Competitive Interactions among Endophagous Parasitoids of Potato Tuberworm Larvae in Southern California

R. V. Flanders and E. R. Oatman
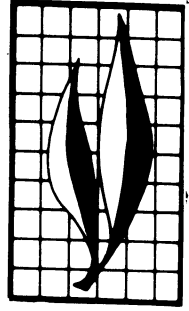
ABSTRACT

Field and laboratory studies were conducted to determine how *Apanteles scutellaris* and *Agathis gibbosa* (Hymenoptera: Braconidae) coexist as solitary endophagous parasitoids of potato tuberworm (PTW) larvae, *Phthorimaea opercullela* (Lepidoptera: Gelechiidae), in southern California. The competitive characteristics of *Orgilus jennieae* (Hymenoptera: Braconidae), an exotic parasitoid of PTW larvae, were compared with those of the native species to determine its potential for establishment. Emergence of the egg-larval parasitoid *Chelonus phthorimaeae* (Hymenoptera: Braconidae) from field-collected PTW larvae was compared with those of the other parasitoids, but its competitive interactions were not considered. Seasonal density changes, mine characteristics, and within-plant distributions of PTW larvae were studied to determine their possible impacts on parasitoid interactions.

Apanteles scutellaris and *A. gibbosa* oviposited in similar host instars, similarly responded to vertical distributions of PTW larvae in plants, and were capable of ovipositing in larvae mining in nearly all potato plant tissues. However, *A. scutellaris* with its short ovipositor more efficiently oviposited in hosts in leaflets and distal portions of petioles, while *A. gibbosa* with its long ovipositor more efficiently oviposited

THE AUTHORS:

R. V. Flanders is an Entomologist, USDA APHIS Biological Control Laboratory, 2534 S. 11th Street, Niles, MI 49120.

E. R. Oatman is Professor and Entomologist, Division of Biological Control, Department of Entomology, University of California, Riverside, CA 92521.

Competitive Interactions among Endophagous Parasitoids of Potato Tuberworm Larvae in Southern California[1]

INTRODUCTION

BIOLOGICAL COMPETITION usually is defined as the active demand by two or more individuals of the same species (intraspecific competition) or of two or more species at the same trophic level (interspecific competition) for a common resource that is actually or potentially limiting (Clements and Shelford 1939). Other definitions also exist (see Milne 1961). Intensity of competition among species relying on the same resource depends on their biological and ecological similarities, as measured by the overlapping of their ecological niches along common resource gradients (May 1973; Miller 1967). The more the ecological niches of two coexisting species overlap, the more intense is their competition. Ultimately, species whose ecological niches broadly overlap exhibit allopatric or parapatric distributions resulting from competitive displacements (DeBach 1966; DeBach and Sundby 1963; Mayr 1963; Miller 1967). Consequently, species that spatially and temporally coexist while utilizing the same resource must sufficiently differ in some characteristics to reduce the intensity of their competition. This suggests that over long periods of time adaptations, specializations, and distributional segregations occurred among the progenitors of currently coexisting species so that the intensity of competition is reduced, compensated for, or avoided (Mayr 1963; Miller 1967).

Importing natural enemies to suppress insect pest densities (classical biological control) may be viewed as an attempt to fill vacant niches in biological communities (Watt 1965). Consequently, the ecological and practical impacts of competition among natural enemies, especially parasitoids, for a common host has been debated among biological control workers for decades (DeBach 1966; DeBach and Sundby 1963; Flanders 1965, 1966; Huffaker and Laing 1972; Pemberton and Willard 1918; Smith 1929; Turnbull 1967; Turnbull and Chant 1961; van den Bosch 1968; Watt 1965). Most debate has centered on the impact of competition between or among parasitoid species on the probability of simultaneously or subsequently establishing imported species, or on the subsequent degree of host density suppression. However, few empirical studies have been conducted.

Analyses of rates of establishment and of biological control successes by Ehler and Hall (1982), Hall and Ehler (1979), and Hall, Ehler, and Bisabri-Ershadi (1980) suggested that the more species of parasitoids attacking a host in a region, the more likely that competitive interactions will affect establishing imported species. Classical biological control has been most frequently and successfully employed against exotic insect pests (Hall and Ehler 1979; Hall, Ehler, and Bisabri-Ershadi 1980; van den Bosch 1968). Such pests usually possess no natural enemies or possess poorly adapted native species that evolved with native hosts. Consequently, when exotic natural enemies are first introduced, most ecological niches at the carnivore trophic level are

vacant or occupied by poorly adapted species, and competition probably has little impact on establishment failures or successes (Ehler and Hall 1982; Hall and Ehler 1979; van den Bosch 1968). However, when initial introductions result in establishing one or more species, subsequent introductions may result in competition among previously established and recently introduced species.

Such interactions may preclude or inhibit establishment of new species, displace previously established species, or have no affect, depending on species similarities and competitive abilities. For example, DeBach and Sundby (1963) documented replacements of species of *Aphytis* with their sequential introduction into California against the California red scale, an exotic pest of citrus. They hypothesized that these replacements occurred because the parasitoids possessed overlapping niches and each newly introduced species was competitively superior to previously introduced species because of greater climatic tolerances and higher searching capacities. However, studies by Luck and Podoler (1985) suggest that *A. lingnanensis* Compere was replaced by *A. melinus* DeBach because *A. melinus* preferred younger or smaller scales for oviposition, thereby causing relative shortages of suitable hosts for oviposition by *A. lingnanensis*. Ehler and Hall (1982), analyzing attempts to establish exotic natural enemies against several exotic pests, suggest that establishment failures due to competition probably have occurred where similar species were sequentially or simultaneously introduced.

Although introducing exotic natural enemies to suppress native pest densities has been advocated (Pimentel 1963), previous attempts have resulted in fewer establishments than have introductions against exotic pests (Hall and Ehler 1979; Hall, Ehler, and Bisabri-Ershadi 1980). This lower establishment rate may be due largely to competition with native species since these pests usually possess adapted complexes of coevolved natural enemies. Consequently, to establish exotic natural enemies against native pests, the exotic species must either fill narrow but still vacant niches or must competitively displace native species, thereby severely lowering the probability of their establishment. However, few studies have been conducted on how complexes of native parasitoids partition their hosts to enable coexistence. Force (1970, 1974) studied several species of parasitoids, all native to California, that attack the midge *Rhopalomyia californica* Felt (Diptera: Cecidomyiidae) that forms galls on coyote brush. However, mechanisms or strategies that allow these coevolved parasitoids to coexist were not clearly established or only implied, as Force emphasized competition rather than coexistence to determine how host densities were affected.

In a study of how three sympatric species of *Megarhyssa* coexist as parasitoids of the pigeon tremex, Heatwole and Davis (1965) found that each species possesses an ovipositor of a different length and each parasitizes host larvae burrowing in wood at depths corresponding to its ovipositor length. No studies have been conducted, however, on how the mechanisms and strategies of coexistence among a group of native parasitoids may affect the ability of imported species to become established. Consequently, we chose to study the potato tuberworm (PTW), *Phthorimaea opercullela* (Zeller) (Lepidoptera: Gelechiidae), in southern California to determine how some of its native parasitoids coexist and how exotic parasitoids may or may not fit into the existing strategies of competition and coexistence.

The PTW is a cosmopolitan pest of field and stored potatoes (Commonwealth Institute of Entomology 1968). It apparently evolved in western South America where its most common host plants, potato and tobacco, also originated (Graf 1917; Lloyd

1972). The PTW readily reproduces on stored potato tubers, enabling it to be easily transported; consequently, it has become established throughout the world (Commonwealth Institute of Entomology 1968; Lloyd 1972). In South America, however, the PTW is a relatively minor pest of potatoes. The reason for its innocuous status there probably is that a diverse complex of natural enemies attacks it (Lloyd 1972). Where the PTW has been introduced, simple natural enemy complexes usually occur and PTW thrives. These complexes usually consist of accidentally or purposefully introduced species, or of native species whose native hosts are ecologically and physiologically similar to PTW (Lloyd 1972).

The PTW was first observed in California more than a century ago (Graf 1917), but circumstantial evidence indicates its presence for a much longer time. Attacking PTW in California are at least 12 species of native parasitoids (table 1; Graf 1917; Oatman and Platner 1974), a more diverse parasitoid complex than generally occurs where it has been introduced (Lloyd 1972). The parasitoid complex in California also is generically similar to those occurring in South and Central America (Lloyd 1972; Oatman and Platner 1974). In addition, these parasitoids effectively suppress PTW in aerial parts of native solanaceous plants in California, but are relatively ineffective on potatoes, especially tubers, in commercial fields (Graf 1917; Oatman and Platner 1974). Most California parasitoids also attack other native lepidopterous hosts that are leaf miners or folders like PTW (table 1; Krombein et al. 1979); this may indicate that they originally evolved on these alternate hosts and subsequently adapted to PTW.

The perennial status of PTW as a pest of potatoes in California prompted attempts to introduce 11 parasitoids (table 1; Lloyd 1972; Oatman and Platner 1974), but none has become established, although many of them were recovered for several years after colonization. For example, Oatman and Platner (1974) reported that *Orgilus lepidus* Muesebeck (Hymenoptera: Braconidae) was recovered in 1968, 3 years after colonizations ceased, but it has not been recovered since. *Copidosoma koehleri* Blanchard (Hymenoptera: Encyrtidae) similarly disappeared after appearing to be established (Oatman and Platner 1974). The inability of exotic parasitoids to become established in California was thought to be because they could not adapt to the new climate, but studies comparing temperature responses of exotic and native species (Cardona and Oatman 1975; Odebiyi and Oatman 1977; Powers and Oatman 1984) suggest that differences in responses were too small to explain all establishment failures. Because all the parasitoids introduced into California were congeners of or ecologically similar to indigenous species (table 1), Oatman and Platner (1974) speculated that the primary reason for the failure of exotic species to become established was that they were competitively displaced by indigenous species. This study was conducted to test this hypothesis.

The most common primary parasitoids of PTW larvae in southern California are *Apanteles scutellaris* Muesebeck, *Agathis gibbosa* Say, and *Chelonus phthorimaeae* Gahan (Graf 1917; Oatman and Platner 1974). The biologies and physical ecologies of these species were reported by Cardona and Oatman (1975), Odebiyi and Oatman (1972, 1977), and Powers and Oatman (1984). All three species belong to the family Braconidae; their larval stages are solitary and occur in the hemolymph of PTW larvae; and their larvae do not emerge from and kill parasitized hosts until the latter spin their pupal cocoons. Their difference: Females of *C. phthorimaeae* oviposit in PTW eggs; *A. scutellaris* and *A. gibbosa* oviposit in larvae. In addition, *A. scutellaris*

TABLE 1. INDIGENOUS AND INTRODUCED PARASITOIDS
OF THE PTW IN CALIFORNIA*

Family	Genus (biological characters†)	Indigenous species (number of hosts‡)	Introduced species (origin)
Braconidae			
	Agathis (I,S,L)	*gibbosa* (8)	*unicolor* (Argentina)
	Apanteles (I,S,L)	*scutellaris* (2)	*subandinus* (S. America)
	Bracon (E,G,L)	*gelechiae* (34)	
		hebetor (10)	
	Chelonus (I,S,E-L)	*phthorimaeae* (3)	*curvimaculatus* (S. Africa)
			kellieae (Costa Rica)
	Microgaster (I,S,L)	*phthorimaeae* (7)	
	Orgilus (I,S,L)	*californicus* (1)	*lepidus* (Argentina)
			parcus (S. Africa)
			jennieae (Costa Rica)
	Parahormius (E,G,L)	*pallidipes* (2)	
Ichneumonidae			
	Campoplex (I,S,L)	*phthorimaeae* (4)	*haywardi* (Argentina)
	Diadegma (I,S,L)	*compressum* (3)	*mollipla* (S. Africa)
			stellenboschense (S. Africa)
	Nepiera (I,S,L)	*fuscifemora* (7)	
	Nythobia (I,S,L)		*Nythobia* sp. (India)
	Pristomerus (I,S,L)	*spinator* (12)	
	Temelucha (I,S,L)		*Temelucha* sp. (Argentina)
Encyrtidae			
	Copidosoma (I,P,E-L)		*koehleri* (S. America)
Eulophidae			
	Sympiesis (E,G,L)	*stigmatipennis* (16)	
	Zagrammosoma (E,G,L)	*flavolineatum* (1)	

*Information extracted from Graf (1917), Krombein et al. (1979), Lloyd (1972), and Oatman and Platner (1974).

†The first letter designates the location of the immature parasitoids relative to the body of the host (E = external, I = internal); second letter, number of immature parasitoids per host (G = gregarious, P = polyembryonic, S = solitary); third letter, stage of host attacked (E-L = oviposition in eggs development completed in larvae, L = oviposition and development in or on larvae).

‡Number of hosts attacked includes the potato tuberworm, but does not include hosts only attacked in the laboratory. Some hosts included in these numbers may not occur in California.

females deposit their eggs in the hemolymph of PTW larvae; *A. gibbosa* females deposit their eggs in ganglia of the ventral nerve cord. The ovipositor of *A. gibbosa* also is about four times longer than that of *A. scutellaris*. Furthermore, *A. scutellaris* possesses only one reported alternate host, *C. phthorimaeae* possesses two, and *A. gibbosa* has at least eight (Krombein et al. 1979). Thus, although all three parasitoids may compete for PTW larvae, their biological characteristics indicate possible mechanisms for coexistence.

Our study sought to determine how the biological differences allow *A. scutellaris* and *A. gibbosa* to partition the host resource sufficiently to reduce the intensity of competition to enable coexistence. Since *C. phthorimaeae* oviposits in PTW eggs,

it may only indirectly compete with the other species by affecting densities of non-parasitized PTW larvae available to searching females of the other species and may only directly compete during immature development in multiply parasitized hosts, if adults of the other species do not discriminate. Consequently, because of these limited competitive interactions (cf., Force 1970, 1974), only certain characteristics of the emergence of *C. phthorimaeae* from field-collected PTW larvae were considered.

Among the parasitoids imported into California before 1972, two were braconid species of the genus *Orgilus* (table 1). *Orgilus lepidus,* imported from Argentina and released in California during 1965, was recovered during 1968 (Oatman and Platner 1974), but subsequently disappeared. Oatman and Platner (1974) also recovered an unidentified species of *Orgilus,* subsequently identified as *O. parcus* Turner from South Africa. This species was released at the time of the Oatman-Platner surveys, but like *O. lepidus,* it has not been subsequently recovered. In addition, Krombein et al. (1979) list *Orgilus californicus* (Provancher) as an apparently native parasitoid of PTW, but field surveys in southern California have not detected it. Biological studies on *O. lepidus* by Oatman, Platner, and Greany (1969) and on *O. parcus* by Broodryk (1969) indicate that both species oviposit in young PTW instars and their immature stages internally and solitarily develop in the hemocoel of PTW larvae (as do *A. gibbosa* and *A. scutellaris*), but the lengths of their ovipositors are more similar to that of *A. gibbosa* and they oviposit in the host's hemocoel like *A. scutellaris.*

Based on these biological similarities and similar climatic conditions between the origins of both exotic species and southern California, we hypothesized that inabilities to establish exotic species of *Orgilus* and the apparent absence of *O. californicus* in southern California probably were due to competitive interactions with *A. scutellaris* or *A. gibbosa.* The importation of *O. jennieae* Marsh from Costa Rica in 1972 offered us an opportunity to test this hypothesis. Studies by Flanders and Oatman (1982) indicated that *O. jennieae* possessed nearly the same biological characteristics as the previously imported species of *Orgilus,* suggesting that competitive interactions among this species, *A. scutellaris,* and *A. gibbosa* would be similar to those of the previously imported species. However, *O. jennieae* was not released in southern California before these studies were initiated. Consequently, laboratory investigations were required to determine its competitive attributes and establishment potentials.

Interspecific competition among parasitoids may be separated into extrinsic interactions that occur among adults in their search for hosts and intrinsic interactions that occur among immatures for possession of multiply parasitized hosts (Smith 1929). To investigate possibly important extrinsic interactions among the PTW parasitoids, we considered several characteristics of PTW larval populations. The PTW larvae mine in various tissues of potato plants and the depth and configuration of their mines are affected by location and height on plants (Graf 1917). Stage of development and density of PTW larvae also may affect the depth and configuration of mines, as well as larval distributions among locations and heights on plants.

Based on these host characteristics and on their possible interactions with parasitoid lengths, as found for coexisting *Megarhyssa* species (Heatwole and Davis 1965), we hypothesized that differences in searching preferences or abilities among the parasitoids may partially explain the coexistence of the native species or the establishment potential of *O. jennieae.* In addition, several studies show that interspecific discrimination abilities and intrinsic competition among immature parasitoids in multiply para-

sitized hosts may affect competition and coexistence (Bartlett and Ball 1964; Fisher 1961, 1962, 1971; Luck and Podoler 1985; McLeod 1972; Pemberton and Willard 1918; Salt 1960). For example, studies on *Orgilus obscurator* indicate that it is adversely affected by other nondiscriminating, intrinsically superior parasitoids of European pine-shoot moth larvae (Arthur and Juillet 1961; Arthur, Stainer, and Turnbull 1964; Juillet 1960; Koehler and Kolk 1969; McLeod 1972; Syme 1969, 1970, 1974). Consequently, we also considered as possible factors enabling coexistence or affecting establishment the ability of PTW parasitoids to interspecifically discriminate and the subsequent outcome of intrinsic competition in multiply parasitized hosts if the females of a species do not discriminate. Our field and laboratory studies were formulated to investigate these possibilities.

MATERIALS AND METHODS

Field Studies

Studies were conducted in pesticide-free potato fields on the University of California's Moreno Field Station. During 1977, a 0.2-hectare field of 'Norgold' potatoes was sampled during October and November. During 1978, a field divided into 0.5 hectare of 'Norgold' and 0.4 hectare of 'White Rose' potatoes was sampled from May to July. During both years, sampling ended when the aerial portions of plants in the fields were mechanically destroyed just before harvest.

Temperature and humidity were continuously recorded with a hygrothermograph located within one kilometer of the fields. Rainfall was recorded daily at the same location as the hygrothermograph. During fall, the mean median daily temperature was 14.8°C, mean minimum daily temperature was 5.0°C, and mean maximum temperature was 23.0°C. The minimum and maximum temperatures were 0.6° and 32.3°C, respectively. Rainfall was intermittent, supplemented with overhead sprinkler irrigation.

During spring, temperatures were higher and rainfall less than during fall. The mean median daily temperature was 20.6°C, mean minimum daily temperature was 10.8°C, and mean maximum daily temperature was 30.3°C. The minimum temperature was 4.4°C; the maximum was 38.5°C. Overhead sprinkler irrigation was applied less frequently than during fall, despite less rainfall. The relatively hot, dry weather caused plants of both cultivars to exhibit moderate water stress.

A sample consisted of all foliage and lateral branches attached to a main stem of a potato plant. Stems were cut at the soil surface, and samples did not include tubers. During 1977, 15 samples (14 on the first sampling date) were randomly taken from the field each week. During 1978, 24 samples, equally divided between 'Norgold' and 'White Rose' plants, were randomly taken each week. Samples were placed in individual paper bags and stored at 10°C for 1 to 5 days before being examined in the laboratory.

The length of the main stem, number of lateral stems, and number of nodes on the main stem were recorded. Samples then were thoroughly searched with a magnifying lens and dissecting microscope for PTW larvae. Sample date, sample number, instar of the larva, and location of the larva's mine were recorded for each larva found. Mine locations were recorded according to the plant tissues involved (stem, bud, leaf petiole,

or leaflet) and the nearest leaf node (numbered from base of stem to terminal bud). Larvae were individually placed in 30-ml clear plastic cups with paper lids. Cups were supplied with cubes of 'Norgold' potato tubers and a shallow layer of sterilized white sand for PTW food and pupation, respectively. Larvae then were incubated at 25 + 1°C and 50 percent RH with a 12:12 (L:D) photoperiod (standard rearing conditions) until PTW or parasitoid adults emerged. The species and sex of emerging adults were recorded with the previously obtained data for each larva.

During spring 1978, *O. jennieae* adults were released in the field being sampled. Releases were made on three dates (April, May, June). Each release consisted of 125 to 300 females (250 to 600 males and females) from the laboratory culture. Altogether, 2,350 adults were released. Adult parasitoids were allowed to escape from paper cartons (about 50 adults per carton) as the cartons were carried at waist level through the field.

Laboratory Studies

Cultures of *A. scutellaris* and *A. gibbosa* were initiated with adults obtained from the field studies. The culture of *O. jennieae* was initiated with individuals imported from Costa Rica by E. R. Oatman in 1972. The PTW and parasitoid cultures were maintained on 'White Rose' potato tubers as described by Cardona and Oatman (1975), Finney, Flanders, and Smith (1947), Flanders and Oatman (1982), Odebiyi and Oatman (1972, 1977), Platner and Oatman (1968, 1972), and Platner, Greany, and Oatman (1969).

Oviposition preferences or efficiencies of each parasitoid species relative to PTW instar and mine location were studied, using potato foliage, by methods similar to those of Flanders and Oatman (1982). 'Norgold' plants were grown from tubers in plastic pots (3.8 L) in a greenhouse until their main stems were about 30 cm long. All but three stems per pot were removed in the laboratory. Ventilated, clear acetate cylinders (51 cm high) were placed over pots and plants to form plant-holding units. The tops of polystyrene containers (bottoms removed) with ventilated snap lids were inserted into the tops of the acetate cylinders to close the units.

For each parasitoid species, 10 plant-holding units were infested with 10 to 25 PTW first instars daily for 8 days. Larvae were randomly dropped into the units so that they initiated mines in all possible locations and tissues on the plants. On the eighth day 1- to 2-day-old mated female parasitoids were individually placed in the units. After 24 hours at standard rearing conditions, the females were removed and the units were disassembled. All plant material in a unit was placed in a paper bag and stored at 10°C for 1 to 5 days before being examined. The PTW larvae were individually removed from the foliage and their instar and mine locations were recorded. Larvae then were placed in cups with sand and pieces of tubers to complete development under standard rearing conditions. The species and sex of emerging adults were recorded with the previously obtained information for each larva.

The searching and oviposition behaviors of *A. scutellaris*, *A. gibbosa*, and *O. jennieae* were compared with host mine characteristics in the different plant locations with second PTW instars. Several plant-holding units were infested with first instars, as in the previous study. After 2 days, larvae and plant tissues associated with mines in

buds, stems, petioles, and leaflets were removed from the plants. Several 2-day-old females of each parasitoid species were individually placed in 50-mm Petri dishes. The females had previously been held in plant-holding units with males and PTW larvae to mate and initiate oviposition. Individual PTW larvae in mines from one of the plant locations then were individually exposed to each female. All behaviors of each female leading to, during, and following oviposition were recorded relative to mine characteristics and host responses. When a female oviposited in a larva, the larva and its mine were replaced with a new larva in a mine from another plant location. Each female was observed until she no longer responded to new hosts (1 to 3 hours). At least 15 females of each parasitoid species were observed.

To determine the ability of females of each parasitoid species to discriminate among PTW larvae that were nonparasitized, parasitized by their own species, and parasitized by other species, potato foliage in several plant units were infested with PTW first instars and held until the larvae developed to the second instar. One day before the discrimination abilities of a parsitoid species were studied, 200 PTW larvae mining in leaflets were removed from the infested plants and isolated in 30-ml plastic cups. One hundred and fifty of these larvae then were individually exposed in Petri dishes to females of each parasitoid species, including the species whose discrimination abilities were to be determined (50 larvae per species). Parasitism of each larva was confirmed by observing individual ovipositions. The parasitized and remaining nonparasitized larvae in their mines then were held in plastic cups for 24 hours under standardized rearing conditions. In addition, several newly emerged females and males of the parasitoid species to be studied were placed in a plant-holding unit infested with PTW larvae 1 day before a study began. This conditioning period allowed test females to mate and oviposit in nonparasitized hosts before the studies, since these experiences may affect subsequent discrimination behaviors (Van Lenteren 1976; Van Lenteren and Bakker 1975).

On the day of a study, 10 randomly selected females of the parasitoid species to be tested were placed in individual plastic Petri dishes (50 mm). The lids of the dishes had two vents (20 mm in diameter) covered with cotton organdy. A small amount of honey was supplied in each dish. Each female was first exposed to three nonparasitized PTW larvae and then alternately to parasitized and nonparasitized larvae. All larvae were still within their original mines in potato leaflets. A maximum of four larvae parasitized by each of the three parasitoid species and 14 nonparasitized larvae were exposed to each of the 10 test females of each species. Observations on a female were considered complete if she responded to at least the first eight nonparasitized larvae exposed to her. If a female stopped responding (no examination of mine or host within 1 hour) before the eighth nonparasitized larva, she was discarded and a new replication initiated. Searching and oviposition behaviors of each female were constantly observed and recorded relative to the parasitism history of each exposed larva. Results of previous observations were used to separate behaviors into four categories: examination of mine or PTW frass with antennae; probing of mine or PTW frass with ovipositor; insertion of ovipositor into larva; and deposition of egg into larva. Observations were conducted at 25°C and under cool, white fluorescent lights. After exposure, the PTW larvae were placed in individual plastic cups with paper lids. After 2 to 3 days of incubation under standard rearing conditions, each larva was dissected to confirm primary parasitism, superparasitism, or multiple parasitism. Immature parasitoid species were

distinguished by their previously described morphologies (Cardona and Oatman 1975; Flanders and Oatman 1982; Odebiyi and Oatman 1972).

When results from the discrimination studies indicated that females of one parasitoid species could not detect PTW larvae parasitized by another species, studies were conducted to determine the intrinsic competitive abilities of their immature stages in multiply parasitized hosts. Potato foliage in several plant units was infested with PTW first instars and held until larvae developed to the second instar, as in the previous study. For each combination of parasitoid species, 30 PTW larvae mining in leaflets were first parasitized by individual females of the parasitoid species that was not discriminated against. Fifteen of these larvae were then immediately exposed to individual females of the nondiscriminating species for multiple parasitism. The remaining 15 PTW larvae were exposed 24 hours later. In addition 15 PTW larvae were exposed to individual females of each parasitoid species for primary parasitization only to verify the accuracy of observations on oviposition behaviors. All parasitized larvae were removed from their mines in leaflets and placed in individual plastic cups with cubes of 'Norgold' potato tuber and sterilized white sand. Larvae then were incubated under standard rearing conditions until adult parasitoids emerged. The parasitoid species that emerged was recorded according to the parasitism history of each PTW Larva.

Data were analyzed by procedures in the Statistical Package for the Social Sciences (Nie et al. 1975). Logarithmic or arc-sine transformations were used when required prior to analyzing data by analysis of variance procedures (Sokal and Rohlf 1969). Frequency data in contingency tables were analyzed by the log likelihood ratio test (G test) (Sokal and Rohlf 1969).

RESULTS AND DISCUSSION

Potato Plant Growth

During fall, sampling began about 4 weeks after the field was planted and the plants were nearly mature on the first sample date. Consequently, the lengths of stems were not significantly different among sample dates ($P > 0.05$; ANOVA) and averaged 24.8 cm (n = 89). The number of nodes per stem also was not significantly different among sample dates and averaged 14.3 (n = 89).

During spring, sampling began 1 week after the field was planted. Consequently, the length of 'White Rose' stems significantly increased ($P < 0.05$; ANOVA) from a mean of 4.8 cm (n = 10) on the first sample date to 74.4 cm (n = 12) on the last sample date. The number of nodes per main stem also significantly increased from 5.6 (n = 10) to 26.3 (n = 12). The lengths of stems and numbers of nodes per stem on 'Norgold' plants significantly increased from a mean of 4.7 cm and 5.2 (n = 10), respectively, on the first sample date, to 49.3 cm and 19.4 (n = 12) on the last sample date. Stems of 'White Rose' plants were significantly longer and possessed significantly more nodes than those of 'Norgold' plants on the last five sample dates ($P < 0.05$; t-tests). In general, 'Norgold' plants were upright and compact; 'White Rose' plants were vinelike and spreading.

Comparing mature 'Norgold' plants between seasons, plants during spring had significantly longer stems and more nodes per stem than during fall ($P < 0.05$; t-tests). This probably was due to the higher temperatures during spring.

PTW Larval Densities

During fall, PTW densities gradually increased from 9.3 to 23.4 larvae per plant (table 2). Only the density on the last sample date was significantly higher than were those on the first two sample dates (P<0.05; ANOVA, Duncan's New Multiple Range Test [DNMRT]). Although PTW populations have multiple overlapping generations in southern California (Graf 1917), sequential changes in percentages of each instar and in density among sample dates resembled those that would be expected during a generation of larvae (table 2). Relatively high proportions of first instars from November 1 to 15 suggested the beginning of a new generation of larvae.

During spring, densities of PTW larvae between cultivars were not significantly different on any sample date (P>0.05; ANOVA). Since 'White Rose' plants had more foliage than 'Norgold' plants during the last half of the season, the nonsignificant density differences suggested that 'Norgold' plants were under more intense feeding pressure by PTW larvae.

Grouped data from both cultivars during spring indicated that PTW densities gradually increased from 0.2 larvae per sample on May 15 to 8.0 on July 10 (table 2). Densities from May 15 to June 12 were not significantly different (P>0.05; ANOVA, DNMRT), but the density on May 15 was significantly lower than on June 19 (P<0.05). Densities from June 19 to July 10 were not significantly different, but densities following June 19 were significantly higher than before June 19. The relatively high percentages of first instars on May 15 and 22, and from June 12 to 16 suggested that two larval generations occurred during sampling, the second initiating during the June 19 transition from lower-to-higher densities.

TABLE 2.   LARVAL DENSITIES AND INSTAR PERCENTAGES OF PTW POPULATIONS INFESTING POTATO FOLIAGE AND STEMS DURING 1977 ('NORGOLD' POTATOES) AND 1978 ('NORGOLD' AND 'WHITE ROSE' POTATOES) AT MORENO, CALIFORNIA

Year	Sample date	Number of samples	Larvae per sample ($\bar{x}$ ± se)		Percent of larvae on sample date			
					First instars	Second instars	Third instars	Fourth instars
1977	Oct 24	14	9.3	7.9	7.7	33.8	36.2	22.3
	Nov 1	15	12.3	7.5	21.7	29.4	31.0	17.9
	Nov 8	15	17.0	12.0	23.5	26.7	39.2	14.5
	Nov 15	15	17.9	7.6	22.0	34.7	24.6	18.7
	Nov 22	15	18.3	11.0	13.1	35.4	33.2	18.2
	Nov 29	15	23.4	12.6	16.6	28.4	33.2	21.8
1978	May 15	24	0.2	0.6	66.7	33.3	0.0	0.0
	May 22	24	1.4	2.3	45.5	36.4	9.1	9.1
	May 29	24	1.7	3.1	2.5	20.0	40.0	37.5
	Jun 5	24	1.2	2.3	3.4	17.2	41.4	37.9
	Jun 12	24	0.9	1.2	18.2	31.8	31.8	13.6
	Jun 19	24	4.0	8.0	15.8	22.1	38.9	23.2
	Jun 26	24	6.4	6.2	13.1	33.3	30.7	22.9
	Jul 3	24	7.7	6.0	9.2	23.9	32.1	34.8
	Jul 10	24	8.0	4.6	12.0	17.8	29.3	40.8

The PTW larval densities were three times higher during fall than during spring just before harvest. Since 'Norgold' plants were smaller and PTW densities were higher during fall, the potential of the PTW population to affect potato yield adversely appeared higher during fall.

Seasonal Parasitism Rates

During fall, parasitism of PTW larvae was not significantly different among sample dates ($P > 0.05$; ANOVA) and over all dates was 52.6 percent, not including larvae that died during rearing (table 3). *Agathis gibbosa* was the most common parasitoid, emerging from 21.9 percent of all hosts. *Chelonus phthorimaeae* was the next most common parasitoid, followed by *A. scutellaris*, *Bracon gelechiae* Ashmead, and *Sympiesis stigmatipennis* Girault. *Apanteles dignus* Muesebeck, reared from a single PTW larva, more commonly parasitizes the tomato pinworm, *Keiferia lycopersicella* (Walsingham) (Lepidoptera: Gelechiidae), in southern California (Oatman 1970).

During spring, parasitism of PTW larvae was significantly higher on 'Norgold' than on 'White Rose' plants on all sample dates but the first ($P < 0.05$; ANOVA). Over all dates, only 22.6 percent of the larvae were parasitized on 'White Rose' plants, compared with 44.4 percent on 'Norgold' (table 3), despite nonsignificant PTW density differences between cultivars. Differences in parasitism rates between cultivars possibly were due to the larger size of 'White Rose' plants and the consequent larger surface areas required to be traversed by adult parasitoids on these plants to locate as many hosts as on smaller 'Norgold' plants. However, no significant dependencies among parasitoid species occurred between cultivars on any or over all sample dates ($P > 0.05$; G tests). This suggests that the cultivars did not differentially affect the searching behavior of any parasitoid species.

Grouped data from both cultivars during spring indicated that parasitism of PTW larvae significantly differed among sample dates ($P < 0.05$; ANOVA). Generally, PTW parasitism rates followed trends similar to those of density with a transition from

TABLE 3. PARASITIZATION OF PTW LARVAE IN POTATO FOLIAGE AND STEMS OVER ALL SAMPLE DATES DURING FALL 1977 AND SPRING 1978 AT MORENO, CALIFORNIA

Year	Potato cultivar	Total PTW larvae*	Percent of larvae not para- sitized	Percent of larvae parasitized by			
				Apanteles scutellaris	*Agathis gibbosa*	*Chelonus phthorimaeae*	Other species†
1977	'Norgold'	1168 (304)	47.4	12.7	21.9	17.2	0.8
1978	'Norgold'	312 (108)	55.8	22.1	7.7	10.9	3.5
	'White Rose'	257 (75)	77.4	14.4	1.6	4.7	2.0
	Both	752 (183)	65.6	18.6	4.9	8.1	2.8

*Numbers of larvae that died while being held in the laboratory are indicated in parentheses. Only larvae from which adult parasitoids or PTW emerged were used to calculate percentages.

†The other species that emerged were *Apanteles dignus*, *Bracon gelechiae*, *Euderus* sp., *Orgilus jennieae*, *Sympiesis stigmatipennis*, and *Temelucha* sp.

lower to higher rates occurring June 19. Parasitism rates among dates before June 19 were not significantly different (14.0 percent overall), but were significantly lower (except for May 29, 29.4 percent) than those following June 19 (35.2 percent overall) (P<0.05; ANOVA, DNMRT). The highest parasitism rate occurred on June 19 (45.7 percent).

Unlike during fall, the most common parasitoid emerging from PTW larvae during spring was *A. scutellaris* followed by *C. phthorimaeae* and *A. gibbosa* (table 3). *Bracon gelechiae* did emerge from spring samples, but *S. stigmatipennis* and *A. dignus* were not detected. In addition, *Temelucha* sp. (Hymenoptera: Ichneumonidae) and *Euderus* sp. (Hymenoptera: Eulophidae) emerged from samples during spring. Emergence of *Euderus* sp. apparently was the first recorded instance of it parasitizing PTW larvae in southern California. Although *O. jennieae* was released into the field during spring, it only emerged from 1 percent of the sampled PTW larvae.

Comparing PTW larval densities and parasitization rates between seasons, parasitization by *A. scutellaris* did not appreciably change even though PTW larval densities were significantly higher during fall. However, parasitization by *A. gibbosa* was lower in spring when PTW densities were low and was higher in fall when densities were high. Similar seasonal changes in parasitization by these species were reported by Oatman and Platner (1974). These results suggest that *A. scutellaris* may possess a higher searching capacity (ability to find hosts at low host densities) than does *A. gibbosa*. However, differences in parasitization by *A. gibbosa* between seasons may have been partially due to its longer generation time and lower net reproductive rate compared with those of *A. scutellaris* (Cardona and Oatman 1975; Odebiyi and Oatman 1977). If relatively few *A. gibbosa* survive the adversities of winter to initiate spring populations, then their low searching capacity and intrinsic rate of increase only allow their densities to gradually increase with PTW densities during the ensuing warmer months and to reach maximum densities and parasitism rates during fall. Conversely, the higher searching capacity and intrinsic rate of increase of *A. scutellaris* may allow it to keep pace with but not suppress PTW density increases so that it exhibits relatively constant parasitism rates between seasons.

Parasitism of PTW Instars

During fall, frequencies of *A. scutellaris, A. gibbosa,* and *C. phthorimaeae* that emerged from PTW larvae significantly depended on the PTW instar (P<0.05; G test) and no significant interaction occurred with the sample date (fig. 1). Higher-than-expected frequencies of *A. scutellaris* emerged from second and third instars and a lower-than-expected frequency from first instars relative to frequencies of all PTW instars sampled during the season. *Agathis gibbosa* emerged from higher-than-expected frequencies of third and fourth instars, and a lower-than-expected frequency of first instars. *Chelonus phthorimaeae* emerged from higher-than-expected frequencies of second and third PTW instars, but from lower-than-expected frequencies of first and fourth instars.

During spring, only the emergence of *A. scutellaris* significantly depended on the PTW instar (P<0.05; G test) and no significant interactions occurred with sample date or cultivar. Over all sample dates and cultivars, the frequency of *A. scutellaris*
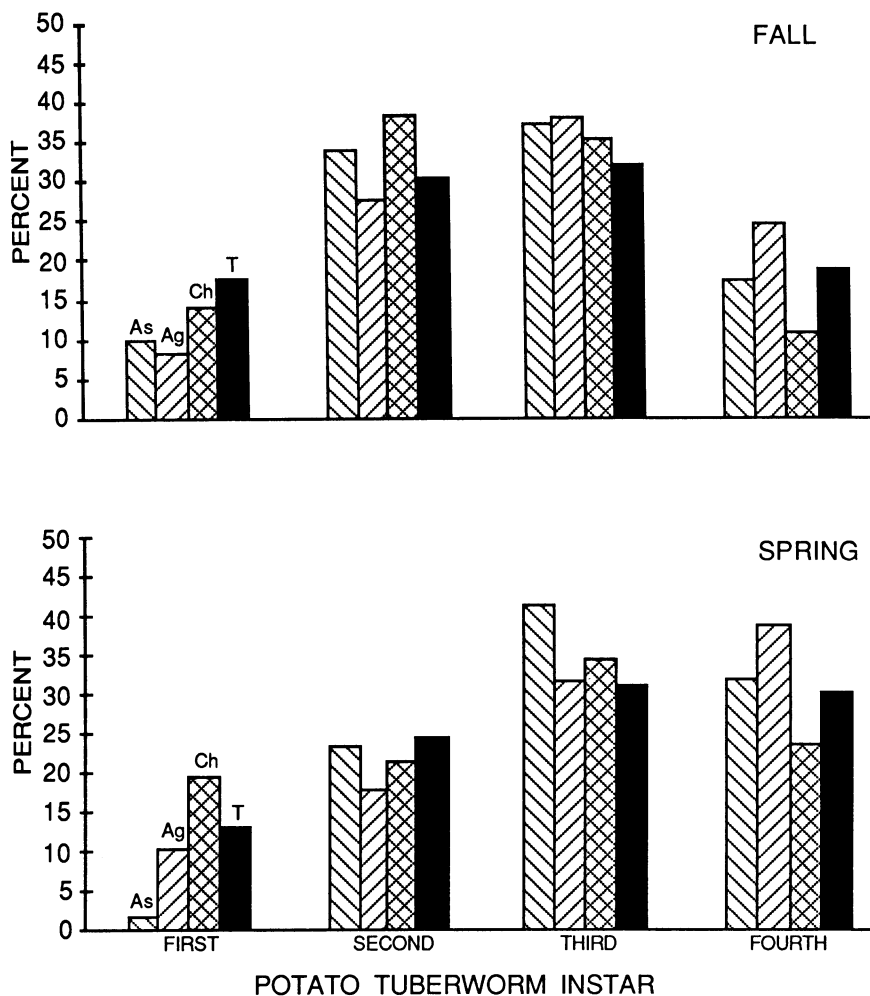
Fig. 1. Emergences of *A. scutellaris* (As), *A. gibbosa* (Ag), and *C. phthorimaeae* (Ch) from each PTW instar as percentages of the total emergence of each species, compared with percentages of each PTW instar (T) sampled during fall 1977 on 'Norgold' potatoes and spring 1978 on 'Norgold' and 'White Rose' potatoes at Moreno, California. Percentages are based on 1,158 host larvae of which 148, 256, and 201 were parasitized by As, Ag, and Ch, respectively, during fall, and on 752 host larvae of which 105, 28, and 46 were parasitized by As, Ag, and Ch, respectively, during spring.

emerging from third instars was higher than expected while emergence from first instars was lower than expected (fig. 1).

Associations among frequencies of PTW instars sampled and of species that subsequently emerged during both seasons suggest that females of *A. scutellaris* and *A. gibbosa* primarily oviposited in second to fourth instars. However, it was difficult to interpret actual parasitoid oviposition preferences because of the possibilities of parasitized PTW larvae accumulating in older instars and of differential survival rates among instars or between parasitized and nonparasitized larvae. For example, the association between frequencies of *C. phthorimaeae* emerging and PTW instars during fall was unexpected, since this species only oviposits in PTW eggs. Consequently, laboratory studies were required to determine actual oviposition preferences and to compare *O. jennieae* with *A. scutellaris* and *A. gibbosa*.

In the laboratory, frequencies of *A. scutellaris, A. gibbosa,* and *O. jennieae* emerging from PTW larvae significantly depended on instar at the time of oviposition (P<0.05; G tests) (fig. 2). *Apanteles scutellaris* females oviposited in higher-than-expected frequencies of second and third instars and in a lower-than-expected frequency of fourth instars, indicating a preference for second and third instars. This result differed from that of Cardona and Oatman (1975) who reported that *A. scutellaris* preferred to oviposit in first instars mining in potato tubers. *Agathis gibbosa* oviposited in higher-than-expected frequencies of first to third PTW instars and lower-than-expected frequencies of fourth instars. Odebiyi and Oatman (1972, 1977) similarly reported that *A. gibbosa* preferred to oviposit in second PTW instars in potato tubers. *Orgilus jennieae* oviposited in higher-than-expected frequencies of first and second instars and in lower-than-expected frequencies of older instars; this was similar to the preferences reported by Flanders and Oatman (1982) for hosts mining in potato tubers. Overall, laboratory results indicate that the three parasitoid species broadly overlap each other in PTW instar preferences for oviposition, but that *O. jennieae* more narrowly prefers younger instars than do the two native species.

PTW Larval Distribution and Parasitism Relative to Leaf Nodes

During fall, a significant association existed between frequencies of PTW larvae and leaf node number (P<0.05; G test), independent of instar and sample date (fig. 3). The distribution of larvae by leaf node number over all dates and instars was bell shaped and skewed to the base of the plant with higher-than-expected frequencies between the fourth and seventh nodes.

During spring, a significant association also occurred between PTW larval frequencies and leaf node numbers (P<0.05; G test), independent of instar. Higher-than-expected frequencies of larvae occurred between the sixth and ninth leaf nodes on both cultivars over all sample dates (fig. 3). However, a significant interaction occurred among larval frequencies, leaf node numbers, and cultivar (P<0.05; G test). Frequencies of larvae at the upper leaf nodes were higher on 'White Rose' than on 'Norgold' plants, apparently due to the presence of more nodes on the larger 'White Rose' plants. Distributions on both cultivars also significantly interacted with sample date,
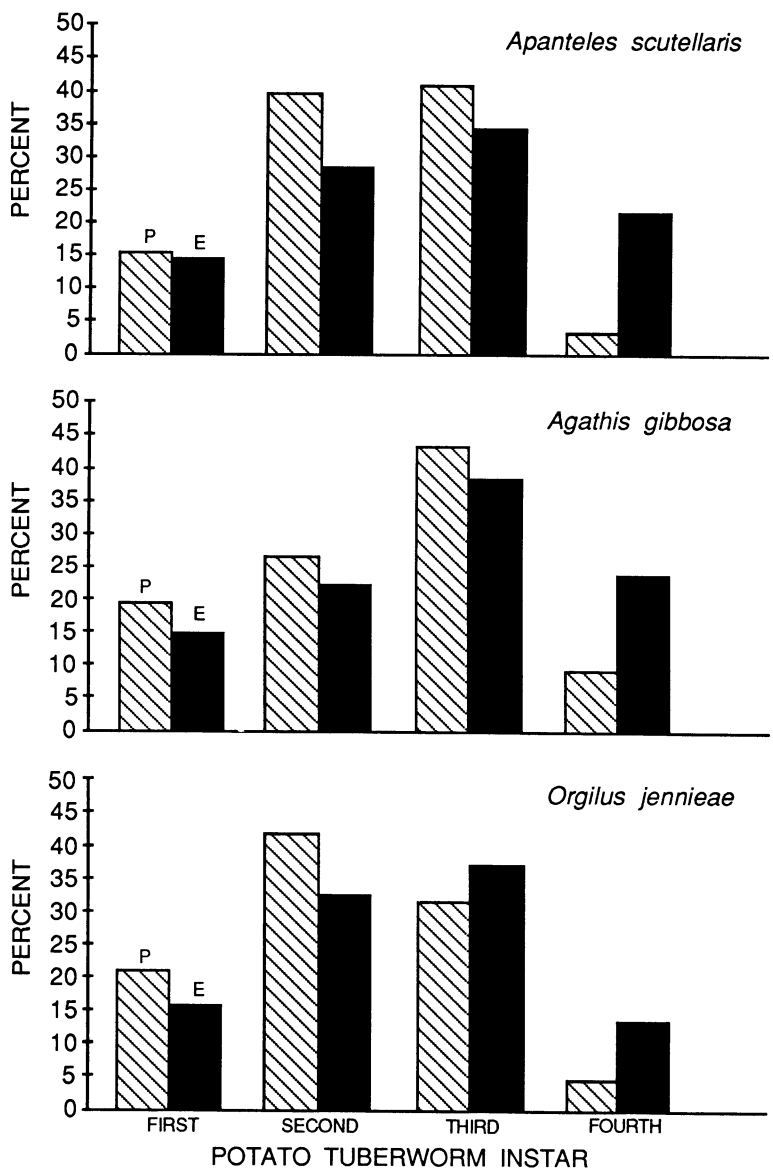
Fig. 2. Emergences of *A. scutellaris, A. gibbosa,* and *O. jennieae* from each PTW instar as percentages of the total emergence of each species (= P), compared with percentages of each PTW instar that were exposed to ovipositing females of the parasitoid species (= E). Results were from 10 isolated females of each parasitoid species individually exposed to 50 to 100 hosts of all instars for 24 hours on 'Norgold' potato foliage at 25°C and with a 12:12 (L:D) photocycle. Percentages are based on 959 exposed and 249 parasitized hosts for *A. scutellaris;* 897 exposed and 126 parasitized for *A. gibbosa;* and 518 exposed and 257 parasitized for *O. jennieae.*
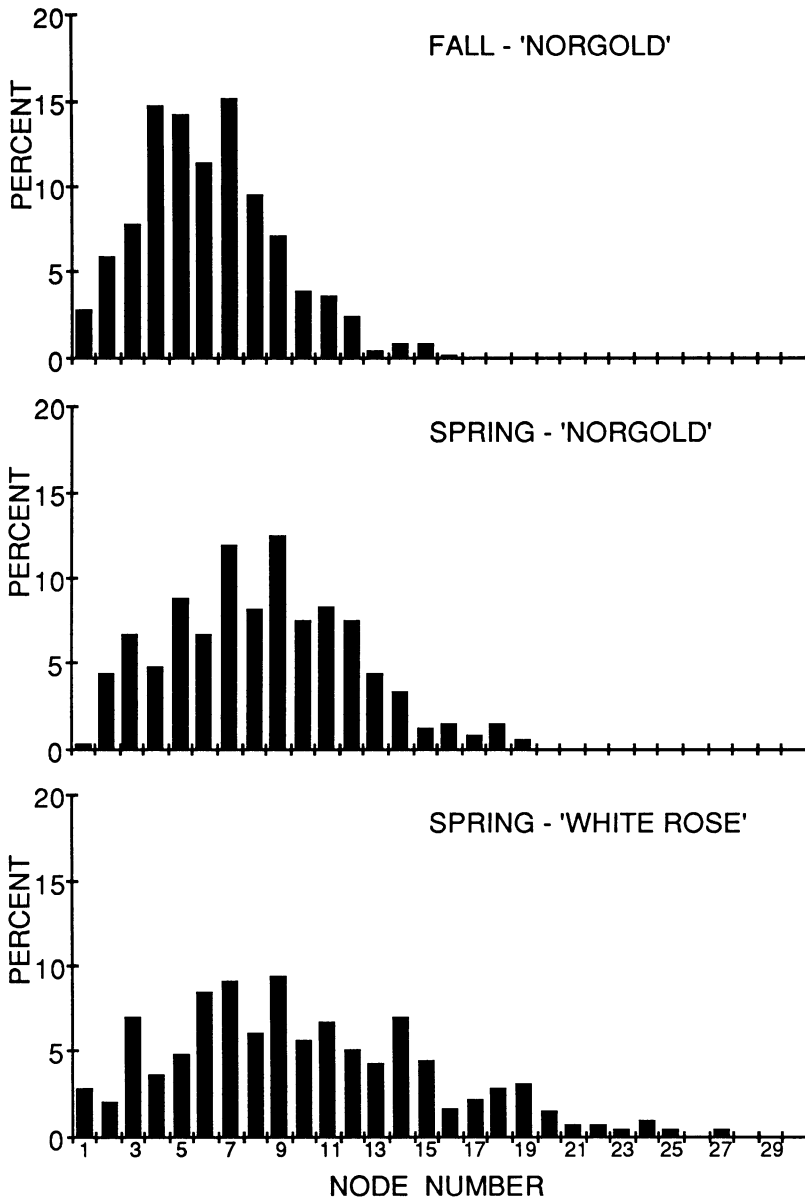
Fig. 3. PTW larvae at each node of potato stems as percentages of all larvae sampled during fall 1977 on 'Norgold' potatoes and during spring 1978 on 'Norgold' and 'White Rose' potatoes at Moreno, California. Node numbers ascend from the soil surface to the terminal bud. Percentages are based on 1,145, 420, and 332 larvae on 'Norgold' plants during fall, on 'Norgold' plants during spring, and on 'White Rose' plants during spring, respectively.

apparently because larvae initiated mines further up stems as the plants grew; this was most significant between larval generations.

Although Graf (1917) reported that PTW females oviposit on all exposed surfaces of potato plants, no eggs were found on stems or leaves in our study. Bacon (1960) and Traynier (1975) reported that PTW females actually oviposit on soil surfaces or debris near bases of potato plants. Distributions of PTW larvae along stems found in our study appear to support these authors' conclusions. The PTW larvae hatching from eggs at the soil surface apparently move relatively short distances up stems to initiate mines. Nonsignificant associations between leaf nodes and instars suggest that once larvae initiate mines, they remain near those leaf nodes during subsequent development. Consequently, PTW larval populations on aerial parts of potato plants are concentrated near the bases of plants, but distributions among cultivars may vary due to differences in plant growth.

Frequencies of parasitoids emerging from PTW larvae were independent of leaf node number during both sampling seasons and no significant interactions occurred with cultivar, sample date, or instar (P>0.05; G tests). These results indicate that ovipositing females of *A. scutellaris* and *A. gibbosa* respond only to overall distributions of PTW larvae along plant stems and do not partition the host population by searching different vertical strata on plants.

PTW Larval Distribution and Parasitism Relative to Plant Tissues

During fall, 75.6 percent of the PTW larvae were extracted from mines in leaflets, 14.0 percent were in leaf petioles, 6.0 percent were in stems, and 4.4 percent were in buds (fig. 4). During spring, 41.2 percent of the larvae were from mines in leaflets, 34.0 percent were in buds, 16.9 percent were in stems, and 7.9 percent were in petioles (fig. 4). Frequencies of PTW larvae by plant locations were independent of sample date during fall and spring and were independent of cultivar during spring (P>0.05; G test). However, analyses of larval frequencies by plant location between seasons indicated that higher-than-expected frequencies occurred in main stems and axillary buds during spring, and frequencies in leaflets were higher than expected during fall (P<0.05; G test). These results may have been due to the hotter, drier conditions during spring that caused larvae to orient to or remain in the more protected central areas of plants (stems and buds) than during fall.

During fall and spring, frequencies of PTW instars depended on plant location (P<0.05; G tests), and sample date and cultivar did not significantly interact with these dependencies. Frequencies of first instars during fall were higher than expected in buds and lower than expected in stems and petioles; third instars were higher in petioles and lower in buds; and fourth instars were higher in stems and lower in buds (fig. 4). During spring, frequencies of first and second instars were higher than expected in buds and lower than expected in stems and petioles; third and fourth instars were lower in buds; third instars were higher in petioles; and fourth instars were higher in stems and leaflets (fig. 4). Results from both seasons suggest that first instars tend to initiate mines in buds more frequently than in other plant tissues, and that older instars extend these mines into petioles and stems. Larvae mining petioles
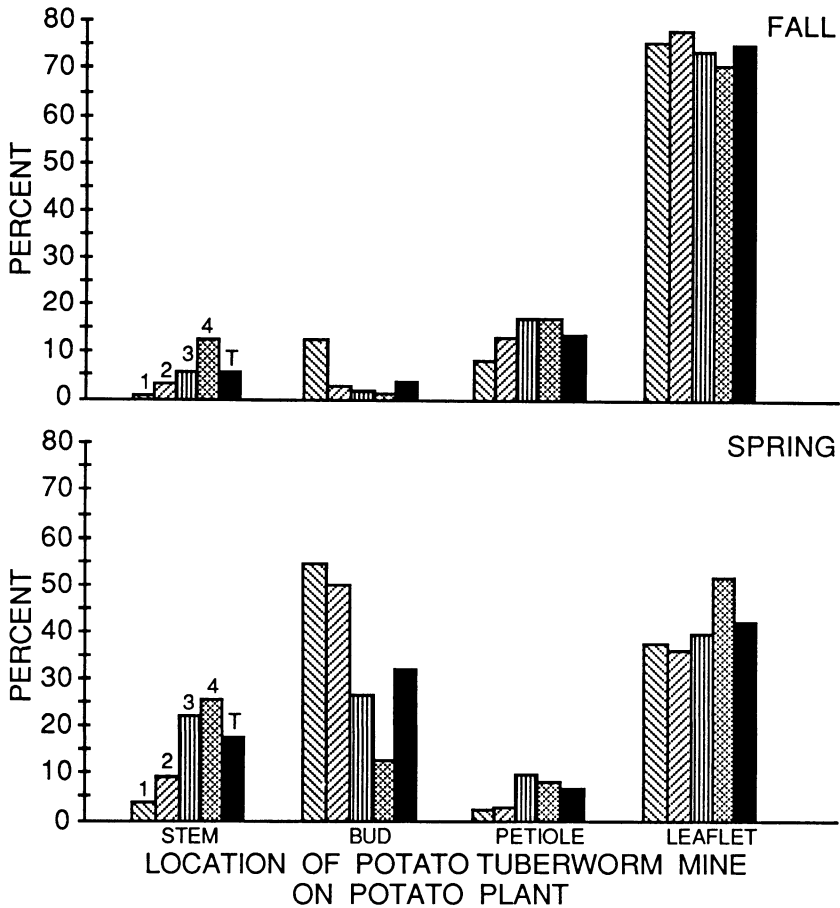
Fig. 4. First (1), second (2), third (3), and fourth (4) PTW instars mining stems, buds, petioles, and leaflets as percentages of all larvae sampled (T) during fall 1977 on 'Norgold' potatoes and during spring 1978 on 'Norgold' and 'White Rose' potatoes at Moreno, California. Percentages are based on 263 first, 456 second, 477 third, and 256 fourth instars during fall, and on 100 first, 184 second, 237 third, and 231 fourth instars during spring.

tend to extend their mines toward stems, resulting in relatively high frequencies of older instars in stems and basal leaf petioles. However, there was a significant interaction between seasons which was due to higher-than-expected frequencies of first and second instars in buds and lower-than-expected frequencies of first through third instars in leaflets during spring as compared with fall (P<0.05; G test). This interaction between seasons suggests that younger larvae tended more than older larvae to orient to or remain in the more central parts of plants during the hotter, drier spring.

During fall, *A. scutellaris* emerged from higher-than-expected frequencies of larvae mining leaflets and lower-than-expected frequencies mining stems, buds, and petioles compared with frequencies of PTW larvae not parasitized by this species ($P<0.05$; G test) (fig. 5). This association was independent of PTW instar, leaf node, and sample date ($P>0.05$). However, frequencies of *A. gibbosa* and *C. phthorimaeae* emerging from PTW larvae were independent of the location of PTW mines at sampling during fall ($P>0.05$).
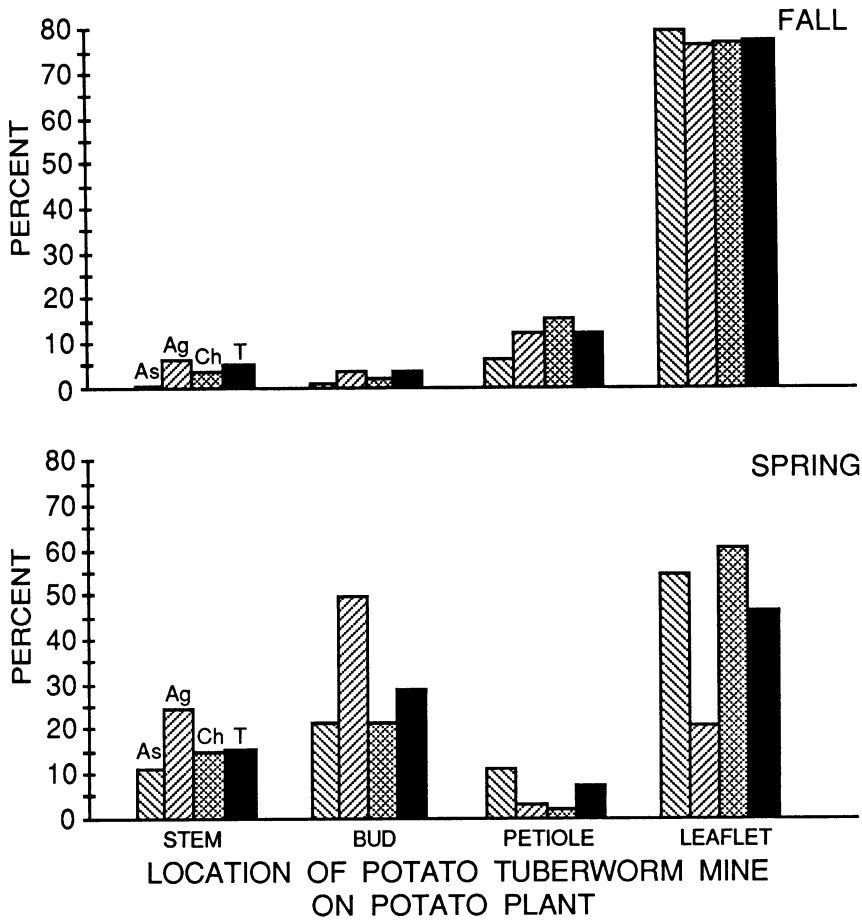
Fig. 5.   Emergences of *A. scutellaris* (As), *A. gibbosa* (Ag), and *C. phthorimaeae* (Ch) from PTW larvae mining potato stems, buds, petioles, and leaflets as percentages of the total emergence of each species, and compared with percentages of all PTW larvae mining in each location (T) during fall 1977 on 'Norgold' potatoes and during spring 1978 on 'Norgold' and 'White Rose' potatoes at Moreno, California. Percentages are based on 1,168 hosts of which 148, 241, and 201 were parasitized by As, Ag, and Ch, respectively, during fall; and on 559 hosts of which 105, 28, and 46 were parasitized by As, Ag, and Ch, respectively, during spring.

During spring, *A. scutellaris* emerged from higher-than-expected frequencies of larvae mining in leaflets and petioles, and lower-than-expected frequencies in stems and buds (P<0.05; G test) (fig. 5). *Agathis gibbosa* emerged from significantly higher frequencies of larvae in stems and buds and from lower frequencies in leaflets and petioles. *Chelonus phthorimaeae* emerged from significantly higher frequencies of larvae in leaflets, and from lower frequencies in stems, buds, and petioles.

Results from both seasons suggest that *A. scutellaris* was more effective or preferred parasitizing larvae mining in leaflets or petioles, whereas *A. gibbosa* was more effective or preferred parasitizing larvae in stems or buds. Significant associations between larvae parasitized by *C. phthorimaeae* and PTW larval mine locations during spring may have been due to differences in behaviors between parasitized and nonparasitized hosts. However, PTW larval movement or expansion of mines from one location to another between parasitoid oviposition and field sampling made interpretation of these results difficult. To overcome this difficulty and to compare *O. jennieae* with *A. scutellaris* and *A. gibbosa*, laboratory studies were conducted.

In the laboratory, parasitism by *A. scutellaris* was independent of the location of PTW mines (P>0.05; G test) and there was no significant interaction with PTW instars (fig. 6). However, emergence of male and female *A. scutellaris* depended on mine location (P<0.05; G test). Higher-than-expected frequencies of females emerged from larvae mining petioles (54 percent female); lower-than-expected frequencies emerged from larvae in stems (20 percent female) compared with emergence from all locations (39 percent female). If females deposit fertilized eggs in hosts in preferred locations, then higher frequencies of females emerging from hosts mining in petioles in the laboratory may indicate preferences similar to those observed in the field. However, sexes of *A. scutellaris* emerging from PTW larvae in the field were independent of PTW locations (P>0.05; G tests). During fall 59.5 percent of the *A. scutellaris* emerging were female; during spring 52.7 percent were female.

Frequencies of PTW larvae parasitized by *A. gibbosa* were significantly associated with mine locations in the laboratory (P<0.05; G test) and this association was independent of instar. Higher-than-expected frequencies of PTW larvae were parasitized by *A. gibbosa* in buds and petioles; lower-than-expected frequencies were parasitized in stems and leaflets (fig. 6). These results suggest that the relatively high frequencies of *A. gibbosa* emerging from PTW larvae in stems in the field may have been due to parasitized hosts moving or extending their mines from petioles and buds where they were initially parasitized into stems. Unlike *A. scutellaris*, emergence of male and female *A. gibbosa* was independent of host location in the laboratory and field (P>0.05; G tests). In the laboratory, 43.7 percent of the *A. gibbosa* emerging were female; in the field during fall and spring, respectively, 68.8 percent and 75.0 percent were female.

In the laboratory, *O. jennieae* parasitized higher-than-expected frequencies of PTW larvae mining in buds and lower-than-expected frequencies in petioles and leaflets (P<0.05; G test; fig. 6). Emergence of male and female *O. jennieae* was independent of PTW location; 41.7 percent were female.

Field and laboratory results suggest that *A. scutellaris* either more frequently oviposits in or produces more female progeny in PTW larvae mining in more exterior parts of potato plants where plant tissues are thinner. Conversely, *A. gibbosa* and
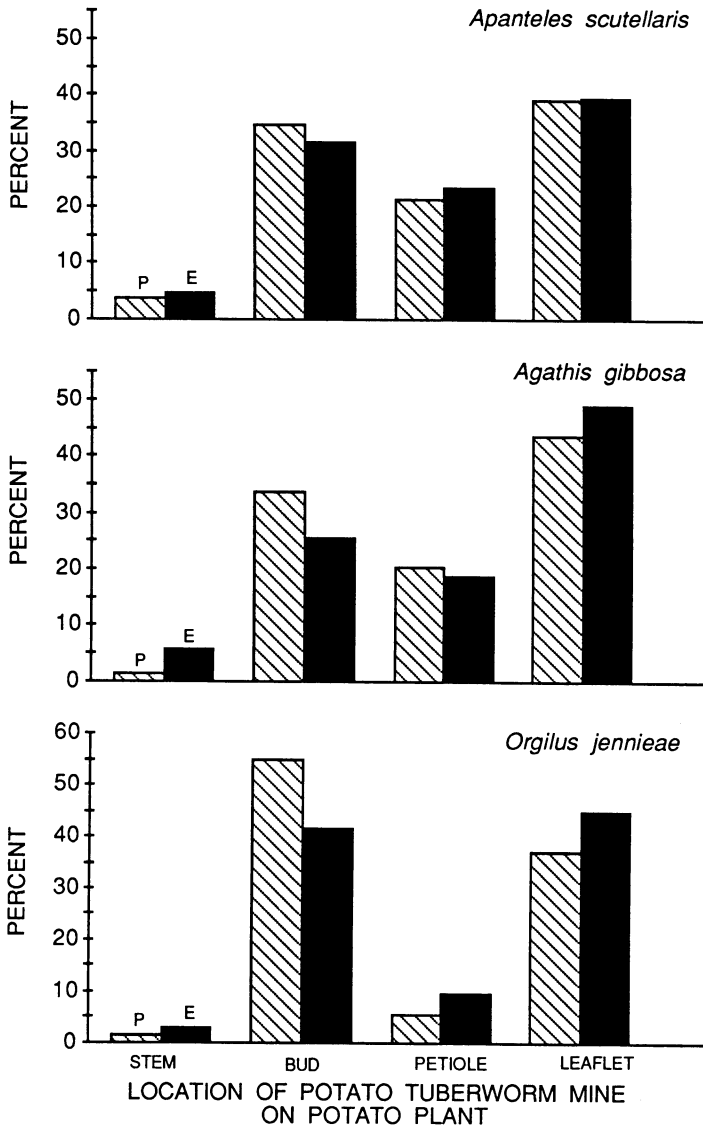
Fig. 6.   Emergences of *A. scutellaris, A. gibbosa,* and *O. jennieae* from PTW larvae mining in stems, buds, petioles, or leaflets of 'Norgold' potatoes in the laboratory as percentages of the total emergence of each species (= P), and compared with host larvae mining in each location as percentages of the total larvae exposed to ovipositing females of each species (= E). Results were from 10 females of each parasitoid species individually exposed to 50 to 100 hosts in all locations for 24 hours at 25°C with a 12:12 (L:D) photocycle. Percentages are based on 959 exposed and 249 parasitized hosts for *A. scutellaris;* 897 exposed and 126 parasitized for *A. gibbosa;* and 518 exposed and 257 parasitized for *O. jennieae.*

O. jennieae appeared to more frequently parasitize hosts in more interior locations where plant tissues are thicker. However, observations of searching and oviposition behaviors were required to confirm and explain these results.

Parasitoid Searching and Oviposition Behaviors

The recognition or finding of PTW mines by *A. scutellaris, A. gibbosa,* and *O. jennieae* females were similar. Females searched for PTW mines by palpating plant surfaces with their antennae while rapidly walking or running. When females contacted frass exuding from mines of PTW larvae, their previous expansive searching behaviors changed to intensive examination with their antennae of the frass piles and surrounding plant tissues. Similar changes in behavior upon contact with frass exuding from PTW mines in potato tubers were reported by Cardona and Oatman (1975) for *A. scutellaris,* by Flanders and Oatman (1982) for *O. jennieae,* by Oatman, Platner, and Greany (1969) for *O. lepidus,* and by Odebiyi and Oatman (1972) for *A. gibbosa.* Hendry, Greany, and Gill (1973) identified two kairomones in PTW frass that mediated host recognition by *O. lepidus,* and based on similar behaviors, these chemicals may be relied on by most parasitoids that oviposit in PTW larvae.

After *A. scutellaris* females located piles of frass, they began examining with their antennae surrounding plant surfaces, especially those surfaces that enclosed PTW mines. While females examined the surfaces of mines in leaflets, the PTW larvae rapidly moved about the interiors of their mines as if to avoid the females on the surface. Females intermittently stopped examining mine surfaces with their antennae and rapidly thrust their ovipositors through the leaflet tissues and into the mines. The movement of the enclosed PTW larvae appeared to stimulate females to thrust their ovipositors into mines. When a female eventually positioned herself over a PTW larva in a mine and her ovipositor contacted the larva during a thrust, the tip of the ovipositor was rapidly inserted into the larva. Oviposition then was completed in 1 to 2 seconds. During oviposition, females stood motionless with their wings characteristically extended slightly above their bodies and with their antennae extended directly forward.

When exposed to PTW larvae mining in petioles, buds, and stems, *A. scutellaris* females attempted to contact larvae more frequently by inserting their ovipositors into piles of frass to locate the mine entrances than by thrusting their ovipositors directly through plant tissues. In addition, as the depth of mines in petioles, buds, and stems successively increased, females less successfully located larvae with their ovipositors. Since *A. scutellaris* possesses a relatively short ovipositor ($\bar{x} = 0.76$ mm, n = 35), females had difficulty contacting larvae in mines deeper than this dimension. In addition, PTW mines in petioles, buds, and stems are linear; those in leaflets are blotchlike, and PTW larvae in linear mines responded to searching females by moving to the deepest areas of their mines. In distal portions of leaf petioles, tunnel-like mines were close enough to the surface and PTW larvae were so restricted in their movements that *A. scutellaris* females located and oviposited in them more rapidly than in leaflets. In addition, mines in distal portions of petioles often extended into leaflets and females rapidly relocated PTW larvae that moved between such areas. In general, *A. scutellaris* females could parasitize PTW larvae mining in all plant locations but spent longer

locating and less successfully oviposited in hosts mining in buds, stems, and basal portions of petioles, compared with those in leaflets and distal portions of petioles.

Agathis gibbosa and *O. jennieae* females exhibited similar behaviors when attempting to locate PTW larvae in their mines, regardless of location. When females located piles of frass exuding from mines in any plant tissue, they briefly examined the frass with their antennae and then attempted to insert their ovipositors into the mines. Ovipositors usually were inserted through mine entrances directly below or adjacent to frass piles, but occasionally were inserted through breaks or weak areas in plant tissues immediately surrounding frass piles. Unlike *A. scutellaris*, females of *A. gibbosa* and *O. jennieae* rarely examined plant surfaces at any great distance from frass piles and never thrust their ovipositors directly through intact plant tissues to gain entrance to mines. Since *A. gibbosa* and *O. jennieae* females possess relatively long ovipositors ($\bar{x}$ = 2.8 and 2.7 mm [n = 35], respectively), they had more difficulty contacting PTW larvae in blotch like mines in leaflets than did *A. scutellaris*. Females frequently spent up to 10 minutes with their ovipositors inserted into mines in leaflets attempting to physically contact evading PTW larvae; frequently they were unsuccessful. However, these species more successfully located and oviposited in PTW larvae mining in buds and stems than did *A. scutellaris*. Since PTW mines in these locations are more linear and tunnel-like, PTW larvae had more difficulty evading the long ovipositors of *A. gibbosa* and *O. jennieae*. In addition, insertion of long ovipositors through frass piles into entrances of mines in these locations directly led to contact with enclosed larvae.

Although mines in petioles also are tunnel-like, the abilities of *A. gibbosa* and *O. jennieae* to locate PTW larvae in such mines depended on whether the mines extended into leaflets. When mines in leaf petioles extended into leaflets, as frequently occurred in distal portions of the leaf, PTW larvae frequently evaded the long ovipositors of *A. gibbosa* and *O. jennieae* by retreating into leaflets. When PTW larvae could not retreat from petioles into leaflets, as often occurred in basal portions of leaves, females rapidly contacted host larvae in their more restrictive tunnel-like mines. Consequently, in contrast to *A. scutellaris*, *A. gibbosa* and *O. jennieae* more efficiently and successfully located PTW larvae mining in buds, stems, and basal portions of leaf petioles, but were less successful and efficient in leaflets and distal portions of leaf petioles.

When the ovipositor of an *O. jennieae* female contacted a PTW larva in its mine, the ovipositor tip was immediately inserted into the larva. Oviposition then required 1 to 3 seconds. Following oviposition, females exhibited characteristic ovipositor flexions, as described by Flanders and Oatman (1982).

When the ovipositor of an *A. gibbosa* female contacted a PTW larva, the ovipositor tip also was immediately inserted. However, females kept their ovipositors inserted for as long as 30 seconds. Impaled PTW larvae became less active during this time, as though they were being paralyzed by the *A. gibbosa* females. Quednau (1970) observed that *Agathis pumila* (Ratzeburg) similarly paralyzed larch casebearer larvae before oviposition. When PTW larvae were nearly immobile, *A. gibbosa* females began to deeply probe into them with their ovipositors. Since *A. gibbosa* deposits eggs in the ganglia of the ventral nerve cord of PTW larvae (Odebiyi and Oatman 1972), these deep probings apparently were to locate oviposition sites. Females frequently removed their ovipositors from paralyzed larvae, and occasionally from mines, and then rein-

serted them apparently to gain better access to ganglia. Eventually females ceased all movement while eggs apparently were being deposited. Although oviposition only required 5 to 10 seconds, the entire process from paralysis of larvae to egg deposition required from 30 seconds to 5 minutes. Parasitized PTW larvae regained normal mobility in 10 to 20 minutes.

Parasitoid Discrimination

Females of the three parasitoid species nearly always accepted nonparasitized PTW larvae for oviposition, but nearly always rejected hosts previously parasitized by their own species (fig. 7). Avoidance of superparasitism occurred at an early stage in the behavioral steps leading to oviposition, and usually occurred before insertion of the ovipositor into a mine or larva. The early rejection of hosts parasitized by conspecifics appeared to be due to the presence or absence of some factor in the frass of the host, especially for *A. scutellaris* and *O. jennieae.*

Females of *A. scutellaris* rejected PTW larvae parasitized by *A. gibbosa* as frequently as those parasitized by their own species (fig. 7). Most *A. scutellaris* females rapidly retreated from mines containing larvae parasitized by *A. gibbosa* as if they possessed some repellent property. However, *A. scutellaris* females did not exhibit this behavior when examining mines occupied by hosts parasitized by *O. jennieae* and oviposited in such hosts significantly more frequently than in hosts parasitized by conspecifics and by *A. gibbosa* ($P < 0.05$; G test). However, hosts parasitized by *O. jennieae* were oviposited in significantly less frequently by *A. scutellaris* females than were previously nonparasitized hosts.

Females of *A. gibbosa* oviposited in significantly more PTW larvae parasitized by *A. scutellaris* and *O. jennieae* than they did those parasitized by conspecifics ($P < 0.05$; G tests) (fig. 7). However, significantly fewer of these parasitized hosts were accepted for oviposition by *A. gibbosa* than were nonparasitized hosts, which was similar to how *A. scutellaris* responded to hosts parasitized by *O. jennieae.* In addition, *A. gibbosa* females were less efficient than *A. scutellaris* females in detecting and rejecting hosts previously parasitized by their own species. Females did not immediately leave mines of hosts parasitized by conspecifics and often spent considerable time examining such mines with their antennae and ovipositors before retreating from them.

Females of *O. jennieae* oviposited in significantly more hosts parasitized by *A. gibbosa* than they did those parasitized by conspecifics and *A. scutellaris,* but significantly fewer than nonparasitized hosts ($P < 0.05$; G tests) (fig. 7). Although females rejected hosts parasitized by *A. scutellaris* for oviposition as frequently as those parasitized by their own species, rejection occurred later in the sequence of behavioral steps leading to oviposition than occurred with hosts parasitized by conspecifics. PTW larvae parasitized by *A. scutellaris* frequently were probed by *O. jennieae* females with their ovipositors before being rejected for oviposition; hosts parasitized by conspecifics rarely were probed.

Results indicate that *A. scutellaris* possesses a highly developed ability to discriminate against hosts parasitized by conspecifics and *A. gibbosa,* but readily oviposits in hosts parasitized by the exotic *O. jennieae. Agathis gibbosa* females apparently do not interspecifically discriminate and readily oviposit in hosts parasitized by *A. scutellaris*
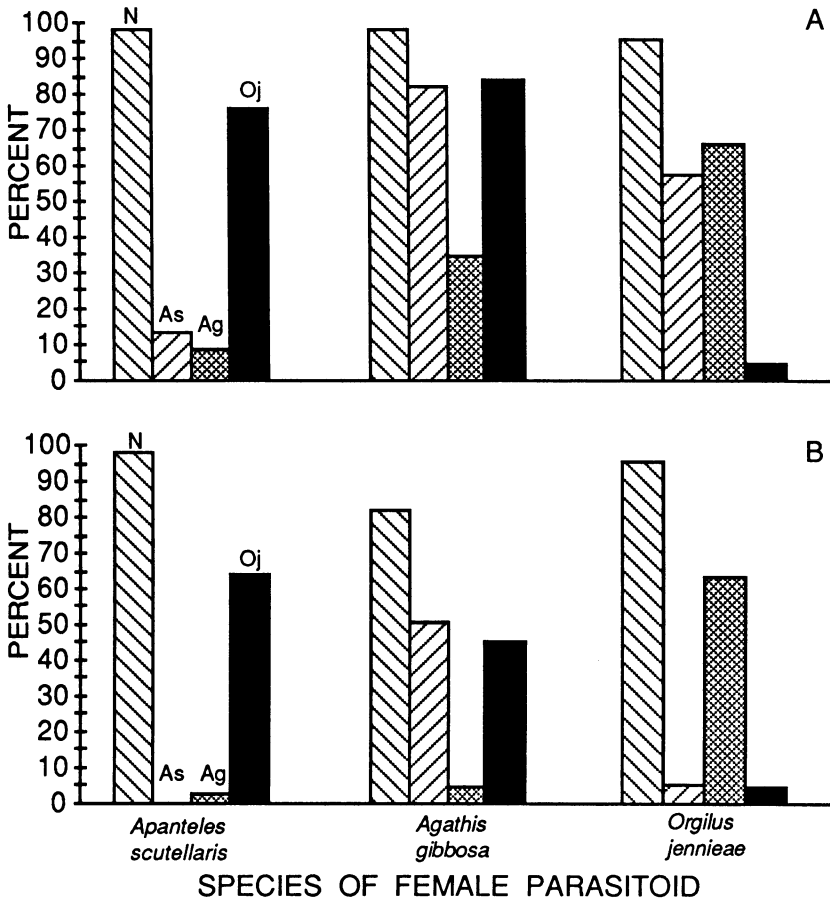
Fig. 7. Behavioral responses of adult females of *A. scutellaris* (Ag), *A. gibbosa* (Ag), and *O. jennieae* (Oj) individually exposed to parasitized and nonparasitized (N) PTW larvae mining 'Norgold' potato leaflets in the laboratory at 25°C. The top chart (*A*) shows percentages of hosts examined by female parasitoids into which the females subsequently inserted their ovipositors, and the bottom chart (*B*) shows percentages of hosts examined by females into which they subsequently oviposited following insertion of their ovipositors. Results are from 10 females of each parasitoid species sequentually exposed to one to four hosts parasitized by each parasitoid species and five to fourteen nonparasitized hosts. Percentages are based on 222 hosts examined by As, 244 by Ag, and 239 by Oj.

and *O. jennieae. Orgilus jennieae* females are capable of discriminating against hosts parasitized by *A. scutellaris,* but readily oviposit in hosts parasitized by *A. gibbosa.* When a species did not reject hosts parasitized by another species, however, acceptance was significantly less frequent than for nonparasitized hosts; this suggests that each species possesses at least a rudimentary ability to interspecifically discriminate.

Parasitoid Survival in Multiply Parasitized Hosts

When *A. scutellaris* females oviposited in hosts parasitized by *O. jennieae*, the species that subsequently emerged depended on the length of time between ovipositions (table 4). *Apanteles scutellaris* emerged from higher-than-expected frequencies of multiply parasitized hosts when females oviposited within 2 hours after *O. jennieae* ($P<0.05$; G test). However, when *A. scutellaris* females oviposited 24 hours after *O. jennieae*, *A. scutellaris* adults emerged from lower-than-expected frequencies of multiply parasitized hosts. Dissection of multiply parasitized hosts revealed that eggs of each parasitoid hatched, but that only one larva survived to the late first instar in each host. Remains of dead first instars frequently were observed floating in hemocoels of hosts with the surviving parasitoid larvae. Consequently, elimination of competitors appeared to occur during the early first instar. Since first instars of both species possess large sicklelike mandibles, elimination of competitors probably was by physical attack using these mandibles as has been described for other species (Bartlett and Ball 1964; Fisher 1961, 1962, 1971; Pemberton and Willard 1918; Salt 1960; Schroeder 1974). Apparently, the species whose egg hatched first had a competitive advantage over the species whose egg hatched later. Since eggs of *A. scutellaris* hatch 1 to 2 days sooner than do those of *O. jennieae*, at least at 25°C (Cardona and Oatman 1975; Flanders and Oatman 1982), *A. scutellaris* has an inherent competitive advantage over *O. jennieae*. This advantage disappears when a sufficient period of time intervenes between ovipositions to allow the eggs of *O. jennieae* to hatch before those of *A. scutellaris*.

When *A. gibbosa* oviposited in hosts parasitized by *A. scutellaris*, the species that subsequently emerged again depended on the time interval between ovipositions (table 4). Higher-than-expected frequencies of *A. gibbosa* emerged when females oviposited shortly after *A. scutellaris*, but higher-than-expected frequencies of *A. scutellaris* emerged when multiple parasitism was delayed by 24 hours. Observations during

TABLE 4. EMERGENCE OF PARASITOIDS FROM MULTIPLY PARASITIZED PTW LARVAE AS AFFECTED BY OVIPOSITION SEQUENCE AND TIME BETWEEN INITIAL AND MULTIPLE PARASITIZATIONS AT 25°C AND 12:12 (L:D) PHOTOCYCLE

Species initially ovipositing in host larvae	Species multiply parasitizing host larvae	Hours between initial and multiple parasitizations	Percent of hosts from which parasitoid that initially oviposited emerged (N)
Agathis gibbosa	None	0	83.0 (15)
	Orgilus jennieae	1	63.6 (11)
	Orgilus jennieae	24	88.9 (9)
Apanteles scutellaris	None	0	100.0 (15)
	Agathis gibbosa	1	42.9 (14)
	Agathis gibbosa	24	88.9 (9)
Orgilus jennieae	None	0	100.0 (15)
	Agathis gibbosa	1	25.0 (12)
	Agathis gibbosa	24	14.3 (14)
	Apanteles scutellaris	1	0.0 (11)
	Apanteles scutellaris	24	100.0 (13)

dissections indicated that some eggs of *A. scutellaris* did not hatch when *A. gibbosa* multiply parasitized hosts. In addition, many first instars of *A. gibbosa* were found dead in the hemocoels of multiply parasitized hosts, but few dead *A. scutellaris* first instars were found. These results and observations suggest that the species emerging from multiply parasitized hosts depends on whether the eggs of *A. scutellaris* have hatched when *A. gibbosa* females oviposit. Paralysis of hosts by *A. gibbosa* may adversely affect the eggs of *A. scutellaris* so that they die or are unable to complete development. However, first instars of *A. scutellaris* apparently were unaffected by paralysis, continued to develop, and subsequently killed *A. gibbosa* first instars when they eclosed from their eggs. Since the eggs of *A. scutellaris* require 24 hours to complete development at 25°C (Cardona and Oatman 1975), oviposition by *A. gibbosa* within 24 hours of *A. scutellaris* resulted in the emergence of *A. gibbosa*, but *A. scutellaris* emerged when oviposition by *A. gibbosa* was delayed 24 hours.

Few *O. jennieae* immatures survived in hosts multiply parasitized by or initially parasitized by *A. gibbosa*, and emergence frequencies were independent of time intervals between initial and subsequent ovipositions (P>0.05; G tests) (table 4). These results and dissections of multiply parasitized hosts suggest that the eggs of *O. jennieae* probably are as adversely affected as are those of *A. scutellaris* when *A. gibbosa* females paralyze hosts. Since the eggs of *O. jennieae* require 1 to 2 days longer than those of *A. scutellaris* to complete development, *O. jennieae* eggs are at risk of being killed by nondiscriminating *A. gibbosa* females for longer than are the eggs of *A. scutellaris*. In addition, recently eclosed first instars of *A. gibbosa* are larger than those of *A. scutellaris* and *O. jennieae* (Cardona and Oatman 1975; Flanders and Oatman 1982; Odebiyi and Oatman 1972), and this larger size may indicate that first instars of *A. gibbosa* are competitively superior to similarly aged but smaller larvae of the other species. However, this competitive advantage is lost when a competing species hatches from its egg sooner and subsequently grows to the same or larger size, as apparently occurs with *A. scutellaris* but not *O. jennieae*. Observations during dissections of PTW larvae initially parasitized by *O. jennieae* and multiply parasitized by *A. gibbosa* suggest that first instars of *O. jennieae* also may be adversely affected during paralysis by *A. gibbosa*. Thus, *O. jennieae* nearly always is at a disadvantage when competing with *A. gibbosa* in multiply parasitized hosts.

SUMMARY AND CONCLUSIONS

Laboratory and field studies indicate that *A. scutellaris* and *A. gibbosa* oviposit in similar host instars, similarly respond to vertical distributions of PTW larvae in plants, and may oviposit in PTW larvae mining in nearly all aerial potato plant tissues. However, *A. scutellaris* with its shorter ovipositor more efficiently located and oviposited in PTW larvae mining in shallower tissues in distal leaf locations, whereas *A. gibbosa* with its longer ovipositor was more efficient in deeper plant tissues in basal leaf petioles, buds, and stems. *Apanteles scutellaris* females also were able to detect and thus avoid multiply parasitizing hosts parasitized by *A. gibbosa*. However, *A. gibbosa* females did not discriminate against and frequently multiply parasitized hosts initially parasitized by *A. scutellaris*. The stage of development of immature *A. scutellaris* at the time of multiple parasitization by *A. gibbosa* determined which

species eventually emerged from hosts. The apparent ability of *A. gibbosa* females to kill *A. scutellaris* eggs during paralysis of hosts enabled the progeny of *A. gibbosa* to emerge from multiply parasitized hosts. However, the rapid development of *A. scutellaris* eggs partially alleviated this susceptibility, since first instars were not affected by ovipositing *A. gibbosa* females and killed *A. gibbosa* larvae when they emerged from eggs in ganglia. These results suggest that differences in oviposition efficiencies relative to the location of PTW mines and the ability of *A. scutellaris* to avoid multiply parasitizing hosts probably are the primary mechanisms that enable these species to coexist. The immunity of *A. scutellaris* first instars to paralysis by *A. gibbosa* females, the ability of *A. scutellaris* first instars to kill those of *A. gibbosa,* and the rapid development of *A. scutellaris* eggs appeared to be compensatory strategies possibly adopted by *A. scutellaris* to reduce progeny losses incurred by nondiscriminating *A. gibbosa* females. These compensatory strategies may secondarily aid coexistence.

Because *A. gibbosa* has several alternate hosts, its inability to discriminate against PTW larvae previously parasitized by *A. scutellaris* and its ability to kill eggs of *A. scutellaris* during host paralysis may be strategies adopted by this species to successfully compete with several parasitoids attacking any of its alternate hosts. These competitive strategies appear to be relatively primitive and unstable forms of exploitation (Miller 1967). Conversely, because of its near monophagy, *A. scutellaris* appears to have compensated for the exploitation strategies of *A. gibbosa* by utilizing a combination of interference (interspecific discrimination) and exploitation (rapid egg development and competitively superior first instars) strategies. Differences in ovipositional efficiencies relative to host locations between these species (exploitation strategies) probably were prerequisites for *A. scutellaris* to evolve the ability to interspecifically discriminate, since these efficiencies appeared to be more primitive morphological and behavioral adaptations to the host. In addition, the evolution of intraspecific discriminatory mechanisms and abilities of both species probably was a prerequisite for *A. scutellaris* to develop its interspecific discriminatory abilities, as discussed by Miller (1967). These results suggest that *A. scutellaris* has primarily adapted to the presence of *A. gibbosa,* rather than vice versa, and that coexistence is now based on a combination of exploitation and interference strategies that compensate for intrinsic and extrinsic competitive advantages and disadvantages of each species.

Contrary to the views of DeBach (1966) and DeBach and Sundby (1963) (see Huffaker and Laing 1972; Luck and Podoler 1985), we believe that intense competition between *A. scutellaris* and *A. gibbosa* occurs only when and where host densities are low, and that only at low host densities has competition been sufficiently intense for *A. scutellaris* to compensate for and adapt to the presence of *A. gibbosa* by the mechanisms it now exhibits. Unfortunately, in the fields we studied, PTW densities were too high and parasitism rates too low to assume that intense competition for hosts between these parasitoids was occurring. Consequently, the locational preferences or efficiencies we did observe probably narrow with decreasing host densities (i.e., overlap of locational niches of the parasitoids decreases as the intensity of competition increases). In addition, PTW densities in potato monocultures in southern California may only rarely be sufficiently low for intense competition to occur. Sufficiently low PTW densities may most commonly occur on spatially and temporally isolated patches of native solanaceous plants. Furthermore, the competitive characteristics we observed probably evolved on such patches before the extensive planting of potato monocultures

in California. However, no studies have been conducted on native solanaceous plants to support this hypothesis.

Field and laboratory results also suggest that *A. scutellaris* possesses a higher searching capacity (ability to find hosts at low host densities) than does *A. gibbosa,* indicating that below certain PTW densities *A. gibbosa* cannot locate sufficient numbers of hosts to survive and compete with *A. scutellaris.* The relatively low parasitization of PTW larvae by *A. gibbosa* during spring when PTW densities were low compared with fall appear to support this possibility. These results suggest that competition between these parasitoids only occurs when PTW densities are low relative to the searching capacity of *A. gibbosa* but are high relative to those of *A. scutellaris,* contrary to our definition of competition and to our perception of the intensity of selection pressures required for *A. scutellaris* to develop interspecific discriminatory abilities. Such selection pressures would only appear to be sufficiently high when host densities are low relative to the searching capacities of both species. A possible explanation for this apparent discrepancy may involve the effect of alternate hosts on the dynamics of *A. gibbosa* populations. High immigration rates from nearby reservoir populations on alternate hosts may enable *A. gibbosa* to maintain its presence when or where low PTW densities occur. Thus, *A. gibbosa* may still parasitize sufficient numbers of hosts at low PTW densities to intensely compete with *A. scutellaris.* However, our field studies were not conducted at sufficiently low PTW densities and no studies have been conducted on interactions among *A. gibbosa* populations parasitizing alternate hosts to support this hypothesis.

Laboratory studies indicate that *O. jennieae* populations in southern California may suffer high mortality because of competition with either native species, but especially with *A. gibbosa.* Similarly to *A. gibbosa* and broadly overlapped by *A. scutellaris,* *O. jennieae* females preferentially or more efficiently parasitized PTW larvae mining in stems, buds, and basal petioles. *Orgilus jennieae* could discriminate against hosts initially parasitized by *A. scutellaris* but not those parasitized by *A. gibbosa;* neither of the native species could discriminate against hosts initially parasitized by *O. jennieae.* In multiply parasitized hosts, *O. jennieae* immatures were nearly always killed by *A. gibbosa,* regardless of which species oviposited first and regardless of time intervals between initial and multiple parasitizations. This apparently was due to *A. gibbosa* females killing *O. jennieae* eggs during host paralysis and was aggravated by the relatively slow development of *O. jennieae* eggs compared with those of *A. scutellaris.* First instars of *O. jennieae* also may have been killed during *A. gibbosa* oviposition or subsequently by competitively superior *A. gibbosa* first instars. When *A. scutellaris* multiply parasitized hosts initially parasitized by *O. jennieae,* the outcome of competition between their first instars depended on the time between ovipositions relative to differences in rates of egg development. Since *O. jennieae* females also preferred to oviposit in younger host instars than did the native parasitoids, many hosts initially parasitized by *O. jennieae* in the field would be susceptible to subsequent parasitization by the nondiscriminating native species, especially *A. gibbosa* with its similar locational efficiencies. Niche characteristics exhibited by *O. jennieae* do not appear sufficiently contractable to reduce the intensity of competition with the native parasitoids, and the ensuing mortality of *O. jennieae* immatures could severely reduce its reproductive potential.

Although the intrinsic rate of increase of *O. jennieae* is higher than that of *A. gibbosa* and nearly equal to that of *A. scutellaris* (Cardona and Oatman 1975; Flanders and

Oatman 1982; Odebiyi and Oatman 1977) and its searching capacity appeared to be nearly equal to that of *A. scutellaris* in the laboratory, these characteristics appear insufficient to compensate for potential progeny losses caused by the native species when and where low host densities occur. Since *O. jennieae* probably would be nearly monophagous in southern California, low PTW densities, in combination with possible invasions of *A. gibbosa* from alternate host populations and with consequent high rates of multiple parasitism, suggest that *O. jennieae* will at least be at a reproductive disadvantage in southern California potato fields. Furthermore, seasonal disruptions in and spatial isolations of potato monocultures with high PTW densities will regularly force *O. jennieae* to rely on low density PTW populations on native solanaceous plants. The ensuing intense competition for hosts with native parasitoids will severely reduce the reproductive potential of *O. jennieae* so that its ability to invade and establish itself in potato fields would progressively decline. These considerations strongly suggest that *O. jennieae* may temporarily become established in southern California, but will eventually disappear. The time of its disappearance will depend on the frequency and intensity of competition with native parasitoids on native solanaceous plants when potato fields are unavailable. Unfortunately, no surveys have been conducted since 1978 in potato monocultures or native solanaceous plants to determine the presence or status of *O. jennieae* in southern California to validate this hypothesis.

These results also suggest that competitive interactions with *A. gibbosa* probably have been the major reason why previously imported species of *Orgilus* have failed to become permanently established and why the native *O. californicus* is so rare or does not occur in southern California. The inabilities of *A. scutellaris* and *A. gibbosa* to discriminate against hosts initially parasitized by *O. jennieae* appeared to operate at the generic, rather than specific, level so that these species would respond similarly to any *Orgilus* species. Furthermore, since possession of a long ovipositor is a generic characteristic, most species of *Orgilus* that parasitize PTW larvae may possess locational efficiencies or preferences similar to those of *A. gibbosa*. Such similar host utilization strategies, along with the competitive strategies of *A. gibbosa*, indicate that severe progeny losses of any *Orgilus* species probably would occur. Consequently, intense competition with *A. gibbosa* probably has been and will continue to be the major obstacle to permanently establishing species of *Orgilus* in southern California. However, initial establishments followed by gradual disappearances of these species may occur because PTW densities in potato monocultures in southern California only occasionally become sufficiently low for intense competition and subsequent displacements to occur, as exemplified by the previously discussed disappearances of *O. lepidus* and *O. parcus*.

Concerning the more general question of attempting to import natural enemies against native or exotic pests that presently possess complexes of natural enemies, our studies suggest that competitive interactions among coexisting native parasitoids may affect the ability to establish exotic species and should be considered before and during such introductions. However, the impact of such interactions on the establishment of exotic species may depend on the degree to which and manners by which the indigenous species have adapted to each other and to the host. The higher the number of parasitoid species attacking a host and the longer they have coexisted, the less likely the possibility that vacant niches exist for inserting new species into an existing complex or the possibility that exotic species can replace indigenous species.

ACKNOWLEDGMENTS

LITERATURE CITED

ARTHUR, A. P., and J. A. JUILLET
   1961. The introduced parasites of the European pine-shoot moth, *Rhyacionia buoliana* (Schiff.) (Lepidoptera: Olethreutidae), with a critical evaluation of their usefulness as control agents. Can. Entomol. 93:297-312.

ARTHUR, A. P., J. E. STAINER, and A. L. TURNBULL
   1964. The interaction between *Orgilus obscurator* (Nees) (Hymenoptera: Braconidae) and *Temelucha interruptor* (Grav.) (Hymenoptera: Ichneumonidae), parasites of the pine-shoot moth, *Rhyacionia buoliana* (Schiff.) (Lepidoptera: Olethreutidae). Can. Entomol. 96:1030-34.

BACON, O. G.
   1960. Control of the potato tuberworm. J. Econ. Entomol. 53:868-71.

BARTLETT, B. R., and J. C. BALL
   1964. The developmental biologies of two encyrtid parasites of *Coccus hesperidum* and their intrinsic competition. Ann. Entomol. Soc. Amer. 57:496-503.

BROODRYK, S. W.
   1969. The biology of *Orgilus parcus* Turner (Hymenoptera: Braconidae). J. Entomol. Soc. S. Afr. 32:243-57.

CARDONA, C., and E. R. OATMAN
   1975. Biology and physical ecology of *Apanteles subandinus* Blanchard (Hymenoptera: Braconidae), with notes on temperature responses of *Apanteles scutellaris* Muesebeck and its host, the potato tuberworm. Hilgardia 43(1):1-51.

CLEMENTS, F. E., and V. E. SHELFORD
   1939. Bio-ecology. New York: John Wiley and Sons. 425 pp.

COMMONWEALTH INSTITUTE OF ENTOMOLOGY
   1968. Distribution maps of insect pests. Series A, No. 10—*Phthorimaea opercullela*. 56 Queens Gate, London, S.W. 7 pp.

DeBACH, P.
   1966. The competitive displacement and coexistence principles. Ann. Rev. Entomol. 11:183-212.

DeBACH, P., and R. A. SUNDBY
   1963. Competitive displacement between ecological homologues. Hilgardia 34(5):105-66.

EHLER, L. E., and R. W. HALL
   1982. Evidence of competitive exclusion of introduced natural enemies in biological control. Environ. Entomol. 11:1-4.

FINNEY, G. L., S. E. FLANDERS, and H. S. SMITH
   1947. Mass culture of *Macrocentrus ancylivorus* and its host, the potato tuber moth. Hilgardia 17(13):437-83.

FISHER, R. C.
   1961. A study in insect multiparasitism, II. The mechanism and control of competition for the host. J. Exp. Biol. 38:605-28.
   1962. The effect of multiparasitism on populations of two parasites and their host. Ecology 43:314-16.
   1971. Aspects of the physiology of endoparasitic Hymenoptera. Biol. Rev. 46:243-78.

FLANDERS, R. V., and E. R. OATMAN
   1982. Laboratory studies on the biology of *Orgilus jenniae* (Hymenoptera: Braconidae), a parasitoid of the potato tuberworm, *Phthorimaea operculella* (Lepidoptera: Gelechiidae). Hilgardia 50(8):1-33.

FLANDERS, S. E.
   1965. Competition and cooperation among parasitic Hymenoptera related to biological control. Can. Entomol. 97:409-22.
   1966. The circumstances of species replacement among parasitic Hymenoptera. Can. Entomol. 98:1009-24.

FORCE, D. C.
   1970. Competition among four hymenopterous parasites of an endemic insect host. Ann. Entomol. Soc. Am. 63:1675-88.
   1974. Ecology of insect host parasitoid communities. Science 184:624-32.

GRAF, J. E.
   1917. The potato tubermoth. USDA Tech. Bull. 427. 56 pp.

HALL, R. W., and L. E. EHLER
   1979. Rate of establishment of natural enemies in classical biological control. Bull. Entomol. Soc. Am. 25:280-82.

HALL, R. W., L. E. EHLER, and B. BISABRI-ERSHADI
   1980. Rate of success in classical biological control of arthropods. Bull. Entomol. Soc. Am. 26:111-14.

HEATWOLE, H., and D. M. DAVIS
    1965.   Ecology of three sympatric insects of the genus *Megarhyssa.* Ecology 46:140-50.
HENDRY, L. B., P. D. GREANY, and R. J. GILL
    1973.   Kairomone mediated host finding behavior in the parasitic wasp *Orgilus lepidus.* Entomol.
        Exp. Appl. 16:471-77.
HUFFAKER, C. B., and J. E. LAING
    1972.   "Competitive displacement" without a shortage of resources?. Res. Pop. Ecol. 14:1-17.
JUILLET, J. A.
    1960.   Immature stages, life histories, and behavior of two hymenopterous parasites of the European
        pine-shoot moth, *Rhyacionia buoliana* (Schiff.) (Lepidoptera: Olethreutidae). Can. Entomol.
        92:342-46.
KOEHLER, W., and A. KOLK
    1969.   Studies on the significance of multiple parasitism in *Rhyacionia buoliana* Schiff. population
        dynamics. Prace Inst. Badaw. Lesnictwa 374:64-86.
KROMBEIN, K. V., P. D. HURD Jr., D. R. SMITH, and B. D. BURKS (eds.)
    1979.   Catalog of Hymenoptera in America north of Mexico. Vol. I, Symphyta and Apocrita
        (Parasitica). Washington, D.C.: Smithsonian. 1198 pp.
LLOYD, D. C.
    1972.   Some South American parasites of the potato tuber moth *Phthorimaea operculella* (Zeller)
        and remarks on those in other continents. Comm. Instit. Biol. Cont. Tech. Bull. pp. 35-49.
LUCK, R. F., and H. PODOLER
    1985.   Competitive exclusion of *Aphytis lingnanensis* by *A. melinus:* potential role of host size.
        Ecology 66:904-13.
MAY, R. M.
    1973.   Stability and complexity in model ecosystems. Princeton, N.J.: Princeton Univ. Press. 265 pp.
MAYR, E.
    1963.   Populations, species, and evolution. Cambridge, Mass.: Harvard Univ. Press. 453 pp.
McLEOD, J. M.
    1972.   A comparison of discrimination and of density responses during oviposition by *Exenterus*
        amictorius and *Exenterus diprionis* (Hymenoptera: Ichneumonidae) parasites of *Neodiprion*
        swainei (Hymenoptera: Diprionidae). Can. Entomol. 104:1313-30.
MILLER, R. S.
    1967.   Pattern and process in competition. Adv. Ecol. Res. 4:1-74.
MILNE, A.
    1961.   Definition of competition among animals. *In* Mechanisms in biological competition. Symp.
        Soc. Exp. Biol. No. 15 (F. L. Milthorpe, ed.). London: Cambridge Univ. Press. pp. 40-61.
NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, and D. H. BENT
    1975.   Statistical package for the social sciences (2nd ed.). New York: McGraw Hill. 675 pp.
OATMAN, E. R.
    1970.   Ecological studies of the tomato pinworm on tomato in southern California. J. Econ. Ento-
        mol. 63:1531-34.
OATMAN, E. R., and G. R. PLATNER
    1974.   Parasitization of the potato tuberworm in southern California. Environ. Entomol. 3:262-64.
OATMAN, E. R., G. R. PLATNER, and P. D. GREANY
    1969.   The biology of *Orgilus lepidus* (Hymenoptera: Braconidae), a primary parasite of the potato
        tuberworm. Ann. Entomol. Soc. Am. 62:1407-14.
ODEBIYI, J. A., and E. R. OATMAN
    1972.   Biology of *Agathis gibbosa* (Hymenoptera: Braconida), a primary parasite of the potato tuber-
        worm. Ann. Entomol. Soc. Am. 65:1104-14.
    1977.   Biology of *Agathis unicolor* (Schrottky) and *Agais gibbosa* (Say) (Hymenoptera: Braconidae),
        primary parasites of the potato tuberworm. Hilgardia 45(5):123-51.
PEMBERTON, C. E., and H. F. WILLARD
    1918.   Interrelations of fruit fly parasites in Hawaii. J. Agric. Res. 12:285-95.
PIMENTEL, D.
    1963.   Introducing parasites and predators to control native pests. Can. Entomol. 95:785-92.
PLATNER, G. R., and E. R. OATMAN
    1968.   An improved technique for producing potato tuberworm eggs for mass production of natural
        enemies. J. Econ. Entomol. 61:1054-57.
    1972.   Techniques for culturing and mass producing parasites of the potato tuberworm. J. Econ.
        Entomol. 65:1336-38.
PLATNER, G. R., P. D. GREANY, and E. R. OATMAN
    1969.   Heat extraction technique for recovery of potato tuberworm larvae from potato tubers. J.
        Econ. Entomol. 62:271-72.

POWERS, N. R., and E. R. OATMAN
    1984.   Biology and temperature responses of *Chelonus kellieae* and *Chelonus phthorimaeae* (Hymenoptera: Braconidae) and their host, the potato tuberworm, *Phthorimaea operculella* (Lepidoptera: Gelechiidae). Hilgardia 52(9):1-32.

QUEDNAU, F. W.
    1970.   Competition and cooperation between *Chrysocharis laricinella* and *Agathis pumila* on larch casebearer Quebec. Can. Entomol. 102:602-12.

SALT, G.
    1960.   Competition among insect parasitoids. Symp. Soc. Exptl. Biol. 15:96-119.

SCHROEDER, D.
    1974.   A study of the interactions between the internal larval parasites of *Rhyacionia buoliana* (Lepidoptera: Olethreutidae). Entomophaga 19:145-71.

SMITH, H. S.
    1929.   Multiple parasitism: its relation to the biological control of insect pests. Bull. Entomol. Res. 20:141-49.

SOKAL, R. R., and F. J. ROHLF
    1969.   Biometry. San Francisco: Freeman. 776 pp.

SYME, P. D.
    1969.   Interaction between *Pristomerus* sp. and *Orgilus obscurator,* two parasites of the European pine-shoot moth. Can. For. Serv. Bi-Monthly Res. Notes 25:30-31.
    1970.   Discrimination by *Hyssopus thymus* (Hymenoptera: Eulophidae) against *Orgilus obscurator* (Hymenoptera: Braconidae) an internal parasite of the European pine-shoot moth, *Rhyacionia buoliana* (Lepidoptera: Olethreutidae). Can. Entomol. 102:1523-27.
    1974.   Interaction between three parasites of the European pine-shoot moth. Can. For. Serv. Bi-Monthly Res. Notes 30:9-10.

TRAYNIER, R. M. M.
    1975.   Field and laboratory experiments on the site of oviposition by the potato moth *Phthorimaea operculella* (Zell.) (Lepidoptera: Gelechiidae). Bull. Entomol. Res. 65:391-98.

TURNBULL, A. L.
    1967.   Population dynamics of exotic insects. Bull. Entomol. Soc. Am. 13:333-37.

TURNBULL, A. L., and D. A. CHANT
    1961.   The practice and theory of biological control of insects in Canada. Can. J. Zool. 39:697-753.

van den BOSCH, R.
    1968.   Comments on population dynamics of exotic insects. Bull. Entomol. Soc. Am. 14:112-15.

VAN LENTEREN, J. C.
    1976.   The development of host discrimination and the prevention of superparasitism in the parasite *Pseudeucoila bochei* (Hymenoptera: Braconidae). Neth. J. Zool. 26:1-83.

VAN LENTEREN, J. C., and K. BAKKER
    1975.   Discrimination between parasitized and unparasitized hosts in the parasitic wasp *Pseudeucoila bochei* a matter of learning. Nature (London) 254:417-19.

WATT, K. E. F.
    1965.   Community stability and the strategy of biological control. Can. Entomol. 97:887-95.

in hosts in buds, stems, and basal portions of petioles. Females of *A. scutellaris* also could detect hosts parasitized by *A. gibbosa*, but *A. gibbosa* females readily multiply parasitized hosts. Eggs of *A. scutellaris* appeared to be adversely affected during host paralysis and oviposition by *A. gibbosa*, but larvae were not affected. Consequently, when nondiscriminating *A. gibbosa* females oviposited before the eggs of *A. scutellaris* hatched, *A. gibbosa* emerged from multiply parasitized hosts; otherwise, *A. scutellaris* emerged. Results suggest that differences in oviposition efficiencies relative to the location of PTW mines and the discrimination abilities of *A. scutellaris* are the primary mechanisms that enable these species to coexist. Influences of alternate hosts and PTW densities, along with the evolution of these competitive strategies, are discussed.

Like *A. gibbosa*, *O. jennieae* most efficiently oviposited in PTW larvae mining potato buds, stems, and basal portions of petioles of potato plants. In addition, *O. jennieae* readily multiply parasitized hosts previously parasitized by *A. gibbosa*, but avoided hosts previously parasitized by *A. scutellaris*. Neither native species discriminated against hosts previously parasitized by *O. jennieae*. In multiply parasitized hosts, *O. jennieae* immatures were nearly always killed by *A. gibbosa* immatures or during host paralysis, despite oviposition sequences and time intervals between ovipositions. When *A. scutellaris* multiply parasitized hosts previously parasitized by *O. jennieae*, the species whose egg hatched first subsequently emerged. *Orgilus jennieae* exhibited a narrower oviposition preference for younger PTW instars than did the native species, possibly increasing the probability of multiple parasitization by the native species. These results, especially those relating to interactions with *A. gibbosa*, along with considerations on searching capacities and potential population increases, suggest that *O. jennieae* is not likely to become permanently established in southern California. Previous failures to establish exotic species of *Orgilus* in southern California and the importation of exotic parasitoids against other native pests that possess coevolved natural enemy complexes are discussed.