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Parasitoid Interactions and Their Contribution to the Stabilization of Auchenorrhyncha Populations

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Table 11.1. Parasitoid families known to attack the Fulgoroidea (from Waloff and Jervis, 1987).

Taxonomic Group	Stage Attacked
Diptera	
Pipunculidae	Nymph/adult
Strepsiptera	
Elenchidae	Nymph/adult
Halictophagidae	Nymph/adult
Hymenoptera	
Aphelinidae	Egg
Dryinidae	Nymph/adult
Encyrtidae	Egg, nymph/adult
Eulophidae	Egg
Mymaridae	Egg
Scelionidae	Egg
Trichogrammatidae	Egg

Introduction

The Fulgoroidea are common herbivores in both agricultural and natural systems, often causing severe damage to their host plants (Chapters 14–20). As a result of their economic importance, much research has been conducted on the ecology of planthoppers and the role that natural enemies play in limiting their damage. Researchers have, through extensive collections and many hours of field work, identified the majority of natural enemies associated with planthoppers.

The Fulgoroidea are attacked by two major groups (guilds) of parasitoids which are distinguished broadly by the host stage they exploit. These are the egg parasitoids and the nymphal/adult parasitoids which span a number of families in primarily three insect orders: the Hymenoptera, Strepsiptera, and Diptera (Waloff and Jervis 1987; Stiling Chapter 13). Most egg parasitoids are Hymenoptera, although wasps in the family Dryinidae attack nymphs and adults as do the Strepsiptera and Diptera (Pipunculidae) (Table 11.1). On average, each planthopper species is host to approximately two species of egg parasitoids and two nymphal/adult parasitoids (Stiling Chapter 13). Parasitism by these natural enemies often accounts for substantial mortality to their planthopper hosts; rates average over 36% for egg parasitoids and 17% for nymphal parasitoids. Although researchers have painstakingly documented rates of parasitism for host species, often from samples taken over a wide spatial range and for a number of years, relatively few studies have attempted to assess the role parasitoids play in planthopper population dynamics. Even fewer studies have taken an experimental approach in the field in attempting to elucidate interactions between planthoppers and their parasitoids.

Critical data on the interaction between planthoppers and their parasitoids (aside from seasonal rates of parasitism) are rare. The paucity of ecological data on the Fulgoroidea led us to extend our review to include information on leafhoppers (Cicadellidae) as well. Because of the close taxonomic and ecological similarity between planthoppers and leafhoppers, we feel that combining these two groups is warranted. We review the interactions between the Auchenorrhyncha and their parasitoids; in particular, we examine parasitoid searching behavior and spatial and temporal patterns of parasitism with respect to host density. The resulting information will be used to assess the importance of parasitoids to the regulation, stability, and persistence of planthopper and leafhopper populations. A comprehensive review by Waloff and Jervis (1987) on the systematics, taxonomy, biology, and ecology of the Auchenorrhyncha provided a valuable initial source of information for the present review.

Parasitoid Behavioral Patterns and Their Influence on Host and Parasitoid Stability

In the broadest ecological sense, stability is avoidance of the two extremes of population eruption and extinction. Between extremes, stability may be

density vague (Strong 1988, 1992) and without forces that impel densities toward some specific "equilibrium," this situation could lead to stochastic boundedness (Chesson 1978). One distinctly different situation is simple equilibrium stability, with a single equilibrium point. Between these two extremes lies a vast spectrum of possibilities (Connell and Sousa 1983). One interesting possibility is that simple equilibrium stability is so weak that the forces toward the specific equilibrium value are extremely difficult to detect given the inevitable stochasticity of the environment (Hassell 1985a, 1986a, 1987). In this context, an important consideration is whether stability is strong enough to prevent extinctions in the face of environmental stochasticity (Morrison and Barbosa 1987; Reeve 1988). Another possibility focuses on multiple point equilibria (Peterson 1984). Additionally, a very topical possibility is chaos, in which deterministic forces are so extremely reactive as to create bewilderingly complicated dynamics. Against this background of possibliites, we are able to weigh evidence largely in the realm of deterministic point equilibrium and density vagueness.

Typically, studies of the interactions between planthoppers and their parasitoids come from field collections of parasitized hosts, and most deal with economically important plant species. There are a few notable exceptions, however, involving planthoppers of grasslands (Waloff 1975; Waloff and Thompson 1980) and those inhabiting salt marshes (Stiling and Strong 1982a; Strong 1989; Cronin and Strong 1990a). Much of the experimental work is laboratory bound, but several field experiments with egg parasitoids have been conducted (Ōtake 1967; Becker 1975; Cronin and Strong 1990a). In the following section, we review the searching behavior of these parasitoids and how these behaviors contribute to host–parasitoid stability.

Parasitoid Functional Response

The number of hosts attacked by each parasitoid female per unit time, the parasitoid functional response, is the per–capita parasitoid effect as a function of host density (Holling 1959a). A Type I response is simply density independent. A Type II response, previously thought to be typical of arthropod predators and parasitoids (Hassell 1978), does not stabilize the interaction because parasitoids are less efficient at higher host densities; it produces inverse density-dependence (Hassell and May 1973). A Type III functional response, however, leads to density dependence up to some host density threshold and can contribute to population stability (Murdoch and Oaten 1975; Oaten and Murdoch 1975a; Murdoch 1979). However, time delays, such as those described by the Nicholson–Bailey difference equations, tend to negate the stabilizing effect of a Type III response. The Type

III response is typical of vertebrate predators, but some arthropods exhibit it as well (Murdoch and Oaten 1975; Hassell 1978).

It should be noted at the outset that discriminating among the categories of functional responses has not involved much statistical rigor (Trexler et al. 1988). It can be tenuous, in practice, to distinguish especially between Type II and Type III responses because any trends in real data are usually awash in great amounts of variability. Discerning nonlinearity, which is the essence of the difference between Type II and Type III responses, is particularly problematical in a typical background of high variance. The difficulty is amplified by the fact that the nonlinearity involves position; where does a Type III response begin and end in the range of host densities? It is possible that a Type III curve occurs over a range of host densities lower than the one spanned by a particular data. If so, is this range below typical natural densities? A functional response evident in the lab might have little or no effect on population dynamics in nature, where fluctuations and variability from other "external" forces are so great that any regulatory forces from the response are overwhelmed.

Because of the need for data on the number of searching parasitoids as well as the parasitism rate per host, only four studies have examined the functional response of planthopper and leafhopper parasitoids, of which three deal with *Anagrus* spp. attacking the egg stage (Moratorio 1977; Chantarasa-ard et al. 1984a; Cronin and Strong present study). The remaining study addresses the response by a dryinid which parasitizes nymphs and adults (Chua et al. 1984). Moratorio (1977) examined the behavior of the egg parasitoids *A. mutans* and *A. silwoodensis* on their shared host, the cicadellid *Cicadella viridis* (L.). Both species exhibited a Type II response (Fig. 11.1A), but *A. mutans* had a greater handling time (T_h), resulting in fewer hosts parasitized at higher host density. A Type II response was also found by Chantarasa-ard et al. (1984a) for *A. incarnatus* Haliday attacking *Nilaparvata lugens* (Stål) (Fig. 11.1B) and by Cronin and Strong (present study) for *A. delicatus* Dozier attacking *Prokelisia marginata* Van Duzee (Fig. 11.1C). Only the dryinid, *Pseudogonatopus flavifemur* Esaki attacking *N. lugens* showed a functional response with sufficient accelerating mortality to be reasonably described by a sigmoid curve (Fig. 11.1D) (Chua et al. 1984). It is important to note that the acceleration occurs at very low densities, so any regulatory effect would not act over most of the range of host densities used in this experiment.

Parasitoid Density and Interference

As parasitoid density increases, the probability that searching females will encounter each other becomes high, especially if parasitoids aggregate at
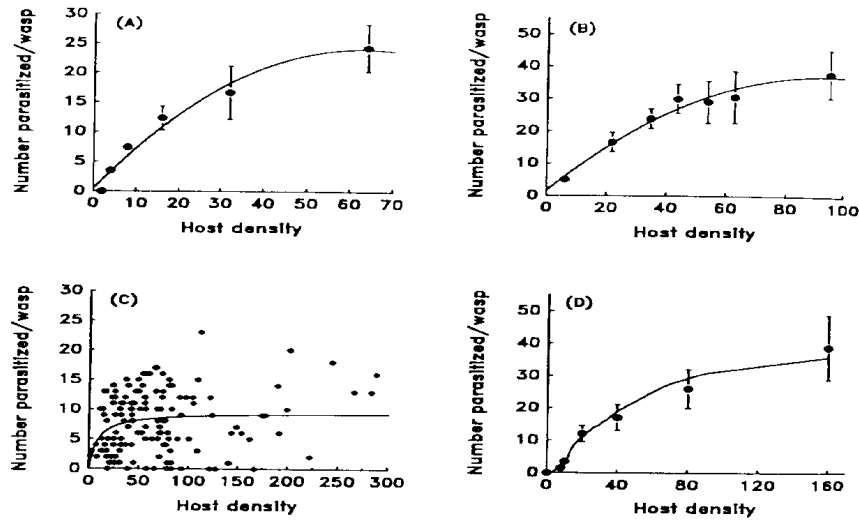
Figure 11.1. Functional responses for parasitoids attacking the Auchenorrhyncha. (A) The mymarid *Anagrus silwoodensis* (Mymaridae) attacking *Cicadella viridis*, Type II (Moratorio 1977). (B) *A. incarnatus* attacking *Nilaparvata lugens*, (Chantarasa-ard et al. 1984a). (C) *A. delicatus* attacking *Prokelisia marginata*, Type II. (D) *Pseudogonatopus flavifemur* (Dryinidae) attacking *N. lugens*, Type III (Chua et al. 1984).

high host density as mainstream models would suggest (Hassell and May 1973). The effects of such encounters can reduce the per capita number of eggs parasitized by causing a decrease in searching efficiency or an increase in handling time as parasitoid density increases (Hassell 1978). In addition, high parasitoid density can lead to a shift in offspring sex ratio toward a male bias (Wylie 1965; Viktorov 1968). Interactions among parasitoids at high parasitoid density is termed mutual interference. Mutual interference can strongly stabilize the otherwise unstable Nicholson–Bailey model, provided the interference constant (m) falls between 0 and 1 (Hassell and May 1973).

Five studies (the same four cited in the previous section on parasitoid functional response, plus Pitcairn et al. 1990) have examined the effects of

parasitoid density on parasitoid behavior. Among the egg parasitoids, Moratorio (1977) found no effect of the density of *A. mutans* or *A. silwoodensis* on their searching efficiency in the laboratory (Fig. 11.2A). These data agreed with previous observations that searching females do not interact with each other. On the other hand, Chantarasa-ard et al. (1984a) and Chua et al. (1984) found significant effects of egg parasitoid and nymphal/adult parasitoid density, respectively, on their searching efficiency in the laboratory (Figs. 11.2B,C).

The remaining two studies (Pitcairn et al. 1990; Cronin and Strong present study) looked for interference among parasitoids in the field. On the basis of a detailed knowledge of host egg and parasitoid larval development rates (degree-day development), Pitcairn et al. (1990) were able to predict the number of adult *A. epos* emerging from blackberry leafhopper (*Dikrella californica*) eggs at time $t + 1$ from leaf samples collected in the field at time t. Their clever method provided an indirect estimate of wasp density at each sample date. During the course of 12 months of biweekly sampling, a marginally significant negative effect of *A. epos* density on performance was found (Fig. 11.2D).

In our study with *A. delicatus*, parasitoid density was directly estimated by trapping of wasps on host plants in a field experiment spanning 20 replicate weeks. Experimentally established patches of host eggs were exposed concurrently with trap plants, providing estimates of both wasp density and parasitism. Further details on this experiment can be found in Cronin (1991) and Cronin and Strong (unpublished data). Among our temporal replicates, we found a significant decline in parasitoid performance as density increased (Fig. 11.2E). A great deal of variability surrounds the line, however.

We (Cronin and Strong unpublished data) performed a series of laboratory experiments to elucidate the mechanism underlying interference in *A. delicatus*. One cause of the decline in wasp searching efficiency is that *A. delicatus* indiscriminantly attacks hosts; wasps do not avoid ovipositing in hosts that have already been parasitized (superparasitism). Interference is indirect ("pseudointerference" sensu Free et al. 1977) and is a consequence of the increasing likelihood of wasting eggs on previously parasitized hosts as the ratio of parasitized to unparasitized hosts increases. *Anagrus delicatus* also demonstrates significant direct ("mutual") interference that involves the nonharmful disruption of conspecific searching on a patch of hosts.

Although data are limited, it appears that interference may be common in the parasitoids of planthoppers and leafhoppers. Four out of six species examined showed strong intraspecific interactions at high parasitoid density. In all three cases of interference, m fell within the range where stability is possible ($m = 0.32–0.59$; Fig. 11.2). Evidence from *A. epos* and *A.*
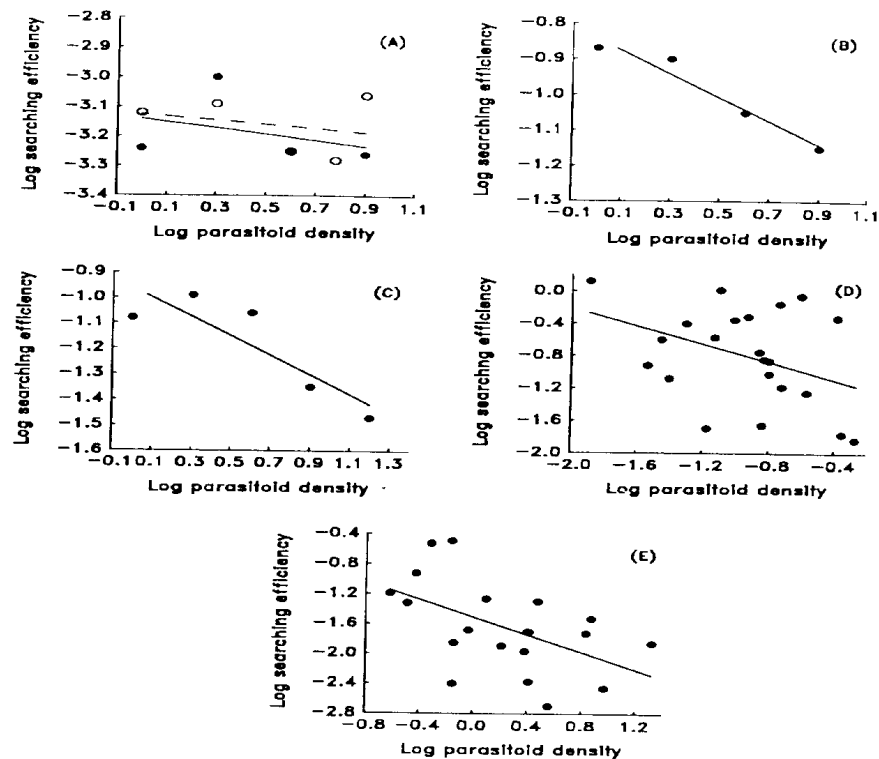
Figure 11.2. Interference among searching parasitoids of the Auchenorrhyncha. (A) The mymarid *Anagrus mutans* (solid circles and line, interference constant; $m = 0.12$) and *A. silwoodensis* (open circles, dashed line; $m = 0.09$) attacking *Cicadella viridis* (no relationship, $P > 0.05$) (Moratorio 1977). (B) *A. incarnatus* ($m = 0.32$) attacking *Nilaparvata lugens* ($R^2 = 0.97, P < 0.05$) (Chantarasa-ard et al. 1984a). (C) The dryinid *Pseudogonatopus flavifemur* ($m = 0.36$) attacking *N. lugens* ($R^2 = 0.58, P < 0.001$) (Chua et al. 1984). (D) *A. epos* ($m = 0.56$) attacking *Dikrella californica* ($R^2 = 0.16, P < 0.07$) (Pitcairn et al. 1990). (E) *A. delicatus* ($m = 0.59$) attacking *Prokelisia marginata* ($R^2 = 0.27, P = 0.02$).

delicatus in the field tends to argue against the conclusion of Griffiths and Holling (1969) that interference is mainly a laboratory phenomenon. Clearly, more detailed laboratory and field studies are needed before we can generalize to all parasitoids of leafhoppers and planthoppers.

Spatial and Temporal Patterns of Parasitism

It has long been recognized that spatial or temporal density-dependent parasitism can stabilize host–parasitoid interactions and maintain populations at low densities (Howard and Fisk 1911; Huffaker 1969; DeBach 1974), a goal that is often sought in biological control programs (Huffaker et al. 1971; Batra 1982). The pattern of density dependence is thought to result from parasitoid aggregation at patches of high host density (Hassell and May 1973). Unfortunately, the evidence supporting the prevalence of spatial (Stiling 1987; Walde and Murdoch 1988) and temporal density dependence in insect populations (Dempster 1983; Stiling 1987, 1988) is equivocal. Independent reviews of field studies during the past several decades show that cases of density dependence and inverse density dependence occur with equal frequency (25%), whereas density independence occurs in about half the studies (Stiling 1987; Walde and Murdoch 1988). On the basis of these reviews, population stability based on density dependence does not appear to be common (but see Hassell 1985a, 1986a, 1987; Hassell et al. 1989).

Recently, however, it has been noted that inverse density dependence can bring about population stability (Hassell 1985b; Chesson and Murdoch 1986). This counterintuitive hypothesis can be easily understood when one examines the distribution of parasitism. In the case of inverse density dependence, hosts are relatively free of parasitism (a partial refuge occurs) at high host density. Some proportion of the host population survives parasitism, imparting stability on the system. As long as the distribution of parasitism is clumped (heterogeneous) in space, such that some proportion of the population is relatively free of attack, stability can occur (see Heterogeneous Parasitism Rates and Stability section below for further discussion). Equilibrium population densities when parasitism is inversely density-dependent are quite high because many hosts (in high-density patches) escape parasitism (Murdoch 1992). As has been noted (Chesson and Murdoch 1986), stability from this sort of interaction can operate counter to the objective of biological control, which is to prevent high host densities.

We examined the literature for the Auchenorrhyncha (combining data from both the planthopper and the leafhopper literature) for spatial and temporal patterns of parasitism. We found a total of 9 published papers (with 10 host–parasitoid comparisons) that explicitly examined spatial density dependence (Table 11.2) and 11 (with 21 comparisons) that examined temporal density dependence (Table 11.3). In each case, we ac-

Table 11.2. Case studies of spatial relationships between host density and parasitism of the Auchenorrhyncha.

Host Species	Parasitoid	Analysis	Study Type	Response Type	Reference
EGG PARASITOIDS					
Mymaridae					
Eupteryx urticae	Anagrus sp. nr. atomus	Regr.*	C	DD	Stiling (1980b)
Laodelphax striatellus	Anagrus nr. flaveolus	Regr.*	E	DI	Ôtake (1967)
Laodelphax striatellus	Anagrus optabilis	Regr.*	C	DI	Miura et al. (1981)
Macrosteles sexnotatus	Anagrus holci	Regr.	E	DD	Becker (1975)
Nephotettix cincticeps	Gonatocerus sp.	Regr.*	C	DI	Miura et al. (1981)
Nilaparvata lugens	Anagrus optabilis	Regr.*	C	DI	Miura et al. (1981)
Nilaparvata lugens	Anagrus sp.	Regr.*	E	DI	Ôtake (1967)
N. lugens/S. furcifera	Anagrus incarnatus	Regr.*	C	DI/INV	Chantarasa-ard et al. (1984b)
Prokelisia marginata	Anagrus delicatus	Regr.	C	DI	Strong (1989)
Prokelisia marginata	Anagrus delicatus	k-value	C	DI-INV	Roderick (1987)
Prokelisia marginata	Anagrus delicatus	k-value	C	INV	Stiling and Strong (1982a)
Prokelisia marginata	Anagrus delicatus	Regr.	C	DI	Cronin and Strong (1990a)
Sogatella furcifera	Anagrus sp.	Regr.*	E	DD	Ôtake (1967)
Sogatella furcifera	Anagrus optabilis	Regr.*	C	DI	Miura et al. (1981)
Typhlocyba pomaria	Anagrus epos	Regr.*	C	DI/DD	Sevedodeslami and Croft (1980)
Trichogrammatidae					
Nephotettix cincticeps	Paracentrobia andoi	Regr.*	E	DD	Sasaba and Kiritani (1972)
Nephotettix cincticeps	Paracentrobia andoi	Regr.*	C	DI	Miura et al. (1981)
Nilaparvata lugens	Paracentrobia andoi	Regr.*	C	DI	Miura et al. (1981)
NYMPHAL/ADULT PARASITOIDS					
Dryinidae					
Nephotettix spp.	Dryinidae	Regr.*	C	DI	Peña and Shepard (1986)
Nilaparvata lugens	Dryinidae	Regr.*	C	DI	Peña and Shepard (1986)
Sogatella furcifera	Dryinidae	Regr.*	C	DI	Peña and Shepard (1986)
Prokelisia marginata	Dryinidae	Regr.	C	DI	Stiling et al. (1991b)
Pipunculidae					
Nephotettix nigropictus	Pipunculidae	Regr.*	C	DI	Peña and Shepard (1986)
Nephotettix virescens	Pipunculidae	Regr.*	C	DI	Peña and Shepard (1986)
Strepsiptera					
Nephotettix spp	Strepsiptera	Regr.*	C	DI	Peña and Shepard (1986)
Nilaparvata lugens	Strepsiptera	Regr.*	C	DI	Peña and Shepard (1986)
Prokelisia marginata	Elenchus koebelei	Regr.	C	DI	Stiling et al. (1991b)
Sogatella furcifera	Strepsiptera	Regr.*	C	DI	Peña and Shepard (1986)

Note: Study type: C = data from field collections, E = data from field experiments. Response type: DD = density dependence, DI = density independence. INV = inverse density dependence. * indicates our own analysis of the author's data.

Table 11.3. Case studies of temporal relationship between host density and parasitism of the Auchenorrhyncha Duration of study is reported in months.

Host Species	Parasitoid	Duration	Analysis	Study Type	Response Type	Reference
EGG PARASITOIDS						
Eulophidae						
Saccharosydne saccharivora	Tetrasticus sp.	24	Life table	C	INV	Metcalfe (1972)
Mymaridae						
Dikrella californica	Anagrus epos	36	Life table	C	DDD[†]	Williams (1984)
Javesella pellucida	Anagrus atomus	48	Regr.[*]	C	DI	Raatikainen (1967)
Laodelphax striatellus	Anagrus nr. flavelous	3	Regr.[*]	E	DI	Ôtake (1967)
Prokelisia marginata	Anagrus delicatus	12	Regr.	C	INV[+]	Strong (1989)
Prokelisia marginata	Anagrus delicatus	12	k-value	C	INV	Stiling and Strong (1982a)
P. marginata and P. dolus	Anagrus delicatus	3	k-value	C	DI	Benrey and Denno (unpublished data)
Prokelisia marginata	Anagrus delicatus	10	Regr.	E	INV	Cronin and Strong (1990a)
Saccharosydne saccharivora	Anagrus flaveolus	24	Life table	C	DI	Metcalfe (1972)
Typhlocyba froggatti	Anagrus armatus	5	Regr.[*]	C	INV[+]	Teulon and Penman (1986)
Trichogrammatidae						
Nephotettix cincticeps	Paracentrobia andoi	36	Life table	C	DD	Sasaba and Kiritani (1972)
NYMPHAL/ADULT PARASITOIDS						
Dryinidae						
Cicadellid complex	Dryinidae	48	Regr.[*]	C	DI	Waloff (1975)
Delphacid complex	Dicondylus bicolor	36	Regr.[*]	C	DI	Waloff (1975)
Dichoptera hyolinata	Dryinus sp. A	12	Regr.[*]	C	DI	Swaminanthan and Ananthakrishnan (1984)
Dicranotropis hamata	Dicondylus bicolor	72	k-factor	C	DDD	Waloff and Thompson (1980)
Javesella pellucida	Dicondylus bicolor	36	Regr.[*]	C	DI	Waloff (1975)
Javesella pellucida	Dicondylus lindbergi	72	Regr.[*]	C	DI	Raatikainen (1967)
Muirodelphax exiguus	Dicondylus bicolor	36	Regr.[*]	C	DD	Waloff (1975)
Nephotettix spp.	Dryinidae	10	Regr.[*]	C	DI	Peña and Shepard (1986)
Nilaparvata lugens	Dryinidae	10	Regr.[*]	C	DI	Peña and Shepard (1986)
Psammotettix confinus	Dryinidae	48	Regr.[*]	C	DI	Waloff (1975)
Sogatella furcifera	Dryinidae	10	Regr.[*]	C	DI	Peña and Shepard (1986)
S. furcifera/N. lugens	Haplogon. orientalis	3	Regr.[*]	C	DI	Ôtake et al (1976)
Prokelisia marginata	Dryinidae	12	Regr.	C	DI	Stiling et al. (1991b)
Nematoda						
S. furcifera/N. lugens	Nematoda	3	Regr.[*]	C	DI	Ôtake et al (1976)
Pipunculidae						
Cicadellid complex	Pipunculidae	48	Regr.[*]	C	DI	Waloff (1975)
Delphacid complex	Cephal. semifumosus	36	Regr.[*]	C	DD	Waloff (1975)
Errastunus ocellaris	Pipunculidae	72	k-factor	C	DI	Waloff and Thompson (1980)
Javesella pellucida	Cephal. semifumosus	36	Regr.[*]	C	DI	Waloff (1975)
Laodelphax elegantulus	Cephal. semifumosus	36	Regr.[*]	C	DI	Waloff (1975)
Muirodelphax exiguus	Cephal. semifumosus	36	Regr.[*]	C	DI	Waloff (1975)
Neophilaenus lineatus	Verrallia aucta	108	k-factor	C	DD	Whittaker (1971)
Nephotettix cincticeps	Pipunculidae	24	Regr.[*]	C	DDD	Kiritani et al (1970)
Nephotettix nigropictus	Pipunculidae	10	Regr.[*]	C	DI	Peña and Shepard (1986)
Nephotettix virrescens	Pipunculidae	10	Regr.[*]	C	DI	Peña and Shepard (1986)
Philaenus spumarius	Verrallia aucta	108	k-factor	C	DD	Whittaker (1973)
Psammotettix confinus	Pipunculidae	48	Regr.[*]	C	DI	Waloff (1975)
S. furcifera/N. lugens	Pipunculidae	3	Regr.[*]	C	DI	Ôtake et al (1976)

(continued)

Table 11.3. (Continued)

Host Species	Parasitoid	Duration	Analysis	Study Type	Response Type	Reference
Strepsiptera						
Delphacid complex	Elenchus tenuicornis	36	Regr.*	C	DI	Waloff (1975)
Javesella pellucida	Elenchus tenuicornis	36	Regr.*	C	DI	Waloff (1975)
Javesella pellucida	Elenchus tenuicornis	72	Regr.*	C	DI/DD	Raatikainen (1967)
Laodelphax elegantulus	Elenchus tenuicornis	36	Regr.*	C	DD†	Waloff (1975)
Muirodelphax exiguus	Elenchus tenuicornis	36	Regr.*	C	DI	Waloff (1975)
Nephotettix spp.	Strepsiptera	10	Regr.*	C	DI	Peña and Shepard (1986)
Nilaparvata lugens	Strepsiptera	10	Regr.*	C	DI	Peña and Shepard (1986)
Nilaparvata lugens	Elenchus sp.	12	Regr.*	C	DI	Kathirithamby (1985)
Paraliburnia dalei	Elenchus tenuicornis	36	Regr.*	C	DD	Waloff (1975)
Poophilus costalis	Halictoph. pontifex	48	Regr.	C	DD	Greathead (1970)
Poophilus lattiusculus	Halictoph. pontifex	48	Regr.	C	DI	Greathead (1970)
Poophilus consperus	Halictoph. pontifex	48	Regr.	C	DI	Greathead (1970)
Cordia peragrans	Halictoph. pontifex	48	Regr.	C	DI	Greathead (1970)
Clovia centralis	Halictoph. pontifex	48	Regr.	C	DI	Greathead (1970)
Clovia quadrispinosa	Halictoph. pontifex	48	Regr.	C	DI	Greathead (1970)
Prokelisia marginata	Halictoph. koebelei	12	Regr.	C	DI	Stiling et al. (1991b)
Ribautodelphax angulosus	Elenchus tenuicornis	36	Regr.*	C	DI	Waloff (1975)
Saccharosydne saccharivora	Stenocranophilus sp.	24	Life table	C	DD	Metcalfe (1972)
Sogatella furcifera	Strepsiptera	10	Regr.*	C	DI	Peña and Shepard (1986)
S. furcifera/N. lugens	Elenchus sp.	3	Regr.*	C	DI	Ötake et al (1976)

Note: Study type: C = data from field collections, E = data from field experiments. Response type: DD = density dependence, DDD = delayed density dependence. DI = density independence. INV = inverse density dependence. * indicates our own analysis of the author's data. † indicates significant serial correlation based on Durbin–Watson statistic (Montgomery and Peck 1982).

cepted the author's interpretation of the data in terms of the response of parasitism to host density. The agricultural literature that we examined contained many additional studies that did not examine the relationship between host density and parasitism, even though information on both host density and levels of parasitism were given. We took the liberty of analyzing these data as well. In all, we found an additional 4 papers (with 18 comparisons) that contained enough data to support examination for spatial patterns and 10 (with 37 comparisons) that we could examine for temporal patterns of parasitism. We attempted to be inclusive in our literature search but may have overlooked some studies; for that we apologize. Regardless of possible oversights, we feel that there are sufficient data in these papers (28 spatial and 58 temporal comparisons total) to reveal the general patterns in the Auchenorrhyncha.

We attempted to be conservative in our reanalysis of others' data. Spatial and temporal patterns of parasitism were examined by means of using simple linear regressions of host density on parasitism. All temporal data were examined for any delayed density dependence by lagging of data by one or two sample dates. Only papers with four or more simultaneous or sequential estimates of host density and parasitism were included in our analysis.

A number of statistical queries have been raised concerning the validity of the use of regression and correlation in detecting density dependence from field data (Reddingius 1971; Pielou 1974; Royama 1977, 1981). Of most significance are the assumptions that measurements of density and parasitism rate are made without error and that no serial correlation (autocorrelation) exists between sample dates (that density values are independent). Parameter estimates can be problematic, especially for measurement of the parasitism rate of hosts with overlapping generations (Van Driesche 1983; Van Driesche et al. 1991). We made no attempt to control for biases in authors' estimates of host density and parasitism. We assume them to be accurate or at the very least to be biased consistently throughout each study such that the bias is independent of host density. Serial correlations in temporal data, on the other hand, can introduce bias that leads to spuriously significant density relationships (a Type I error) (Varley and Gradwell 1968). To identify possible errors of this type, we use the Durbin–Watson statistic (Montgomery and Peck 1982) to test for serial correlations. This statistic is applied to all cases of significant temporal density relationships (density dependence and inverse density dependence) found in Table 11.3. For studies with a significant response to density and a significant serial correlation of densities through time, we do not reverse response type (to density independence). Instead, we simply urge caution in their interpretation.

SPATIAL PATTERNS

Approximately three-quarters of the cases examined showed no spatial density dependence (Table 11.4). The remaining 25% is split fairly evenly between cases of density dependence and inverse density dependence. It is interesting to note that all cases of inverse density dependence come from one system: the egg parasitoid *A. delicatus* and its host *P. marginata*. Only the egg parasitoids demonstrated any density dependence (35%); cases involving nymphal/adult parasitoids showed only density independence. Significant relationships (density dependence and inverse density dependence) occurred more frequently among the egg parasitoids than among nymphal/adult parasitoids (Fisher's exact test, $P = 0.026$). In total, fewer significant relationships occurred among the Auchenorrhyncha (26%) than for all host–parasitoid systems (50%) reviewed by Stiling (1987) (Fisher's exact test, $P = 0.011$).

For *A. incarnatus* parasitizing *N. lugens* (Chantarasa-ard et al. 1984b) and *A. delicatus* parasitizing *P. marginata* (Stiling and Strong 1982a; Strong 1989; Cronin and Strong 1990a; Roderick 1987; Benrey and Denno unpublished data), the spatial response to host density supports the laboratory findings of a Type II functional response for each species. A parasitoid that exhibits a Type II response should have a density-independent attack rate at lower host densities, but as the response reaches a plateau, parasitism should tend toward inverse density dependence. For both parasitoids, parasitism was either inversely density dependent or density independent.

The fact that egg parasitoids are more responsive to host density is puzzling. We could advance many ad hoc reasons why the sedentary egg stage may incur a higher frequency of significant responses, but no single reason appears compelling enough to justify invoking it over other alternatives. In the absence of detailed studies of parasitoid foraging behavior, it would be fruitless, at this point, to speculate about the cause of this pattern among the Auchenorrhyncha.

We can offer no concrete reasons for why fewer cases of density dependence or inverse density dependence should occur among planthoppers and leafhoppers. The lack of statistical power that results from the typically small sample sizes may have inflated the number of nonsignificant patterns. Results may also be biased toward density independence because appropriate spatial scales were not examined (Heads and Lawton 1983, but see Strong 1989). Only 5 of the 27 comparisons examined more than 1 spatial scale, 4 of which dealt with the same host–parasitoid system (Stiling and Strong 1982a; Chantarasa-ard et al. 1984b; Strong 1989; Cronin and Strong 1990a; Roderick 1987). Three of the 5 studies showed a significant density response (all inverse) at some spatial scale (Stiling and Strong 1982a; Chantarasa-ard et al. 1984b; Roderick 1987). For example, Stiling and Strong (1982a) examined the effects of parasitism by the egg parasitoid *A. delicatus* in a north Florida salt marsh at a range of spatial scales from within leaves to among plants and finally among small islands. The pattern of parasitism, however, was inversely density dependent at all spatial scales. Ecologists today appear to be more aware of the potential problem of studying only one spatial scale, and it is likely that more studies in the future will address this issue. Until then, we can only suggest that doing so may reduce the likelihood of finding a significant response. According to Hassell (1985a, 1986a, 1986b, 1987), it may be very difficult to extract true patterns of parasitism from field data as a result of the great environmental variability so typical of natural populations. Underlying density dependence may be hidden by stochastic processes or time delays, resulting in an overestimate of the prevalence of density-independent processes in field collections. However, if density dependence in parasitism rate is so feeble, then population dynamics are not likely to be affected by it.

We have attempted to circumvent this problem by performing well-controlled experiments that are replicated in time and over spatial scales that are relevant to the searching behavior of the parasitoid involved (Cronin and Strong 1990a). We controlled host age, patch size, host plant quality, and exposure time by experimentally forcing *Prokelisia* spp. to lay eggs on

Table 11.4 Summary of studies examining spatial and temporal density dependence (see Tables 11.2 and 11.3) for egg and nymphal/adult parasitoids, separately and combined. Numbers in parentheses are proportions of studies showing response to density.

Pattern	Parasitoid Guild	Response to Host Density		
		DD	DI	INV
Spatial	Egg	5	13	3
		(0.24)	(0.62)	(0.14)
	Nymphal/adult	0	10	0
		(0.0)	(1.0)	(0.0)
	Total	5	23	3
		(0.16)	(0.74)	(0.10)
Temporal	Egg	2	4	5
		(0.18)	(0.36)	(0.45)
	Nymphal/adult	11	37	0
		(0.23)	(0.77)	(0.0)
	Total	13	41	5
		(0.22)	(0.69)	(0.09)

Note: DD = density dependence, DI = density independence, INV = inverse density dependence.

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Pattern	Parasitoid Guild	Response to Host Density		
		DD	DI	INV
Spatial	Egg	5 (0.24)	13 (0.62)	3 (0.14)
	Nymphal/adult	0 (0.0)	10 (1.0)	0 (0.0)
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Temporal	Egg	2 (0.18)	4 (0.36)	5 (0.45)
	Nymphal/adult	11 (0.23)	37 (0.77)	0 (0.0)
	Total	13 (0.22)	41 (0.69)	5 (0.09)

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cordgrass leaves in well-defined patches over a 2-day period. Plants were exposed to searching *A. delicatus* in the field for a 3-day period and then returned to the lab. This procedure permitted accurate estimates of parasitism and was repeated on 20 separate occasions to account for any temporal variation in parasitism. Despite these precautions, we still found no evidence for density dependence, a result that corresponds closely with observational data collected by Stiling and Strong (1982a) and Strong (1989). We suggest that the observational data reviewed in this chapter can provide valid inferences about density relationships and that the results of the reviews should not be lightly dismissed.

TEMPORAL PATTERNS

Temporal density independence was the pattern most frequently observed among the 58 available comparisons (Table 11.4). Sixty-nine percent of these studies showed no density dependence, whereas 22% showed direct density dependence and 9% revealed inverse density dependence. Of those 18 significant responses, only 4 showed significant serial correlations among sample densities (Table 11.3). Three come from egg parasitoids and one from a nymphal-adult parasitoid. Because omission of these studies from subsequent analysis would only further magnify the preponderance of nonsignificant responses, we elected to include them. The proportion of significant temporal responses was significantly lower than that found in Stiling's (1987) review for all insect parasitoids (Fisher's exact test, $P = 0.008$). Among the Auchenorrhyncha, egg parasitoids showed more significant responses (63%) than did nymphal/adult parasitoids (23%) (Fisher's exact test, $P = 0.011$). Again, the difference between egg and nymphal/adult parasitoids is difficult to explain with the data at hand. Bias, however, may have been introduced into this analysis because 40% of the egg parasitoid data are from one host–parasitoid interaction (*P. marginata* and *A. delicatus*), which represented three of the five inverse responses. Other forms of bias may be introduced if host and parasitoid species are represented by multiple comparisons. In any event, this result corresponds with the evidence from the spatial data that egg parasitoids more often exhibit significant responses to host density.

Hassell et al. (1989; see also Solow and Steele 1990) have recently argued that the preponderance of density independence in temporal studies may simply be the result of the short duration typical of most analyses. They argue that as the experimental period increased, so did the probability that a significant density response would occur. We categorized the temporal data from Table 11.3 by duration (<1, 2, 3, 4, and >5 years) and plotted the proportion of reports in each category of a significant density response. We

found that, as the duration of the study increased, significant density patterns became more likely (Fig. 11.3), but much of this pattern is driven by the low proportion of density responses for studies of less than 1 year. Beyond 1 year, the proportion of density responses is not strongly affected by time.

The data from our review of the literature do not provide strong support for stability due to simple point equilibrium of host–parasitoid interactions. However, environmental variability, lack of statistical power, and the short duration of these studies may be obscuring density-dependent patterns of parasitism (Hassell 1985a, 1986a, 1987; Hassell et al. 1989; but see Mountford 1988). Before we can draw any sound conclusions about the universality of density-dependent processes in the Auchenorrhyncha, more detailed studies will have to be performed. In particular, long-term studies involving a hierarchy of spatial scales can be most informative. In addition, experimental studies manipulating hosts such as those by Ôtake (1967), Sasaba and Kiritani (1972), Becker (1975), and Cronin and Strong (1990a) would help ferret out any underlying density dependence in natural populations. Until studies like these can be performed, the controversy surrounding the role of density dependence in population regulation will remain unresolved.
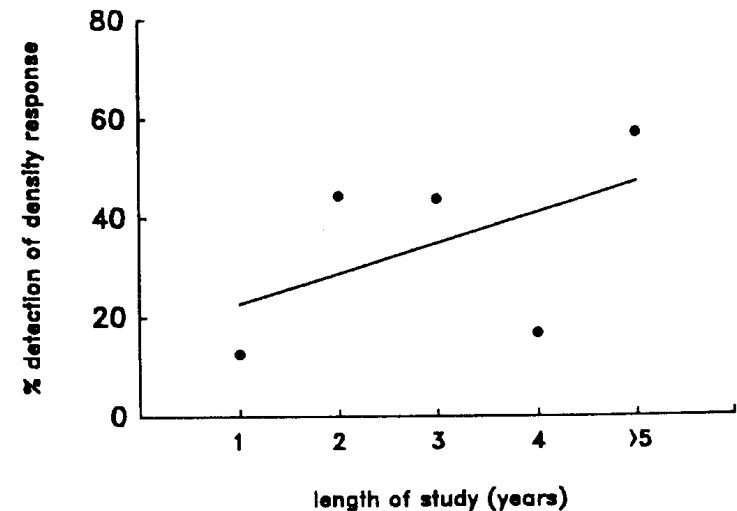

Figure 11.3. The relationship between the length of study and the probability of detecting a significant response of parasitism to host density (density dependence and inverse density dependence). Data were angular transformed and weighted by the inverse of the variance ($1/4n$, where n = number of studies in that time period). Line fit by least squares regression ($R^2 = 0.42$, $P < 0.001$).

Heterogeneous Parasitism Rates and Stability

The proponderance of cases of spatial density independence (74%) found in our review of the Auchenorrhyncha is not *prima fascie* evidence for the instability of planthopper- and leafhopper-parasitoid interactions. Many of these density-independent relationships are characterized by high variance in parasitism rate per host patch, which is considered to be a powerfully stabilizing force (Hassell 1985b; Chesson and Murdoch 1986). Recently, Pacala et al. (1990) and Hassell et al. (1991) have provided a general criterion, the $CV^2 > 1$ rule, for determining whether sufficient heterogeneity in parasitism exists to theoretically stabilize the host-parasitoid interaction. In their review, Pacala and Hassell (1991) found that 9 of 34 case studies exhibited sufficient heterogeneity to satisfy the $CV^2 > 1$ rule. For eight of these nine cases, the principal source of heterogeneity was density-independent.

We do not evaluate the role of heterogeneous parasitism rates in stabilizing all 31 case studies in Table 11.2 (see below). Instead, we exemplify the CV^2 approach with a parasitoid whose biology and ecology is most familiar to us: the fairyfly *A. delicatus*. J. D. Reeve, J. T. Cronin, and D. R. Strong (unpublished data) estimated the CV^2 from data on *A. delicatus* parasitism obtained in Strong (1989) and Cronin and Strong (1990a). On 24 of 28 sampling dates, the CV^2 exceeded 1 (14 were significantly greater than 1), and over all dates averaged 3.34 ± 0.78 ($\pm$ 1SE). Because parasitism was independent of host density in these data (Table 11.2) the source of heterogeneity was also density-independent. However, stability, in a theoretical sense, is not proved in this example. A critical assumption of the stability criterion is violated: The life cycle of *P. marginata* and *A. delicatus* are not completely synchronous. Asynchronous development tends to destabilize host-parasitoid interactions and generally requires heterogeneity (CV^2) greater than 1 to stabilize the interaction (Godfray and Hassell 1989; J. D. Reeve, J. T. Cronin, and D. R. Strong unpublished data).

Serious consideration of the heterogeneity in parasitoid foraging is an important advancement in the study of host-parasitoid interactions; it may well prove to be an important cause of stability. However, the $CV^2 > 1$ rule for evaluating the contribution of heterogeneity to stability must be used judiciously. The assumptions of random parasitoid search and oviposition within a patch, discrete nonoverlapping host and parasitoid generations, and synchronous host and parasitoid development must be met before the $CV^2 > 1$ rule for stability can be considered valid. The robustness of this stability criterion is largely unexplored with respect to deviations from most of these assumptions. Unless we are certain the assumptions are met, or until we more fully understand the consequence of violating these as-sumptions, the CV^2 rule may be of little practical use. We, therefore, advise a fundamental understanding of host-parasitoid biology and parasitoid foraging behavior **before** a test of the stabilizing effect of heterogeneity is considered. In light of the paucity of these kinds of data for host-parasitoid systems listed in Table 11.2, we decline to evaluate the stability criterion for these systems.

Refugia from Parasitism

We have already mentioned that aggregation of parasitism produces a partial refuge in which some hosts may escape parasitism and that this process can confer stability on the host-parasitoid interaction or prevent extinctions (Murdoch et al. 1989). Many other types of refugia can exist in natural populations that confer some protection from parasitism. In general, any biological or physical factor that makes the host species less vulnerable can contribute to the stability of the system (Bailey et al. 1962; Murdoch and Oaten 1975; Hassell 1978; but see McNair 1986). Such factors as host size, age, and distribution can act as refuges from parasitism, as can physical refugia.

Some planthopper hosts are relatively invulnerable to parasitism beyond a certain developmental stage. May (1971) found that *A. stenocrani* completely avoids parasitizing *Stenocranus minutus* (Fabricius) eggs later in development. In addition, Cronin and Strong (1990b) found that successful parasitism of host eggs declined with egg age; well-developed eggs produced almost no offspring. Ôtake (1968) found more subtle differences with hosts age; parasitoid development was simply protracted in older hosts. Size-dependent parasitism (which is often correlated with age) has also been documented. Greathead (1970) found that parasitism by the strepsipteran *Halictophagus pontifex* Fox increased with the size of its cercopid host, allowing smaller hosts to be relatively free of parasitism. Not only would host age or size provide a refuge from parasitism, but it may also reduce a parasitoid's efficiency and/or increase handling time, by causing parasitoids to waste eggs or time on an invulnerable developmental stage or size class (Walde et al. 1989). Both could contribute to the stability (or persistence) of the system.

Environmental factors have also contributed to the protection of planthoppers from their parasitoids. These refugia either exclude natural enemies from the host habitat or interfere with or prevent the detection of the host. Stiling and Strong (1982a), for example, found that host eggs of *P. marginata* were concentrated in the basal portions of their cordgrass host, whereas parasitism by *A. delicatus* was concentrated in the apical leaves. They argued that, as a result of the tides, basal leaves were more protected

from parasitoids because they were submerged for longer periods of time. Tides, then, could effectively reduce the time available for parasitizing the abundant hosts at the basal portions of the plant, which could lead to the inverse pattern of parasitism found by Stiling and Strong (1982a). Recently, however, Roderick (1987) concluded that the tides had little effect on parasitism rates in a California salt marsh. More information will be needed to determine the importance of tidal inundation as a refuge from parasitism. Tay (1972) also found distributional differences of the cicadellid *Cicadella viridis* within its host plant *Juncus* that were similar to those found in the salt marsh. Leafhoppers were concentrated low on the Juncus stems, and egg parasitism in these areas was much lower than at the stem tips. A similar situation was found by Arzone (1974). Either parasitoids do not search as often near the ground or they are less effective at high host density (inverse density dependence); either way, a partial refuge is created. Differential susceptibility of hosts to parasitism within different microhabitats of the host plant appears to be a relatively common phenomenon among parasitoid species (Lawton 1986).

There is also evidence that the host plant can confer some protection from parasitoids. Parasitoids may locate hosts by first cueing in on the host plant (Price et al. 1980; Vinson 1981). Hosts on plants that are outside of the sensory range of a parasitoid would, therefore, be overlooked. Hosts on different plant species may also come to differ markedly in quality through ingestion of secondary metabolites (Vinson 1976, 1981; Price et al. 1980; Gibson and Mani 1984; Barbosa 1988), which can influence the host selection process. Abdul-Nour (1971) found that the strepsipteran *Halictophagus languedoci* in grasslands attacked a complex of leafhoppers that fed on the grass *Brachypodium phaenicoides* but did not attack those feeding on either *B. ramosum* or *Bromus erectus*, even though host plants occurred within the same localized habitat. In common garden experiments, A. M. Rossi, J. D. Reeve and J. T. Cronin, (unpublished data) found that parasitism of *Carneocephala floridana* eggs by *Gonatocerus* sp. was significantly higher on grasses (*S. alterniflora* and *Distichlis spicata*) than on herbaceous perennials (*Salicornia virginica* and *Borrichia frutescens*). Whether variations in host susceptibility result from differences in plant nutrition that affect leafhopper quality, and ultimately parasitoid quality, or from differences in parasitoid foraging behavior among host plants is not known. Regardless of the cause, the less-susceptible host plants act as a partial refuge from parasitism.

The plant may also function as a refuge by limiting access of searching parasitoids to their hosts. For example, host eggs that are buried deep within stems, leaves, or buds may escape attack from egg parasitoids that have ovipositors too short to reach them. Planthoppers that can insert eggs

deeper into the plant tissue may be relatively immune from attack by a larger portion of the parasitoid population. Host-species differences in the placement of eggs apparently result in different parasitoid complexes attacking each species (Claridge and Reynolds 1972; Ali 1979). Settle and Wilson (1990) demonstrated that parasitism of the grape leafhopper is higher than that of the variegated leafhopper because the former's eggs are more readily detected by foraging *Anagrus epos*. The greater depth at which variegated leafhopper eggs are buried is presumably the cause of their reduced detection. Intraspecific differences in susceptibility to parasitoid attack have also been found. Raatikainen (1967) found that *Javesella pellucida* eggs in cereal stems were invulnerable to attack by *A. atomus*, whereas eggs in leaf blades incurred high levels of parasitism. In oats, thin-walled stems had a higher incidence of parasitism than thick-walled stems, suggesting an inability of the wasp to detect or gain access to more deeply concealed hosts. We, on the other hand (Cronin 1991; Cronin and Strong unpublished), find that the host plant provides no physical barrier to *A. delicatus* searching for *Prokelisia* spp. eggs concealed within the leaf. Even the wasps with the shortest ovipositors had free access to the most deeply embedded host eggs. We are aware of no other studies that have considered differential susceptibility of individual planthoppers or leafhoppers within a population to their natural enemies. However, the phenomenon has been found among other host–parasitoid systems involving such diverse groups as gall-making and other endophytic flies (Weis 1983; Price and Clancy 1986; Weis and Abrahamson 1985; Price 1988; Romstöck-Völkl 1990), moths (Graham and Baumhofer 1927; Cronin and Gill 1989), and bark beetles (Ball and Dahlsten 1973).

The potential for refugia among the Auchenorrhyncha is certainly much greater than the evidence at hand would suggest. Few researchers have explicitly considered looking for refugia in their field studies, and the necessary experiments needed to identify them have rarely been performed. Because a refuge can exist in so many different forms and can have a large effect on the stability and/or persistence of host–parasitoid populations, more emphasis should be placed on experimental testing for mechanisms of escape from parasitism.

Role of Alternate Hosts in Host–Parasitoid Stability

A broad host range can contribute significantly to the persistence and stability of host–parasitoid systems. When densities of preferred hosts fall to low levels, polyphagous parasitoids can switch (not necessarily exclusively) to more abundant alternate hosts. This frequency-dependent switch-

ing from one host to another should result in a Type III, sigmoid functional response (Murdoch 1969; Hassell 1978). Because a host and its parasitoid are less coupled and because of the parasitoid's broader diet, time delays should be absent from the functional response (Murdoch and Oaten 1975). In the absence of time delays, a Type III response can be strongly stabilizing because mortality can be directly density dependent (Hassell 1986b). In essence, a broader host range can buffer the parasitoid population against fluctuations in the abundance of hosts. When one host becomes locally extinct because of local catastrophes or simply seasonal changes in abundance of susceptible host stages, alternate hosts may be the only means by which a parasitoid can persist. That is to say, not only can alternative hosts contribute to population stability, but more fundamentally, they can allow parasitoid populations to persist.

Host records for the parasitoids of planthoppers and leafhoppers are largely incomplete and, therefore, probably reflect an underestimate of the degree of polyphagy among these parasitoids. Existing records suggest that the egg parasitoids of the Auchenorrhyncha are relatively monophagous or oligophagous (Waloff and Jervis 1987). Data from the Mymaridae suggest that the oviposition site of the host is an important determinant of whether an egg will be parasitized (Claridge and Reynolds 1972; Ali 1979). Claridge and Reynolds (1972) suggested that *Polynema euchariforme* and *P. bakkendorfi* were restricted in host range by the oviposition sites of their *Oncopsis* hosts. *Polynema euchariforme* was restricted to eggs of host species that were laid deep within birch buds, whereas *P. bakkendorfi* was restricted to hosts that laid eggs closer to the surface. Similar results were found by Ali (1979) with *Anagrus* spp. In support of host site specificity, Ali (1979) found that some *Anagrus* spp. rejected oviposition sites of unnatural hosts but accepted these unnatural hosts when they were placed among eggs of their natural hosts. Successful development was possible from these unnatural host species, although survival of offspring was not always as high (Ali 1979; Walker 1979). Monophagy may be the rule among egg parasitoids, but until more complete records can be obtained and the taxonomy of the Mymaridae improved (Huber 1986), we must view this statement with some skepticism.

Polyphagy appears to be the rule among the Pipunculidae, Strepsiptera, and Dryinidae (Waloff and Jervis 1987). For example, in a grassland community, Waloff (1975) and Waloff and Thompson (1980) found that the majority of parasitoids were generalists. In woodland forests of South Wales, Jervis (1980) found that all five pipunculids and three of the four dryinids that attack the typhlocybine leafhoppers were polyphagous. The polyphagy appears to extend to one host family, which appears to be a general pattern among nymphal/adult parasitoids; few exceptions exist (Waloff and Jervis

1987). In addition, few of these parasitoids are restricted to attacking hosts on a single plant species (Waloff and Jervis 1987).

A number of studies involving the Auchenorrhyncha suggest the importance of alternative hosts for the persistence and stability of host–parasitoid interactions. Evidence for frequency-dependent host selection comes from the studies by Whittaker (1971, 1973) in grasslands of southern England. When the cercopid *Neophilaenus lineatus* was more abundant than the alternate host, *Philaenus spumarius*, it incurred higher rates of parasitism by the pipunculid *Verrallia aucta* (Fig. 11.4). In years when *P. spumarius* was more abundant, it incurred higher rates of parasitism. This switching between hosts involves switching habitats as well because the two hosts feed on different plant species. Adult mortality of both host species was density-dependent when the effects of the pipunculid were included, and the degree of density dependence was greatest when the two species were treated together (Whittaker 1973). This result led Whittaker (1973) to conclude that populations of *P. spumarius* and *N. lineatus* were more stable in the presence of each other than when occurring alone.

A classic example of the importance of alternative hosts in host–parasitoid interactions comes from the agricultural literature on the pests of
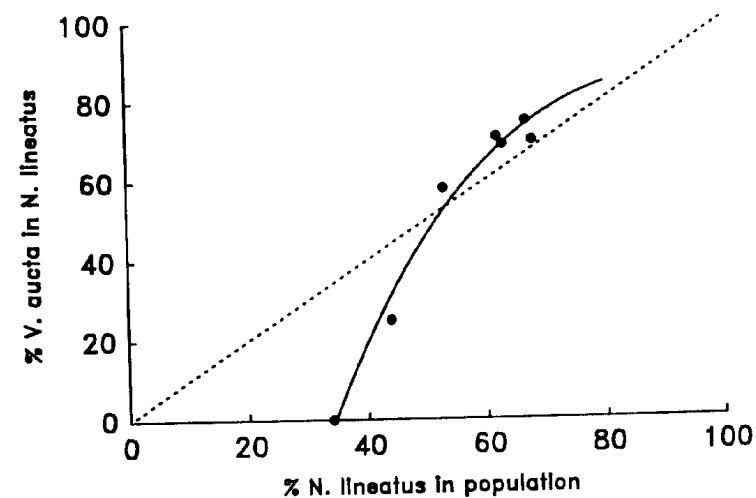

Figure 11.4. Host switching behavior by the pipunculid *Verrallia aucta* between its two cercopid hosts, *Neophilaenus lineatus* and *Philaenus spumarius*. Percentage of *V. aucta* in *N. lineatus* is greater than expected on the basis of random foraging (straight line) in years when *N. lineatus* is most abundant. In years when *N. lineatus* is rare (< 50%), the parasitoid is underrepresented in this host. Data are from Whittaker (1973), and switching curve is fit by eye.

grapes in California, USA. The grape leafhopper, *Erythroneura elegans*, became a serious pest of the Old World grape, *Vitis vinifera*, soon after the grape's introduction into the New World in 1781. The leafhopper's eggs are attacked by the mymarid *Anagrus epos*, which has significantly contributed to the control of this pest. The success of this parasitoid in controlling the grape leafhopper is directly tied to the availability of its alternative host, *Dikrella cruentata*, which feeds on wild *Rubus* spp. (Doutt and Nakata 1965, 1973; Williams 1984). As temperatures warm in the spring and grape leafhoppers resume egg laying, *A. epos* numbers respond rapidly. By late summer, parasitism rates can reach levels greater than 90%. During late fall and winter, adult leafhoppers cease oviposition and undergo reproductive diapause. The wasps do not undergo diapause, and grape leafhopper eggs are absent during the winter months (Doutt and Nakata 1973). In winter, *A. epos* parasitizes only *D. cruentata*, whose eggs can be found year round. Parasitism of this alternative host in northern California is temporally density-dependent (Williams 1984), as might be expected when frequency-dependent host selection occurs (Hassell 1978, 1986b).

It is clear from the above data that both host species are necessary for *A. epos* to utilize the large populations of the grape leafhopper. A number of other studies implicate the lack of synchronization (the presence of a suitable host developmental stage) as a cause of host switching (Raatikainen 1967; Claridge and Reynolds 1972; Waloff 1975; Hulden 1984). Jervis (1980), on the other hand, found little evidence that polyphagy among dryinids and pipunculids of typhlocybine leafhoppers was the result of poor synchronization with one or several hosts. Suitable stages (nymphs and adults) of all host species were available during periods when foraging parasitoids were active. Instead, he suggested that host range was delimited by discriminative oviposition or defensive behavior of nymphs, among other things.

There is little doubt of the importance of these alternative hosts in buffering parasitoid populations against potential extinction. However, support for the role of alternative hosts in contributing to interaction stability is mostly anecdotal. More detailed analyses of the regulatory power of parasitoids on their entire host ranges are needed.

Parasitoid Dispersal

There is little question that parasitoid dispersal contributes to the persistence of the interactions between the Auchenorrhyncha and their parasitoids. Evidence from the importance of alternate hosts to polyphagous par-

asitoids have already demonstrated this point. *Anagrus epos* must disperse from vineyards (Doutt and Nakata 1965, 1973), and *A. atomus* must disperse from oat fields in search of suitable overwintering hosts (Raatikainen 1967). Some parasitoids travel great distances in search of suitable host habitats. An example is the egg parasitoid *A. delicatus*, which regularly disperses up to several kilometers in search of new hosts (Antolin and Strong 1987; Cronin unpublished data). Several other examples exist that document the dispersiveness of parasitoids of leafhoppers and planthoppers (Ôtake 1970, 1976; Raatikainen 1972).

The role of dispersal has been addressed in the context of formal stability models. In the simplest abstract models without environmental variability, migration among spatially subdivided units of a population has either no effect or even a detrimental one on stability (Allen 1975). Introducing some forms of environmental variability and the notion of "nonequilibrium coexistence," Caswell (1978) showed how the disturbance caused by a predator could greatly prolong the coexistence of unstable combinations of competitors. For predator–prey and parasitoid–host models, perhaps the major key to persistence of deterministically unstable interactions is desynchronization of subpopulations; local populations that go extinct are refounded by immigrants (Crowley 1981; Nachmann 1987). In the metapopulation model, local extinctions must be complemented by other, extant subpopulations that can supply immigrants. Reeve (1988) has elaborated this principle in hybrid, equilibrium with nonequilibrium, modeling, showing how greatly the relative levels of dispersal and environmental variability can affect persistence of subdivided populations. Persistence of unstable ensembles of subpopulations can be greatly enhanced when variability caused by environmental stochasticity is complemented by low to moderate rates of migration among subpopulations. This is to say that groups of local populations, which would all become extinct if isolated, can persist if they are sufficiently desynchronized.

There is a long tradition in ecology of verbal–graphic models that rely on dispersal for the long-term persistence of parasitoid–host populations (Andrewartha and Birch 1954; den Boer 1968; Reddingius and den Boer 1970; Roff 1974a, 1974b). Population dynamics are much affected by random external forces that generate extinction and asynchrony among subpopulations. Predation, parasitism, and the weather act in a nonregulatory fashion to depress population densities and can cause local extinctions, but because subpopulations are no longer synchronous, extinction of the metapopulation (the collection of subpopulations) is rare. Vacant patches are eventually recolonized by individuals dispersing from nearby local subpopulations. The fitness of organisms in this type of environment could be

increased by dispersal among a number of subpopulations, that is, by "spreading the risk" of extinction among a number of host patches (den Boer 1968).

Such a situation appears to exist among populations of the salt marsh-inhabiting delphacid *P. marginata* and its mymarid egg parasitoid *A. delicatus* (Strong 1988; Cronin and Strong unpublished data). Hosts are dispersed among many discrete patches of salt-marsh cordgrass, isolated as a result of man-made development, erosion, and the physical contour of the marsh. In addition, oyster bars and islands along the Gulf coast of north Florida contain populations separate from those on the mainland. Among these heterogeneous islands, planthopper population densities and net reproductive rates differ from island to island (Strong et al. 1990). Although extinctions can be difficult to document absolutely, evidence does suggest that island populations occasionally approach extinction of hosts and parasitoids (Antolin and Strong 1987; Strong unpublished data). Recolonization of vacant island habitats occurs by the regular dispersal of both macropterous adult planthoppers and female parasitoids (Strong and Stiling 1983; Antolin and Strong 1987).

Evidence for risk spreading by *A. delicatus* in such a variable environment comes from their pattern of oviposition in host patches (Cronin and Strong unpublished data). In nature, parasitoids lay only a small fraction of their eggs in patches containing abundant hosts. An average of two eggs were laid per parasitoid per leaf containing experimentally placed host eggs, and then wasps dispersed. This low number of eggs laid per host patch is not the result of egg depletion or sperm limitation, nor is it related to the density of hosts per leaf. In the laboratory, time on a patch prior to dispersal is quite variable but also independent of host density. Dispersing wasps are very adept at locating new host patches, even at long distances within the marsh. At least a few wasps locate experimentally isolated host patches (> 300 m from other hosts) within just a few days and can cause high per capita rates of parasitism (Antolin and Strong 1987; Cronin and Strong unpublished data). Submaximal oviposition rates coupled with frequent bouts of dispersal, despite the presence of abundant hosts, appear to be a common feature of this system and fit well within the framework of risk-spreading theory. Presently, we have no data on the risks involved in remaining and ovipositing within a single or few host patches, but the data would suggest that there has been strong selection against such a strategy. A risk-spreading strategy, in concert with weakly stabilizing factors such as mutual interference (Fig. 11.2D), and heterogeneous parasitism can contribute greatly to long-term persistence of the *P. marginata–A. delicatus* interaction.

Discussion and Conclusions

Data on the ecology of the Auchenorryncha are presently incomplete. Only limited evidence exists that addresses the regulatory power of the parasitoids of planthoppers and leafhoppers, and the data are equivocal. Most evidence comes from an analysis of the spatial and temporal relationship between host density and parasitism from field collections of hosts. More than 70% of the studies reviewed found density independence, and an additional 10% found inverse density dependence, leaving only about 20% of the studies that showed some regulatory power. This is probably a slight underestimate of the importance of density dependence because of low sample sizes, short durations of study, and environmental noise, all of which could bias results toward density independence. However, if density dependence exists in these populations, it is probably a weak stabilizing force in the face of other environmental factors.

A myriad of other factors can contribute to the overall stability of planthopper–parasitoid interactions, despite any or all being weak forces. Parasitoid interference, heterogeneous parasitism, the presence of refugia, alternate hosts, and alternate strategies of risk spreading can all contribute toward the long-term persistence of natural populations. For example, in *A. delicatus*, parasitoid interference or heterogeneous parasitism rates may weakly contribute to the regulation and stability of the system, but neither alone is likely sufficient to cause host–parasitoid persistence. The presence of an invulnerable developmental stage (Cronin and Strong 1990b), the availability of alternate hosts (*Prokelisia dolus*), and an apparent risk-spreading strategy (Strong 1988; Cronin and Strong unpublished data) can act together with these weak regulatory mechanisms to provide strong population stability. This situation probably exists in other planthopper systems where no strong regulatory role is played by their parasitoids.

Until more critical experiments are performed on the ecology of planthopper–parasitoid interactions, we can only speculate as to the role parasitoids play in stabilizing host populations. We need to progress beyond basic sampling programs that provide only indirect data on parasitoid behavior, through estimates of rates of parasitism. Only long-term manipulative field experiments, spanning many generations and spatial scales, will aid in resolving the controversy of the regulatory power of parasitoids. Experimental studies of the dynamical behavior of parasitoids within host patches will be most useful in providing information on the broad-scale effects of parasitism on population persistence. Patch-level studies can reveal information on the host location and selection process, presence of refugia, patterns of parasitoid foraging behavior, and so on. Such an ap-

proach has been fruitfully employed by Kareiva and Odell (1987) in their study of the role of coccinellids in controlling their aphid prey. Without such studies, we will not be able to further our understanding of the role of parasitoids in the population dynamics of their planthopper and leafhopper hosts.

Summary

1. Parasitoids are common natural enemies of planthoppers and leafhoppers and often contribute substantial mortality to host populations. High mortality in itself does not, however, provide evidence for population regulation or control.

2. We review the interactions between the Auchyenorrhyncha and their parasitoids in terms of their effect on stability or population persistence. Our review concentrates on parasitoid searching behavior and the spatial and temporal patterns of parasitism with respect to host density.

3. Direct studies of paratisoid functional response and interference are few and provide equivocal evidence for the regulatory power of parasitoids. On the other hand, spatial and temporal relationships between host density and parasitism are predominantly density independent (> 70% of the studies reviewed), indicating no or weak regulation by parasitoids.

4. Other potentially stabilizing factors, such as heterogeneous parasitism rates, the presence of refugia for hosts, host switching by parasitoids, and less traditional nonequilibrial strategies by parasitoids, have received very little consideration.

5. The critical data needed to assess the regulatory power of planthopper and leafhopper parasitoids are largely unavailable. It is imperative that long-term manipulative field experiments over many generations and spatial scales, coupled with detailed examination of parasitoid searching behavior, be performed if we hope to resolve this issue.

12

Transmission Biology, Vector Specificity and Evolution of Planthopper-Transmitted Plant Viruses

Lowell R. Nault

Introduction

Special attention has been paid to a number of planthopper species because of the impact they have on crop production. Few would argue that one of the best studied planthoppers, *Nilaparvata lugens* (Stål), is also one of the world's most destructive insects. Each year, *N. lugens* causes more than $1.23 billion in losses to rice in Southeast Asia (Herdt 1987). These losses are caused by damage from feeding injury and by plant viruses transmitted by the planthopper. *N. lugens* is one of more than two dozen planthopper species known to transmit plant pathogens.

No book on planthoppers would be complete without a discussion of their role as vectors. This coverage of the subject mainly is limited to transmission of the plant viruses because currently little is know about the vector–pathogen relationships of planthopper-transmitted, mycoplasma-like organisms. The chapter is written with two groups of scientists in mind. The first is insect biologists, including those familiar with planthoppers, who do not have a background in plant virology. The second is virologists and plant pathologists unfamiliar with the biology of planthoppers and their homopteran relatives. Accordingly, in this chapter the characteristics of plant virus groups that have planthopper vectors are reviewed and the mechanisms by which planthoppers transmit them are discussed. My discussion on vector specificity is founded on this understanding of transmission mechanisms. The origin and evolution of planthopper-transmitted viruses are also speculated. Finally, a discussion of why planthoppers are ill-suited to transmit some plant viruses and better-suited to transmit others