

Biology and Ecology of *Anagrus takeyanus* (Hymenoptera: Mymaridae), an Egg Parasitoid of the Azalea Lace Bug (Heteroptera: Tingidae)

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ABSTRACT Mean duration of development of the parasitoid *Anagrus takeyanus* Gordh in the eggs of the tingid *Stephanitis pyrioides* (Scott) was 36.7, 26.1, and 16.4 d at 21, 24, and 27°C, respectively. The average lifespan of *A. takeyanus* adults provided with honey-water solution was 1.35, 1.07, and 0.88 d at 21, 24, and 27°C, respectively, and <1 d at all 3 temperatures when given water only. Male *A. takeyanus* occurred rarely and emerged from host eggs <2 d later than females. The male wasp, previously unreported, has 13 antennal segments; antennae of female wasps have 9 segments. There were 5 emergence peaks in 1992 and 1993 in the Georgia Piedmont. *A. takeyanus* emerged from overwintering *S. pyrioides* eggs synchronously with or slightly later than its host in 1992 and synchronously with or earlier than its host in 1993. Parasitism of *S. pyrioides* eggs averaged 19, 18, and 17% at 3 sites in the Georgia Piedmont in 1992, and 14, 9, and 7% in 1993. Parasitism of *S. pyrioides* eggs by *A. takeyanus* was widespread in Georgia and also was detected in Alabama, North Carolina, and Florida.

KEY WORDS *Stephanitis pyrioides*, *Rhododendron*, natural enemy

THE AZALEA LACE bug, *Stephanitis pyrioides* (Scott), is the most important pest of evergreen azaleas, *Rhododendron* spp., in the landscape (Raupp and Noland 1984). The aesthetic and physiological damage caused by *S. pyrioides* is of major economic concern to growers and landscapers because azaleas are among the most widely planted flowering shrubs (Raupp and Noland 1984). Feeding by *S. pyrioides* adults and nymphs results in stippled or bleached leaves when viewed from above, with tar-like frass and exuviae below. Females oviposit along the mid-rib and secondary veins, frequently covering eggs with frass.

Anagrus takeyanus Gordh was described originally from *Stephanitis takeyai* Drake & Maa, in Connecticut (Gordh and Dunbar 1977) and was reported as a natural enemy of *S. pyrioides* in Georgia (Braman et al. 1992). *S. pyrioides* and *S. takeyai* were inadvertently introduced from Asia before 1945 (Drake and Ruhoff 1965). Because eggs of lace bugs in the genus *Stephanitis* are not commonly parasitized in America, Gordh and Dunbar (1977) suggested that *A. takeyanus* may have been introduced with *S. takeyai*. Azalea lace bugs have few natural enemies, thus current management strategies consist primarily of chemical

control efforts (Neal et al. 1991, Wise et al. 1992, Braman and Beshear 1994). Predaceous mirids (Henry et al. 1986, Neal et al. 1991) and the parasitoid *A. takeyanus* (Braman et al. 1992) have potential as biological control agents against *S. pyrioides*. However, detailed information concerning the role of *A. takeyanus* in *S. pyrioides* population dynamics is lacking.

Despite the value of the Mymaridae for controlling pest populations, few genera have been studied (Meyerdirk and Moratorio 1987, Cronin and Strong 1990). Wasps in the large genus *Anagrus* are primarily parasitoids of heteropteran and homopteran insects (Gordh and Dunbar 1977). Six species have been reported in North America (Gordh and Dunbar 1977), and of these, the biologies of 4 species that parasitize cicadellids or delphacids, *Anagrus epos* Girault, *A. armatus* Ashmead, *A. delicatus* Dozier, and *A. giraulti* Crawford, have been studied in detail (Doutt and Nakata 1973, Meyerdirk and Moratorio 1987, Cronin and Strong 1990).

Here, we present information on the development and longevity of *A. takeyanus*, describe its seasonal activity in the Piedmont region of Georgia, and examine intraplot factors influencing parasitism. We determine the distribution of *A. takeyanus* within Georgia and document its presence regionally. This information, combined with phenological information on *S. pyrioides* (Neal and

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Douglass 1988, Braman et al. 1992), provides a foundation for integrated pest management decisions regarding this important pest of evergreen azaleas.

Materials and Methods

Insect Rearing. *S. pyrioides* was maintained in the laboratory at 24°C and a photoperiod of 15:9 (L:D) h in wooden frame cages (61 by 61 by 64 cm) covered with 32-mesh nylon screen. Adults were provided *Rhododendron* sp. 'Hino Red' azaleas for feeding and oviposition. Plants were replaced weekly, so infested plants used in all studies contained *S. pyrioides* eggs 7–14 d old available for parasitism by *A. takeyanus*.

To provide a continual source of parasitoids, azalea leaves exhibiting lace bug damage were collected from landscape plantings in Spalding and Clarke counties in the Georgia Piedmont. Samples of 3–4 leaves were placed in covered petri dishes with a small square of damp paper towel over the petioles to provide moisture. Dishes were kept at room temperature and checked daily for adult wasp emergence. Condensation in each dish was removed daily. Additional wasps were reared from infested azalea leaves collected during January and February 1993 in Monticello, FL.

Development. Duration of *A. takeyanus* development was determined at 21, 24, and 27°C and a photoperiod of 15:9 (L:D) h. Temperatures were chosen to represent a range of those that occur in Georgia when *A. takeyanus* is active. Newly emerged wasps were placed in 32-ml clear plastic cups (Jet Plastica, Hatfield, PA). Infested leaves on an azalea terminal were fitted through a hole (1 cm diameter) in the center of the cup lid, and a small piece of damp cellulose sponge was wrapped around the stem of the terminal to seal the hole in the lid. The damp sponge served as a water source for the parasitoid and prevented its escape. The cup containing the wasp(s) was attached to the lid. A small piece of paper towel dampened with honey-water solution was placed in the cup with the wasp. Plants, with plastic cups attached, were kept in environmental chambers at each experimental temperature. Parasitoids were removed from the plant after 24 h and terminals were tagged with masking tape marked with the date.

Leaves from parasitoid-exposed terminals were removed from plants before parasitoid emergence and placed in petri dishes with a square of damp paper towel over the petioles. The dishes were then checked daily at 0800 and 1600 hours for *A. takeyanus* emergence. Date, time of emergence, and the sex of each wasp were recorded.

Developmental times at each temperature were calculated using time measured as the interval between the midpoint of the 24 h during which a wasp was placed in a cup with *S. pyrioides* eggs and the midpoint between the time a newly emerged wasp was first observed and the last time

that dish was checked. These data were averaged to establish duration of development at each temperature. The Student *t*-test was used to determine significant differences in developmental rates between female and male *A. takeyanus*.

Voucher specimens of both sexes of *A. takeyanus* were deposited in the University of Georgia Natural History Museum, Athens.

Longevity. Longevity of *A. takeyanus* adults was measured at 21, 24, and 27°C. Twenty wasps were placed individually in petri dishes containing *S. pyrioides*-infested leaves and a small square of paper towel dampened with honey-water. An additional 20 wasps were housed in the same manner but given water only. The dishes were kept in an environmental chamber (Percival, Boone, IA) at the desired temperature with a photoperiod of 15:9 (L:D) h and checked daily for wasp mortality. An unbalanced analysis of variance (ANOVA) for 2-way designs (PROC GLM procedure, SAS Institute 1985) was used to determine if longevity was influenced by temperature and water versus honey-water availability.

Parthenogenesis. The majority of wasps transferred to newly infested azalea leaves were virgin females; either no other wasps were present in the petri dishes containing the azalea leaves from which females emerged, or if multiple wasps were discovered, they were determined, upon microscopic examination, to be female. Thelytokous reproduction of *A. takeyanus*, reported by Gordh and Dunbar (1977), was confirmed by recording emergence of offspring of these unmated females: the sex of emerging offspring was recorded.

Seasonal Activity and IntraPlot Distribution. To determine the phenology of *A. takeyanus*, leaf samples were collected weekly from 1 *S. pyrioides*-infested site in Spalding County, Georgia, and 2 infested sites 160 km away in Clarke County, Georgia, from 4 April through 30 October 1992 and from 11 January through 30 September 1993. Each site consisted of 7–10 mature evergreen azaleas of mixed varieties. The 2 Clarke County sites were ≈7 km apart. In Spalding County and at 1 Clarke County site, plants were bordered by turf; the 3rd site was in a wooded landscape. Each plant was divided into the following quadrants: upper and lower interior, upper and lower exterior. Four samples of 10 leaves exhibiting lace bug damage were collected randomly within each of the 4 quadrants for a total of 160 leaves per site and 480 leaves per week. Sampling was conducted in this manner to determine if *A. takeyanus* preferentially parasitizes *S. pyrioides* eggs according to their location within a plant and to ensure that leaf samples would be representative of seasonal activity if the lace bug or the parasitoid (or both) demonstrated a distributional bias within plants. Leaves were taken to the laboratory and examined for lace bug eggs and parasitoids.

Data from samples collected between 4 April and 31 July 1992 were used to examine intraplant

Table 1. Mean \pm SE developmental time (d) and longevity of *A. takeyanus* at 3 temperatures

Temp. °C	Mean d to develop		Longevity	
	♀	♂	Water only	Honey-water
21	36.73 \pm 2.24	N/A	0.92 \pm 0.10	1.35 \pm 0.16
24	26.05 \pm 0.66	27.38 (\pm 0.99)	0.95 \pm 0.13	1.07 \pm 0.12
27	16.39 \pm 1.06	N/A	0.66 \pm 0.09	0.88 \pm 0.24

distribution of parasitized lace bug eggs. Evidence of parasitoid emergence is the round hole the wasp chews in the lace bug egg operculum when it emerges; eggs from which lace bug nymphs have emerged have the entire operculum removed. Thus, *S. pyrioides* eggs in leaves examined under the microscope were categorized as intact (unhatched), having had an *S. pyrioides* nymph emerge (hatched), or having had an *A. takeyanus* adult emerge. Contingency tables were used to determine differences in percentage parasitism among the quadrants within the plant. Seasonal percentage parasitism was calculated for each site after emergence of the last generation of parasitoids.

Statewide Distribution. During February and March 1992, 10 *S. pyrioides*-infested azalea plantings were identified in each of 4 widely separated counties of Georgia: Cherokee County (northern Georgia), Spalding County and Clarke County, 160 km apart (central Georgia), and Tift County (southern Georgia). The percentage of leaves exhibiting symptoms of lace bug damage—chlorotic stippling on the upper leaf surface and lace bug frass and cast skins on the lower surface—on each of 12 terminals per site was calculated by dividing the number of damaged leaves on a terminal by the total number of leaves on the terminal.

Sixty *S. pyrioides*-infested leaves were collected randomly from each site, placed in plastic bags, taken to the laboratory, and examined under the microscope for the presence of *S. pyrioides* eggs. Unhatched (intact) eggs represented the overwintering generations of *S. pyrioides* and *A. takeyanus*; hatch did not occur until mid-March. The effectiveness of *A. takeyanus* in suppressing *S. pyrioides* populations during the previous season was, therefore, measured by calculating percentage parasitism based on hatched eggs and those from which a parasitoid had emerged; intact eggs were excluded from analysis. Relationships between degree of *S. pyrioides*-induced visible damage and percentage parasitism, damage and total number of eggs per site, and percentage parasitism and total number of eggs per site were examined with regression analysis (SAS Institute 1985).

Additional leaf samples of azalea collected in eastern Alabama ($n = 500$ leaves collected in Auburn, AL, September 1992), northern Florida ($n > 500$ leaves, Monticello, FL, January–February 1993) and northcentral North Carolina ($n > 500$ leaves, 6 sites, 1992) were examined for additional

Table 2. Two-way ANOVA of *A. takeyanus* longevity at 3 temperatures given water or honey-water

Source of variation	df	F
Temp	2	2.67*
Food source	1	4.15**
Temp \times food source	2	0.58

*, $P < 0.10$; **, $P < 0.05$.

evidence of parasitism of *S. pyrioides* eggs within the southern region of the United States.

Results

Development. Adult *A. takeyanus* emerged from parasitized *S. pyrioides* eggs at all temperatures in this study, and developmental time was inversely related to temperature (Table 1). The range in developmental time within each temperature narrowed with increasing temperature (Table 1), from 32 d at 21°C to 13 d at 27°C.

Males were observed only at 24°C and had an average \pm SE developmental time of 27.4 \pm 0.99 d, whereas females required 26.05 \pm 0.66 d to develop at 24°C ($t = 0.4834$, $df = 59$, $P > 0.05$). Eighteen wasps emerged at 27°C, and of the 15 where gender could be positively determined, all were female. Although fewer wasps emerged at this temperature, the average developmental rate of 16.4 d was relatively rapid. Azalea plants, as well as leaves in petri dishes, tended to desiccate more rapidly at 21 and 27°C than at 24°C. Declining plant quality may have affected parasitoid development and emergence; however, wasps emerged from eggs in comparatively dry leaves.

Longevity. *A. takeyanus* was short-lived at all temperatures, regardless of honey availability (Table 1). Longevity differed with temperature and food source (plain water versus honey-water; Tables 1 and 2). However, *A. takeyanus* lived only slightly > 1 d at the most optimum temperature and when fed honey-water.

Parthenogenesis. Progeny of unmated *A. takeyanus* females were female. Seven male *A. takeyanus* were observed and all of these emerged in June 1992 from laboratory-infested azalea leaves. Males, not previously reported, are readily identified as they lack ovipositors and their antennae have 13 segments. In contrast, antennae of females have 9 segments.

Seasonal Activity. *A. takeyanus* emerged at each of 3 sampling sites during both years (Fig. 1). During 1992, we observed 5 peaks in parasitoid emergence at each site, which suggested 5 generations of *A. takeyanus*. The overwintering generation of parasitoids emerged in March 1992, shortly after overwintered, unparasitized *S. pyrioides* eggs hatched. Increased parasitoid emergence tended to occur shortly after lace bug emergence as indicated by greater proportions of parasitized eggs

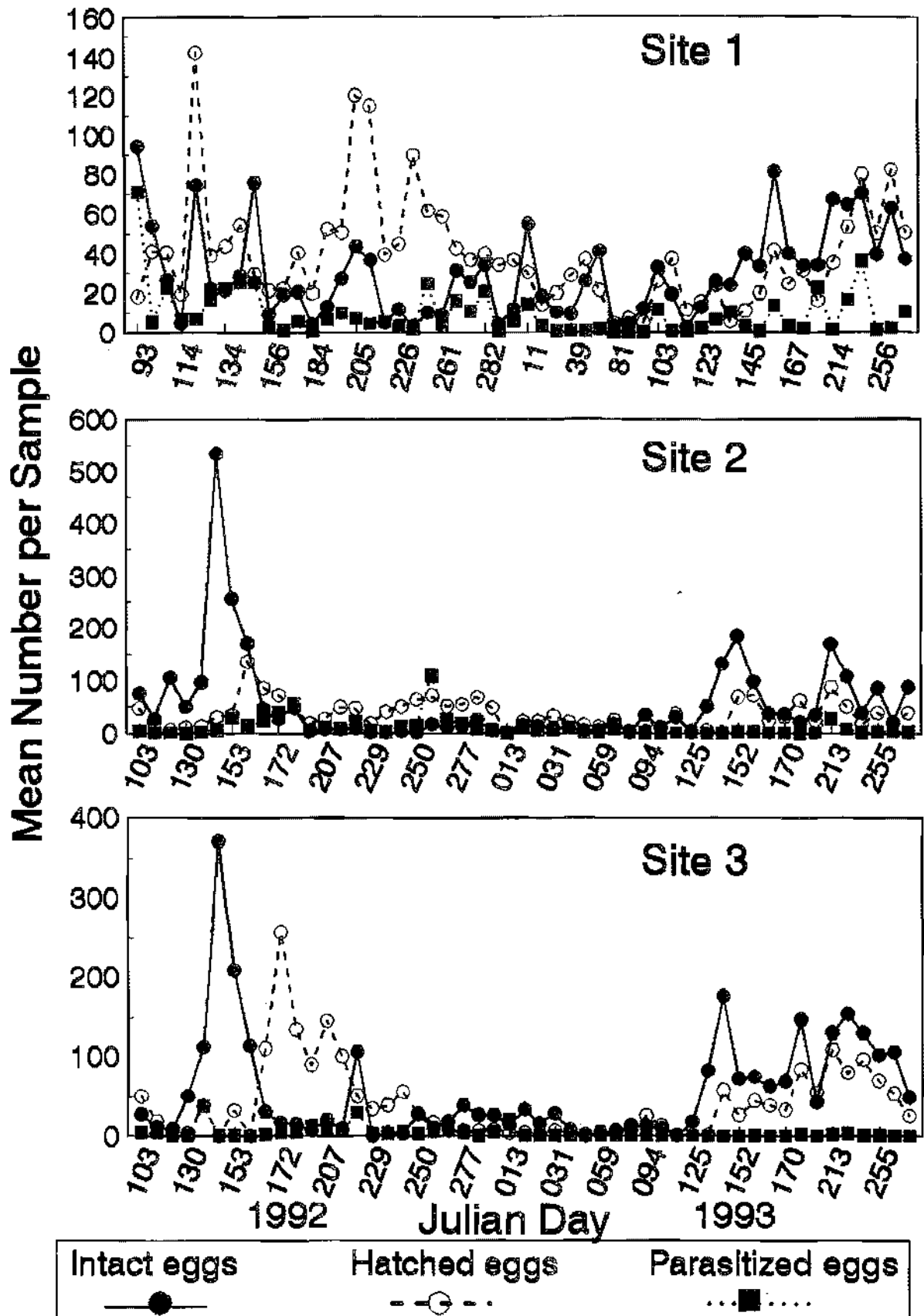


Fig. 1. Seasonal activity of *A. takeyanus* parasitizing *S. pyrioides* eggs during 1992 and 1993.

Table 3. Distribution of parasitized *S. pyrioides* eggs within azaleas in Clarke and Spalding counties, Georgia, April–July 1992

Level	Hatched	Parasitized	% parasitized	χ^2 parasitized eggs
Upper exterior	2,666	603	18.4	
Upper interior	1,965	546	21.7	
Lower exterior	2,235	500	18.3	
Lower interior	1,648	350	17.5	
Upper exterior versus upper interior				9.70*
Upper exterior versus lower exterior				0.03
Upper exterior versus lower interior				0.72
Upper interior versus lower exterior				9.83*
Upper interior versus lower interior				12.48*
Lower exterior versus lower interior				0.46

*. Statistically significant difference in parasitism ($P < 0.05$).

relative to hatched or parasitized eggs. During 1992, at Spalding County, at site 1, wasp emergence also peaked in mid-May (Julian day 136), mid-July (Julian day 199), early August (Julian day 226), and late September (Julian day 247) (Fig. 1). In Clarke County, 1992, at site 2, *A. takeyanus* emergence was observed in early June (Julian day 153). Three additional periods of increased emergence occurred in early July (Julian day 186), early August (Julian day 222), and mid-September (Julian day 260) (Fig. 1). *A. takeyanus* emergence occurred synchronously with that of *S. pyrioides* or shortly thereafter at sites 2 and 3. Parasitoid emergence at site 1 was more variable than that of the host.

Anagrus takeyanus emerged during mid-April, 1993 (Julian day 103) in Spalding County (Fig. 1), and mid-March (Julian day 079) at Clarke County, site 2 (Fig. 1). In Clarke County, parasitoid emergence peaks occurred again in June (Julian day 152), August (Julian day 213), and September (Julian day 264). In Spalding County (Fig. 1), parasitoid emergence again peaked in early May (Julian day 135), late July (Julian day 207), early September (Julian day 245), and late September (Julian day 270).

Recall that the distinguishing emergence holes of lace bug nymphs versus *A. takeyanus* adults remain visible on the undersides of leaves. During each season, mean percentage parasitism of *S. pyrioides* eggs was estimated on each date as the ratio of eggs from which parasitoids had emerged: (eggs from which nymphs had emerged + eggs from which parasitoids had emerged). During 1992, parasitism of *S. pyrioides* eggs at site 1 in Spalding

County ranged from 1 to 77% (mean = 19%). Parasitism at site 2 ranged from 0 to 62% (mean = 18%), and from 0 to 54% (mean = 17%) at site 3 in Clarke County. During 1993, parasitism at these 3 same experimental sites was lower and did not exceed 65% at any location on any date, averaging 14, 9, and 7% at sites 1, 2, and 3, respectively. These figures are conservative because parasitized eggs in which wasps failed to develop, and eggs which were otherwise damaged, perhaps by wasp probing, were indistinguishable from unparasitized eggs. Unhatched eggs were not dissected to determine their contents.

Intraplot Distribution. Percentage parasitism of eggs located in various plant strata collected from April through July 1992 ranged from 17.5 to 21.7% (Table 3). Slightly higher parasitism of *S. pyrioides* eggs by *A. takeyanus* was found in leaves in the upper interior level of azalea plants than in the other 3 plant regions (Table 3).

Statewide Distribution. Parasitism of *S. pyrioides* eggs by *A. takeyanus* was found in each of the 4 Georgia counties surveyed and at 32 of the 40 sampled sites within the state. Incidence of parasitism was highest in Spalding County with mean percentage parasitism of 33.1% and a range of 0–64.5% (Table 4). Parasitized *S. pyrioides* eggs also were recovered in leaf samples collected in Alabama, North Carolina, and Florida.

Estimates of percentage lace bug feeding damage ranged from 26.2% to 97.0% at the 10 sites sampled in Spalding County, Georgia. The proportion of leaves exhibiting visible lace bug damage (stippling) was an effective estimate of *S. pyrioides* infestation (number of lace bug eggs) ($F = 5.5$; $df = 1, 8$; $P < 0.05$). Visible damage may remain, however, following lace bug dispersal and may not be a consistent means of population estimation. Regression analysis revealed that degree of infestation (lace bug egg density or damage estimates) was not a good predictor of parasitoid activity: no relationship was found between the total number of eggs in a leaf sample and percentage parasitism.

Table 4. Mean percentage of parasitism and range of parasitism of azalea lace bug eggs by *A. takeyanus* in 4 Georgia counties during February and March 1992

County	Range of parasitism		Mean % parasitism
	Min, %	Max, %	
Cherokee	0.0	9.0	2.4
Tift	3.4	13.6	8.4
Clarke	2.2	44.4	15.9
Spalding	0.0	64.5	33.1

Discussion

Parasitoid development times are variable among species within the genus *Anagrus*, although development accelerates at warmer temperatures for all species studied. For example, at 24°C, *A. takeyanus* required almost 2 wk longer to emerge than *A. giraulti* (Meyerdirk and Moratorio 1987). Developmental times of *A. takeyanus* and *A. delicatus* were more similar. At 22°C, *A. delicatus* required 35.9 d to complete development in eggs of *Prokelisia marginata* (Van Duzee) (Cronin and Strong 1990); at 21°C, *A. takeyanus* emerged in 35.8 d, on average, from *S. pyrioides* eggs.

Developmental time of these parasitoids may be adapted to the life cycles of their hosts. McKenzie and Beirne (1972) found that, as a parasitoid of *Erythroneura zizac* Walsh, *A. epos* emerged shortly after its host and had an apparent development period of 14–17 d in May in British Columbia. This same species completed development in 16–21 d on *E. elegantula* Osborn and in about 14 d on *Dikrella cruentata* (Gillette) throughout the season in northern California (Doutt and Nakata 1973).

The life cycle of *A. takeyanus* closely followed that of its host. In 1992, the peaks in *A. takeyanus* populations that occurred shortly after each *S. pyrioides* generation suggested a response to the host increase occurring as each *S. pyrioides* generation matured and deposited eggs (Fig. 1). Reduced lace bug and parasitoid populations were observed in 1993. After the overwintering generation of lace bugs matures, a continual source of host eggs is available for parasitism because adult females of the 4 overlapping generations of *S. pyrioides* oviposit throughout the season (Braman et al. 1992).

With a mean adult lifespan of <2 d, *A. takeyanus* is the shortest-lived of the studied *Anagrus* wasps. *A. giraulti* is the longest-lived with an average lifespan of 11.4 d (Meyerdirk and Moratorio 1987). Thelytokous reproduction has been observed for *A. takeyanus* (Cordh and Dunbar 1977) and *A. delicatus* populations in the San Francisco area of California (J. T. Cronin, personal communication). Arrhenotoky has been observed in Florida populations of *A. delicatus* (J. T. Cronin, personal communication). Thelytoky is an adaptation suited to the short lifespan of *A. takeyanus*. *A. takeyanus* males emerge in much lower numbers and later than females, possibly ensuring mate availability. In arrhenotokous *Anagrus* spp., males emerge simultaneously with or earlier than females (Cronin and Strong 1990).

The generally unbiased pattern of *S. pyrioides* egg parasitism among plant strata observed for *A. takeyanus* also was reported for *A. delicatus* Dozier, a parasitoid of *Prokelisia marginata* Van Duzee, a planthopper on salt marsh cord grass, *Spartina alterniflora* Coisel (Cronin and Strong 1990). This unbiased distribution was suggested to be a response of the parasitoid to the disturbed habitat

of its host (Stiling and Strong 1982, Strong 1989); however, azaleas, although commonly planted in urban environments, are not regularly disturbed and probably represent a stable habitat for *S. pyrioides* and *A. takeyanus*.

The variable levels of naturally occurring parasitism of *S. pyrioides* eggs by *A. takeyanus* indicate that the parasitoid can have a localized, temporal impact on its pest host. Evidence of *A. takeyanus* activity was widespread throughout Georgia and was observed in Florida, Alabama, and North Carolina. A comparison of parasitism of *S. pyrioides* eggs on azaleas treated with 9 different insecticides indicated that treatments did not affect development of *A. takeyanus* or its ability to colonize treated plants relative to untreated controls (Balsdon et al. 1993). This suggests that chemical and biological suppression methods for *S. pyrioides* are potentially compatible. Use of resistant azalea species and cultivars may be a lace bug management option (Braman and Pendley 1992, Schultz 1993, Balsdon et al. 1995). Additional research is required to determine whether biological control using *A. takeyanus* is compatible with host plant resistance strategies.

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