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Spatial patterns of goldenrod aphids and the response of enemies to patch density

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Summary. The two aphid species feeding on goldenrod (*Solidago altissima*) in northern Florida (U.S.A) exhibited behavioral differences that resulted in characteristic spatial patterns. *Uroleucon nigrotuberculatum* alates (winged forms) aggregated when colonizing stems and subsequent non-winged generations were relatively sedentary, resulting in a clumped spatial pattern. *U. tissoti* colonized stems singly and was more mobile; these behaviors resulted in its more random spatial pattern within fields of goldenrod.

Manipulations of aphid density in the field revealed that although patches with high densities of aphids accumulated more predators than patches with few aphids, predation pressure (measured as number of predators per aphid) was lower in dense patches. As a result, aphids in dense patches had a higher per capita change in density than aphids in sparse patches. However, when the fungal pathogen, *Neozygites fresenii*, became the dominant mortality agent, the influence of aphid density on mortality was reversed; aphids in dense patches were then more vulnerable than aphids in sparse patches. Thus the spatial patterns exhibited by the *U. nigrotuberculatum* and *U. tissoti* resulted in differences in their relative vulnerability to different natural enemies.

Key words: Aphids – Density dependence – Host-pathogen interactions – Predator-prey interactions – Spatial patterns

Theoreticians seeking to understand the population dynamics of phytophagous insects have been interested in spatial heterogeneity for more than a decade. Although numerous models have incorporated the effects of spatial heterogeneity in enemy attack (e.g., Hassell and May 1974; Murdoch and Oaten 1975; Hassell 1985; Chesson and Murdoch 1986), few incorporate explicitly spatial differences in victim density (Murdoch and Reeve 1987). This is unfortunate because phytophagous insects vary greatly in their typical spatial patterns; some aggregate onto their host plant resource, whereas others are more regularly dispersed in space (Taylor et al. 1978; Stamp 1980; Edson 1982, 1985).

In addition, most phytophagous insects are attacked by a large number of natural enemies, ranging from generalist predators to specialist parasitoids and diseases. Each type of enemy is likely to respond in a different fashion to variation in prey or host density. Thus, insects with different spatial patterns are likely to differ in their vulnerability to the various types of mortality agents.

In this study, I compared the spatial patterns of two species of goldenrod-feeding aphids, *Uroleucon nigrotuberculatum* and *U. tissoti*. Observations on naturally occurring patches differing in number of aphids, as well as manipulations of aphid density in the field, were used to determine the influence of aphid density on predation and on mortality caused by a fungal pathogen.

Natural history

The two aphids, *Uroleucon nigrotuberculatum* and *U. tissoti*, were studied at Tall Timbers Research Station, Leon County, Florida. Both feed primarily on the goldenrod *Solidago altissima*, a widespread perennial plant of abandoned fields. *U. nigrotuberculatum* occurs on goldenrod throughout the eastern U.S. and has been studied in North Carolina (Edson 1982, 1985), Rhode Island (Kareiva 1984) and New York (Cappuccino 1987). The range of *U. tissoti* extends northward into North Carolina (Edson 1982, 1985), but this species is replaced further north by the morphologically and behaviorally similar *U. caligatum* (Cappuccino 1987). *U. nigrotuberculatum* and *U. tissoti* share a common set of natural enemies in Florida, which include numerous species of coccinellid beetles, larvae of both hemerobiid and chrysopid lacewings, larvae of syrphid flies, tettigoniid grasshoppers, fire ants (*Solenopsis invicta*), aphidiid wasps and the fungal pathogen *Neozygites fresenii*.

Methods

On 27 May 1984, I assessed *U. tissoti* dispersion in an old field in which occurred a vigorous stand of *Solidago altissima*. I walked along two transects (each approximately 125 m long) and haphazardly chose a stem every 5 m. Each stem was searched for both *U. nigrotuberculatum* and *U. tissoti*. Because *U. nigrotuberculatum* did not appear in this sample, and because upon further observation I found no *U. nigrotuberculatum* colonies (I use "colony" to refer to the aphids on one stem) in this field, I sampled an adjacent field for this species.

To determine the mechanisms responsible for the spatial patterns of the two species, I looked specifically at the aggregation behavior of alates and the predator avoidance behavior of apterae. To see if alates of either species respond to conspecifics when colonizing goldenrod stems, I

chose 20 pairs of *S. altissima* stems; paired plants were <0.5 m apart and similar in height and appearance. All aphids were removed from these stems. One member of each pair of plants then received 10–15 first instar *U. tissoti* nymphs. All nymphs readily initiated feeding within 15 min of transfer. I checked the stems after 24 h and counted all *U. tissoti* alates that colonized the stems. Six stems lost their nymphs to predators and these were excluded from analysis. One week later, when *U. nigrotuberculatum* alates were noticed colonizing stems in this field, I repeated the experiment with *U. nigrotuberculatum* nymphs.

I also tested apterous adults and fourth instar nymphs of both species for their response to medium-sized coccinellid larvae. I found 18 *U. tissoti* colonies and 6 *U. nigrotuberculatum* colonies on stems free from predators. All of the aphids in these colonies were feeding (stylets inserted into stems), none were wandering around on the stems or sitting under leaves. Onto half of the *U. tissoti* stems and half of the *U. nigrotuberculatum* stems I placed one second instar coccinellid larva. I recorded the position of the aphids after 3 h.

Between 4 and 8 June the response of predators to aphid patch density was tested by manipulating the number of *U. nigrotuberculatum* in 1/2 m^2 patches of goldenrod. The experiment was done with *U. nigrotuberculatum* for two reasons: 1) the more sedentary *U. nigrotuberculatum* individuals were more likely to remain in the spatial pattern in which I placed them, and 2) there were no *U. nigrotuberculatum* already at this site at the time of the experiment. All *U. nigrotuberculatum* individuals used in this experiment were grown in a 5 m × 5 m predator exclusion screen cage.

I measured a 9 m × 5 m grid in the field and tagged sixty 1/2 m^2 patches of goldenrod at 1 m intervals within the grid. Patches were randomly designated to receive low (1–29), medium (30–99), or high (100–600) densities of aphids. (These densities were not always achieved; the goal was merely to establish a range of patch densities.) Aphids were transferred to stems in the patches by cutting "donor" stems bearing aphids from within the predator exclusion cage and attaching them to "recipient" stems with a twist-tie. Within a day, when the donor stems had wilted and the aphids had moved onto the recipient stems, I removed the twist ties and donor stems and counted the aphids. Twice daily for 3 d I recorded the number of aphid adults and nymphs, and predators in the patches. I repeated the experiment on 12–16 June, after first removing any residual aphids (they were few) and predators from the patches, and reassigning the patches to density treatment.

On 18 June when cadavers of aphids killed by the fungal pathogen *Neozygites fresenii* were seen at one end of the field, I tagged the colonies in 38 naturally occurring patches of *U. nigrotuberculatum*. I counted the aphids in these colonies every day, removing any predators seen feeding there and counting cadavers of aphids that had succumbed to the disease.

Results

U. nigrotuberculatum individuals were more clumped onto goldenrod stems than *U. tissoti* individuals (Fig. 1); stems contained either no *U. nigrotuberculatum* or many, whereas most stems sampled for *U. tissoti* contained a few individuals. This difference in dispersion was partly the result of

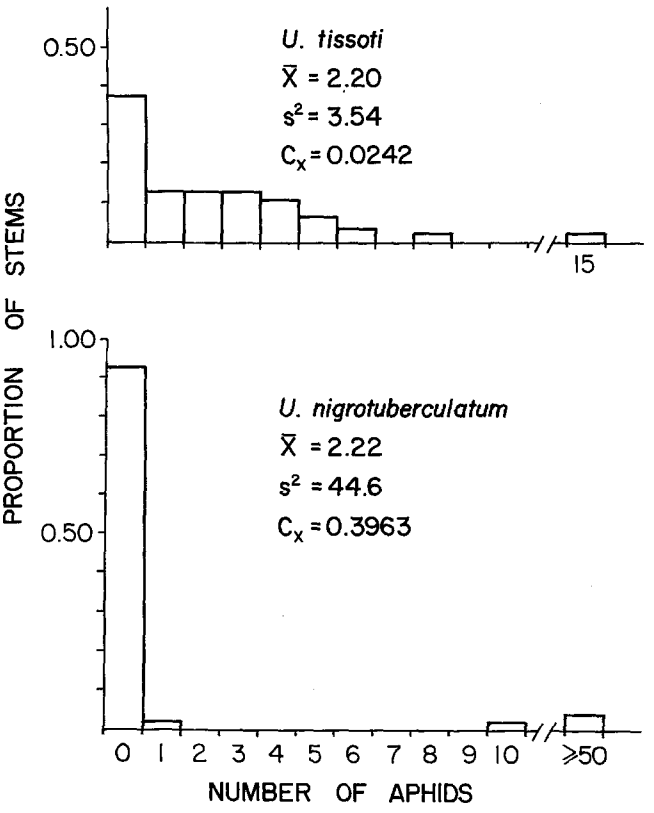

Fig. 1. Distribution of *U. nigrotuberculatum* and *U. tissoti* onto stems. Mean ($\bar{X}$) and variance (s^2) in the number of aphids per stem, as well as Green's (1966) aggregation index (C_x) are included on the Fig.

a response of *U. nigrotuberculatum* alates to conspecifics. Stems with *U. nigrotuberculatum* nymphs attracted more alates than those without (Wilcoxon signed-ranks test, $P=0.006$). *U. tissoti* alates showed no such tendency to colonize stems with nymphs more frequently than stems without nymphs (Wilcoxon signed-ranks test, $P=0.265$). This difference in spatial pattern was exaggerated by the different responses to disturbance exhibited by the two species. When disturbed by second instar coccinellid larvae, *U. tissoti* individuals were much more likely than *U. nigrotuberculatum* individuals to stop feeding and wander about on the plant (Table 1). Predators did not influence the likelihood that *U. nigrotuberculatum* individuals would stop feeding (Table 1). By having no aggregative response when initiating colonies and by walking away from disturbances, *U. tissoti* takes on its characteristic dispersion of numerous small colonies scattered throughout a field of goldenrod.

In both density manipulation trials, there were more predators in patches of high aphid density (Fig. 2A). However, the number of predators per aphid (and hence predation pressure) was lower in dense patches (Fig. 2B). Dense patches of aphids had significantly higher (log) percentage increase than patches with few aphids (Table 2). Not surprisingly, percentage increase was also higher in patches with a greater proportion of adults (Table 2) – a result of greater reproduction in these patches.

Pathogen-induced mortality was significantly greater for aphids in dense patches than for those in sparse patches (Fig. 3). Within patches, larger colonies tended to show sign of infection sooner than small colonies. Although few of these within patch correlations between colony size and date

Table 1. Response of *U. nigrotuberculatum* and *U. tissoti* to second instar coccinellid larvae. Aphid colonies either received one predator or none (controls) and aphids responded by either moving or not moving

	G_{adj}	significance
3-way *G*-test:		
species × predator treatment × response	3.35	ns
2-way *G*-tests:		
U. tissoti:		
predator treatment × response	90.72	$P<0.0001$
U. nigrotuberculatum:		
predator treatment × response	1.99	ns
with predator:		
species × response	69.25	$P<0.0001$
no predator (control):		
species × response	0.004	ns

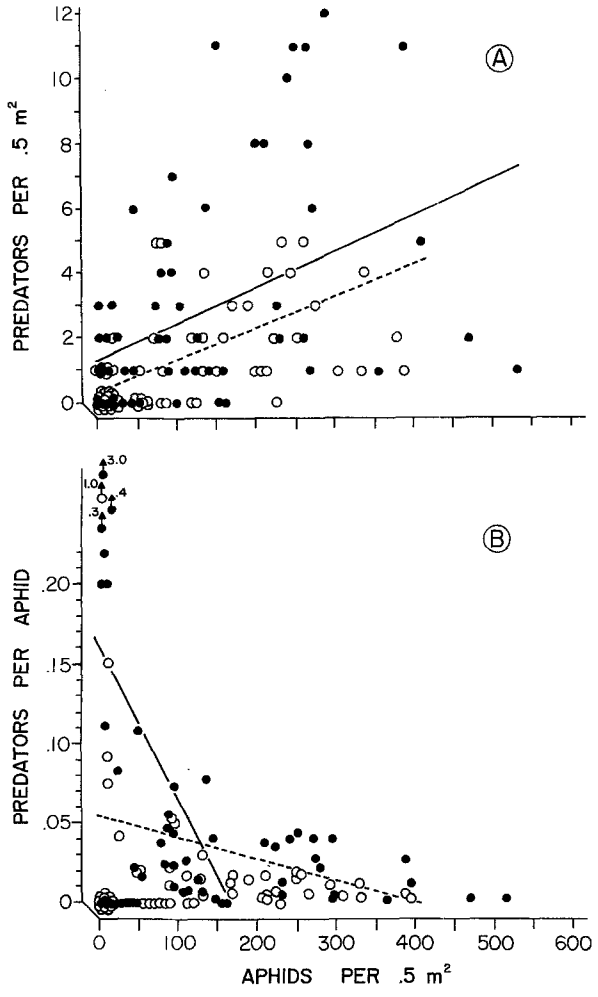

Fig. 2. **A)** Predators per 0.5 m^2 patch as a function of initial aphid density per patch. Trial 1 (solid dots and line) regression equation: $Y=1.346+0.013\,X$, $F=15.87$, $P<0.0001$. Trial 2 (open dots and broken line) regression equation: $Y=0.430+0.007\,X$, $F=20.21$, $P<0.0001$; **B)** Predators per aphid as a function of initial aphid density. Trial 1 (solid dots and line) regression equation: $Y=0.166-0.001\,X$, $F=2.06$, $P=0.113$. Trial 2 (open dots and broken line) regression equation: $Y=0.054-0.0001\,X$, $F=1.592$, $P=0.123$

Table 2. Regression of log transformed percent change in aphid number on percent adults in patches and initial patch density

Trial	Independent Variable	Coefficient	*F*	*P*
1	percent adults	3.557	7.51	0.009
	initial density	0.0014	6.44	0.015
2	percent adults	−0.570	0.33	ns
	initial density	4.530	20.54	0.0001

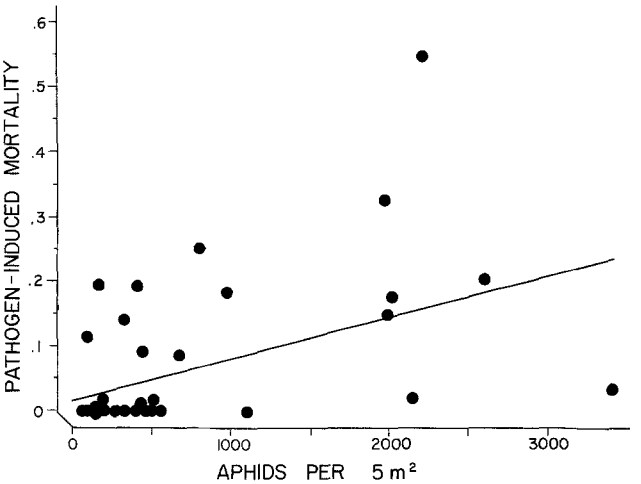

Fig. 3. Pathogen-induced mortality as a function of initial aphid density. Regression equation: $Y=0.0436+0.00005\,X$, $F=4.65$, $P=0.0397$

of first infection were significant at $P=0.05$, 11 of the 14 were negative (sign test, $P<0.05$).

Although there were significant relationships between aphid density and both predation and disease, there was nonetheless considerable variance in the effect of density on the risk of an aphid being killed by these mortality agents (Figs. 2 and 3). Although aphids in sparse patches were at a significantly higher risk of being eaten by a predator, many sparse patches escaped predation entirely. Likewise, two patches with high aphid density lost relatively few aphids to the fungal pathogen.

Discussion

The differences in the spatial patterns of the two goldenrod-feeding aphids, *Uroleucon nigrotuberculatum* and *U. tissoti*, which result from differences in the colonization patterns of alates and the local movement of apterae, fit a tpyical dichotomy in aphid spatial behavior (Dixon 1958). In his scheme, aphids are either a) sedentary, clumped, aposematically colored, toxic and/or ant-tended, or b) mobile, more randomly dispersed and cryptic. *U. nigrotuberculatum* does not appear to be toxic to its predators, and it is unlikely that its arthropod predators are deterred by its color (Cappuccino 1987). Birds may be less likely to eat red aphids. Although I never observed birds eating either *U. nigrotuberculatum* or *U. tissoti* in Florida, North Carolina, Rhode Island or New York, I have seen gnatcatchers (*Polioptila* sp.) eating aphids from *Encelia farinosa* stems in Arizona. Although the stems bore both red and green aphids, similar in size and appearance to *U. nigrotuberculatum* and *U.*

tissoti, it was unclear whether the gnatcatchers were being selective in which species they took.

U. nigrotuberculatum and *U. tissoti* exhibited the same spatial patterns in Florida as they do in eastern North Carolina (Edson 1982, 1985), and western North Carolina (personal observation). Furthermore, *U. nigrotuberculatum* displays the same behavior in Rhode Island (Kareiva 1984), and New York (Cappuccino 1987). *U. caligatum* replaces *U. tissoti* in New York and is similar in color (green), behavior and spatial pattern (Cappuccino 1987). Moran (1986) has shown that a pair of *Uroleucon* species feeding on *Solidago nemoralis* show a similar behavioral dichotomy; *U. nigrotibium*, a specialist on *S. nemoralis*, forms large colonies, whereas *U. gravicoryne*, a more general feeder, forms small colonies and disperses more frequently by producing alates at lower densities. *U. nigrotibium*, however, is more likely to escape enemies by walking to adjacent stems, but because of the highly clumped dispersion of *S. nemoralis* (several stems emerge from the same woody caudex), this behavior does not spread *U. nigrotibium* over a large area as it does for *U. tissoti* on *S. altissima*.

Although dense aggregations of *U. nigrotuberculatum* "attract" or otherwise accumulate more predators than sparse patches, the number of predators per aphid (predation pressure) is lower in dense patches. This lighter predation pressure in dense patches is reflected in the relationship between percentage change and initial density – patches with more aphids had a higher per capita change in density than patches with few aphids. Although aggregations of some insect species have been shown to facilitate feeding and enhance reproduction (e.g., Hayamizu 1984), Cappuccino (1987) has shown that this was not the case for *U. nigrotuberculatum*. Thus, the higher per capita change in density for aphids in dense patches was the result of lower mortality not greater reproduction.

U. tissoti does not aggregate and may be more vulnerable to predators as a result. Although *U. tissoti* adults and large nymphs are probably able to escape predators by walking, small nymphs are less mobile and more vulnerable to predators (Cappuccino 1987). This vulnerability is likely to be enhanced by the fact that mobile *U. tissoti* adults deposit their nymphs in numerous small colonies instead of single large aggregations.

Although it may aid in numerically "escaping" predators, aggregation increases the likelihood of aphids succumbing to the fungal pathogen, *Neozygites fresenii*. Like its congener, *U. tissoti* is also susceptible to *Neozygites*; I have been able to infect *U. tissoti* in the laboratory by exposing them to sporulating *U. nigrotuberculatum* cadavers. However, I have not observed *U. tissoti* populations in Florida or North Carolina, or *U. caligatum* populations in New York, annihilated by this pathogen, even where large *U. nigrotuberculatum* aggregations in the same field were completely destroyed. The widely scattered spatial pattern of *U. tissoti* and *U. caligatum* apparently affords these two species protection from the density-dependent mortality imposed by *Neozygites*.

Thus, there is a reversal in the relative advantage of the spatial strategies of these two species when the fungal pathogen *Neozygites* supplants predators as the most important cause of aphid mortality. When enemies act in an inverse density-dependent manner, as did the predators in this study, the dispersion exhibited by *U. nigrotuberculatum* is, on average, more advantageous. When faced with a strongly density-dependent mortality agent, such as a pathogen, it is more advantageous to have a dispersion such as that of *U. tissoti*. With the diversity of natural enemies faced by most phytophagous insects (Root 1973; Cappuccino unpublished work), any one strategy for avoiding enemies is likely to work against only a subset of enemies. Thus, insect spatial pattern becomes an important niche variable, in the sense that different spatial patterns result in limitation by different types of enemies.

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