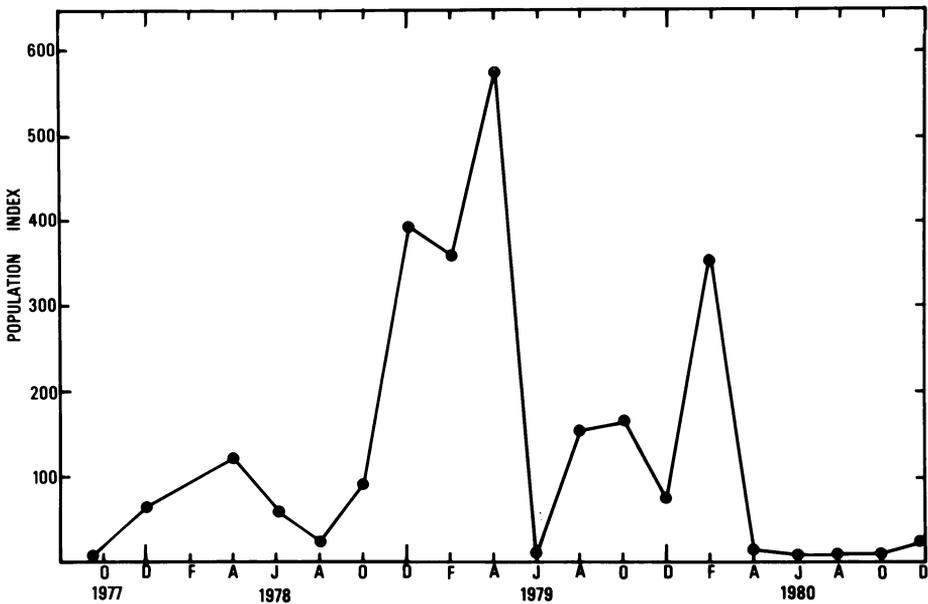


Fig. 1. Population trends of *Rhopalomyia californica* from December, 1977, to December, 1980. Population index = (number of galls collected/minute) X (number chambers/gall). Each point is the average value for three sites.

By October of 1978, the midge population had begun to increase (fig. 1). Only three species of parasites were recovered, but total parasitization was comparatively high (avg. = 62.1%); *T. koebelei* was clearly the dominant species among the parasites (table 4). Midge survival was very low (avg. = 0.8%). Despite this poor midge survival rate and rather high rate of parasitization, the population increased in December to a level

TABLE 2
PARTIAL LIFE TABLES FOR COHORTS OF *RHOPALOMYIA CALIFORNICA* COLLECTED ON APRIL 21, 1978

Age interval (x)*	dxF	Site 1 (49 galls)			Site 2 (49 galls)			Site 3 (50 galls)			Mean		
		lx	dx	100rx	lx	dx	100rx	lx	dx	100rx	lx	dx	100rx
Larva†	Parasites	1310			1151			1125			1195.3		
	<i>T. koebelei</i>	14	1.1		0	0		27	2.4		13.7	1.1	
	<i>T. baccharidis</i>	22	1.7		22	1.9		13	1.2		19	1.6	
	<i>Z. capitis</i>	76	5.8		91	7.9		56	5		74.3	6.2	
	<i>P. californica</i>	199	15.2		211	18.3		91	8		167	14	
	<i>Mesopolobus</i> sp.	0	0		1	0.1		0	0		0.3	0.003	
	<i>Tetrastichus</i> sp.	0	0		0	0		0	0		0	0	
	Undetermined	0	0		0	0		0	0		0	0	
	Total	311	23.8		325	28.2		187	16.6		274.3	22.9	
	Residual	181	13.8		166	14.4		166	14.8		171	14.3	
Pupa	Residual	818	11	0.8	660	8	0.7	772	8	0.7	750	9	0.8
Adult‡	Not assessed		Σ=	Σ=		Σ=	Σ=		Σ=	Σ=		Σ=	Σ=
		807	503	38.4	652	499	43.4	764	361	32.1	741	454.3	38

*Key to symbols: x = age interval; dxF = mortality factor; lx = number of individuals entering stage x; dx = number of individuals dying during stage x; 100rx = dx as a % of lx for larvae.

†Population index = 131, 115, and 112.5, for sites 1, 2, and 3, respectively.

‡Sex ratio (♀ : ♂) = 1.3:1, 1.5:1, and 1.2:1 for sites 1, 2, and 3, respectively.

TABLE 3
PARTIAL LIFE TABLES FOR COHORTS OF *RHOPALOMYIA CALIFORNICA* COLLECTED ON JUNE 26, 1978

Age interval (x)*	dxF	Site 1 (49 galls)			Site 2 (49 galls)			Site 3 (50 galls)			Mean		
		lx	dx	100rx	lx	dx	100rx	lx	dx	100rx	lx	dx	100rx
Larva†	Parasites	674			555			779			669.3		
	<i>T. koebelei</i>	262	38.9		271	48.8		335	43		289.3	43.2	
	<i>T. baccharidis</i>	2	0.3		3	0.5		7	0.9		4	0.6	
	<i>Z. capitis</i>	84	12.5		63	11.4		99	12.7		82	12.3	
	<i>P. californica</i>	10	1.5		6	1.1		26	3.3		14	2.1	
	<i>Mesopolobus</i> sp.	0	0		0	0		2	0.3		0.7	0.1	
	<i>Tetrastichus</i> sp.	0	0		0	0		0	0		0	0	
	Undetermined	0	0		0	0		0	0		0	0	
	Total	358	53.1		343	61.8		469	60.2		390	58.3	
	Residual	262	38.9		196	35.3		264	33.9		240.6	35.9	
Pupa	Residual	54	1	0.2	16	0	0	46	3	0.4	38.7	1.3	0.2
Adult‡	Not assessed		Σ=	Σ=		Σ=	Σ=		Σ=	Σ=		Σ=	Σ=
		53	621	92.1	16	539	97.1	43	736	94.5	37.3	632	94.4

*Key to symbols: x = age interval; dxF = mortality factor; lx = number of individuals entering stage x; dx = number of individuals dying during stage x; 100rx = dx as a % of lx for larvae.

†Population index = 33.8, 46.2, and 86.7, for sites 1, 2, and 3, respectively.

‡Sex ratio (♀ : ♂) = 1.9:1, 1.3:1, and 1.4:1 for sites 1, 2, and 3, respectively.

> 2X that observed in April (fig. 1). In the December samples, total parasitization was actually lower than that observed in October (avg. = 43.5%), even though there were six species of parasites present (table 5). The sixth and final species to colonize was *Tetrastichus* sp. which was first detected in the December samples. Among the parasites, *P. californica* was clearly dominant. Midge survival was somewhat higher (avg. = 10%) than in October. By February, 1979, the midge population was comparable to that ob-

TABLE 4
PARTIAL LIFE TABLES FOR COHORTS OF *RHOPALOMYIA CALIFORNICA* COLLECTED ON OCTOBER 20, 1978

Age interval (x)*	dxF	Site 1 (50 galls)			Site 2 (48 galls)			Site 3 (48 galls)			Mean		
		lx	dx	100rx	lx	dx	100rx	lx	dx	100rx	lx	dx	100rx
Larva†	Parasites	822			882			986			896.7		
	<i>T. koebelei</i>	469	57.1		448	50.8		532	54		483	53.9	
	<i>T. baccharidis</i>	0	0		0	0		0	0		0	0	
	<i>Z. capitis</i>	37	4.5		72	8.2		43	4.4		50.7	5.7	
	<i>P. californica</i>	24	2.9		22	2.5		8	0.8		18	2	
	<i>Mesopolobus</i> sp.	0	0		0	0		0	0		0	0	
	<i>Tetrastichus</i> sp.	0	0		0	0		0	0		0	0	
	Undetermined	6	0.7		8	0.9		1	0.1		5	0.6	
	Total	536	65.2		550	62.4		584	59.2		556.7	62.1	
	Residual	275	33.5		325	36.8		398	40.4		332.7	37.1	
Pupa	Residual	11	0	0	7	1	0.1	4	0	0	7.3	0.3	0.003
Adult‡	Not assessed		Σ=	Σ=		Σ=	Σ=		Σ=	Σ=		Σ=	Σ=
		11	811	98.7	6	876	99.3	4	982	99.6	7	889.7	99.2

* Key to symbols: x = age interval; dxF = mortality factor; lx = number of individuals entering stage x; dx = number of individuals dying during stage x; 100rx = dx as a % of lx for larvae.

† Population index = 91.2, 81.9, and 98.6 for sites 1, 2, and 3, respectively.

‡ Sex ratio (♀ : ♂) = 1.8:1, 2:1, and 3:1 for sites 1, 2, and 3, respectively.

TABLE 5
PARTIAL LIFE TABLES FOR COHORTS OF *RHOPALOMYIA CALIFORNICA* COLLECTED ON DECEMBER 21, 1978

Age interval (x)*	dxF	Site 1 (50 galls)			Site 2 (46 galls)			Site 3 (49 galls)			Mean		
		lx	dx	100rx	lx	dx	100rx	lx	dx	100rx	lx	dx	100rx
Larva†	Parasites	896			876			1124			965.3		
	<i>T. koebelei</i>	144	16.1		26	3		94	8.4		88	9.1	
	<i>T. baccharidis</i>	4	0.4		1	0.1		23	2		9.3	0.8	
	<i>Z. capitis</i>	19	2.1		22	2.5		60	5.3		33.7	3.5	
	<i>P. californica</i>	157	17.5		235	26.8		365	32.5		252.3	26.1	
	<i>Mesopolobus</i> sp.	0	0		1	0.1		0	0		0.3	0.03	
	<i>Tetrastichus</i> sp.	16	1.8		8	0.9		13	1.2		12.3	1.3	
	Undetermined	35	3.9		8	0.9		30	2.7		24.3	2.5	
	Total	375	41.9		301	34.4		585	52		420.3	43.5	
	Residual	430	48		528	60.3		372	33.1		443.3	45.9	
Pupa	Residual	91	10	1.1	47	0	0	167	3	0.3	101.7	4.3	0.4
Adult‡	Not assessed		Σ=	Σ=		Σ=	Σ=		Σ=	Σ=		Σ=	Σ=
		81	815	91	47	829	94.6	164	960	85.4	97.3	868	90

* Key to symbols: x = age interval; dxF = mortality factor; lx = number of individuals entering stage x; dx = number of individuals dying during stage x; 100rx = dx as a % of lx for larvae.

† Population index = 299.3, 292.6, and 573.5, for sites 1, 2, and 3, respectively.

‡ Sex ratio (♀ : ♂) = 2.7:1, 1.1:1, and 2.5:1 for sites 1, 2, and 3, respectively.

served in December (fig. 1), as was total parasitization (avg. = 44.7%) (table 6). Again, all six species of parasites occurred in samples and *P. californica* was dominant. Midge survival increased from December (avg. = 22.7%). By April, 1979, the population index had reached the highest level observed in this study (fig. 1); and it was evident that the efficiency of the parasites had not increased (table 7). Only four species of parasites were detected in the samples; and, *T. koebelei*, *Z. capitis*, and *P. californica* were all compar-

TABLE 6
PARTIAL LIFE TABLES FOR COHORTS OF *RHOPALOMYIA CALIFORNICA* COLLECTED ON FEBRUARY 19, 1979

Age interval (x)*	dxF	Site 1 (50 galls)			Site 2 (50 galls)			Site 3 (50 galls)			Mean			
		lx	dx	100rx	lx	dx	100rx	lx	dx	100rx	lx	dx	100rx	
Larva †	Parasites	772			1018			995			915			
	<i>T. koebelei</i>		56	7.3		45	4.4		54	5.7		51.7	5.7	
	<i>T. baccharidis</i>		7	0.9		2	0.2		16	1.7		8.3	0.9	
	<i>Z. capitis</i>		38	4.9		50	4.9		42	4.4		43.3	4.7	
	<i>P. californica</i>		162	21		342	33.6		382	40		295.3	32.3	
	<i>Mesopolobus</i> sp.		1	0.1		0	0		0	0		0.3	0.03	
	<i>Tetrastichus</i> sp.		11	1.4		7	0.7		11	1.2		9.7	1.1	
	Undetermined		0	0		0	0		0	0		0	0	
	Total		275	35.6		446	43.8		505	52.9		408.7	44.7	
	Residual		222	28.8		250	24.6		366	38.3		279.3	30.5	
Pupa	Residual		275	17	2.2	322	32	3.1	84	9	0.9	227	19.3	2.1
Adult ‡	Not assessed			Σ=	Σ=		Σ=	Σ=		Σ=	Σ=		Σ=	Σ=
			258	514	66.6	290	728	71.5	75	880	92.1	207.6	707.3	77.3

* Key to symbols: x = age interval; dxF = mortality factor; lx = number of individuals entering stage x; dx = number of individuals dying during stage x; 100rx = dx as a % of lx for larvae.

† Population index = 257.8, 509, and 319, for sites 1, 2, and 3, respectively.

‡ Sex ratio (♀ : ♂) = 1.7:1, 1.6:1, and 2:1 for sites 1, 2, and 3, respectively.

TABLE 7
PARTIAL LIFE TABLES FOR COHORTS OF *RHOPALOMYIA CALIFORNICA* COLLECTED ON APRIL 19, 1979

Age interval (x)*	dxF	Site 1 (50 galls)			Site 2 (50 galls)			Site 3 (50 galls)			Mean			
		lx	dx	100rx	lx	dx	100rx	lx	dx	100rx	lx	dx	100rx	
Larva †	Parasites	1297			1440			1052			1263			
	<i>T. koebelei</i>		268	20.7		193	13.4		126	12		195.7	15.5	
	<i>T. baccharidis</i>		0	0		0	0		0	0		0	0	
	<i>Z. capitis</i>		124	9.6		130	9		86	8.2		113.3	9	
	<i>P. californica</i>		145	11.2		100	6.9		181	17.2		142	11.2	
	<i>Mesopolobus</i> sp.		0	0		0	0		0	0		0	0	
	<i>Tetrastichus</i> sp.		11	0.8		3	0.2		4	0.4		6	0.5	
	Undetermined		20	1.5		0	0		12	1.1		10.7	0.8	
	Total		568	43.8		426	29.6		409	38.9		467.7	37	
	Residual		368	28.4		323	22.4		401	38.1		364	28.8	
Pupa	Residual		361	90	6.9	691	141	9.8	242	61	5.8	431.3	97.3	7.7
Adult ‡	Not assessed			Σ=	Σ=		Σ=	Σ=		Σ=	Σ=		Σ=	Σ=
			271	1026	79.1	550	890	61.8	181	871	82.8	334	929	73.6

* Key to symbols: x = age interval; dxF = mortality factor; lx = number of individuals entering stage x; dx = number of individuals dying during stage x; 100rx = dx as a % of lx for larvae.

† Population index = 648.5, 720, and 351.4 for sites 1, 2, and 3, respectively.

‡ Sex ratio (♀ : ♂) = 1.1:1, 1.4:1, and 1.6:1 for sites 1, 2, and 3, respectively.

actively abundant. However, total parasitization (avg. = 37%) was even lower than in the previous two samples and midge survival was also comparatively high (avg. = 26.4%). Clearly, the midge population had escaped from any previous level of control exerted by the parasites and had increased accordingly. By June, 1979, the midge population had crashed precipitously, and galls were rare. Of the 41 galls (228 chambers) collected

TABLE 8
PARTIAL LIFE TABLES FOR COHORTS OF *RHOPALOMYIA CALIFORNICA* COLLECTED ON AUGUST 20, 1979

Age interval (x)*	dxF	Site 1 (50 galls)			Site 2 (50 galls)			Site 3 (42 galls)			Mean		
		lx	dx	100rx	lx	dx	100rx	lx	dx	100rx	lx	dx	100rx
Parasites		679			1180			484			780		
Larva†	<i>T. koebelei</i>	61	9		146	12.4		39	8.1		82	10.5	
	<i>T. baccharidis</i>	0	0		0	0		0	0		0	0	
	<i>Z. capitis</i>	3	0.4		54	4.6		1	0.2		19.3	2.5	
	<i>P. californica</i>	6	0.9		30	2.5		9	1.9		15	1.9	
	<i>Mesopolobus</i> sp.	0	0		0	0		0	0		0	0	
	<i>Tetrastichus</i> sp.	3	0.4		1	0.1		1	0.2		1.7	0.2	
	Undetermined	14	2.1		2	0.2		18	3.7		11.3	1.4	
	Total	87	12.9		233	19.7		68	14.1		129.3	16.6	
	Residual		550	81.4		907	76.9		413	85.3		623.3	79.9
Pupa	Residual	39	37	5.5	40	16	1.4	3	1	0.2	27.3	18	2.3
Adult‡	Not assessed		Σ=	Σ=		Σ=	Σ=		Σ=	Σ=		Σ=	Σ=
		2	674	99.7	24	1156	98	2	482	99.6	9.3	770.6	98.8

* Key to symbols: x = age interval; dxF = mortality factor; lx = number of individuals entering stage x; dx = number of individuals dying during stage x; 100rx = dx as a % of lx for larvae.

† Population index = 135.2, 241, and 82.6 for sites 1, 2, and 3, respectively.

‡ Sex ratio (♀ : ♂) = 2:0, 1.7:1, and 1:1 for sites 1, 2, and 3, respectively.

TABLE 9
PARTIAL LIFE TABLES FOR COHORTS OF *RHOPALOMYIA CALIFORNICA* COLLECTED ON OCTOBER 22, 1979

Age interval (x)*	dxF	Site 1 (46 galls)			Site 2 (41 galls)			Site 3 (24 galls)			Mean		
		lx	dx	100rx	lx	dx	100rx	lx	dx	100rx	lx	dx	100rx
Parasites		1061			1005			245			770		
Larva†	<i>T. koebelei</i>	316	29.8		206	20.5		63	25.7		195	25.3	
	<i>T. baccharidis</i>	0	0		0	0		0	0		0	0	
	<i>Z. capitis</i>	14	1.3		10	1		0	0		8	1	
	<i>P. californica</i>	6	0.6		16	1.6		1	0.4		7.7	1	
	<i>Mesopolobus</i> sp.	0	0		0	0		0	0		0	0	
	<i>Tetrastichus</i> sp.	5	0.5		3	0.3		8	3.3		5.3	0.7	
	Undetermined	53	5		20	2		7	2.9		26.7	3.5	
	Total	394	37.1		255	25.4		79	32.2		242.6	31.5	
	Residual		643	60.6		726	72.2		166	67.8		511.7	66.5
Pupa	Residual	24	0	0	24	3	0.3	0	0	0	16	1	0.1
Adult‡	Not assessed		Σ=	Σ=		Σ=	Σ=		Σ=	Σ=		Σ=	Σ=
		24	1037	97.7	21	984	97.9	0	245	100	15	755.3	98.1

* Key to symbols: x = age interval; dxF = mortality factor; lx = number of individuals entering stage x; dx = number of individuals dying during stage x; 100rx = dx as a % of lx for larvae.

† Population index = 192.4, 264.5, and 42.4 for sites 1, 2, and 3, respectively.

‡ Sex ratio (♀ : ♂) = 3.8:1, 0.3:1, and 0:0 for sites 1, 2, and 3, respectively.

among all the sites, the following insects emerged: 18 *T. koebelei*, one *P. californica*, and one *Tetrastichus* sp. Population index was 18.5, 8.9, and 5.3 for sites 1, 2, and 3, respectively. Total parasitization was only 8.8 percent; however, midge survival—at least in these samples—was zero. Whether or not the parasites actually caused the population crash could not be ascertained. However, it was quite clear that midge abundance during

TABLE 10
PARTIAL LIFE TABLES FOR COHORTS OF *RHOPALOMYIA CALIFORNICA* COLLECTED ON DECEMBER 18, 1979

Age interval (x)*	dxF	Site 1 (50 galls)			Site 2 (50 galls)			Site 3 (50 galls)			Mean			
		lx	dx	100rx	lx	dx	100rx	lx	dx	100rx	lx	dx	100rx	
Larva†	Parasites	445			536			427			484.3			
	<i>T. koebelei</i>		170	38.2		250	46.6		115	24.4		178.3	36.8	
	<i>T. baccharidis</i>		1	0.2		2	0.4		4	0.8		2.3	0.5	
	<i>Z. capitis</i>		25	5.6		32	6		11	2.3		22.7	4.7	
	<i>P. californica</i>		6	1.3		18	3.4		65	13.8		29.7	6.1	
	<i>Mesopolobus</i> sp.		1	0.2		1	0.2		1	0.2		1	0.2	
	<i>Tetrastichus</i> sp.		12	2.7		2	0.4		33	7		15.7	3.2	
	Undetermined		37	8.3		22	4.1		38	8.1		32.3	6.7	
	Total		252	56.6		327	61		267	56.6		282	58.2	
	Residual		179	40.2		191	35.6		182	38.6		184	38	
Pupa	Residual		14	6	1.3	18	4	0.7	23	3	0.6	18.3	4.3	0.9
Adult‡	Not assessed		8	437	98.2	14	522	97.4	20	452	95.8	14	470.3	97.1

*Key to symbols: x = age interval; dxF = mortality factor; lx = number of individuals entering stage x; dx = number of individuals dying during stage x; 100rx = dx as a % of lx for larvae.

†Population index = 74.1, 59.5, and 94.4 for sites 1, 2, and 3, respectively.

‡Sex ratio (♀ : ♂) = 7:1, 1.8:1, and 2.3:1 for sites 1, 2, and 3, respectively.

TABLE 11
PARTIAL LIFE TABLES FOR COHORTS OF *RHOPALOMYIA CALIFORNICA* COLLECTED ON FEBRUARY 21, 1980

Age interval (x)*	dxF	Site 1 (49 galls)			Site 2 (45 galls)			Site 3 (49 galls)			Mean			
		lx	dx	100rx	lx	dx	100rx	lx	dx	100rx	lx	dx	100rx	
Larva†	Parasites	852			916			436			734.6			
	<i>T. koebelei</i>		0	0		0	0		34	7.8		11.3	1.5	
	<i>T. baccharidis</i>		0	0		0	0		0	0		0	0	
	<i>Z. capitis</i>		38	4.5		65	7.1		12	2.8		38.3	5.2	
	<i>P. californica</i>		334	39.2		371	40.5		139	31.9		281.3	38.3	
	<i>Mesopolobus</i> sp.		0	0		1	0.1		1	0.2		0.7	0.1	
	<i>Tetrastichus</i> sp.		0	0		0	0		9	2.1		3	0.4	
	Undetermined		14	1.6		13	1.4		4	0.9		10.3	1.4	
	Total		386	45.3		450	49.1		199	45.6		345	47	
	Residual		432	50.7		370	40.4		201	46.1		334.3	45.5	
Pupa	Residual		34	8	0.9	96	1	0.1	36	9	2.1	55.3	6	0.8
Adult‡	Not assessed		26	826	96.9	95	821	89.6	27	409	93.8	49.3	685.3	93.3

*Key to symbols: x = age interval; dxF = mortality factor; lx = number of individuals entering stage x; dx = number of individuals dying during stage x; 100rx = dx as a % of lx for larvae.

†Population index = 435, 509, and 111.1, for sites 1, 2, and 3, respectively.

‡Sex ratio (♀ : ♂) = 1.4:1, 1.6:1, and 3.5:1 for sites 1, 2, and 3, respectively.

the second population cycle was much greater than during the first, even though six species of parasites were present compared to four or five in the previous cycle.

By August, 1979, the midge population had increased to a level greater than that observed during the spring of 1978 (fig. 1), although parasitization was not comparable (table 8). Only four species of parasites were detected in the samples, and these together parasitized an average of only 16.6 percent of the hosts. Among the parasites, *T. koebelei*

TABLE 12
PARTIAL LIFE TABLES FOR COHORTS OF *RHOPALOMYIA CALIFORNICA* COLLECTED ON APRIL 18, 1980

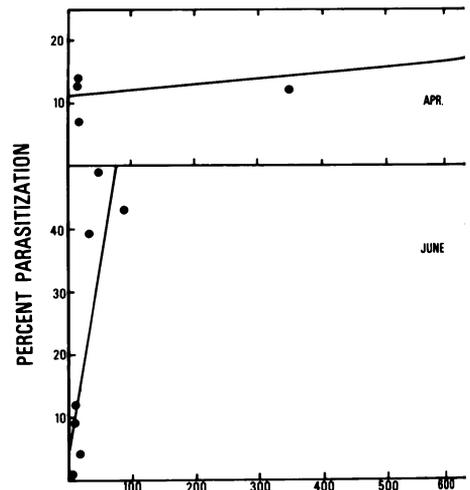
Age interval (x)*	dxF	Site 1 (24 galls)			Site 2 (10 galls)			Site 3 (13 galls)			Mean			
		lx	dx	100rx	lx	dx	100rx	lx	dx	100rx	lx	dx	100rx	
Larva†	Parasites	148			72			67			95.7			
	<i>T. koebelei</i>		10	6.8		10	13.3		9	13.4		9.7	10.1	
	<i>T. baccharidis</i>		0	0		0	0		0	0		0	0	
	<i>Z. capitis</i>		22	14.9		0	0		2	3		8	8.3	
	<i>P. californica</i>		38	25.7		4	5.6		7	10.4		16.3	17	
	<i>Mesopolobus</i> sp.		0	0		0	0		0	0		0	0	
	<i>Tetrastichus</i> sp.		6	4.1		0	0		1	1.5		2.3	2.4	
	Undetermined		1	0.7		0	0		4	6		1.7	1.8	
	Total		77	52.2		14	19.4		23	34.3		38	39.7	
	Residual		70	47.3		58	80.6		44	65.7		57.3	59.9	
Pupa	Residual		1	0	0	0	0	0	0	0	0.3	0	0	
Adult‡	Not assessed		Σ=	Σ=		Σ=	Σ=		Σ=	Σ=		Σ=	Σ=	
			1	147	93.3	0	72	100	0	67	100	0.3	95.3	99.6

* Key to symbols: x = age interval; dxF = mortality factor; lx = number of individuals entering stage x; dx = number of individuals dying during stage x; 100rx = dx as a % of lx for larvae.

† Population index = 17.1, 15.8, and 13.4, for sites 1, 2, and 3, respectively.

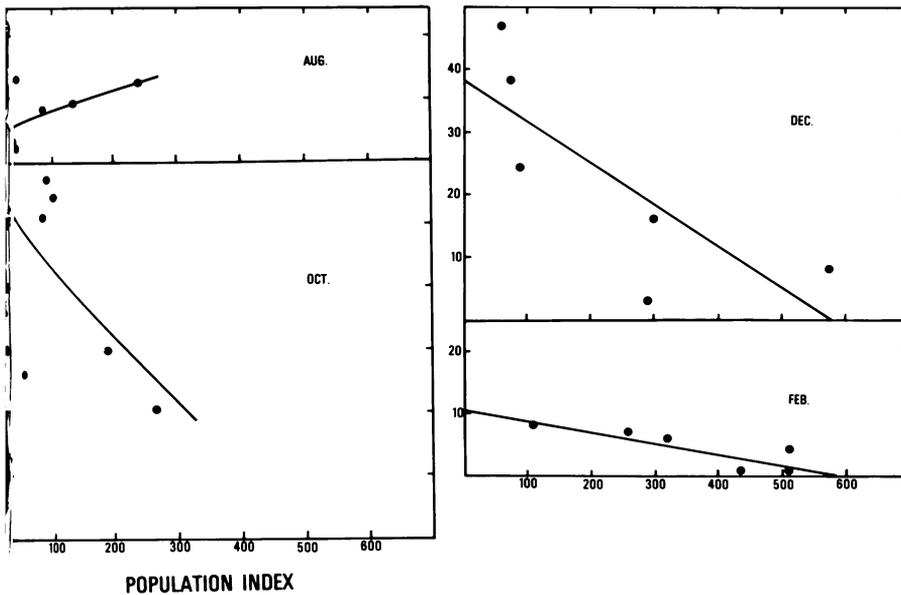
‡ Sex ratio (♀ : ♂) = 0:1 at site 1.

Fig. 2. Statistical relationships between percent parasitization by *Torymus koebelei* and host population index. Regression and correlation statistics as follows: April, $Y = 11.1 + 0.008X$, $r^2 = 0.33$; June, $Y = 4.7 + 0.581X$ ($P < 0.01$), $r^2 = 0.70$; August, $Y = 5.0 + 0.032X$, $r^2 = 0.35$; October, $Y = 53.1 + (-0.105X)$, $r^2 = 0.29$; December, $Y = 38.4 + (-0.067X)$, $r^2 = 0.62$; February, $Y = 10.5 + (-0.018X)$, $r^2 = 0.64$.



was the dominant species. Midge survival was quite low (avg. = 1.2%). The population index in October, 1979, was comparable to that observed during the previous August (fig. 1), although parasitization was considerably higher (table 9). Total parasitization averaged 31.5 percent, and *T. koebelei* was the dominant species among the four species of parasites present. Midge survival was again quite low (avg. = 1.9%). The population declined in December, 1979 (fig. 1), although parasitization increased considerably (table 10). All six species of parasites were detected at each site, and these together parasitized an average of 58.2 percent of the midge population. Among the parasites, *T. koebelei* was dominant. Midge survival remained relatively low (avg. = 2.9%). At this point, the population was declining, and the parasites appeared to be having a considerable impact. However, by February, 1980, the midge population had increased substantially (fig. 1), even though parasitization remained relatively high (table 11). Although five species of parasites were collected, only two were taken at site 1 and only three at site 2. Regardless of site, *P. californica* was dominant. As a group, the parasites destroyed an average of 47 percent of the midge larvae. Midge survival was slightly higher than in previous samples (avg. = 6.7%). By April, 1980, the midge population had crashed (fig. 1), but parasitization remained comparatively high (table 12). Four species of parasites were recorded at sites 1 and 3 compared to only two at site 2. Total parasitization averaged 39.7 percent. Midge survival was very low (avg. = 0.4%); no parasite species was dominant.

The population remained at low levels from June through December, 1980 (fig. 1). In June, only three galls (12 chambers) were collected, and these yielded two *Tetrastichus* sp. and one female midge. The population index was one, two, and zero for sites 1, 2, and 3, respectively. Similarly, in August, 1980, only one gall (15 chambers) was collected; no insects emerged from this particular gall. In this case, the population index was zero, three, and zero for sites 1, 2, and 3, respectively. In October, only seven galls (44 chambers) were collected; the population index was 3.4, 5.6, and 5.5 at sites 1, 2, and 3, respectively. Percent mortality breakdown was: *P. californica*, 18.2; *Tetrastichus*, 2.3;



undetermined parasites, 4.6; and residual, 75. By December, the population had increased; the index for sites 1, 2, and 3 was 37.5, 9.9, and 41.9, respectively. Of the 57 galls collected (354 chambers), the following emerged: *T. koebelei* (3.1%), *Z. capitis* (5.9%), *P. californica* (1.1%), *Mesopolobus* sp. (0.3%), and undetermined (2.8%). Residual mortality was 80.8 percent and only 3.4 percent of the midges emerged as adults.

Analysis of mortality factors

Parasitization by *T. koebelei* was a major mortality factor affecting the midge population during fall and late spring to early summer but not during winter. This is consistent with observations by Force (1974) who noted this species was tolerant of high-temperature conditions and apparently diapaused during winter. Percent parasitization by *T. koebelei* ranged from 0 to 57.1, 0 to 50.8, and 0 to 54 at sites 1, 2, and 3, respectively. However, this species was not a consistent regulatory factor (fig. 2). From an ecological standpoint, the data in figure 2 suggest the following responses to host density: density independence in April, direct density dependence in June, direct density dependence (weak) in August, and inverse density dependence in October, December, and February. However, the direct response in June was the only statistically significant one. (Data points in these and related graphs represent values of the population index and appropriate 100 rx [see tables 1 to 12] for individual sites [through June, 1980] rather than overall averages.) Thus, *T. koebelei* is capable of regulating the midge population, but evidence of regulation was seldom detected. Temperature probably plays a major role in precluding effective host regulation by *T. koebelei*; however, this should best be regarded as an hypothesis, at least until adequate empirical evidence is available.

Parasitization by *T. baccharidis* was generally insignificant and followed no particular seasonal pattern. Percent parasitization ranged from 0 to 1.7, 0 to 1.9, and 0 to 1.7 at sites 1, 2, and 3, respectively. Poor performance of *T. baccharidis* was likely due to: (1) its relatively low reproductive rate (Force, 1970); (2) its apparent adaptedness to the milder coastal climate rather than the hot Central Valley (see Douth, 1961; Force, 1974); and (3) its inferior competitive ability.

Parasitization by *Z. capitis* was intermediate between that observed for each of the previous two species and followed no apparent seasonal pattern. Percent parasitization ranged from 0 to 14.9, 0 to 11.4, and 0 to 12.7 at sites 1, 2, and 3, respectively. Thus, even though *Z. capitis* is a facultative secondary parasite, it contributed significantly to total parasitization on some occasions. However, parasitization by this species was not a major mortality factor associated with midge populations. Performance of this parasite may be hampered by inadequate reproductive capacity, although this is only an hypothesis.

Parasitization by *P. californica* was a major mortality factor affecting the midge population during winter and early spring but not during late spring, early summer, or fall. This seasonal pattern is not surprising, as Force (1974) stated this species was not tolerant of high temperatures. Percent parasitization by *P. californica* ranged from 0 to 39.2, 0 to 40.5, and 0 to 40 at sites 1, 2, and 3, respectively. It also showed regulatory capabilities (fig. 3). From an ecological view, the data in figure 3 suggest the following responses to host density: density independence in April, direct density dependence (weak) in June, direct density dependence (weak) in August, density independence in October, direct density dependence in December (strong) and February (weak). However, from a statistical standpoint, only the direct responses in June and December were significant. Thus,

P. californica (like *T. koebelei*) is capable of effecting regulation, but evidence of such regulation was not consistently detected. Here again, temperature probably exerts a major influence.

Percent parasitization by *Mesopolobus* sp. was generally insignificant and followed no apparent seasonal pattern; it ranged from 0 to 0.2, 0 to 0.2, and 0 to 0.6 at sites 1, 2, and 3, respectively. This facultative secondary parasite is apparently more adapted to coastal conditions (see Doult, 1961) and this must account, at least in part, for its poor performance in Davis.

Percent parasitization by *Tetrastichus* sp. was not generally significant and showed no obvious seasonal trend; it ranged from 0 to 50, 0 to 0.9, and 0 to 7 at sites 1, 2, and 3, respectively. The maximum rate (50% at site 1) was very atypical and probably an artifact of small sample size; the next highest figure for this site was 4.1 percent. Such an overall poor performance by *Tetrastichus* sp. is consistent with previous accounts (Force, 1974). Thus, despite its comparatively high reproductive rate, its tolerance of higher temperatures, and its superior performance under laboratory conditions (in the absence of competitors) (see Force, 1970; 1974), *Tetrastichus* sp. is decidedly ineffective under most field conditions. There are at least two hypotheses which would account for this: (1) *Tetrastichus* sp. is suppressed by allospecific competitors, and (2) it is suppressed by hyperparasitism due to *Z. capitatus* (primarily) and *Mesopolobus* sp. Some evidence supports each hypothesis, although considerably more data are required.

Parasitization by all six species was a major mortality factor affecting the midge population. Percentage ranged from 3.1 to 65.2, 0 to 62.4, and 9.6 to 60.2 at sites 1, 2, and 3, respectively. However, total parasitization was not a consistent regulatory factor (fig. 4). From an ecological standpoint, the data illustrated in figure 4 suggest the following responses: density independence in April, direct density dependence in June (largely the contribution of *T. koebelei*), direct density dependence in August, inverse density dependence in October and December, and density independence in February. However, only the direct density dependent response in June was statistically significant.

Residual mortality (unaccounted for) was of major importance on virtually every sampling date. For larvae + pupae, the percentage ranged from 14.6 to 96.9, 15.1 to 100, and 15.5 to 88.1 at sites 1, 2, and 3, respectively. Data summarized in figure 5 suggest the following responses: density independence in April, inverse density dependence in June and August, direct density dependence in October, and density independence in December and February. The only statistically significant relationship was the inverse one detected in June. Thus, there is no good reason to believe that the residual mortality contains any consistent regulatory element.

Population dynamics of *R. californica* in Davis

Population growth of *R. californica* characteristically occurred during late fall, winter, and early spring. Growth ceased in late spring, summer, early fall and resumed again in late fall. No one species of parasite or the aggregate of parasite species associated with midge larvae consistently regulated the population. Whereas *P. californica* showed a direct density-dependent response in December and *T. koebelei* a similar response in June, the peak population levels characteristically occurred between these periods (February to April). Therefore, there is no justification for concluding that either of these parasites consistently regulated the population. Also, there is no reason to assume that parasitization by these species behaved in a delayed-density dependent fashion, which

would have regulated the midge population. In fact, there is no solid evidence to suggest that even all six species of the parasites acting in concert consistently regulated the midge population. Total parasitization never exceeded 70 percent. In other words, the parasites—especially *T. koebelei* and *P. californica*—apparently can regulate the midge population when it is at relatively low levels (in December or June) but none is capable of consistently doing so. Midge “outbreaks” thus occur and are eventually regulated by some other factor, such as intraspecific competition. However, the factor(s) responsible for midge population regulation was not established in this study.

Interspecific interactions

Analysis of the data designed to assess certain interspecific interactions among members of the parasite guild revealed that only *T. koebelei* and *P. californica* occurred in sufficient numbers and combinations of galls to permit analysis. These results are summarized in figures 6 through 10. In virtually every case, percent parasitization for either *T. koebelei* or *P. californica* was highest when these species occurred alone compared to when they occurred in combination with other species. Thus, some form of interspecific competition occurred and adversely affected the performance of both species. However, total percent parasitization was consistently higher in mixed-species samples compared to single-species samples. Thus, even though interspecific competition occurred, the total amount of mortality inflicted on the host was greatest in those galls containing more than one species compared to galls containing a single species. In other words, the interspecific competition detected did not appear to have an adverse affect on the overall degree of natural biological control.

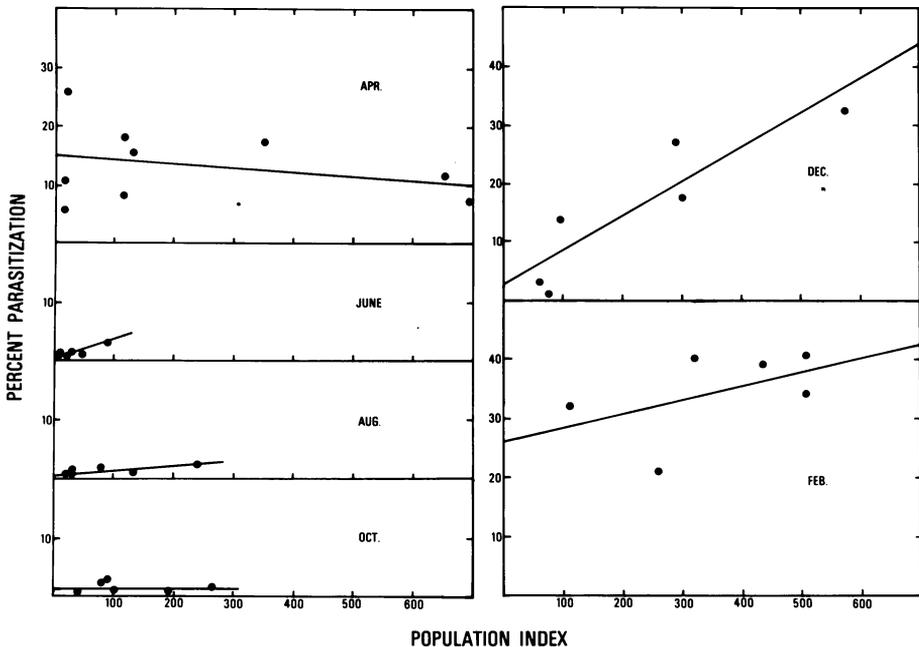


Fig. 3. Statistical relationships between percent parasitization by *Platygaster californica* and host population index. Regression and correlation statistics as follows: April, $Y = 14.8 + (-0.007X)$, $r^2 = 0.08$; June, $Y = -0.08 + 0.036X$ ($P < 0.01$), $r^2 = 0.87$; August, $Y = 0.37 + 0.009X$, $r^2 = 0.53$; October, $Y = 1.57 + (-0.0008X)$, $r^2 = 0.004$; December, $Y = 2.8 + 0.056X$ ($P < 0.01$), $r^2 = 0.82$; February $Y = 26 + 0.023X$, $r^2 = 0.25$.

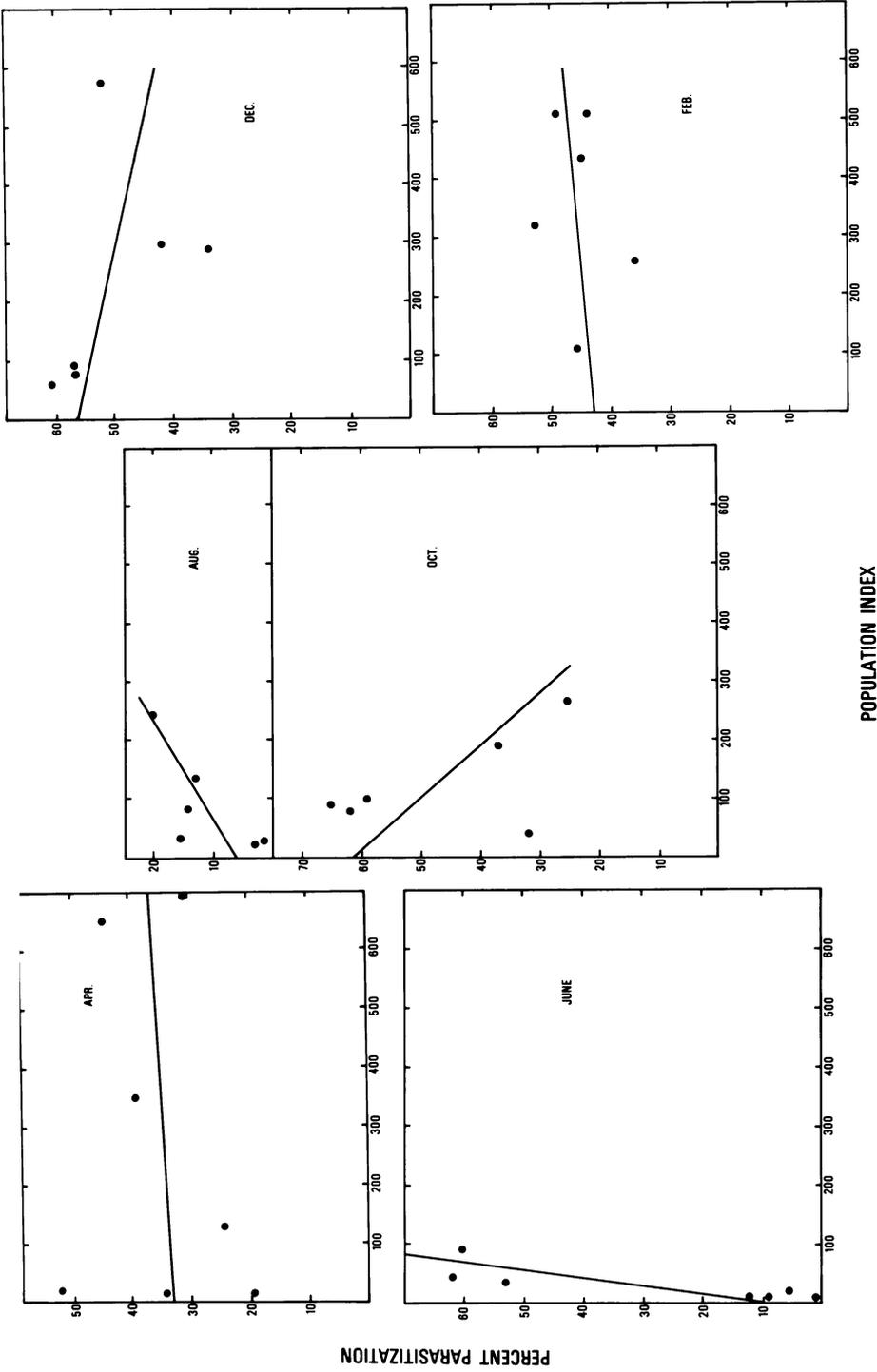


Fig. 4 Statistical relationships between total percent parasitization and host population index. Regression and correlation statistics as follows: April, $Y = 33.3 + 0.005X$, $r^2 = 0.02$; June, $Y = 62 + (-0.117X)$, $r^2 = 0.32$; August, $Y = 6.3 + 0.784X$, $r^2 = 0.05$; October, $Y = 55.9 + (-0.023X)$, $r^2 = 0.21$; February, $Y = 42.7 + 0.008X$, $r^2 = 0.04$; December, $Y = 5.8 + 0.061X$, $r^2 = 0.53$.

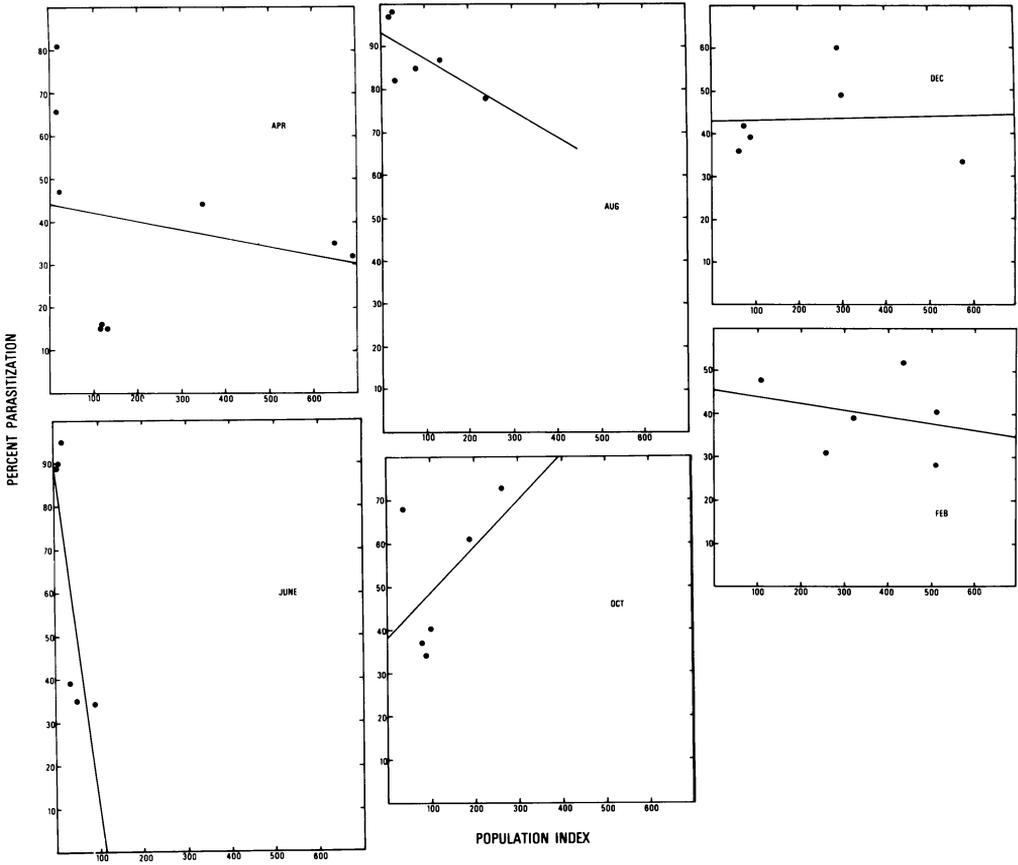


Fig. 5. Statistical relationship between residual mortality and host population index. Regression and correlation statistics as follows: April, $Y = 43.9 + (-0.021X)$, $r^2 = 0.06$; June, $Y = 90.4 + (-0.804X)$ ($P < 0.05$), $r^2 = 0.66$; August, $Y = 93.5 + (-0.061X)$, $r^2 = 0.44$; October, $Y = 38.1 + 0.107X$, $r^2 = 0.28$; December, $Y = 43.2 + 0.0005X$, $r^2 = 0.00009$; February, $Y = 45.4 + (-0.016X)$, $r^2 = 0.07$.

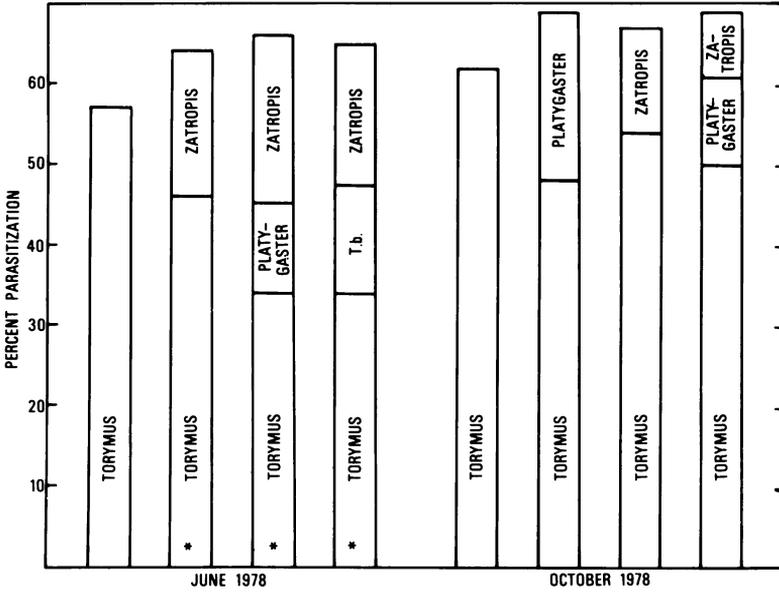


Fig. 6. Influence of other species on percent parasitization by *Torymus koebelei* in June and October, 1978. (T.b. = *Torymus baccharidis*.) Sample sizes for histograms (left to right) = 31, 75, 13, 6, 59, 8, 59, 13. Asterisk at base of histogram indicates significant reduction in parasitization for *T. koebelei*.

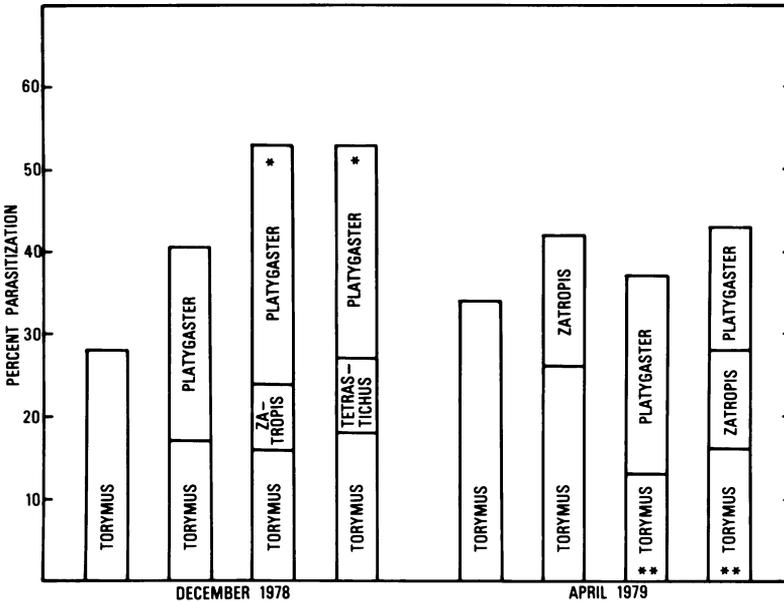


Fig. 7. Influence of other species on percent parasitization by *Torymus koebelei* in December, 1978 and April, 1979. Sample sizes for histograms (left to right) = 6, 20, 12, 10, 14, 24, 7, 52. Asterisks at base of histogram indicate significant reduction in parasitization for *T. koebelei*; asterisks at top of histogram indicate significant increase in total parasitization compared to parasitization by *T. koebelei* alone.

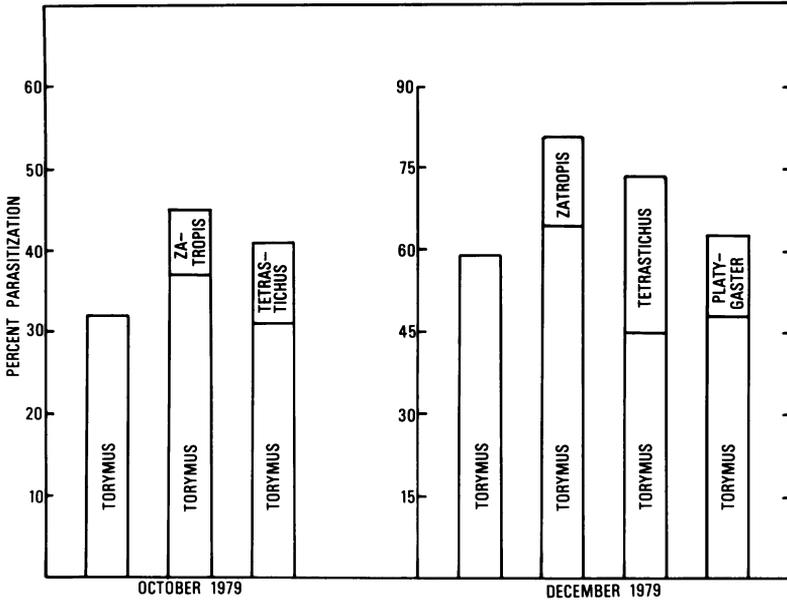


Fig. 8 Influence of other species on percent parasitization by *Torymus koebelei* in October and December, 1979. Sample sizes for histograms (left to right) = 59, 10, 8, 35, 15, 8, 9. No significant differences were detected.

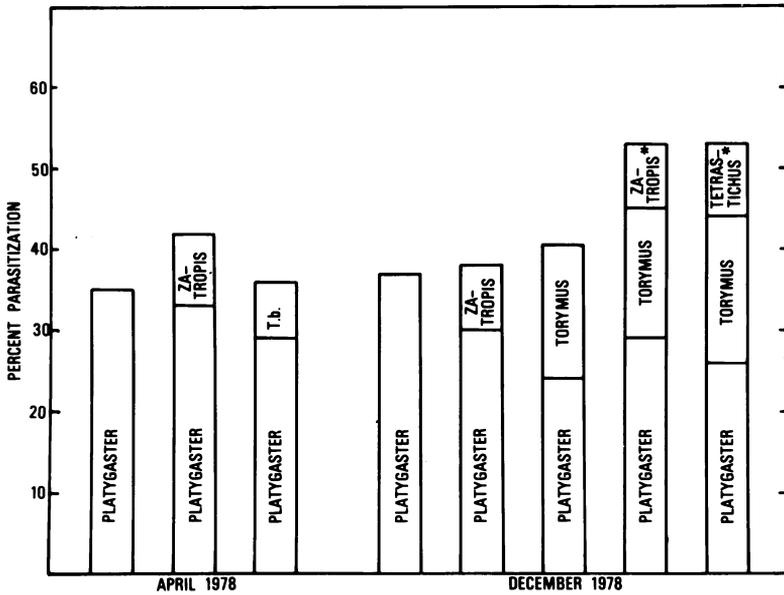


Fig. 9. Influence of other species on percent parasitization by *Platygaster californica* in April and December, 1978. (T.b. = *Torymus baccharidis* and *Torymus* = *T. koebelei*.) Sample sizes for histograms (left to right) = 18, 20, 6, 31, 15, 20, 12, 10. Asterisks at top of histogram indicate significant increases in total parasitization compared to parasitization by *P. californica* alone.

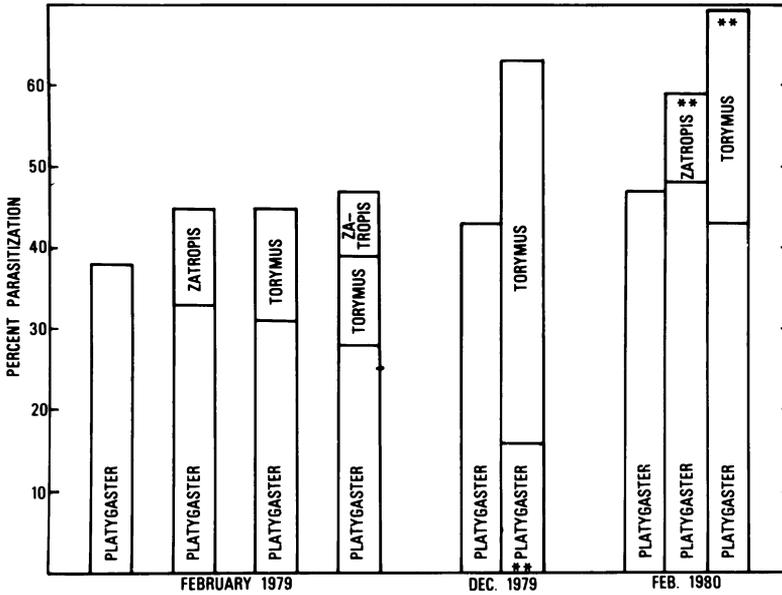


Fig. 10. Influence of other species on percent parasitization by *Platygaster californica* in February and December, 1979 and February, 1980 (*Torymus* = *T. koebelei*). Sample sizes for histograms (left to right) = 21, 33, 32, 19, 9, 9, 46, 42, 7. Asterisk at base of histogram indicates significant reduction in parasitization for *P. californica*; asterisks at top of histogram indicate significant increases in total parasitization compared to parasitization by *P. californica* alone.

Relevance to Biological Control

The results obtained are relevant to a number of topics in modern biological control. These include the use of native plants in urban environments, the question of single versus multiple species introductions, assessing competitive interactions among parasites prior to introduction, the use of facultative secondary parasites in biological control, and the relevance of the theory of r and K selection. These topics will be treated in considerable detail in this section.

Use of native plants

The use of native California plants in the urban landscape has received considerable attention in recent years (Lenz, 1956; Mathias, Lewis, and Kimball, 1977; Walters *et al.*, 1977; Labadie, 1978; Schmidt, 1980). Many conservation-minded urban residents find native plants to be aesthetically pleasing. Moreover, there can be distinct horticultural advantages to using such native plants—e.g., certain species may be well adapted to local environmental conditions.

From an entomological standpoint, native plants could be of considerable value in the urban environment if native plant-feeding insects normally associated with the particular plant are maintained at low levels by their natural enemies. This concept is generally

consistent with the basic premise in biological control, which can be summarized as follows: in the native home (area of origin) of a given plant-feeding insect, there should exist a natural enemy, or complex of natural enemies, which maintains (or is capable of maintaining) the insect at comparatively low levels. This phenomenon is normally termed "natural biological control." From a theoretical standpoint, there are at least two conditions which should be met for such natural biological control to result in an urban setting. First, there must be some degree of structural similarity in the natural enemy guild in the urban environment compared to that observed in the natural or endemic environment. Second, given some degree of structural similarity, the natural enemies in question must be capable of effecting adequate or comparable levels of biological control in the urban environment.

The question of structural similarity was the subject of an investigation of the arthropod fauna associated with live oak (*Quercus fusiformis*, *Q. virginiana*) in urban and natural stands in central Texas (Frankie, Tucker, and Welch, 1979). Arthropods were systematically sampled during 1975 from live oak located in three habitats in Austin, Texas: a suburban shopping plaza, the campus of the University of Texas, and a natural stand adjacent to the Colorado River. Analysis of the mite (Acari) fauna associated with live oak foliage indicated that such structural similarity could be obtained. In this case, the same taxa were dominant at each site (Ehler and Frankie, 1979a). With respect to a family of predaceous mites (Phytoseiidae), the same four species occurred at each site but in differing proportions. However, an index of species richness was similar for each site. The authors suggested that the phytoseiid guild was in equilibrium at each site and that intraspecific competition was playing a critical role in effecting this balance of species. Among the oribatid mites, further evidence for structural similarity of arthropod communities in urban versus non-urban environments was detected (Ehler and Frankie, 1979b). Although evidence for structural similarity was obtained in this study, the ecological impact of natural enemies was not thoroughly assessed.

In the present case, the structure of the parasite guild in Davis was qualitatively similar to that observed in two endemic environments at approximately the same latitude. Of the 7,655 individuals (midges + parasites) which emerged from galls collected during 1978 in Davis, *T. koebelei* was the dominant species (35%) followed by *P. californica* (17.8%), *Z. capitis* (9.5%), *T. baccharidis* (1.3%), *Tetrastichus* sp. (0.5%), and *Mesopolobus* sp. (0.07%). The results for 1979 were similar: of the 6,351 insects reared from the galls, *T. koebelei* was again dominant (33.5%), followed by *P. californica* (23.1%), *Z. capitis* (9.8%), *Tetrastichus* sp. (1.8%), *T. baccharidis* (0.5%), and *Mesopolobus* sp. (0.06%). In contrast, data obtained by Force (personal communication) from 1967 through 1972 in the endemic environment were as follows: (1) of the 12,802 individuals reared from galls collected at Tomales Bay, *P. californica* was the dominant species (32.2%) followed by *T. baccharidis* (16.3%), *T. koebelei* (12.7%), *Mesopolobus* sp. (5.9%), *Z. capitis* (1.6%), and *Tetrastichus* sp. (0.5%); (2) at Bodega Bay, of the 11,412 individuals reared from the galls, *P. californica* was again the dominant species (27.4%), followed by *T. baccharidis* (21.9%), *Mesopolobus* sp. (7.9%), *T. koebelei* (7%), *Z. capitis* (2%), and *Tetrastichus* sp. (1%). To summarize, *T. koebelei* and *P. californica* were the dominant species in Davis whereas *P. californica* and *T. baccharidis* were dominant in the endemic environment. Also, the six species of parasites most frequently collected in the endemic environment were the same species collected in Davis. The quantitative differences in the parasite guilds in the urban versus non-urban environments were presumably due to differences in climate—i.e., the sites at Tomales Bay and Bodega Bay are near the coast and are subject to a milder climate compared to the sites in Davis

which are in the Central Valley.

Despite the fact that the parasite guild in Davis was structurally similar to its non-urban counterpart, this complex of parasites was apparently not able to truly regulate (or control) the midge population and to maintain it at comparatively low levels. As noted previously, both *P. californica* and *T. koebelei* are apparently capable of effecting regulation of the midge population; however, in the present study evidence of such regulation was not consistently detected. At the same time, the mortality brought about through the action of the entire parasite complex was not shown to be a consistent regulatory factor either. Furthermore, the midge population in Davis was much more abundant than in the endemic environment. For example, the average (\pm S.E.) population index for February was 356.8 ± 64.3 in Davis (1979, 1980) compared to 41.8 ± 2.2 at Bodega and 35.7 ± 17.1 at Tomales for 1967, 1968 and 1969. In April, the index averaged 236 ± 91.6 in Davis (1978, 1979, 1980) compared to 59.9 ± 18.3 at Bodega and 35.8 ± 7.8 at Tomales for 1969 and 1970. The data for Bodega and Tomales were calculated from original data kindly provided by D.C. Force. To summarize, the midge population was from 4 to 10 times more abundant in Davis than in the endemic environment at approximately the same latitude.

Thus, parasite guilds associated with native phytophagous insects which are in turn associated with native plants in urban areas may very well be structurally similar to their non-urban counterparts. However, it should not be assumed, *a priori*, that because of such structural similarity, adequate or even comparable natural biological control will result. The evidence obtained in the present study adequately illustrates this. Furthermore, introduced phytophagous species which are not host-specific may also adversely affect native plants. For example, black scale (*Saissetia oleae* [Oliv.]) can be a serious pest of coyote brush and may even kill the plant in some cases (Hagen, van den Bosch, and Dahlsten, 1971). Other insects associated with coyote brush can also cause problems from time to time (cf. Koehler, 1980). Also, human influence on host-plant physiology (e.g., via cultural practices) can alter native plant-herbivore interactions and possibly result in increased densities of native phytophagous insects (see Frankie and Ehler, 1978). Therefore, use of native plants in urban areas could be a mixed blessing: there may be aesthetic and horticultural advantages, but attendant pest problems may not be solvable through reliance on naturally occurring biological control.

Multiple-species introductions (MSI)

Introducing more than one species of natural enemy for control of a target pest species has been one of the most controversial practices in the history of biological control. The critics of such multiple-species introductions (MSI) suggest that intense interspecific competition, which might occur among the various natural enemies, could in fact be detrimental to the project in that it could allow higher pest densities and/or more frequent outbreaks (Turnbull and Chant, 1961; Watt, 1965; Force, 1974). On the other hand, proponents of MSI contend that such competition should not be expected to be harmful and could even result in increased levels of biological control (Huffaker, Messenger, and DeBach, 1971; Huffaker, Simmonds, and Laing, 1976). Part of the reasoning in the latter case is that the total amount of biological control of the target pest obtained by two or more species acting in concert should be greater than that achieved by any one of the species acting alone.

The data summarized in figures 6 through 10 provide empirical support for the latter prediction. In each case, the primary parasite (i.e., *T. koebelei* or *P. californica*) was more efficient (i.e., on a per gall basis) when operating alone compared to when it was in combination with one or more of the other species. Thus, some form of interspecific competition occurred and reduced the effectiveness of a given species. However, the interspecific competition did not result in lower levels of total parasitization; total parasitization in mixed-species samples was consistently higher than that obtained in any of the single-species samples. It appears that, as a general ecological principle, interspecific competition among primary parasites in a guild should result in (1) a reduction in effectiveness in the individual species but (2) an increase in the effectiveness of the aggregate of species (Ehler, 1979a). The above evidence then can be taken as supportive of the practice of multiple-species introduction in biological control. However, whereas this evidence can be considered "necessary" with respect to MSI, it is not "sufficient." This is because other avenues of interspecific competition among the parasites were not assessed—e.g., among adult females.

However, still other necessary evidence for MSI was not obtained—i.e., the effect of interspecific competition on *T. baccharidis* and *Tetrastichus* sp. These species simply did not occur alone in sufficient numbers of galls to permit analysis. This circumstance was particularly unfortunate in the case of *Tetrastichus* sp., because Force (1974) showed under laboratory conditions that *Tetrastichus* sp. acting alone was more effective than any other combination of species. In other words, there may be exceptions to the ecological principle stated above; however, no good demonstration of such a case under field conditions has been reported. In this regard, *Tetrastichus* sp. would be a logical choice as an experimental animal.

Pre-screening natural enemies

Another question concerns the necessity of detailed, pre-introduction studies of candidate natural enemies. Some have argued that it is best to conduct such studies in order to determine the best species or the proper sequence of species to be introduced (Turnbull and Chant, 1961; Zwolfer, 1971; Pschorn-Walcher, 1977). However, others have questioned the need for such studies on the basis that these investigations are largely unnecessary (Huffaker, Messenger, and DeBach, 1971). One aspect of this question is the feasibility of assessing competitive interactions among candidate primary parasites (Ehler, 1979a). There are at least two justifications for proceeding with such pre-introduction studies. First, in the case of multiple-species introductions, it is logically possible (perhaps not very likely) that interspecific competition among parasites could, in fact, lead to reduced levels of overall pest population control. Where the parasites in question occur sympatrically in the endemic region of the host, it might be valuable to investigate the competitive interactions among the species. Second, in those cases where a competitive hierarchy exists, it would be helpful to know the competitive relationships among the various species so that, if desired, the poorest competitor could be imported and colonized first. The more superior competitors could then be colonized if need be at a later date. This practice has been advocated by Zwolfer (1971) and Pschorn-Walcher (1977).

The method used to assess competitive interactions in the present paper could very well be used to assess competitive interactions among members of the parasite guild in the native home. However, such investigations are constrained because in a given number of subsamples, a given species must occur alone and again with other species in an

adequate number of subsamples. Such a natural experimental design is necessary to compare the efficiency of a given species alone versus in combination with at least one or more other species. In the present case, such analysis was only possible for two of the four species of primary parasites (i.e., *T. koebelei* and *P. californica*).

Despite the abundance of evidence obtained with respect to influence of other species on these two primary parasites, only one of the two original questions could be satisfactorily answered. That is, interspecific competition involving either of these primary parasites resulted in (1) reduced efficiency of the individual species but (2) increased efficiency of the aggregate species. This is fully consistent with current theory and could be taken as an indication of how these species might interact in a new environment. However, despite earlier indications (cf. Ehler, 1979*a*), these data did not clearly suggest which species was the inferior competitor and which was the superior competitor. In other words, *P. californica* was not necessarily more or less suppressed through interspecific competition compared to *T. koebelei*. Furthermore, the two remaining species of primary parasites—which were not available for analysis—may very well be the inferior competitors. In fact, Force (1974) believed that *Tetrastichus* sp. was the inferior competitor in the guild. Nevertheless, pre-introduction studies of the sort described here would be an improvement over the current practice of simply releasing all available species of natural enemies in the hope that the best species or combination of species will be sorted out in the field.

Facultative secondary parasites

It is standard practice in classical biological control to not introduce secondary parasites (van den Bosch, 1971; Huffaker, Simmonds, and Laing, 1976). However, it is important to distinguish between obligate and facultative secondary parasites. An obligate secondary parasite must parasitize a primary parasite; the latter is a parasite of a nonparasitic host. A facultative secondary parasite can parasitize either the primary parasite or the nonparasitic host. Intentional exclusion of obligate secondary parasites in biological control remains a sound practice; however, this is not necessarily the case with respect to facultative secondary ones.

According to Ehler (1979*b*), a facultative secondary parasite would be of value in biological control under the following conditions: (1) that the impact on host density brought about by a primary parasite and a facultative secondary one acting in concert be greater than that brought about by the primary parasite acting alone, and (2) that the facultative secondary parasite not have an adverse effect on other parasites or parasite guilds in the environment. Investigating the above conditions with respect to a candidate, facultative secondary parasite would involve both laboratory (e.g., Weseloh, Wallner, and Hoy, 1979) and field investigations (e.g., Ehler, 1979*b*) before introduction.

The analytical technique used in the present paper to assess interspecific interactions among the parasites can also be used to assess condition (1) above. The major experimental requirement is that each candidate primary parasite occur both singly and with the candidate facultative secondary parasite in an adequate number of subsamples. In this way, the efficacy of the primary parasite can be assessed when it occurs alone compared to when it occurs in combination with the facultative secondary parasite.

The impact of *Z. capitis* (a facultative secondary parasite) on the efficiency of two primary parasites (*T. koebelei* and *P. californica*) can be deduced from the data in figures 6 through 10. In virtually every case, the presence of the facultative secondary parasite

led to a reduction in percent parasitization by the primary parasite; however, total percent parasitization was greatest in samples containing both the primary parasite and the facultative secondary one compared to samples containing only the primary parasite. In these instances, the result conformed to what we would expect when several species of obligate primary parasites act together: as the number of parasite species is increased, the efficiency of the individual species declines but the efficacy of the aggregate of species increases. With respect to ecological impact, the effect of the facultative secondary parasite was essentially the same as that of a competing species of a primary parasite.

We thus have some indication of how this particular species of facultative secondary parasite behaves in its native home. Similar results with a candidate facultative secondary parasite would justify additional research—particularly laboratory investigations—designed to further assess how this species might behave in a new environment. However, there were additional points not addressed in the present analysis—e.g., (1) the effect of *Z. capitatus* on the other two species of primary parasites in the guild and (2) the effect of the second facultative secondary parasite (*Mesopolobus* sp.) on all four of the primary parasites in the guild. Unfortunately, the combinations of species available for analysis were not sufficient to enable an assessment of these questions.

Theory of r- and K-selection

The theory of r and K selection is essentially an ecological classification of species. The terms r and K selection were coined by MacArthur and Wilson (1967); in this case K refers to carrying capacity of the environment, whereas r refers to intrinsic rate of natural increase (r_m). Pianka (1970) provided an elegant summary of the theory of r and K selection. According to him, there is a hypothetical r-to-K continuum, and a given organism is positioned at a particular point along it. The r end of the spectrum represents the perfect or near perfect ecological vacuum with virtually no density effects and very little competition. In this situation, the optimum evolutionary strategy would be to put all matter and energy into reproduction and to produce as many progeny as possible. On the other hand, density effects are maximal when the environment is saturated at the K end of the spectrum. Competition should be keen; therefore, the optimal strategy would be to channel available matter and energy into maintenance and production of a few extremely fit offspring. Thus, K selection should lead to increased efficiency of utilization of resources, whereas r selection should lead to higher productivity.

From an entomological standpoint, much of the work relevant to r and K theory has dealt with parasite guilds. Force (1970, 1974) studied the competitive ability and reproductive potential of the four species of primary parasites in the guild under consideration in this paper and constructed an r-to-K continuum for these species. The most r-selected member of the guild was *Tetrastichus* sp.; it was the poorest competitor yet had the highest reproductive rate. The most K-selected was *T. koebelei*; it was the superior competitor and had one of the lowest reproductive rates. *Platygaster californica* and *T. baccharidis* were at intermediate points on the continuum. Force (1972) further observed that, in undisturbed sites, *Tetrastichus* sp. was least dominant numerically and was rarely responsible for more than 1 percent mortality of the host. However, at a particular disturbed site (in this case, plants were removed or cut low to the ground), parasitization by *Tetrastichus* sp. increased sharply from 1 to 46 percent and continued at that level for several months. As the habitat returned to normal, parasitization by *Tetrastichus* sp. declined to the previously low levels. Force (1972, 1974) then suggested that in classical

biological control of insects, natural enemies which are more r-selected might be best suited for highly disturbed or temporary agro-ecosystems. He further suggested that these natural enemies would be those species which are (1) least dominant numerically in undisturbed situations, (2) found consistently over a wide geographical or ecological range, and (3) relatively more abundant in newly disturbed habitats.

However, data from Force's (1970) laboratory experiments on competition were equivocal in some cases. He conducted a series of transplant experiments in which a given species was introduced into an experimental universe containing one allospecific incumbent species. His results were as follows: *P. californica* the incumbent and *T. koebelei* introduced, *T. koebelei* was the superior competitor; *T. baccharidis* the incumbent and *T. koebelei* introduced, result in doubt; *T. koebelei* the incumbent and *Tetrastichus* introduced, *T. koebelei* was the superior competitor; *T. koebelei* the incumbent and *T. baccharidis* introduced, no multiparasitism or competition detected; *Tetrastichus* the incumbent and *T. koebelei* introduced, *Tetrastichus* was the superior competitor; *P. californica* the incumbent and *T. baccharidis* introduced, *T. baccharidis* was the superior competitor; *T. baccharidis* the incumbent and *Tetrastichus* introduced, outcome in doubt; *Tetrastichus* the incumbent and *T. baccharidis* introduced, *Tetrastichus* was superior competitor; *P. californica* the incumbent and *Tetrastichus* introduced, result in doubt.

These results illustrate the problems associated with ranking species of parasites according to their competitive superiority (or inferiority). First, co-occurrence of two species does not necessarily result in interspecific competition. For example, *T. koebelei* showed virtually no restraint with respect to multiple parasitization, whereas *Tetrastichus* showed great restraint; on the other hand, *T. baccharidis* showed complete restraint in cases involving *T. koebelei* and little or no restraint in cases involving *P. californica* or *Tetrastichus* (Force, 1970). (Because *P. californica* is an egg-larval parasite, it does not encounter hosts [eggs] parasitized by the other three species of primary parasites.) Whether or not interspecific competition occurs between two larvae thus depends especially on the degree of restraint exercised by the ovipositing female. Second, the outcome of interspecific competition may well depend on which species is the incumbent. Force's (1970) data illustrate this problem nicely—e.g., *T. koebelei* the incumbent species and *Tetrastichus* introduced, *T. koebelei* is the superior competitor; *Tetrastichus* the incumbent species and *T. koebelei* introduced, *Tetrastichus* is the superior competitor! In the latter case, the "inferior" competitor (*Tetrastichus*) was superior to the "superior" competitor (*T. koebelei*) in the guild! If we were to add confounding features to such an interaction (e.g., environmental heterogeneity, a third competing species, variable temperatures, and the like), the problem of assigning positions for species in a competitive hierarchy approaches the point of being operationally intractable.

The prediction that the r-strategist (or strategists) in a given guild is necessarily a colonizing species (and therefore well suited for biological control in disturbed habitats) is also in need of investigation. In this regard, Gadgil and Solbrig (1972) argued that r-strategists need not necessarily be colonizing species. Data from the present study provide some support for this prediction.

Coyote brush considered in the present paper was planted in early summer of 1975, and by late summer of 1977, the first galls of *R. californica* were observed. The first parasites to colonize the habitat were *Z. capitis* and *P. californica*. These were present in the first samples taken near the end of late fall of 1977. By spring of 1978, *T. koebelei*, *T. baccharidis*, and *Mesopolobus* sp. were first detected in samples from the habitat. It was not until December, 1978, that the first galls containing *Tetrastichus* sp. were collected.

Thus, at least in this case, the species presumed to be most r-selected in the guild (*Tetrastichus* sp.) colonized a newly available habitat about one year after colonization by the host and about 8 to 10 months after colonization by the more K-selected members of the guild.

If these findings indicate the colonization potential of the species in this guild, it suggests that r-strategists be divided into colonizing (= fugitive) and non-colonizing species. It may be that at least two kinds of parasite guilds occur with respect to r and K theory. Certain guilds, especially those associated with stable environments, may well have r-strategists that are not colonizing species. In these cases, the more K-selected members in the guild may in fact be the best colonizers. On the other hand, certain parasite guilds, particularly those associated with unstable environments, may well have r-strategists which are superior colonizing species. However, considerably more empirical evidence is needed, and, with respect to applied ecology, the so-called "theory of r and K selection" should best be regarded as an hypothesis. In other words, the deductive consequences or predictions from the hypothesis should be used in testing and empirically verifying the hypothesis, rather than in deriving strategies for solving ecological problems such as in biological control.

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