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

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15 ABSTRACT

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

29 Keywords: *Anagrus* egg parasitoids, *Erythroneura* leafhoppers, *Vitis*, vineyard,
30 parasitism rate, density dependence

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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 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,

54 some climatic conditions – such as wind, rain, or extreme temperatures – may restrict the
55 activity of the parasitoids and reduce their foraging efficiency, and, thereby, their ability
56 to track their hosts (Stacey, 2003; Stiling, 1987). The structure of the landscape (*e.g.*, its
57 complexity or fragmentation) may also affect the rate of parasitism and how it interacts
58 with host density (Cronin, 2003; Kruess and Tschardt, 2000; Menalled et al., 2003).

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

74 Parasitoid wasps of the genus *Anagrus* (mainly *A. daanei* and *A. erythroneuræ*)
75 are among the most important natural enemies of leafhoppers in grape systems in
76 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). *Anagrus 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 contents. Damaged leaves have a reduced photosynthetic capacity and may eventually senesce and fall off. *Erythroneura* spp. females deposit eggs singly or in clusters under the leaf epidermal tissue or along leaf veins (Daane and Costello, 2000). I found three species of leafhoppers in my field sites: (i) the western grape leafhopper (GLH) *Erythroneura elegantula* Osborn, which is native to California, was found in all field sites; (ii) the variegated leafhopper (VLH) *Erythroneura variabilis* Beamer, which has invaded California over the past few decades (Settle and Wilson, 1990), was found in three vineyards and in one natural site; and (iii) the Virginia creeper leafhopper (VCLH) *Erythroneura ziczac* Walsh, which is new to California (Segoli and Rosenheim, 2013a; Segoli and Rosenheim, 2013b), was found in three vineyards and in one natural site.

2.2 Sampling

The study was conducted during 2010 and 2011 in Northern California. In 2010, I sampled grape leaves (*Vitis* spp) in two field sites: a vineyard that is grown for non-commercial purposes in Village-Homes neighborhood, Davis, CA, and a vineyard in a private farm in Solano County, south-east of Davis. Each of these two field sites was sampled four times during the growing season (July, August, September and October). In 2011, I sampled grape leaves from eight vineyards and from eight sites in riparian habitats in Sonoma, Napa, Yolo, Solano, Sacramento and San Joaquin counties in northern California. With the exception of one unmanaged vineyard, all vineyards received irrigation, fertilization and weed suppression. Vineyards differed in age, size and management regimes. Riparian habitats were along riverbeds or water canals mostly in nature or recreation parks (e.g., American River, Bothe State Park, Putah Creek Nature Park) where native grape vines typically grow over trees or other riparian vegetation. For additional details of field sites see (Segoli and Rosenheim, 2013b). Each of these 16 field sites was sampled once during August or September, 2011.

2.3 Leafhopper density and parasitism rate measurements

To quantify leafhopper density per leaf, I collected, in each sampling, 30 grape leaves from each site. I collected the leaves from sections of the field where some damage from leafhopper, even if minor, was apparent, as those areas are more relevant to the foraging parasitoids. This might have precluded sections where hosts were extremely rare, but where parasitism rate could not have been estimated accurately. However, such sections are not likely to contribute significantly to host or parasitoid populations. I counted the total number of leafhopper eggs on the top and bottom of half of each leaf,

and distinguished between eggs of the three leafhopper species based on their distribution pattern and location on the leaf: GLH lay their eggs singly under the epidermis, VLH lay their eggs singly along the veins, and VCLH lay their eggs in clusters under the epidermis. To quantify parasitism rate, I counted the number of parasitized eggs, easily identified by their darker color or by the emergence holes left by the parasitoids. Although this inevitably excluded some recently parasitized eggs that had not yet changed color, this bias was consistent across field sites. I defined the rate of parasitism per leaf as the number of parasitized eggs (both hatched and unhatched) divided by the total number of eggs on a leaf, excluding leaves with fewer than 5 eggs. I defined the rate of parasitism per field site as the number of parasitized eggs (both hatched and unhatched) divided by the total number of eggs collected (per sample) in the field.

2.4 Statistical analyses

To identify effects at the leaf scale, I used a General Linear Model (GLM) with field site, month of collection (only in 2010), and host density per leaf as the independent factors, and parasitism rate per leaf as the dependent factor. To identify effects at the field scale, I used a GLM with habitat type and host density per field as the independent factors, and parasitism rate per field as the dependent factor. Data were log-transformed where necessary to meet model assumptions.

3. Results

3.1 Parasitism rate in two vineyards across the season-2010

Parasitism rate differed between the two sampled field sites ($F_{1,149} = 25.91$, $P < 0.001$; Fig. 1), increased throughout the season ($F_{3,149} = 11.79$, $P < 0.001$, Fig. 1), and was inversely-correlated with total host density ($F_{1,149} = 4.76$, $P = 0.03$; Fig. 2).

Parasitism rate was independent of host density when considering each leafhopper species separately ($P = 0.99, 0.86$ and 0.38 for GLH, VLH and VCLH respectively). Host density differed between the two sampled vineyards ($F_{1,235}=44.67, P < 0.001$) and between sampled month ($F_{3,235} = 3.40, P = 0.019$), generally increasing towards the end of the season (Median [range] = 6.5 [0-98] eggs per leaf in July; 5.5 [0-80] in August; 14 [0-135] in September and 13.5 [0-197] in October).

3.2 Parasitism rate in multiple agricultural and natural sites-2011

The relationship between parasitism rate and host density at the leaf level was analyzed for samples collected in four natural and five agricultural sites, as in the other field sites the number of eggs per leaf was too small. The results showed a significant effect of field site ($F_{8,114} = 5.55, P < 0.001$), but no effect of host density ($F_{1,114} = 1.56, P = 0.21$) on parasitism rate. Parasitism rate was positively correlated with host density at the field site level ($F_{1,13} = 5.83, P = 0.031$; Fig. 3, pooling hosts of all leaves collected within a site), but was not affected by field type (*i.e.*, natural or agricultural; $F_{1,13} = 0.09, P = 0.77$; Fig. 3). Similar results were obtained when considering field sites that harbored GLH only ($P = 0.034$ for host density and 0.907 for habitat type).

4. Discussion

The results of this study demonstrate that parasitism patterns are highly dynamic in time and space and depend on the scale of observation. Parasitism rate was independent or inversely-dependent on host density at the leaf scale, but it was positively-dependent on host density at the field scale. This finding suggests that different mechanisms and processes that affect parasitism rates operate at the different spatial scales.

4.1 The leaf scale

Parasitoids often aggregate in host-rich patches (Godfray, 1994; Hassell, 2000), but this aggregation does not necessarily result in higher parasitism rates (Heimpel and Casas 2008). For example, aggregation of *Diadegma* spp. foraging for diamondback moth larvae did not lead to density-dependent parasitism (Legaspi and Legaspi, 2005; Waage, 1983). This phenomenon was explained by oviposition rate being limited by handling time in patches of higher host densities. In the leafminer parasitoid *Closterocerus tricinctus*, parasitism rate was inversely related to host density despite a higher visitation rate in leaves with higher leafminer densities (Connor and Cargain, 1994). This finding was explained by more time spent rejecting previously parasitized hosts at high host densities.

Personal observations in the field suggest that *Anagrus* parasitoids aggregate to some degree on host rich patches- as foraging parasitoids are more readily found via direct observations or branch shaking (Segoli and Rosenheim, 2013c) on leaves that exhibit high leafhopper damage. Nevertheless, parasitism per leaf was found to be density independent (in 2011) or inversely density dependent (in 2010). This result suggests that, similar to the examples discussed above, some processes restrict the rate of oviposition on leaves that carry many host eggs. Further investigation is required to characterize these processes, but potential explanations may include egg depletion (Segoli and Rosenheim, 2013a), direct mutual interference with other ovipositing females on a leaf, or indirect interference due to encounters with already-parasitized hosts. Indeed, observations of female *Anagrus* foraging for host eggs on leaves indicated that, although they do not seem to be aggressive towards other females, the foraging females often

bump into each other, which disrupts searching and oviposition behavior. In addition, female *Anagrus* were observed to probe plant tissues containing hosts without ovipositing, a behavior that may indicate attempts to locate suitable hosts (Agboka et al., 2003; Al-Wahaibi and Walker, 2000; Cronin and Strong, 1993). Inversely-dependent parasitism was only apparent when all leafhopper species were considered together, suggesting that processes limiting parasitism rate of one host species may be dependent on the presence of the other hosts. For example, a single female may become egg depleted following successive parasitism of several host species, or a female parasitizing a host of one species may interfere with a female parasitizing a host of another species.

4.2 The field scale

Aggregation at the field level is likely to be governed mostly by demographic processes. For example, aggregation may result from more frequent long distance immigration to – or less frequent emigration from – field sites with many hosts (Fellowes et al., 2005; Heimpel and Casas, 2008). While it is extremely difficult to study dispersal by minute parasitoids such as *Anagrus*, Cronin and Strong (1999) documented the dispersal of *Anagrus sophiae* into experimental floating islands of vegetation located up to 250 m from shore. In addition, Corbett and Rosenheim (1996) documented the dispersal of *Anagrus* spp. in vineyards by releasing and recapturing parasitoids marked with fluorescent dust. They found that some individuals dispersed upwind at a rate of up to few hundred meters per day. Upwind dispersal raises the possibility of oriented movement toward host patches based on chemical cues, which may potentially lead to aggregation in host-rich habitats. Many parasitoids are attracted to host-related cues such as volatiles released from plants during feeding by herbivores, host sex pheromones, and

host mating calls (Hassell and Southwood, 1978). Although host eggs are typically characterized by a low emission of volatile cues, evidence suggest that parasitoids are able to exploit plant compounds that are produced as a consequence of egg laying by their hosts (Colazza et al., 2004; Conti et al., 2010; Fatouros et al., 2008; Hilker et al., 2002). In addition, feeding leafhoppers may contaminate the leaf surface with chemicals emanating from their bodies or their feces, which may potentially attract parasitoids. Indeed, studies of *Anagrus* parasitoids in other systems demonstrated that host adults and nymphs, host exuvia, honeydew, nymph-damaged plants and plants with host eggs all elicited host searching behavior (Lou and Cheng, 2001), and that the combination of plant and host cues acted as the strongest attractant to foraging parasitoids (Chiappini et al., 2012). The possibility of oriented dispersal by *Anagrus* in grape systems, as well as the possibility of reduced emigration from host-rich habitats, should be further explored.

Another mechanism that may lead to aggregation at the field level involves faster population growth in fields with more hosts. Previous studies have suggested that female *Anagrus* from vineyards with higher leafhopper densities lay more eggs during their lifetime than females from fields with lower host densities (Segoli and Rosenheim, 2013a). Moreover, females from host-rich vineyards were shown to have higher egg loads at emergence, suggesting local adaptation in egg loads to reduce the risk of egg limitation (Andreazza et al., 2015; Segoli and Rosenheim, 2013b). Increased population growth in host-rich habitats, as compared to host-poor habitats, is likely to be amplified by multiple generations completed by *Anagrus* during a growing season (Murphy et al., 1996). Indeed, in spite of an increase in host density, parasitism was shown consistently to increase throughout the season. This supports the notion that the parasitoids reproduce

faster than their hosts, completing multiple generations for each host generation, as previously reported (Daane and Costello, 2000).

4.3 Habitat type

Modern agriculture has simplified the agricultural landscape, increased the field size of crops, and reduced the amount of non-crop habitats (Bianchi et al., 2006). These changes likely reduced the availability of food resources and sheltering habitats for parasitoids and other natural enemies (Altieri and Letourneau, 1982; Coll, 1998).

Therefore, maintaining a high habitat complexity often leads to an increase in the diversity and abundance of parasitoids (Chaplin-Kramer et al., 2011). However, habitat complexity may also directly affect parasitoids' searching efficiency (Andow and Prokrym, 1990) and host densities (Thies et al., 2005). Therefore, the increase in parasitoid abundance does not necessarily result in higher parasitism rates or a stronger control of the host population in complex habitats (Chaplin-Kramer et al., 2011). In the only experimental study testing the simultaneous effects of host density and habitat complexity, habitat type had no effect on parasitism rate (Costamagna et al., 2004). In accordance with that study, I found no difference in parasitism rate or in density-dependent parasitism between natural riparian habitats and simplified agricultural vineyards, when controlling for host density. This finding may be attributed to the relatively small sample size (8 natural and 8 agricultural fields), but may also reflect the inconsistency of the effect of habitat complexity on parasitoid success.

4.4 Implications for biological control

The ability of *Anagrus* parasitoids to aggregate and maintain relatively high parasitism rates in vineyards with high host densities is likely to contribute to their ability

to reduce leafhopper populations. Nevertheless, parasitism rates per field in this study did not exceed 60%, which may be partially attributed to factors limiting oviposition rates at the leaf level (see above) or to additional limiting factors in the field. For example, low abundance of nectar resources may restrict survival and reproduction of *Anagrus* and other parasitoids (Heimpel and Casas, 2008; Segoli and Rosenheim, 2013c). Variation in the availability of food resources may potentially explain the differences in parasitism rates among field sites, as observed in this study. Other factors that may limit parasitoid success include predation pressure (Rosenheim, 1998), climatic conditions (Stacey, 2003) and the use of pesticides, in particular, sulfur (Martinson et al., 2001). In order to improve biological control of leafhoppers by *Anagrus*, multiple limiting factors for parasitoid success should be considered simultaneously.

4.5 Conclusions

An examination of parasitism of leafhopper eggs by *Anagrus* and its dependency on host density revealed a complex pattern that varied spatially and temporally. Additional work is required to characterize processes that limit the oviposition rate at the leaf level and that promote aggregation at the field level. Although the ability of *Anagrus* to aggregate at the field level is likely to increase their efficiency for biological control in vineyards, additional limiting factors are likely to prevent parasitism rates from reaching higher values.

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497 Figure legends:

- 498 1. Parasitism rate of *Anagrus* on leafhopper eggs across the season, at the two field
499 sites sampled in 2010.
- 500 2. Parasitism rate of *Anagrus* on leafhopper eggs vs. leafhopper egg density per leaf
501 at the two field sites sampled in 2010.
- 502 3. Parasitism rate of *Anagrus* on leafhopper eggs vs. leafhopper egg density per field
503 for eight vineyards and eight natural sites sampled during 2011.
- 504

504

Figure 1

505

Figure 3

Leaf scale

Field scale