



Effects of habitat type and spatial scale on density dependent parasitism in *Anagrus* parasitoids of leafhopper eggs



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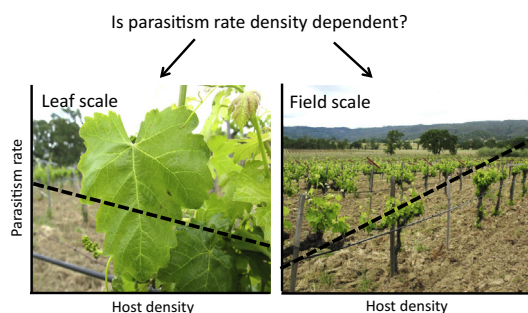
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HIGHLIGHTS

- Parasitism patterns are highly dynamic and depend on the scale of observation.
- Parasitism rate differed among sites and increased across the season.
- Parasitism rate was not affected by habitat type (natural vs. agricultural).
- At the leaf scale parasitism was independent or inversely dependent on host density.
- At the field scale, parasitism rate was positively dependent on host density.

GRAPHICAL ABSTRACT



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ABSTRACT

The ability of parasitoids to maintain a high rate of parasitism under varying conditions is considered crucial to their ability to control the populations of their hosts. Here, I tested parasitism rate by *Anagrus* parasitoids and its dependency on the density of *Erythroneura* leafhopper eggs at two spatial scales (leaf and field) and two habitat types (natural vs. agricultural). The rate of parasitism differed among field sites, increased across the season, and was similar in natural and agricultural sites. At the leaf scale, the rate of parasitism was density-independent or inversely density-dependent, consistent with a weak aggregation of parasitoids on leaves with high host densities and with limited oviposition-rate or egg supply. At the field scale, in contrast, parasitism rate was positively dependent on host density, which may be explained by demographic processes, such as higher recruitment and higher fecundities of females in host-rich field sites. Overall, the results demonstrate that parasitism patterns are highly dynamic in time and space and depend on the scale of observation.

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1. Introduction

According to theories based on optimal foraging or on parasitoid–host dynamics, a positive correlation between the rate

of parasitism and the density of the host (*i.e.*, positive density-dependent parasitism) is predicted to be a common phenomenon in both natural and agricultural systems (Hassell, 2000; Pacala and Hassell, 1991). However, in reality, the rate of parasitism is often independent, or even inversely-dependent, on the density of the host (Lessells, 1985; Pacala and Hassell, 1991; Stiling, 1987; Walde and Murdoch, 1988). This may have significant implications for the ability of parasitoids to control host populations, as

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well as on the stability of parasitoid–host interactions (Bonsall and Bernstein, 2008; Hassell and Waage, 1984).

Several explanations can potentially account for the lack of observed positive density-dependent parasitism. First, factors related to the life history and behavior of the parasitoid may be involved. Density-dependence is promoted by the aggregation of adult parasitoids in areas wherein host density is high, but several factors – such as mutual interference among parasitoids in the patch, long host-handling time, or a high risk of egg limitation – may restrict parasitism rates at high host densities and result in density-independence, or in inversely density-dependent patterns (Bonsall and Bernstein, 2008; Hassell, 2000; Heimpel and Casas, 2008; Ives, 1992; Lessells, 1985; Umbanhowar et al., 2003). Second, factors related to the biology of the host may also be of importance. For example, hosts that are specialist herbivores (i.e., consume a single type of plant) or that are sedentary may be easier for the parasitoid to track in space than hosts that are generalists, mobile, or capable of finding refuge within plants (Price, 1988; Romstock-Volkl, 1990; Stiling, 1987). Third, environmental factors may play a role. For example, some climatic conditions – such as wind, rain, or extreme temperatures – may restrict the activity of the parasitoids and reduce their foraging efficiency, and, thereby, their ability to track their hosts (Stacey, 2003; Stiling, 1987). The structure of the landscape (e.g., its complexity or fragmentation) may also affect the rate of parasitism and how it interacts with host density (Cronin, 2003; Kruess and Tscharrntke, 2000; Menalled et al., 2003).

In addition to the biological and environmental considerations mentioned above, the nature and accuracy of the scientific observation itself may restrict our ability to detect density-dependent parasitism patterns. For example, such patterns may not be apparent if the unit of observation (e.g., a leaf, a cluster of hosts, or a group of plants) is too small or too large relative to the “unit” that is relevant to the foraging parasitoid (Fellowes et al., 2005; Hassell and Southwood, 1978). Indeed, spatial patterns of parasitism have been shown to depend upon the scale of observation (Cronin, 2003; Doak, 2000; Heads and Lawton, 1983; Norowi et al., 2000; Rosenheim et al., 1989). Moreover, some patterns of parasitism may also change on a temporal scale, becoming apparent only in a certain year or season (Menalled et al., 2003; Rosenheim, 1989). Finally, our ability to detect patterns of density-dependence may be better when we consider a complex of hosts and their parasitoids, rather than when we consider a single interaction (Stiling, 1987). However, despite these numerous limitations, most studies investigate density-dependence within single spatial and temporal scales and consider a single host–parasitoid interaction.

Parasitoid wasps of the genus *Anagrus* (mainly *Anagrus daanei* and *Anagrus erythroneurae*) are among the most important natural enemies of leafhoppers in grape systems in California, including both cultivated grapes and wild grapes growing in riparian habitats (Bentley, 2009). The parasitoids forage on grape leaves, lay their eggs and complete their entire development (egg to adult) inside eggs of leafhoppers. The spatial density of the leafhoppers varies within and between field sites and is generally higher in agricultural vineyards than in natural riparian habitats (Daane and Costello, 2000; Segoli and Rosenheim, 2013b).

Some features of the interaction between *Anagrus* and their leafhopper hosts may promote, and others are likely to reduce, positive density-dependent parasitism. On the one hand, the accessibility of the leafhoppers' eggs on the leaves, and their specificity for grape plants may enable *Anagrus* parasitoids to readily track and aggregate in host-rich patches. Moreover, handling of a host egg is minimal, especially in comparison to parasitoids that attack larvae or adult hosts that often resist the attack (Godfray, 1994). In addition, it has been shown that female *Anagrus* parasitoids from

vineyards, where host densities are relatively high, emerge from the host with more eggs than females from natural sites, wherein host densities are lower (Segoli and Rosenheim, 2013b). Such a local adaptation may promote the ability of the parasitoid to maintain a high rate of parasitism in host-rich habitats. On the other hand, because adult *Anagrus* are minute (<1 mm), they may be sensitive to environmental disturbances, reducing their ability to track their hosts in space. In addition, despite the higher egg loads at emergence observed in females from host-rich habitats, it has been estimated that approximately 10% of the female *Anagrus* parasitoids become egg-limited in the field (Segoli and Rosenheim, 2013a), a risk that may restrict parasitism rates in host-rich patches.

These opposing factors may potentially balance each other, resulting in density-independent parasitism by *Anagrus* parasitoids on their hosts. Alternatively, parasitism patterns may differ depending on the spatial scale of observation, as different factors may have a different influence on the rate of parasitism at different spatial scales. For instance, demographic processes – such as long-distance dispersal, reproduction, or survival – may be more important on a larger scale, whereas factors related to parasitoid behavior and oviposition rate within the patch are more important at smaller scales.

In the current work, I tested density-dependent parasitism of leafhopper eggs by *Anagrus* parasitoids during two consecutive years (2010 and 2011) and at two spatial scales (leaf and field). In 2010, I sampled grape leaves from two vineyards across the growing season (July–October); and, in 2011, I obtained one sample from each of eight vineyards and eight riparian habitats. This allowed me to explore density-dependent parasitism while using a wide range of host densities and to search for differences in density dependence patterns at different scales, timings and habitats.

2. Methods

2.1. Parasitoids and hosts

A. daanei Triapitsyn and *A. erythroneurae* Triapitsyn Chiappini (Hymenoptera, Mymaridae) parasitize the eggs of *Erythroneura* spp. leafhoppers (Homoptera: Cicadellidae) in vineyards and riparian habitats of northern California (Bentley, 2009; Douth and Nakata, 1973; Kido et al., 1983). These parasitoids are solitary (i.e., they develop singly inside the leafhopper egg), proovigenic (i.e., they emerge with their full egg load) (Jepsen et al., 2007) and short lived, even under the most benign laboratory conditions (English-Loeb et al., 2003). They develop rapidly from the egg to adult stage in comparison to the leafhopper populations, completing as many as three generations for each leafhopper generation in the field (Daane and Costello, 2000). To identify the relative abundance of parasitoid species in the field, I collected grape leaves from the different sites and kept them in emergence cages until the emergence of the parasitoids. I distinguished male from female wasps and *A. daanei* from *A. erythroneurae* wasps by using a phase-contrast microscope (Triapitsyn et al., 2010). *A. daanei* comprised $80 \pm 10\%$ of all female parasitoids emerging from grape leaves collected in 2010 ($N = 197$ females; 8 collections) and $88 \pm 17\%$ of the females collected in 2011 ($N = 270$ females in 15 collections).

Erythroneura spp. leafhoppers overwinter as adults. Overwintering adults move onto vines shortly after bud break (February–March) and oviposition typically begins in March–April following leaf growth. Leafhoppers complete three to four generations per season, increasing in density with each generation, and reaching their highest peak towards the end of the growing season (September–October). Both nymphs and adults feed on grape leaves by using piercing mouthparts to puncture leaf cells and suck out their

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