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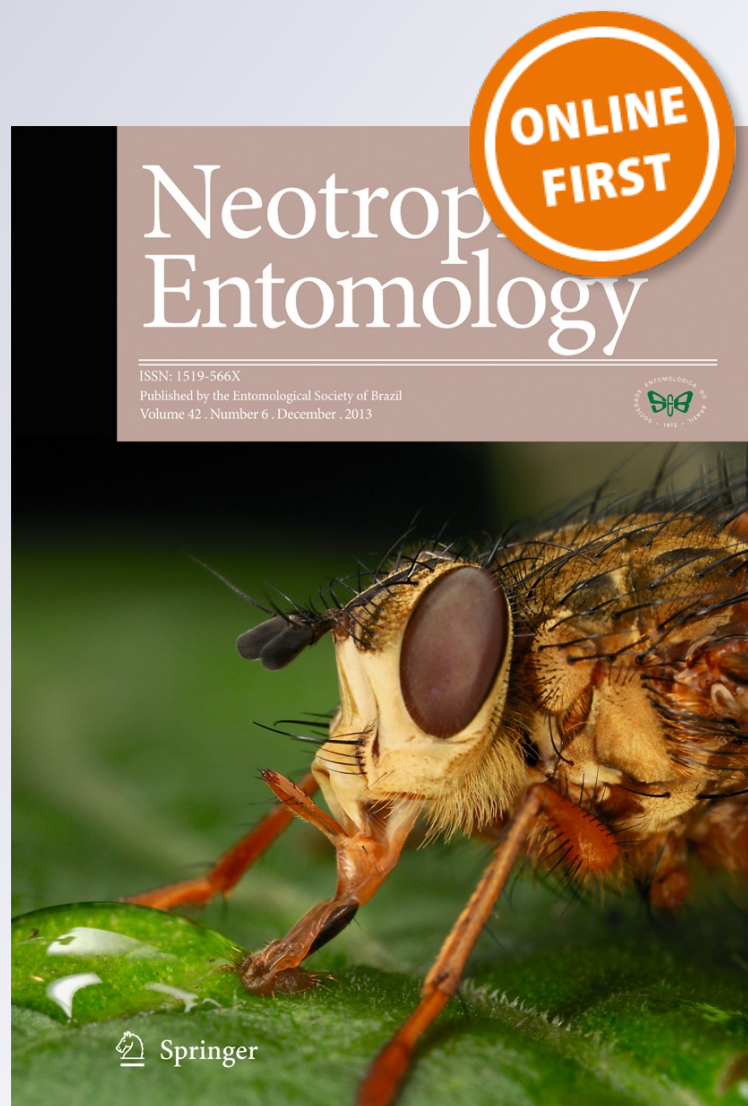
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Susceptibility of *Nezara viridula* (L.) (Hemiptera: Pentatomidae) Egg Masses of Different Sizes to Parasitism by *Trissolcus basalis* (Woll.) (Hymenoptera: Platygasteridae) in the Field

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Keywords

Stink bugs, egg mass size, egg parasitoids, field parasitism

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Abstract

Egg masses of *Nezara viridula* (L.) are commonly parasitized by *Trissolcus basalis* (Woll.), and we investigated the role of size of egg masses on parasitization by *T. basalis*. Sentinel egg masses were exposed to parasitism in the field for 6–7 days, when they were collected for evaluation of parasitoid emergence. We recorded the number of eggs per egg mass, the number of emerged hosts, and the number of empty and parasitized eggs. We calculated the proportion of attacked host egg masses (DE), the proportion of parasitized eggs per attacked egg mass (PE), and total parasitism (PI). The total number of egg masses exposed to parasitism was 330. The minimum, mean, and maximum egg mass sizes were 25, 75.2, and 111, respectively. DE and PE varied widely between different fields, and they were independent of egg mass size. In 14.2% of all parasitized egg masses, we found simultaneous emergence of *T. basalis* and *N. viridula* independently of host egg mass size. PE exhibited low variability compared with PI and DE, which were linearly related. PI and DE values from other field studies are consistent with the linear relationship, suggesting that PI is mostly related to the proportion of the DE. This also suggests that total parasitism is independent of egg mass size, of possible differences in plant species, and *T. basalis* density and strains.

Introduction

In host–parasitoid systems, hosts often occur in discrete patches (Godfray 1994), and at a given spatial scale, the proportion of patches (e.g., egg masses) discovered and parasitized may increase with host patch density (Lill 1998). However, if more than one female parasitoid would be initially attracted to denser patches (e.g., larger egg masses), the proportion of parasitized hosts could not differ between patches of different densities because, as parasitoids aggregate, interference between them could negatively affect their parasitism efficiency (Hassell & Varley 1969, Broadhead & Cheke 1975, Field 1998). Parasitism efficiency is an indicator of host finding capacity, which in turn implies a number of factors, such as parasitoid behavior, parasitoid learning, and habitat characteristics (Bin & Vinson 1990, Nordlund 1994, Gingras *et al* 2008). As each parasitized host cannot

contribute to the growth of the host population, parasitoid searching efficiency is central to parasitoid–host dynamics and to the application of parasitoids as natural enemies of insects (Vet 2001).

The stink bug *Nezara viridula* (L.) (Hemiptera: Pentatomidae) is a cosmopolitan, polyphagous herbivore which develops up to four generations per growing season (from mid-spring to mid-autumn) and has been considered an important pest of several crops in different countries (Kiritani 1963, Panizzi & Slansky 1985, Jones *et al* 1996). It is a synovigenic species that oviposits eggs in masses. The relatively high potential fecundity, >300 eggs per female, depends on the number and size of the oviposited egg masses, which in turn can be influenced by several factors, such as female size and age, and the quality of consumed food. Fecundity depends also on whether females are from the first or the last generation of a given season (Liljesthröm & Bernstein 1990,

Fortes et al 2006). Kiritani (1963) observed an increase with succeeding generation in the mean number of eggs developed in each ovariole: five eggs in the post-diapause adults, six in the next generation, and seven in the last generation (here called first, second, and third adult host generations, respectively).

Nezara viridula oviposits egg masses preferably on the underside of leaves of different species of herbaceous plants. Relevant aspects of the ecology of this stink bug have been treated extensively (Kiritani et al 1966, Liljeström & Coviella 1999, Tillman 2006 and references therein). In the study area (see below), a key factor analysis on the population dynamics of *N. viridula* during four growing seasons (from mid-October to mid-April of the following year) identified three, almost-discrete generations which last approximately 8 weeks (Liljeström & Bernstein 1990). Parasitism of *N. viridula* adults by *Trichopoda giacomellii* (Blanchard) (Diptera: Tachinidae) significantly shortened the host reproductive period (Liljeström 1993), and in consequence, successive host generations occurring during a growing seasons are much less overlapped than in the absence of parasitism by *T. giacomelli*.

Each *N. viridula* egg mass constitutes a discrete patch for oophagous parasitoids, such as *Trissolcus basalis* (Woll.) (Hymenoptera: Platygasteridae). This parasitoid is a solitary and weakly synovigenic (most eggs are mature at emergence, Jervis et al 2001) endoparasitoid of pentatomid eggs, which has been used as a biological control agent of its main host, *N. viridula*, in several countries (Corrêa-Ferreira 1993, Jones et al 1996). It was imported into Argentina and established since 1978–1979 (La Porta & Crouzel 1984). During the early phases of host location, searching is mediated by volatile synomones induced by feeding and oviposition activity of *N. viridula*, which do not seem to be plant specific (Colazza et al 2004). Additionally, host kairomones allow *T. basalis* to recognize host eggs (Mattiacci 1993). Adult females are capable of mating and ovipositing the same day of emergence (Powell & Shepard 1982, Field et al 1998), and total fecundity varies among different strains (*sensu* Diehl & Bush 1984) from ~90 to ~180 eggs/female (Powell & Shepard 1982, Field et al 1998, Catalán & Verdú Gallardo 2005). In laboratory experiments, when more than one *T. basalis* female are allowed to exploit an egg mass simultaneously, aggressive encounters take place between them. However, if the attacks are sequential, superparasitism occurs (Field et al 1997, Field 1998).

Total parasitism depends on the proportion of attacked egg masses as well as on the proportion of parasitized eggs per attacked egg mass. In field studies, both components vary widely. In Hawaii and Australia, while the proportion of attacked egg masses was high, in the former each attacked egg mass showed only few parasitized eggs (Jones & Westcot 2002), whereas in Australia the proportion of parasitized eggs per egg mass was near unity (Seymour & Sands 1993). Jones (1995) suggested that the difference between the

proportion of parasitized eggs per attacked egg mass in Australia and Hawaii could be due to egg predation, which in Hawaii was much higher than in Australia. Moreover, Jones (1995) suggested that, in the framework of Foraging Theory, it makes little sense for *T. basalis* to parasitize every host egg in an egg mass, particularly when predation of egg masses is high. In addition, in Italy, Colazza & Bin (1995) reported that total parasitism of *N. viridula* eggs by *T. basalis* in soybean ranged from ~13% to 52%, and the proportion of parasitized eggs per attacked egg mass decreased with an increase of the egg mass' size: from 0.98 for egg masses of 40–70 eggs/egg mass to 0.74 for egg masses of 101–135 eggs/egg mass. This apparent, inverse density dependence could be due to the functional response of *T. basalis* which saturates at certain host egg mass size (Laumann et al 2008). However, other field studies in the USA (Hoffmann et al 1991, Shepard et al 1994) and in Argentina (Liljeström & Cameán 1992) showed much higher levels of total *N. viridula* egg parasitism (>70%), possibly due to denser local *T. basalis* populations. We hypothesize that the acceptance of *N. viridula* egg masses to parasitism by *T. basalis* is independent of mass size and that total parasitism is related to the proportion of attacked masses.

In this work, we addressed the following questions: (1) is the proportion of parasitized eggs per attacked egg mass higher in larger than in smaller egg masses?; (2) are larger *N. viridula* egg masses discovered and parasitized in greater proportion than smaller ones?; and (3) is total parasitism more related to the proportion of discovered and attacked egg masses than to the proportion of parasitized individual eggs per attacked egg mass?

Material and Methods

To analyze only the possible effects of host egg mass size, we avoided comparisons of egg masses from different host generations. We analyzed published information on three *N. viridula* generations from five growing seasons (Liljeström & Bernstein 1990, Liljeström & Cameán 1992) and new data. The study areas were situated in Berisso and La Plata counties (34°35'S, 57°17'W), Argentina. One of them was a weedy plot of 2.25 ha dominated by *Ricinus communis*, *Brassica* sp., and *Raphanus* sp., from which we obtained information on the first five growing seasons. The new data came from a study area located in a field of the School of Agronomy of the La Plata National University. We collected samples from small plots (approximately 9 m²) of soybean (*Glycine max*) and alfalfa (*Medicago sativa*) within a larger area of 2.7 ha where other crops such as corn (*Zea mays*) and rice (*Oryza sativa*) were present. At weekly intervals, 10–15 egg masses of *N. viridula* 12- to 48-h old obtained in the laboratory were glued individually to a 2×3 cm thin

paper card and exposed to parasitism in the field by stapling them to the underside of the leaves of plant species where *N. viridula* natural oviposition was observed (Liljesthrom & Bernstein 1990). After 6–7 days, the egg masses were taken to the laboratory and kept at 25±1°C, 65±10% RH and a photophase of 14 h in test tubes until parasitoid emergence. In addition, host egg masses found by inspecting plants were also taken to the laboratory, and added to the total sample size of laboratory-produced masses.

We registered the number of egg masses, the number of eggs per egg mass, the number of *N. viridula* emerged nymphs and the number of empty eggs, as well as the number of parasitized eggs. Eggs were considered parasitized when a pupa or an adult of the parasitoid were found dead inside it, when adult parasitoids emergence was registered, or when they had a concave operculum and undefined yellowish content. The oophagous parasitoids were taxonomically identified by Dr. Marta Loiácono and Dr. Cristina Monetti, from the Department of Entomology of the La Plata Museum of Natural Sciences, and egg masses parasitized by species other than *T. basalis* were eliminated from the analysis (n=2).

We analyzed data by three indices defined by Bin & Vinson (1990) (in Colazza & Bin 1995): the “discovery efficiency” (DE), defined as the proportion of attacked egg masses (i.e., number of egg masses with at least one parasitized egg/total number of offered egg masses); the “parasitism efficiency” (PE), defined as the proportion of parasitized eggs per attacked egg mass (i.e., number of parasitized eggs/number of eggs of all the discovered egg masses); and the “parasitoid impact” (PI), defined as the proportion of parasitized eggs across egg masses (i.e., number of parasitized eggs/number of exposed eggs). Both DE and PE are affected by the host's egg mass size. DE is relevant to parasitoid's searching ability and depends on parasitoid density, weather factors, and the phenology and structure of the vegetation (Colazza & Bin 1995), while PE depends on the parasitoid female's complement of eggs, if only one parasitoid female attacks the egg mass (Colazza & Bin 1995).

Proportion of parasitized eggs and of host survivorship from parasitized egg masses, as a function of egg mass size

The proportion of parasitized eggs and the proportion of host survivorship (the latter was not always the complement of the former due to the presence of empty eggs considered infertile) from individual egg masses were plotted against the corresponding egg mass size. After the angular transformation of parasitism proportion (y-axis), we calculated the regression equations. If the individual egg mass size had no effect on the proportion of parasitized eggs or on the proportion of host survivorship, the slopes of the

regression equations should not differ significantly from zero (Zar 1996). In a complementary analysis, we relaxed the former criterion which excluded comparison of egg masses from different host generations and grouped all the egg masses in the following eight classes: <40, 40–49, 50–59, 60–69, 70–79, 80–89, 90–99, and >99 eggs per egg mass, recording for each class the mean number of eggs parasitized or not. If PE was independent of the egg mass size, the expected frequencies of the eight classes could be calculated as the independent product of the proportion in each egg mass size and the overall PE. We compared expected versus observed frequencies via a χ^2 test (Zar 1996).

Proportion of parasitized egg masses as a function of egg mass size

In a complementary analysis, we grouped all egg masses exposed to parasitism in the field, irrespective from host generation and growing season, into four categories (<51, 51–70, 71–90, and >90 eggs/egg mass), and the expected and observed number of parasitized egg masses were compared using the χ^2 test. If the egg mass size had no effect, then the number of observed parasitized egg masses should not differ significantly from the number expected by chance (Zar 1996).

For the *j*th generation (*j*=1, 3) from the *k*th growing season (*k*=1, 6), we characterized the discovery efficiency, $DE_{(j, k)}$, the parasitism efficiency, $PE_{(j, k)}$, and the parasitoid impact, $PI_{(j, k)}$ of *T. basalis* on *N. viridula*.

We used $PE_{(j, k)}$ and $DE_{(j, k)}$ to calculate the parasitoid impact, $CPI_{(j, k)}$, as: $CPI_{(j, k)} = DE_{(j, k)} \cdot PE_{(j, k)}$, and then we compared this estimation to the parasitoid impact values obtained directly from field data, $PI_{(j, k)}$. If all egg masses exposed in the field had the same size, it holds that $PI_{(j, k)} = CPI_{(j, k)}$, as expressed in:

$$\frac{\# \text{ of parasitized eggs}}{\text{Total \# of eggs}} = \left[\frac{\# \text{ of parasitized egg masses}}{\text{Total \# of egg masses}} \right]$$

$$\left[\frac{\# \text{ of parasitized eggs}}{(\# \text{ of parasitized egg masses}) \cdot (\text{average size of par. egg masses})} \right]$$

As host egg masses exposed in the field were of different sizes (see below), if the parasitoids would only attack the larger egg masses and the parasitism within an egg mass would be density-independent (i.e., PE is independent of the egg mass size), then $PI_{(j, k)} > CPI_{(j, k)}$ because the numerator of $PI_{(j, k)}$ increases and the denominator remains unchanged, while $CPI_{(j, k)}$ remains unchanged due to the density independence. On the contrary, if the parasitoid would only attack the smaller egg masses, then $PI_{(j, k)} < CPI_{(j, k)}$, because the numerator of $PI_{(j, k)}$ is now smaller while the denominator remains unchanged. Finally, if the

parasitoid would attack the host egg masses independently of their size, then $PI_{(j, k)} \cong CPI_{(j, k)}$. To test the hypothesis that the susceptibility of the host egg masses to parasitism is independent of the egg mass size, we simulated the following conditions: ten egg masses of five different sizes were “offered”: 50, 60, 70, 100, and 120 eggs/egg mass; 5 egg masses (i.e., $DE=0.5$) were “parasitized” and the proportion of parasitized eggs per attacked egg mass (i.e., PE) was made to vary randomly between 0.01 and 1 independently from the egg mass size.

We considered three extreme situations taking into account frequent *N. viridula* egg mass sizes (Kiritani 1963, Liljeström & Bernstein 1990, Corrêa-Ferreira 1993): (a) parasitoids attack egg masses of all sizes, (b) parasitoids attack only the smaller egg masses, 50, 60, and 70 eggs/egg mass, and (c) parasitoids attack only the larger egg masses 100, and 120 eggs/egg mass.

Eighty simulations of each situation were made, and we calculated the corresponding PI as well as the PE. Differences between the mean PI and DE·PE for each one of the situations, as well as between $PI_{(j, k)} = CPI_{(j, k)}$ were evaluated by the *t* test after the angular transformation.

Total parasitism, proportion of discovered and attacked egg masses, and proportion of parasitized individual eggs per attacked egg mass

To analyze if parasitoid impact, $PI_{(j, k)}$, was related more to the proportion of parasitized individual eggs per attacked egg mass, $PE_{(j, k)}$, or to the proportion of discovered and attacked egg masses, $DE_{(j, k)}$, we plotted $PE_{(j, k)}$ on $PI_{(j, k)}$ and $DE_{(j, k)}$ on $PI_{(j, k)}$. The corresponding regression equations were calculated. If $PE_{(j, k)}$ was independent of $PI_{(j, k)}$ we expected the slope of the equation not to differ significantly from zero, while if $DE_{(j, k)}$ was related to $PI_{(j, k)}$ we expected the slope of the equation not to differ significantly from one. In a complementary analysis we calculated the Spearman correlation coefficient, *rs*: if $PE_{(j, k)}$ was independent of $PI_{(j, k)}$, we expected *rs* not to differ from zero. Similarly, if $DE_{(j, k)}$ was related to $PI_{(j, k)}$ we expected *rs* to be near 1 and differ from zero.

Results

The total number of eggs and egg masses of *N. viridula* exposed to parasitism was 24,825 (22,095 lab-reared and 2,730 field collected) and 330 (291 lab-reared and 39 field collected) respectively. On average, 55.0 ± 2.03 ($n=6$) egg masses were exposed to parasitism during each growing season. The mean egg mass size was 76.3 ± 1.07 eggs/egg mass ($n=330$) and minimum and maximum number of eggs per egg mass were 25 and 111.

Proportion of parasitized eggs and of host survivorship from parasitized egg masses, as a function of egg mass size

The proportion of parasitized eggs per attacked egg mass (PE) calculated from individual egg masses was independent of the egg mass size ($y=76.45+0.051x$; $t_{(149)}=0.842$; $p=0.401$). Similarly, PE was independent of egg mass-size category ($\chi^2_{(7)}=6.287$; $0.5 < p < 0.75$).

The total number of parasitized egg masses from which emergence of host nymphs was registered was 30 (14.15% of all parasitized egg masses). The slope of the linear equation between host survivorship on the corresponding egg mass size did not differ significantly from zero ($y=10.606+0.1842x$, $t_{(27)}=1.67$; $p=0.107$), suggesting that host survivorship was independent of egg mass size.

Parasitism of egg masses as a function of egg mass size

Calculated (simulated) parasitism impacts, CPI, are shown in Fig 1. While the product $DE \cdot PE$ had the same value than PI for egg masses of all sizes were attacked by *T. basalis*, when the parasitoid attacked only the smaller egg masses then $DE \cdot PE$ was higher than PI ($t_{(79)}=33.69$, $p < 0.001$). On the contrary, if the parasitoid attacked only the larger egg masses, then $DE \cdot PE$ was lower than PI ($t_{(79)}=-34.44$, $p < 0.001$).

Similar results were obtained from field data: the average parasitoid impact estimated directly from all egg masses exposed to parasitism during the six growing seasons ($PI_{(j, k)}=0.589$) did not differ from the calculated parasitoid impact $CPI_{(j, k)}=0.588$ ($t_{(34)}=0.007$; $p=0.994$, two tails test).

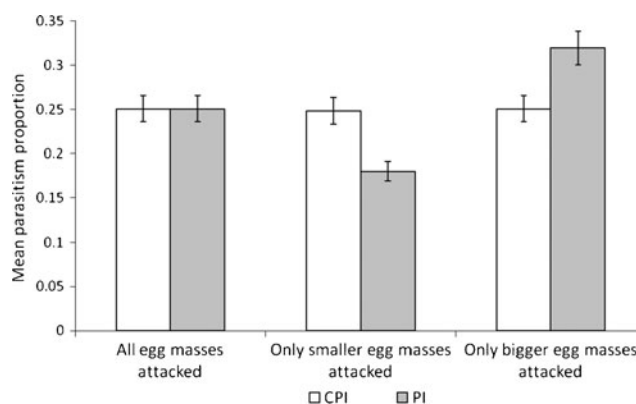


Fig 1 Calculated (simulated) parasitoid impact (CPI) and observed parasitoid impact values obtained directly from field data (parasitoid impact (PI)=number of parasitized eggs/number of exposed eggs), of *Nezara viridula* eggs parasitized by *Trissolcus basalis*. Case 1: all host egg masses parasitized independently from their sizes (CPI equals PI ($t_{(79)}=-0.24$, $p=0.81$); case 2: only smaller egg masses parasitized (CPI was higher than PI ($t_{(79)}=33.69$, $p < 0.001$); or case 3: only larger egg masses parasitized (CPI was lower than PI ($t_{(79)}=-34.44$, $p < 0.001$). Different letters indicate significant differences within each case.

In a complementary analysis, when all egg masses were grouped into four categories, we found that 16.9% of the egg masses had less than 51 eggs, 17.8% had 51–70 eggs, 34.7% had 71–90 eggs, and 30.5% had more than 90 eggs. DE values for each one of the four categories were: $DE_{(<51)}=0.672$, $DE_{(51-70)}=0.66$, $DE_{(71-90)}=0.72$, and $DE_{(>90)}=0.74$. When the number of discovered egg masses was analyzed in terms of the egg mass size categories, the Chi-square test indicated that the differences between categories were not statistically significant ($\chi^2=3.72$; $df=3$; $0.25 < p < 0.50$).

Total parasitism, proportion of discovered and attacked egg masses, and proportion of parasitized individual eggs per attacked egg mass

The above results showed that PE of individual egg masses was density independent within egg masses, and that egg masses are parasitized independently of their size, which in turn suggests that PI would be directly related to DE. The slope of the regression equation between $DE_{(j, k)}$ and $PI_{(j, k)}$ did not differ significantly from 1 ($y=0.027+1.0477y$; $t_{(16)}=1.308$; $0.5 > p > 0.1$). Complementarily, the Spearman correlation between the above mentioned variables was significantly different from zero ($r_s=0.981$; $p < 0.0001$). The slope of the regression equation between $PE_{(j, k)}$ and $PI_{(j, k)}$ did not differ significantly from zero ($y=0.873+0.068x$; $t_{(16)}=0.913$; $p=0.375$) (Fig 2). Again, similar results were obtained by the Spearman correlation: $r_s=0.224$ ($p=0.372$).

In Fig 2, we also included field values of DE and PI by Colazza & Bin (1995) from a six years study in soybean plots in Perugia (Italy) (DE and PI values in Colazza & Bin 1995, Tables 1 and 6, respectively), and data by Jones *et al* (1996) from a soybean plot in South Carolina (USA; mean annual DE

and PI were calculated by us from published values). These values, although having a lower total parasitism (or parasitoid impact), are consistent with the trend of the relationship between DE and PI found in our study.

Discussion

Nezara viridula egg masses constitute discrete patches for the parasitoid *T. basalis*. Egg masses frequently differ in size due to female's size and age, and the quality of food consumed, among other factors (Slansky & Panizzi 1987, Fortes *et al* 2006). Stink bug hibernation (winter diapause) is another source of differences in the mean size of egg masses, as clutches from the post-hibernating generation are smaller than those from the other generations that develop along a growing season (Kiritani 1963, Liljeström & Bernstein 1990).

Trissolcus basalis hibernate in the adult stage (Doetzer & Foerster 2007), and in our study area the surviving post-hibernating adults parasitize *N. viridula* eggs form the first generation of a growing season. The numerical response may produce significant differences in *T. basalis* population's density, leading to the higher egg parasitism on the second host generation registered in a key-factor analysis of the local *N. viridula* population dynamics (Liljeström & Bernstein 1990). Therefore, we analyzed field data to eliminate the effects of different parasitoid population densities, which may obscure the effect of egg mass size. Moreover, when egg masses were grouped without consideration of the host generation we obtained congruent results.

In host–parasitoid systems, even if parasitoids are initially attracted to larger egg masses, the proportion of parasitized individual hosts may not differ between patches of different densities (Lill 1998), because as parasitoids aggregate, interference between them could negatively affect their parasitism efficiency (Broadhead & Cheke 1975, Field 1998). In other cases, such as in the interaction between *Prokelisia marginata* (Van Duzee) (Hemiptera: Delphacidae) and *Anagrus delicatus* Dozier (Hymenoptera: Mymaridae), the parasitoid only oviposits a small fraction of eggs in a host clutch before dispersing (Cronin & Strong 1990).

In this study, we found simultaneous emergence of *T. basalis* adults and *N. viridula* nymphs in 14% of all parasitized egg masses, and this was independent of the host's egg mass size. In the case of larger egg masses which were parasitized only by one *T. basalis* female, parasitoid egg limitation could explain this result, as shown for *T. basalis* parasitizing egg masses of *Euschistus heros* (F.) (Hemiptera: Pentatomidae) in the laboratory (Laumann *et al* 2008). If two or more *T. basalis* adult females would discover the same host egg mass almost simultaneously, apart from superparasitism, aggressive behavior among them (Field *et al* 1997, Field 1998) could negatively affect their parasitism efficiency. The dynamic

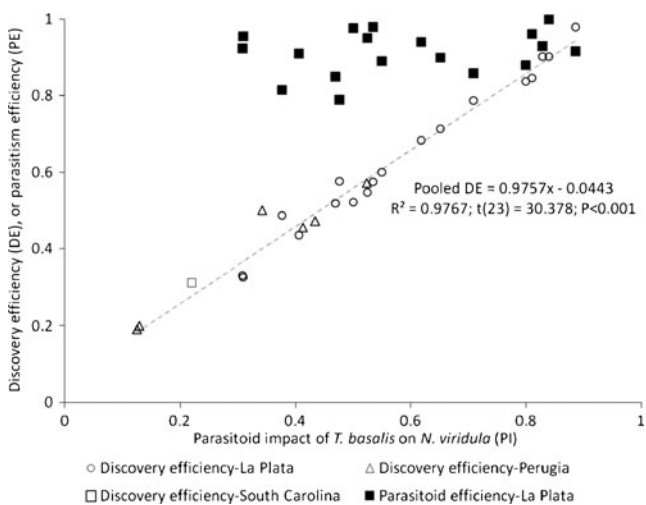


Fig 2 Relationship between the discovery efficiency and the parasitoid impact of host egg masses parasitized in the field. The slopes of the regression equations between DE and PI for La Plata and for Perugia did not differ significantly ($t_{(22)}=0.249$; $p > 0.75$).

effect of these mechanisms could be viewed as a “partial refuge” for *N. viridula*, which could add to other regulatory mechanisms already present in the population dynamics of this stink bug, such as the interaction with the tachinid *T. giacomellii* (Blanchard) in the same study area (Liljesthrom & Rabinovich 2004).

In host–parasitoid systems, it has been found that parasitism can be spatially density dependent, spatially density independent, or spatially inverse density dependent (Walde & Murdoch 1988, Lill 1998). Parasitoid aggregation on patches of higher host density requires long range attraction of parasitoids, usually in response to chemical cues, and once in a dense patch aggregation is maintained through a restriction on re-dispersal (Hassell & May 1974). With respect to *T. basalis*, it was shown that females can learn to associate visual and olfactory stimuli with successful host location, and use such stimuli in making foraging decisions (Dauphin et al 2009).

The index DE is relevant to parasitoid searching ability, which seems to be mainly chemically mediated (Conti et al 2003), and depends on parasitoid density, weather factors and vegetation phenology and structure (Colazza & Bin 1995). In turn, PE depends on the female parasitoid's limited egg availability, mainly when attacking larger host egg masses (Colazza & Bin 1995). However, if egg masses are discovered by more than one *T. basalis* female and super-parasitism occurs, the saturation of the functional response (i.e. egg depletion) would not be evident.

Our findings suggest that DE was independent of egg mass size, in agreement with Colazza & Bin (1995). Regarding PE, our results suggest that it was high (a mean value higher than 0.9) and independent of the individual host's egg mass size. This result is in disagreement with Colazza & Bin (1995) who found in their field study that PE by *T. basalis* decreased with an increase of the host's egg mass size. One possible explanation could be that in our field study the probability of host egg masses being discovered and attacked by *T. basalis* was higher than in Italy, due to a higher local parasitoid population density relative to *N. viridula* (see Fig 2). Furthermore, during our study two and up to three *T. basalis* adult females were observed on or near the same egg mass on various occasions (GGL, pers. observ.). In this case, the typical saturation exhibited by the functional response of *T. basalis* and other platygastriids, which would explain the findings by Colazza & Bin (1995), would not be evident (Allahyari et al 2004, Laumann et al 2008).

In our study, PE exhibited a relatively low variability compared with PI and DE, and variations in PI reflected more tightly variations in DE than in PE. These findings, and the three simulated conditions relating PI with the product DE·PE, suggest that in our study host egg masses were attacked by *T. basalis* independently of their size. The linear relationship between PI and DE was also confirmed when

incorporating values from field studies in Italy and USA, despite differences in plant species and possible differences in *T. basalis* density and strains. This suggests that the fundamental interactions between *T. basalis* and its main host, *N. viridula*, remain similar despite environmental differences and stink bug densities. Finally, the similar pattern exhibited by PE or DE during the six growing seasons of this study showed the importance of *T. basalis* as a mortality factor of the *N. viridula* population, and suggests a stable *N. viridula*–*T. basalis* interaction.

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