

George E. Heimpel · Jay A. Rosenheim · Marc Mangel

Predation on adult *Aphytis* parasitoids in the field

Received: 1 April 1996 / Accepted: 27 November 1996

Abstract We report on predation on adult females of the parasitoids *Aphytis aonidiae* and *A. vandenboschi* (Hymenoptera: Aphelinidae) foraging in the field. During 89.6 h of observation, we witnessed 18 encounters with predators, 6 of which resulted in parasitoid capture. Three classes of generalist predators attacked *Aphytis*: spiders (unidentified Salticidae and Thomisidae), workers of the Argentine ant, *Linepithema humile*, and nymphs of the assassin bug *Zelus renardii* (Hemiptera: Reduviidae). Although observations were conducted during most months of the year, encounters with predators occurred only during September, October and November. During these months, encounters with predators occurred on average every 3.2 h of observation, with one in three encounters resulting in parasitoid capture. Peaks in predation coincided with population peaks of *A. aonidiae*, but were unrelated to population dynamics of any of the predators. We compare these results with previously published laboratory studies on longevity of *Aphytis* parasitoids, and conclude that predation pressure has the potential to severely limit parasitoid fitness in the field.

Key words *Aphytis* parasitoids · Predation pressure · Population dynamics

Introduction

The adult females of insect parasitoids forage for hosts, which are typically the immature stages of other insect species. Females lay one or more eggs in, on or near the host, and the resulting progeny that develop successfully consume and kill the host. The realized fecundity of female parasitoids depends on a large number of factors, including physiological interactions between immature parasitoids and their hosts, physiological features associated with egg production, individual foraging strategies, and population- and community-level factors which affect host encounter rates (Godfray 1994). One factor that is likely to have an important impact on realized fecundity is the mortality rate of adult female parasitoids. Potential sources of mortality in the field include abiotic factors (DeBach et al. 1955; Roitberg et al. 1992, 1993; Fink and Völkl 1995), starvation (Heimpel and Collier 1996; Jervis et al. 1996), and predation (Rees and Onsager 1982; Völkl 1992; Völkl and Mackauer 1993; Rosenheim et al. 1995), among others. Actual field mortality rates from any of these factors remain largely unknown, but morphological and behavioral features of some parasitoids suggest the evolution of anti-predator defenses (Townes 1939; Quicke 1984; Gauld 1987; Quicke et al. 1992; Godfray 1994), and a number of authors have implicated certain groups of parasitoids in Batesian and/or Mullerian mimicry complexes (e.g. Marshall 1902; Shelford 1902; Townes 1939; Mason 1964; Linsley 1959; Quicke 1986; Eggleton 1991; Quicke et al. 1992). The limited experimental and observational evidence available on predation in the field suggests that adults of some parasitoid species are at a substantial risk of being preyed upon (Pierce and Mead 1981; Rees and Onsager 1982; Völkl 1992).

Predators that attack parasitoids in the field include various species of ants (e.g. Pierce and Mead 1981; Völkl 1992; Itioka and Inoue 1996), spiders (Messing and Jang 1992; Visser 1994) nabid bugs (Jervis 1990; Wheeler 1977), anthocorid bugs (Wheeler 1977), asilid flies

G. E. Heimpel (✉)¹ · J. A. Rosenheim
Department of Entomology, University of California,
Davis, CA 95616, USA

M. Mangel²
Section of Evolution and Ecology, University of California,
Davis, CA 95616, USA

Present addresses:

¹ Department of Entomology, University of Wisconsin,
Madison, WI 53706, USA

² Department of Environmental Studies, University of California,
Santa Cruz, CA 95064, USA

(Wheeler 1977; Rees and Onsager 1982), and lizards (Messing and Jang 1992). Documentation of predation on adult parasitoids ranges from casual observations of predation events (Wheeler 1977; Pierce and Mead 1981; Jervis 1990; Visser 1994; Messing and Jang 1992), to detailed observations of parasitoid-predator interactions (Völkl 1992) and studies manipulating predator densities in large field cages (Rees and Onsager 1982). In a series of controlled field observations in which individual aphid parasitoids were released into aphid colonies that were being tended by the ants *Lasius niger* (L.) or *Myrmica ruginodes* (Nyl.), Völkl (1992) showed that one parasitoid, *Trioxys angelicae* (Haliday) was consistently attacked and killed by both ant species while another parasitoid, *Lysiphlebus cardui* (Marshall) was consistently ignored. Völkl and Mackauer (1993) hypothesized that *L. cardui* was protected from predation by cryptic behavior and possibly chemical mimicry. Rees and Onsager (1982) studied predation on three sarcophagid (Diptera) parasitoids of grasshoppers by five species of asilid flies. They documented very high levels of adult parasitoid mortality in the field and tested the hypothesis that asilid predation could explain a substantial portion of this mortality. Results from experiments that compared survivorship of parasitoids in large field cages with or without asilids were in broad agreement with their hypothesis; survivorship without predators approached the high levels observed in laboratory studies, while no parasitoids survived in the cages with predators. As far as we know, however, no studies have used field observations of naturally foraging parasitoids to estimate the risk of predation. The advantages of such an approach include the direct identification of predators as well as the absence of potential artifacts that can arise when laboratory-reared individuals are released and observed.

Here, we report on predation events on the parasitoids *Aphytis aonidiae* (Mercet) and *A. vandenboschi* DeBach and Rosen (Hymenoptera: Aphelinidae) that occurred during observations of females foraging freely in the field, and conclude that adults of these parasitoid species face a substantial risk of predation during specific times of the year.

Materials and methods

Natural history and field site description

Both *A. aonidiae* and *A. vandenboschi* are minute (c. 1 mm long), parasitoids of the San Jose scale, *Quadraspidiotus perniciosus* (Comstock) (Homoptera: Diaspididae). *Q. perniciosus* is native to eastern China and was accidentally introduced into California around 1870 (Gentile and Summers 1958). *A. aonidiae* is holarctic, while *A. vandenboschi* is thought to be native to Japan (Rosen and DeBach 1979). It is not known whether *A. aonidiae* is native to North America or whether it was introduced with *Q. perniciosus* or some other diaspidid scale insect(s). It is also unclear when *A. vandenboschi* entered the United States. *A. aonidiae* appears to be the dominant natural enemy of *Q. perniciosus* in California (Gulmahamad and DeBach 1978a; G.E. Heimpel and J.A. Rosenheim, unpublished work), and *A. vandenboschi* is dominant in

certain parts of Utah (Titayavan and Davis 1988). No releases of *A. aonidiae* or *A. vandenboschi* were made at or near our study site prior to or during this study.

Reproduction for both species is by thelytokous parthenogenesis; unmated females produce daughters, and males occur only rarely (Gulmahamad and DeBach 1978b; Rosen and DeBach 1979; Titayavan and Davis 1988). Eggs of both species are deposited between the scale body and scale cover, singly in the case of *A. aonidiae* (Gulmahamad and DeBach 1978b; Heimpel et al. 1996). Hosts can also be used for adult host feeding, which is the consumption of host fluids by adult female parasitoids. The average handling times in the field for oviposition and host feeding by *A. aonidiae* are 10 and 25 min, respectively (Heimpel 1995).

The study was conducted in a 2.5-ha block of a 25-ha, organically-managed almond orchard (*Prunus dulcis*) in Northern California (Sutter Co.), United States, with a moderate infestation of *Q. perniciosus*. *Q. perniciosus* grows mainly on the bark of twigs and branches of its host tree. Although both species of *Aphytis* use flight to move from tree to tree (G.E. Heimpel and J.A. Rosenheim, unpublished work), within-tree host location is almost exclusively achieved by walking along twigs and branches (G.E. Heimpel and J.A. Rosenheim, personal observations).

Field observations

As part of a study of the oviposition and host-feeding behavior of *A. aonidiae*, observations of parasitoids freely foraging in the field were conducted in May–November 1992, March–May and October–November 1993, and September–October 1994 (Heimpel et al. 1996). Parasitoids were found by scanning branches and young twigs of the almond trees, and were either foraging, resting or handling hosts when found. They were observed continuously until (i) a host encounter which involved more than 1 min of probing was completed, (ii) they were captured by predators, or (iii) they were lost to the observer. In all, 212 *A. aonidiae* and 23 *A. vandenboschi* were observed during 89.6 h. Duration of observations ranged between 1 and 120 min, and parasitoid behavior prior to the encounter with predators was classified as either foraging or host handling, which included host probing, oviposition, and host feeding (Heimpel et al. 1996).

We estimated the rate of encounter with predators and the predation rate by dividing the number of events (encounters with predators or deaths due to predation) by the total time spent observing parasitoids. These estimates were confirmed using maximum likelihood estimation (Edwards 1992). A bootstrapping method was used to compute 95% confidence intervals for the estimates derived by simple division (Efron and Tibshirani 1993).

Predator censuses

To aid in interpretation of seasonal patterns of predator encounters, we conducted censuses of adult *A. aonidiae* and *A. vandenboschi* as well as their potential predators by counting the number of individuals seen during visual scans of individual trees. In 1993, 3-min scans were conducted on 36 trees at weekly intervals between August and November. The trees chosen for scans were spaced evenly throughout the study site and were used repeatedly throughout the season. In 1994, 10-min scans were conducted on ten evenly spaced trees every 2–4 weeks between June and October.

Results

During 89.6 hours of observation of *Aphytis* parasitoids, we witnessed 18 encounters between *Aphytis* adults and one of three classes of predators: spiders (unidentified Salticidae and Thomisidae), workers of the Argentine

Table 1 Incidence of encounters with predators by *Aphytis aonidiae* and *A. vandenboschi* adults during parasitoid observations

Date	<i>Aphytis</i> species	Predator	<i>Aphytis</i> handling host?	Parasitoid capture?
15 Sept 92	<i>A. aonidiae</i>	Unid. Salticid	No	Yes
15 Sept 92	<i>A. aonidiae</i>	<i>Zelus renardii</i>	No	Yes
28 Sept 92	<i>A. aonidiae</i>	<i>Linepithema humile</i>	No	No
5 Oct 92	<i>A. aonidiae</i>	<i>Z. renardii</i>	Yes	Yes
14 Oct 92	<i>A. aonidiae</i>	<i>L. humile</i>	Yes	Yes
15 Oct 92	<i>A. aonidiae</i>	<i>L. humile</i>	No	No
16 Oct 92	<i>A. vandenboschi</i>	<i>L. humile</i>	No	No
16 Oct 92	<i>A. vandenboschi</i>	<i>L. humile</i>	No	Yes
16 Oct 92	<i>A. aonidiae</i>	<i>Z. renardii</i>	No	No
19 Oct 92	<i>A. vandenboschi</i>	Unid. Salticid	No	No
23 Oct 92	<i>A. vandenboschi</i>	<i>L. humile</i>	Yes	No
23 Oct 92	<i>A. vandenboschi</i>	<i>L. humile</i>	No	No
26 Oct 92	<i>A. vandenboschi</i>	Unid. Thomisid	No	No
4 Nov 92	<i>A. aonidiae</i>	Unid. Thomisid	No	No
7 Oct 93	<i>A. vandenboschi</i>	<i>L. humile</i>	No	No
7 Oct 93	<i>A. aonidiae</i>	<i>L. humile</i>	No	No
22 Oct 93	<i>A. aonidiae</i>	<i>L. humile</i>	No	No
6 Sept 94	<i>A. aonidiae</i>	Unid. Thomisid	No	Yes

ant, *Linepithema humile* (Mayr), and nymphs of the assassin bug *Zelus renardii* (Kolenati) (Hemiptera: Reduviidae) (Table 1). Six of these encounters resulted in successful capture of the *Aphytis* parasitoids. The number of observations was insufficient to test for an influence of predator class, *Aphytis* species, or whether or not parasitoids were handling hosts, on the likelihood of parasitoid capture. Although Fisher's exact tests of independence suggested that the relationship for all three of these factors was not significant ($P > 0.15$ for each independent variable tested separately), power analyses using bootstrapped data sets (Efron and Tibshirani 1993) produced significance values of less than or equal to 0.05 when sample sizes were multiplied by factors of four or more (the power analysis is outlined in Appendix 1). Because significant results were obtained when the sample sizes were increased, there do appear to be some trends for an influence of these factors on predation risk, and thus it would be premature to conclude that they have no effect. More work is needed to adequately assess the effects of predator class, *Aphytis* species, and whether or not parasitoids are handling hosts or not on predation risk.

Encounters with predators were observed exclusively during the months of September, October and November (Fig. 1). This seasonal pattern was not due solely to a temporal bias in sampling effort. We used computer simulation and bootstrapping to show that the seasonal distribution of predator encounters that we observed was significantly different from the expected distribution of encounters under the assumption of no seasonality. The simulations and accompanying hypothesis test are outlined in Appendix 2.

Given the significant seasonal trend in predator encounters, we restricted our calculation of encounter and predation rates to the months during which encounters with predators occurred, i.e., September, October, and November. The total time spent in observation during these months (with years pooled) was 57.63 h. The ob-

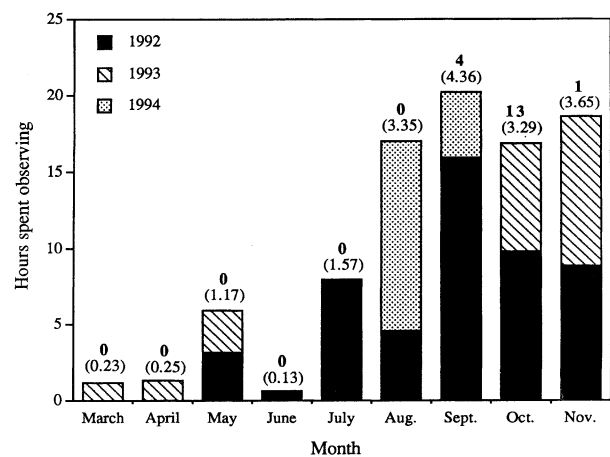


Fig. 1 Hours spent observing *Aphytis* adults between May 1992 and September 1994. Numbers in bold above columns are the number of encounters between predators and parasitoids observed during that month (years pooled). Numbers in parentheses are the expected number of encounters under the null hypothesis that there is no seasonal trend in the probability of encounter, i.e., (proportion of total observation time spent in a given month) \times (total number of encounters)

served rate of encounter with predators, r , was therefore $18/57.6 = 0.312$ encounters per hour (95% confidence interval: 0.189–0.428), and the predation rate, m , was $6/57.63 = 0.104$ parasitoid captures per hour (95% confidence interval: 0.025–0.180). These estimates were confirmed using maximum likelihood estimation (Edwards 1992), which yielded very similar values of r and m (see Appendix 3). Confidence limits for the rate estimates were calculated using standard bootstrapping procedures by randomly resampling the original data sets with replacement 1000 times to generate estimates of variance for r and m (Efron and Tibshirani 1993).

We can translate the encounter and predation rates into probabilities of encountering predators and of pa-

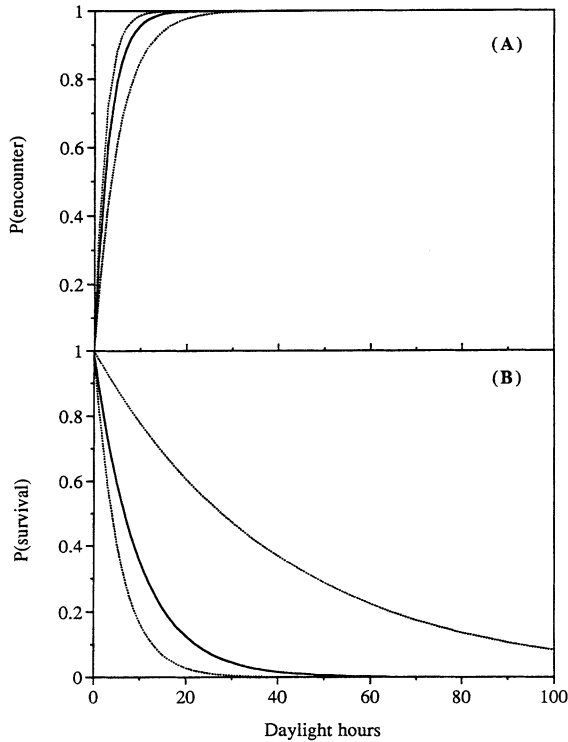


Fig. 2 Probability of **A** predator encounter and **B** survival for *Aphytis* adults in the field during September, October and November with years pooled. Dotted lines are bootstrapped 95% confidence limits

parasitoid survival by setting the probability of not encountering a predator, or of not being preyed upon, as the zero term of a Poisson distribution. Thus, the probability of encountering a predator by time t is $(1 - e^{-t})$, and the probability of surviving until time t is e^{-mt} . Figure 2 shows these probabilities as a function of time. Since all of our observations took place during the day, we consider the appropriate time scale to be daylight hours.

In 1993 and 1994, the numbers of adult *A. aonidiae* seen during visual scans of trees showed distinct peaks during October, while the numbers of predators did not (Fig. 3, 4).

Discussion

Predation on *Aphytis*

We showed that *A. aonidiae* and *A. vandenboschi* adults are subject to a substantial risk of mortality from predator attack during September, October and November. During these months, encounters with predators occurred on average every 3.12 h of observation, with one in three encounters resulting in parasitoid capture. This suggests that the “half-life” of a cohort of *Aphytis* (i.e., the age at which half of the adults will have died or m 0.5) during this time of year should be approximately 6.7 daylight h (Fig. 2).

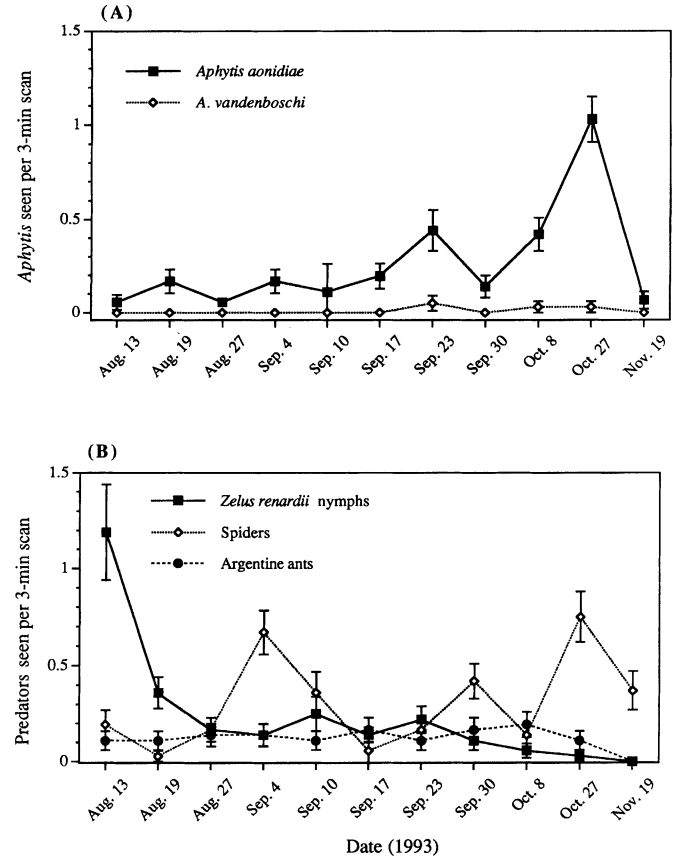


Fig. 3 Mean numbers (\pm SEs) of **A** *Aphytis* adults and **B** predators seen during 36 3-min visual scans of almond trees in 1993. Numbers of ants refers to the number of trees harboring ant “trails”, each of which consisted of numerous individuals

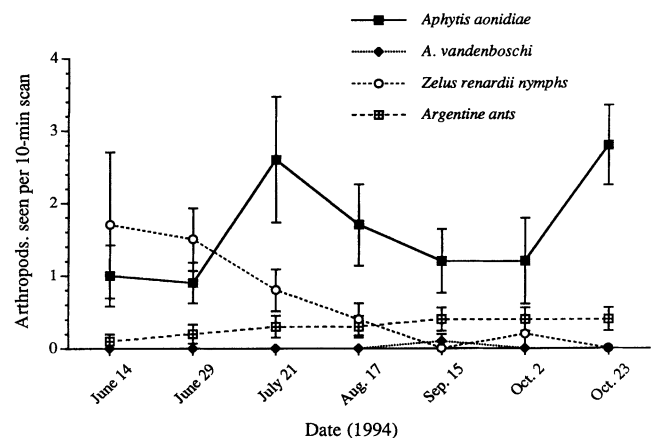


Fig. 4 Mean numbers (\pm SEs) of arthropods seen during ten 10-min visual scans of almond trees in 1994. Numbers of ants refers to the number of trees harboring ant “trails”, each of which consisted of numerous individuals. Spiders were not counted in 1994

At least two caveats accompany this result. First, our observations were conducted only during daylight hours. Some parasitoid species forage at night (Gauld and Huddleston 1976; Gauld and Mitchell 1977; Huddleston and Gauld 1988; Gauld 1987; Quicke 1992), and

nighttime foraging has been postulated as an adaptation for avoiding predators (Gauld 1987; Godfray 1994). Whether or not *Aphytis* spp. forage at night in the field is not known, but DeBach and White (1960) reported anecdotally that parasitism in the laboratory by *Aphytis lingnanensis* Compere occurred mainly during the day. Second, there may be age-related differences in parasitoid behavior that could introduce an observational bias. If younger parasitoids are more likely to rest than are older parasitoids, and more active parasitoids are more likely to be (i) seen by an observer and (ii) encountered by a predator, our calculations could overestimate the actual predator encounter rate by biasing observations toward individuals engaged in relatively high-risk behavior. Although no information is available for *Aphytis* species, laboratory experiments with a number of other parasitoid species have documented a post-emergence period of resting that can last from one to several hours (Forsse et al. 1992; van Lenteren et al. 1992; Pompanon et al. 1995).

Even if we allow for these caveats, however, survival from predators during the fall months should rarely exceed 5 days, and it should often not exceed 2 days. How does this estimate of longevity in the field compare with laboratory estimates of longevity? When *A. aonidiæ* adults are provided with honey in the laboratory, longevity is approximately 30 days (Gulmahamad and DeBach 1978b). The longevity of *A. vandenboschi* adults fed honey is strongly dependent on temperature; below 23°C, Titayavan and Davis (1988) reported mean longevities between 10 and 32 days, while mean longevities above 28°C were 4 days or less. Similar, but less extreme, temperature-dependent results are reported by Avidov et al. (1971) for *A. coheni* DeBach, and DeBach et al. (1955) reported high mortality of adult *A. lingnanensis* at low temperatures. In general, adult *Aphytis* live between 2 and 6 weeks in the laboratory when fed sugar and held at optimum temperatures (e.g., DeBach and White 1960; Bartlett 1962; Quednau 1964; Avidov et al. 1970; Gulmahamad and DeBach 1978b; Takagi and Ogata 1990; Rosenheim and Hoy 1988; Heimpel et al. 1994, submitted; Heimpel and Rosenheim 1995; Collier 1995). If a sugar source is withheld, however, *Aphytis* adults die from starvation within 1–2 days, even if host feeding is allowed (DeBach and White 1960; Heimpel et al. 1994, in press). Thus, the mortality rate from predation that we have documented here rivals starvation and extreme temperature as a source of mortality. Since *Aphytis* parasitoids mature eggs throughout most of their adult life (Quednau 1964; Gulmahamad and DeBach 1978b; Rosenheim and Hoy 1988; Heimpel et al. in press) and have a maximum fecundity that greatly exceeds their maximum egg complement at emergence (Rosenheim and Rosen 1991; Collier 1995; Heimpel and Rosenheim 1995; Heimpel et al. in press), achieving maximum fecundity is only possible for long-lived individuals. Our results suggest that intense predation occurring during the fall months will prevent most parasitoids from realizing their maximum potential fecundity.

Predation by generalists

All of the arthropods that preyed on *Aphytis* adults in this study were generalist predators that were presumably not dependent on *Aphytis* adults for their survival. Indeed, a number of other, more abundant arthropod species were present at our site that probably served as prey for all of the predators discussed in this paper (most notably chironomid flies and various mite species). The (unknown) population dynamics of these and other alternate prey species may contribute to an apparent lack of correlation between predator numbers and the risk of predation for *Aphytis* (Figs. 1, 3, 4). Our results do, however, suggest that a correlation between *Aphytis* population size and predation risk may exist. A test for density dependence of the predation rate was not possible because of a lack of population data from 1992 (the year during which most predation occurred), but the fact that intense predation in all three years occurred during the fall months, which coincided with *Aphytis* population peaks in 1993 and 1994, suggests that predation by generalist predators may contribute to parasitoid population regulation. Murdoch et al. (1995) recently showed that the presence of Argentine ants contributed only slightly to stability and parasitism rates in the *A. melinus*/California red scale system in citrus, but the collective influence of all relevant generalist predators on *Aphytis* host/parasitoid population dynamics remains unexplored.

All of the classes of predators that we observed are known to feed on both herbivores and their natural enemies in various agricultural systems (reviewed by Rosenheim et al. 1995). Indeed, *Z. renardii* has recently been implicated in the disruption of biological control by feeding on the predators of pest aphids (Rosenheim et al. 1993). In addition, Argentine ants and a number of other ant species, can disrupt parasitoid activity in a number of agricultural (e.g., Bartlett 1961; Rosenheim et al. 1995; Itioka and Inoue 1996) and natural systems (e.g., Pierce and Mead 1981; Völkl 1992; Völkl and Mackauer 1993). Usually, the disruption involves ants defending honeydew-producing homopteran insects or larvae of lycaenid butterflies against their parasitoids. However, parasitoids whose hosts are not tended by ants can also be subject to attacks by ants. In these cases, ants are presumably tending a co-occurring insect, and/or are foraging for prey. Interactions between ants and *Aphytis* parasitoids provide a classical case of this scenario in citrus groves. Although diaspidid scale insects do not produce honeydew, and are not tended by ants, ants can cause substantial (DeBach et al. 1951; DeBach 1958), or slight (Murdoch et al. 1995) disruption of *A. melinus* controlling the California red scale, *Aonidiella aurantii* (Maskell). In these and other studies, it was not specified whether disruption of biological control was caused solely by non-predatory interference with parasitoids, or by a combination of predation and other forms of interference. We showed in this study that Argentine ants capture a substantial fraction of the *Aphytis* adults that they encounter.

In conclusion, our study supports the claims of a number of ecologists that host-parasitoid interactions are likely to be affected by community-level dynamics (Hawkins and Sheehan 1994). Specifically, we demonstrated the potential of generalist predators to operate on the fourth trophic level and strongly affect the life-time reproductive success of insect parasitoids.

Acknowledgements We thank Edward Sills for allowing us to use his private land for this study; D. Kattari, J.M. Adams and F. Hernandez for assistance in the field and laboratory; D. Rosen for parasitoid identification and P. Ward for ant identification. We also thank S. Ben-Shalom, T.R. Collier, L.E. Ehler, K. Hobson, A.R. Ives, M.A. Jervis, P.J. Ode, M.S. Strand and an anonymous reviewer for comments on the manuscript. This research was supported in part by USDA competitive grant 9202357 to JA Rosenheim, and a University of California Statewide IPM project grant to GE Heimpel and JA Rosenheim.

Appendix 1 A power analysis for predation risk

We outline the power analysis used to investigate the effect of *Aphytis* species on parasitoid capture. Analogous methods were used for predator class and whether or not parasitoids were handling hosts at the time of predator encounter. The initial data set included 12 observations of *A. aonidiae* (five of which resulted in parasitoid capture) and 6 observations of *A. vandenboschi* (one of which resulted in parasitoid capture) (Table 1). Each of these data sets was sampled randomly with replacement 200 times (Efron and Tibshirani 1993). The significance level of Fisher's exact test of independence,

$$P = \frac{(a+b)!(c+d)!(a+c)!(b+d)!}{a!b!c!d!n!} \quad (1.1)$$

was then computed for each data set, in which a = the number of *A. aonidiae* captured, b = the number of *A. vandenboschi* captured, c = the number of *A. aonidiae* not captured, d = the number of *A. vandenboschi* not captured, and n = the total number of observations. P is the probability of obtaining a , b , c , and d by chance (Sokal and Rohlf 1981). P was averaged over the 200 runs, and average P values were calculated for runs in which the size of the initial data set was multiplied by factors of 1–6

Appendix 2 Testing for seasonal differences in predation risk

The expected number of encounters per month, $N_m(\text{exp})$, is the total number of encounters (= 18) multiplied by the proportion of the total observation time spent in a given month (Fig. 1). Additional data sets were simulated under the assumption of no seasonality as follows. Numbers between 0 and 1 were drawn at random and assigned to a given month based on the proportion of observation time allocated to that month. In this way, the 18 encounters were spread evenly over the observation time. The sum of encounters for each month, $N_m(\text{sim})$, constituted a simulated data set under the null hypothesis of no seasonality. These values were used to characterize the distribution of a test statistic,

$$T_{\text{null}} = \sum_1^M [N_m(\text{sim}) - N_m(\text{exp})]^2 \quad (2.1)$$

which was calculated 10,000 times to capture the potential variability in the number of encounters per month under the null hypothesis (M is the number of months in the study, with years pooled). Next, we calculated T_{obs} for the observed data (i.e., substituting $N_m(\text{sim})$ with the actual numbers of encounters observed; Fig. 1), to perform the test of seasonality. The null hypothesis of no seasonality was

rejected because T_{obs} was greater than more than 95% of the values of T_{null} (indeed, T_{obs} was greater than all 10,000 simulated values of T_{null}). T_{null} was 30.3 with SE 7.5, and T_{obs} was 116.5

Appendix 3 Maximum likelihood estimation of predation rates

We begin by assuming that the probability of being preyed upon can be described by an exponential distribution, so that,

$$P(\text{predation by time } t) = 1 - e^{-mt} \quad (3.1)$$

in which m is the predation rate, and t is time. We seek the joint likelihood for the observation times of those parasitoids that survived predation and those that did not. From Eq. 3.1, the probability that a parasitoid survives past t is e^{-mt} , so that if $\{t_p(i)\}$, $i = 1, 2 \dots N$, are the observation times for parasitoids that did not survive predation and $\{t_{np}(k)\}$, $k = 1, 2 \dots M$, the observation times for the parasitoids that survived predation, the likelihood is

$$L = \prod_{i=1}^N (1 - e^{-mt_p(i)}) \prod_{k=1}^M e^{-mt_{np}(k)} \quad (2)$$

and the negative log-likelihood is

$$\text{NLL} = - \sum_{i=1}^N \ln(1 - e^{-mt_p(i)}) + \sum_{k=1}^M mt_{np}(k) \quad (3)$$

We used an iterative method to determine the value of m that minimized the negative log-likelihood. This resulting estimate was $m = 0.107$ predation events per hour (recall that the value computed in the text was 0.104).

We estimated the rate of encounter with predators in the same way by substituting r for m in Eq. 3.1, 3.2, and 3.3. The resulting estimate was $r = 0.325$ encounters per hour (recall that the value computed in the text was 0.312).

References

- Avidov Z, Balshin M, Gerson U (1970) Studies on *Aphytis coheni*, a parasite of the California red scale, *Aonidiella aurantii* in Israel. *Entomophaga* 15:191–207
- Bartlett BR (1961) The influence of ants upon parasites, predators, and scale insects. *Ann Entomol Soc Am* 54:543–551
- Bartlett BR (1962) The ingestion of dry sugars by entomophagous insects and the use of this feeding habit for measuring the moisture needs of parasites. *J Econ Entomol* 55:749–753
- Collier TR (1995) Host feeding, egg maturation, resorption and longevity in the parasitoid *Aphytis melinus*. *Ann Entomol Soc Am* 88:206–214
- DeBach P (1958) The role of weather and entomophagous species in the natural control of insect populations. *J Econ Entomol* 51:474–484
- DeBach P White EB (1960) Commercial mass culture of the California red scale parasite, *Aphytis lingnanensis*. *Cal Agric Exp Stn Bull* 770:1–57
- DeBach P, Fleschner CA, Dietrich EJ (1951) A biological check method for evaluating the effectiveness of entomophagous insects. *J Econ Entomol* 44:763–766
- DeBach P, Fisher TW, Landi J (1955) Some effects of meteorological factors on all stages of *Aphytis lingnanensis*, a parasite of the California red scale. *Ecology* 36:743–753
- Edwards AWF (1992) Likelihood, expanded edn. Johns Hopkins University Press, Baltimore
- Eggleton P (1991) Patterns in male mating strategies of the Rhysini, a holophyletic group of parasitoid wasps (Hymenoptera: Ichneumonidae). *Anim Behav* 41:829–838
- Efron B, Tibshirani RJ (1993) An introduction to the bootstrap. Chapman and Hall, New York
- Fink U, Völkl W (1995) The effect of abiotic factors on foraging and oviposition success of the aphid parasitoid, *Aphidius rosae*. *Oecologia* 103:371–378

- Forsse E, Smith RS, Bouchier RS (1992) Flight initiation in the egg parasitoid *Trichogramma minutum*: effects of ambient temperature, mates, food, and host eggs. *Entomol Exp Appl* 62:147–154
- Gauld ID (1987) Some factors affecting the composition of tropical ichneumonoid faunas. *Biol J Linn Soc* 30:299–312
- Gauld ID, Huddleston T (1976) The nocturnal Ichneumonoidea of the British Isles, including a key to genera. *Entomol Gaz* 27:35–49
- Gauld ID, Mitchell PA (1977) Nocturnal Ichneumonidae of the British Isles: the genus *Alexeter* Foerster. *Entomol Gaz* 28:51–55
- Gentile AG, Summers FM (1958) The biology of the San Jose scale on peaches with special reference to the behavior of males and juveniles. *Hilgardia* 27:269–285
- Godfray HCJ (1994) Parasitoids: behavioral and evolutionary ecology. Princeton University Press, Princeton
- Gulmahamad H, DeBach P (1978a) Biological control of the San Jose scale *Quadraspidiotus perniciosus* (Comstock) (Homoptera: Diaspididae) in southern California. *Hilgardia* 46:205–238
- Gulmahamad H, DeBach P (1978b) Biological studies on *Aphytis aonidiae* (Mercet) (Hymenoptera: Aphelinidae), in important parasite of the San Jose scale. *Hilgardia* 46:239–256
- Hawkins BA, Sheehan W (eds) (1994) Parasitoid community ecology. Oxford University Press, Oxford
- Heimpel GE (1995) Host-feeding strategies of *Aphytis* parasitoids. PhD thesis, University of California, Davis
- Heimpel GE, Collier TR (1996) The evolution of host-feeding behaviour in insect parasitoids. *Biol Rev* 71:373–400
- Heimpel GE, Rosenheim JA (1995) Dynamic host feeding by the parasitoid *Aphytis melinus*: the balance between current and future reproduction. *J Anim Ecol* 64:153–167
- Heimpel GE, Rosenheim JA, Adams JM (1994) Behavioral ecology of host feeding in *Aphytis* parasitoids. *Norw J Agric Sci Suppl* 16:101–115
- Heimpel GE, Rosenheim JA, Mangel M (1996) Egg limitation, host quality and dynamic behavior by a parasitoid in the field. *Ecology* 77:2410–2420
- Heimpel GE, Rosenheim JA, Kattari D Adult feeding and lifetime reproductive success in the parasitoid *Aphytis melinus* (1997) *Entomol Exp Appl* (in press)
- Huddleston T, Gauld ID (1988) Parasitic wasps (Ichneumonoidea) in British light-traps. *Entomologist* 107:134–154
- Itioka T, Inoue T (1996) The consequences of ant-attendance to the biological control of the red wax scale insect *Ceroplastes rubens* by *Anicetus beneficus*. *J Appl Ecol* 33:609–618
- Jervis MA (1990) Predation of *Lissonota coracinus* (Gmelin) (Hymenoptera: Ichneumonidae) by *Dolichonabis limbatus* (Dahlbom) (Hemiptera: Nabidae). *Entomol Gaz* 41:231–233
- Jervis MA, Kidd NAC, Heimpel GE (1996) Parasitoid adult feeding behaviour and biological control – a review. *Biocontrol News Info* 17:11–26
- Lenteren JC van, Szabo P, Huisman PWT (1992) The parasite-host relationship between *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae) XXXVII. Adult emergence and initial dispersal pattern of *E. formosa*. *J Appl Entomol* 114:392–399
- Linsley EG (1959) Mimetic form and coloration in the Cerambycidae (Coleoptera) *Ann Entomol Soc Am* 52:125–131
- Marshall GAK (1902) Common warning colours in south African hymenoptera and the mimicry of them by insects of other orders. *Trans R Entomol Soc Lond* 1902:525–536
- Mason WRM (1964) Regional color patterns in the parasitic Hymenoptera. *Can Entomol* 96:132–134
- Messing MH, Jang EB (1992) Response of the fruit fly parasitoid *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae) to host-fruit stimuli. *Environ Entomol* 21:1189–1195
- Murdoch WW, Luck RF, Swarbrick SL, Walde S, Yu DS, Reeve JD (1995) Regulation of an insect population under biological control. *Ecology* 76:206–217
- Pierce NE, Mead PS (1981) Parasitoids as selective agents in the symbiosis between lycaenid butterfly larvae and ants. *Science* 211:1185–1187
- Pompanon F, Fouillet P, Bouletreau M (1995) Emergence rhythms and protandry in relation to daily patterns of locomotor activity in *Trichogramma* species. *Evol Ecol* 9:467–477
- Quednau FW (1964) An evaluation of fecundity, host-mutilation and longevity on three species of diaspine scale in *Aphytis lingnanensis* Compere (Hymenoptera: Aphelinidae) *S Afr J Agric Sci* 7:521–530
- Quicke DLJ (1984) Evidence for the function of white-tipped ovipositor sheaths in Braconinae (Hymenoptera: Braconidae). *Proc Trans Br Ent Nat Hist Soc* 17:71–79
- Quicke DLJ (1986) Preliminary notes on homeochromatic associations within and between the afrotropical Braconinae (Hym., Braconidae) and Lamiinae (Col., Cerambycidae). *Entomol Monthly Mag* 122:97–110
- Quicke DLJ (1992) Nocturnal Australasian braconinae (Hym: Braconidae). *Entomol Monthly Mag* 122:97–109
- Quicke DLJ, Ingram SN, Proctor J, Huddleston T (1992) Batesian and Mullerian mimicry between species with connected life histories with a new example involving braconid wasp parasites of *Phoracantha* beetles. *J Nat Hist* 26:1013–1034
- Rees NE, Onsager JA (1982) Influence of predators on the efficiency of the *Blaesoxipha* spp. parasites of the migratory grasshopper. *Environ Entomol* 11:426–428
- Roitberg BD, Mangel M, Lalonde RG, Roitberg CA, Alphen JJM van, Vet L (1992) Seasonal dynamic shifts in patch exploitation by parasitic wasps. *Behav Ecol* 3:156–165
- Roitberg BD, Sircom J, Roitberg CA, Alphen JJM van, Mangel M (1993) Life expectancy and reproduction. *Nature* 364:108
- Rosen D, DeBach P (1979) Species of *Aphytis* of the world. Junk, The Hague
- Rosenheim JA, Hoy MA (1988) Sublethal effects of pesticides on the parasitoid *Aphytis melinus* (Hymenoptera: Aphelinidae). *J Econ Entomol* 81:476–483
- Rosenheim JA, Rosen D (1991) Foraging and oviposition decisions in the parasitoid *Aphytis lingnanensis*: distinguishing the influences of egg load and experience. *J Anim Ecol* 60:873–893
- Rosenheim JA, Wilhoit LR, Armer CA (1993) Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia* 96:439–449
- Rosenheim JA, Kaya HK, Ehler LE, Marois JJ, Jaffee BA (1995) Intraguild predation among biological-control agents: theory and evidence. *Biol Control* 5:303–335
- Shelford R (1902) Observations on some mimetic insects and spiders from Borneo and Singapore. *Proc Zool Soc Lond* 1902:230–284
- Sokal RR, Rohlf FJ (1981) Biometry, 2nd edition. Freeman, New York
- Takagi M, Ogata T (1990) Reproductive potential of *Aphytis yanonensis* DeBach & Rosen and *Coccobius fulvus* (Compere et Annecke) (Hymenoptera: Aphelinidae), parasitoids of *Unapsis yanonensis* (Kuwana) (Homoptera: Diaspididae). *Appl Entomol Zool* 25:407–408
- Titayavan M, Davis DW (1988) Studies of a uniparental form of *Aphytis vandenboschi* (Hymenoptera: Aphelinidae), a parasite of the San Jose scale in northern Utah. *Great Basin Nat* 48:388–393
- Townes HK (1939) Protective odors among the Ichneumonidae (Hymenoptera). *Bull Brooklyn Entomol Soc* 34:29–30
- Visser ME (1994) The importance of being large: the relationship between size and fitness in females of the parasitoid *Aphaereta minuta* (Hymenoptera: Braconidae). *J Anim Ecol* 63:963–978
- Völkl W (1992) Aphids or their parasitoids: who actually benefits from ant-attendance? *J Anim Ecol* 61:273–281
- Völkl W, Mackauer M (1993) Interactions between ants attending *Aphis fabae* spp. *cirsiiacanthoidis* on thistles and foraging parasitoid wasps. *J Insect Behav* 6:301–312
- Wheeler AG (1977) Studies on the arthropod fauna of alfalfa VII. predaceous insects. *Can Entomol* 109:423–427