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RESOURCE AVAILABILITY AND PARASITOID ABUNDANCE IN THE ANALYSIS OF HOST-PARASITOID DATA

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 David W. Williams^{1,3}

Population models have suggested that host regulation by natural enemies is achieved by the density-dependent response of natural enemies to temporal and spatial changes in host density. However, surveys of insect host-parasitoid systems (Morrison and Strong 1980, Dempster 1983, Stiling 1987) indicate that few field studies provide unambiguous evidence of density-dependent relationships. It has been argued that density dependence may be obscured by various behavioral and stochastic elements involved in the interaction, rendering our methods for its detection inadequate (Morrison and Strong 1980, Stiling and Strong 1982, Hassell 1985, Lessels 1985, Morrison 1986, Stiling 1987, Price 1988). Hassell (1985) has suggested that the regulatory role of natural enemies may be detected by examining the relationship between the per capita searching efficiency and parasitoid density. The per capita searching efficiency is calculated as:

$$A = (1/P)\log_e(N/S) \quad (1)$$

where P is the abundance of searching parasitoids, N is the number of susceptible hosts, and S is the number of hosts surviving (not parasitized). A major problem with this method, however, is the difficulty in determining the abundance of the parasitoid population. In this note, we examine the relationship between a leafhopper species and its egg parasitoid and, using Hassell's suggestion, investigate the relationship between parasitoid searching efficiency and per capita host abundance. Because parasitoid adult density was not measured directly, the number of searching parasitoids was estimated from the number of parasitoid immatures occurring earlier.

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Methods

Anagrus epos Girault (Hymenoptera: Mymaridae) is a solitary endoparasitoid that develops in the eggs of the blackberry leafhopper, *Dikrella californica* (Lawson), and of the grape leafhopper, *Erythroneura elegantula* Osborn. Its adults have a mean life-span of 3–4 d (range: 1–8 d) and a total fecundity of 10–20 eggs (Williams 1984). *D. californica* is commonly found on wild blackberry in riparian habitats throughout California. *E. elegantula* is found on wild grape in riparian habitats and, more commonly, on cultivated grape in commercial vineyards where it can cause serious damage. *A. epos* is an effective biological control agent of *E. elegantula* in commercial vineyards, maintaining the leafhopper populations below damaging levels throughout the growing season (Doutt and Nakata 1973). All three species are native to California.

Williams (1981, 1984) performed field studies from 22 January 1979 through 1 February 1980 to investigate the interaction between *A. epos* and *D. californica* on wild blackberry (*Rubus procerus* Mueller) in a riparian habitat in central California (wild grape and *E. elegantula* were not present at this site). *D. californica* egg abundance was monitored by removing blackberry leaves taken at random throughout the canopy. Before May 1979, each sample consisted of 10–20 compound leaves; after May 1979, 120 terminal leaflets were removed. Leaf samples were obtained every 2 wk (monthly during the winter months). Eggs were dissected from the leaf tissue under a microscope and identified as unparasitized or containing a 1st-instar parasite larva, 2nd-instar parasite larva, parasite pupa, or fully formed, unemerged parasite adult (Williams 1984).

The egg-to-adult developmental period of *A. epos* is 244.5 degree-days (base 7.16°C) (Williams 1984). M. S. Moratorio (1977 and *personal communication*) determined the relative proportion of development for immature *Anagrus silwoodensis* Walker, a species of whose biology is similar to *A. epos*. Based on these data, the period of development from oviposition to the mid-point of the 1st-instar, 2nd-instar, and pupal stages was 110, 220, and 370 degree-days (base 7.16°), respectively.

Adult parasitoid abundance was estimated as follows. The abundance of each immature stage was plotted on a physiological time scale (degree-days) (e.g., Fig. 1). Interpolating linearly between data points, the number of adults at time t was estimated as the sum of the number of 1st instars 330 degree-days earlier, of 2nd instars 220 earlier, of pupae 70 earlier, and of unemerged adults 20 earlier. This value estimates the total number of adults at each sample date. Few dead immature parasitoids were found in dissected host eggs,

and thus we assumed no immature mortality. The study area was large enough to account for movement throughout the plant canopy; migration into and out of the study area was not measured. The sex ratio of adults reared from field-collected hosts was 52% female (Williams 1984); therefore the number of searching adults was estimated as one half the total number of adults. This method would not be appropriate for parasitoid populations whose period of adult activity is longer than a few days.

On any sample date our best estimate of parasitoid success was the number of host eggs with 1st-instar larvae, which occurred ≈ 110 degree-days following oviposition. As a result, the number of searching adults and the number of susceptible hosts (total eggs minus eggs with 2nd-instar and older parasitoids) were estimated as their abundance 110 degree-days prior to each sample date.

Results and Discussion

The seasonal abundance of susceptible leafhopper eggs and host eggs with 1st-instar parasitoids showed two peaks (Fig. 1). Parasitism during the first peak was low, but was higher during the second peak. Plotting the percentage of parasitism against host density shows no clear relationship (Fig. 2A). In contrast, parasitism as a function of the number of hosts per parasitoid shows a distinct pattern (Fig. 2B). When the per capita resources were low, the proportion of hosts parasitized was variable. Since host eggs on a leaf are not clumped, some parasitoids may have left the leaf before all eggs were found. When there were >4 hosts per parasitoid, all observed rates of parasitism were $<35\%$. Thus, by normalizing host density as the number of hosts per searching parasitoid, the data show a clear inverse density-dependent relationship. Using Eq. 1, we calculated

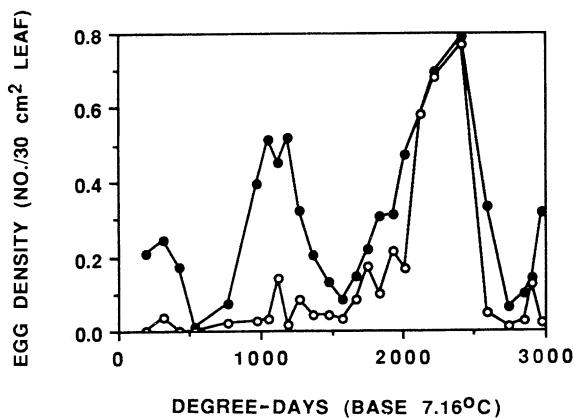


FIG. 1. Temporal variation in *Dikrella californica* egg density (● susceptible eggs; ○ parasitized eggs). All values are standardized to 30-cm² leaf area.

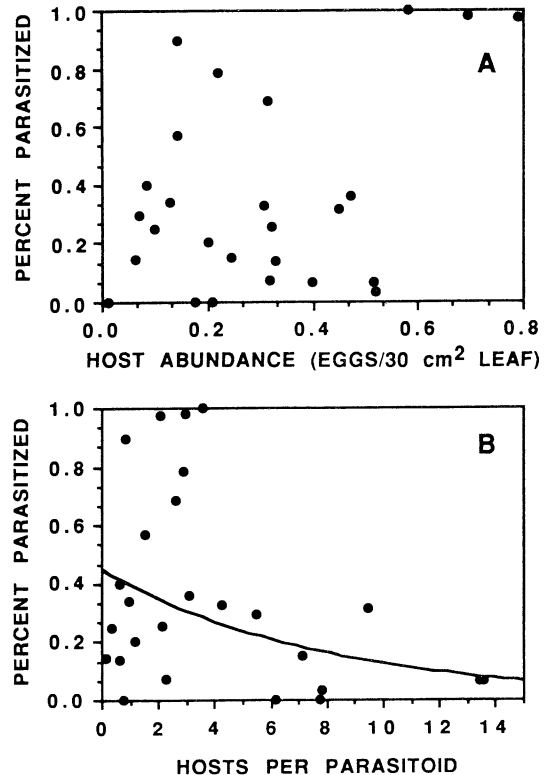


FIG. 2. A. Relation between proportion of eggs parasitized and the number of susceptible host eggs per 30 cm² leaf area. B. Relation between proportion of eggs parasitized and the number of susceptible hosts per adult parasitoid per 30-cm² leaf area: $Y = 0.4492 \cdot 10^{(-0.1106 \cdot X)}$, $r^2 = 0.26$, $P < .02$.

the searching efficiency of the adult parasitoid population for each sample date. Plotting searching efficiency against parasitoid abundance reveals a decrease in efficiency with increasing parasitoid abundance (Fig. 3). This suggests that the density-dependent relationship is primarily in terms of resources available per capita exploiter (hosts per parasitoid) rather than in terms of the total resources (hosts) available (see Getz 1984, Arditi and Ginzburg 1989).

The intention of this note is not to draw conclusions concerning the density-dependent relationships in this system, or to debate which mechanisms are the most important in determining the persistence of host-parasitoid interactions. Rather, we wish to restate Hassell's (1985) suggestion that the dynamics of host-parasitoid systems may be better understood by investigating the per capita relationships between the parasitoid population and its host or, more generally stated, the resources available per capita exploiter (Getz 1984). Our analysis of the *A. epos*-*D. californica* interaction reveals a striking decline in parasitoid searching efficiency with increasing parasitoid density (Fig.

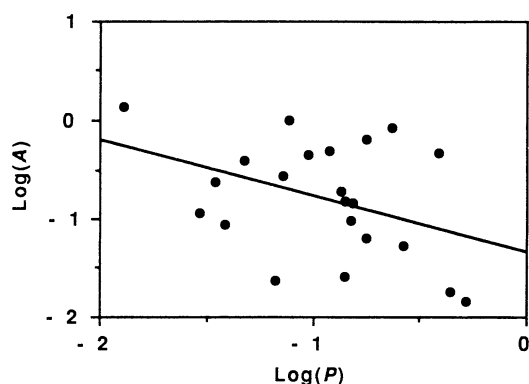


FIG. 3. Relationship between \log_{10} searching efficiency (A) and \log_{10} parasitoid abundance (P): $Y = -0.1620 - 0.5647 \cdot X$, $r^2 = .16$, $P < .07$.

3). Hassell (1985) has already pointed out that such declines in parasitoid searching efficiencies can be stabilizing. It remains to be seen how common these sorts of patterns are, and what behavioral mechanisms underlie reduced parasitoid efficiency with increasing numbers of parasitoids per host.

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EARLY 19TH-CENTURY FIRE DECLINE FOLLOWING SHEEP PASTURING IN A NAVAJO PONDEROSA PINE FOREST

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Pattern in ponderosa pine (*Pinus ponderosa* Laws.) forests in the American Southwest is significantly influenced by fire (Cooper 1960). The fire-scar record in

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tree rings reveals that the occurrence of fire has been greatly reduced throughout the region in the past century (Swetnam, *in press*). Many authors have argued that this decline was caused by dramatic land-use changes associated with European settlement in the last two decades of the 19th century (Weaver 1951, Cooper 1960, Biswell et al. 1973, Dieterich 1980a, Madany 1981). Herd numbers of domestic grazing animals, particularly sheep, rose steeply in the Southwest at that time (Bailey and Bailey 1986). Intense grazing removed the grass that had fueled light, episodic surface fires. After grazing herds dwindled in the 20th century, active fire-suppression policy maintained low fire frequency.

A second thesis, that reduced fire frequency at the turn of the century is responsible for major structural changes in ponderosa pine communities, has been postulated by a long lineage of studies (Arnold 1950, Weaver 1951, Cooper 1960, Biswell et al. 1973, Wright 1978, Allen 1989). In the early decades of the 20th