Migratory Aphid (Hemiptera: Aphididae) Habitat Selection in Agricultural and Adjacent Natural Habitats

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ABSTRACT Paired suction traps were used to study the habitat choice of migrating aphids in adjacent crop and natural habitats in east central Illinois. Traps were placed in a row-crop field and a restored prairie for 4 yr at one site, and a row-crop field and a wooded plot for 3 yr at another. Row crops were corn or soybean, rotated annually. We did not wish to sample aphids that were native to the local habitats because they would be in a habitat by circumstance of birth, and not necessarily by choice. We therefore removed from the habitat choice analysis any aphid species that colonize plants in either the agricultural or natural habitat. Numbers of aphids from outside sources in the two adjacent habitats were compared. In 2 of 4 yr, outside-source aphids were more abundant in the row-crop than the restored prairie, despite the absence of potential host plants in both habitats. In all 3 yr, outside-source aphids were trapped in greater numbers in the crop than in the woods. Selection of the crop over the natural habitat occurred during almost all sampling periods throughout the summers. We present possible explanations for the aphids' apparent preference for crop habitats and provide brief discussions of abundant aphids, local—as well as outside—source species, trapped in our study. We also discuss the relevance of our study to the understanding of long- and short-distance aphid migration and aphid vectoring of plant pathogens.

KEY WORDS Aphididae, migratory flight, habitat selection, suction trap

APHIDS ARE SERIOUS pests in most regions of the world because of their high fecundity and vectoring of plant viruses. Although much is known about the mechanisms of virus transmission (Nault 1997), relatively little is known about the factors guiding the dispersal of migratory aphids and hence the long-distance spread of aphid-vectored plant pathogens. The current study was designed to assess whether or not aphids are capable of selecting when and where to terminate their migratory flight.

Most work on aphid flight behavior has examined trivial flight, the plant to plant flight of an aphid searching for a suitable host. Trivial flight is horizontal and for short distances, and always well within the atmospheric boundary layer (Kring 1972). During trivial flight, the aphid lands on a plant, probes it a few times with its stylets, and either decides it is suitable and settles, or flies again toward another plant to repeat the process.

In contrast, migratory flight, from birth colony to new host, bypasses potential targets nearby (Hardie 1993), and so is a means of dispersal to geographically distant locations. Just how distant is a matter of some contention. Because migratory aphids are carried by the wind, and because of a few exceptional reports of finding aphids 1,000 km from the nearest possible source (Elton 1925, Kring 1972), certain workers have emphasized long-distance migration of aphids ranging into the hundreds of kilometers (Hendrie et al. 1985, Irwin and Thresh 1988, Riley et al. 1995). In contrast, other aphidologists dismiss long-distance migration as uncharacteristic of most aphids, and emphasize the importance of shorter distance migrations of 20 km or less (Loxdale et al. 1993).

Be it long- or short-distance migration, aphids terminate migratory flight and arrive in a particular habitat to then enter trivial flight and search for a suitable host. One hypothesis is that migratory aphids, as aerial plankton, have little or no control over when and where they stop. That is, they stop their migratory flight whenever and wherever the wind stops, and descend into whatever habitat they happen to be above at the time. Another hypothesis is that aphids actually do have significant control over when and where they end migratory flight and enter trivial flight. Hardie (1989) called this ending of the migratory flight behavior attacking flight.

Termination of migratory flight and aphid landing is clearly a complex process, mediated by many factors. Irwin and Hendrie (1987) hypothesized four possible principal mechanisms for termination of aphid migratory flight: (1) physical, weather-related phenomena (e.g., down-drafts); (2) aphid physiological response to exhaustion; (3) environmental stimuli (e.g., vegetation cues); and (4) some combination of 2 and 3. Hendrie et al. (1987) added that despite these four possibilities, most evidence suggests that landings are behaviorally motivated, and that aphids guide themselves to appropriate habitats at ground level (i.e., during trivial flight).

Historically, migrating aphids have been sampled by airplane (Taylor 1960), helicopter (Hollinger et al.

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1991), and tall suction traps (Halbert et al. 1990), but these methods sample aphids exclusively during migration, and not immediately thereafter. Attacking aphids are typically sampled by pan- and sticky-traps. Irwin and Hendrie (1987) tried using a rotating sticky trap system in which fresh traps were automatically deployed in 3-h increments. This and other trapping methods sample aphids almost exclusively during trivial flight, however, and not immediately before they begin trivial flight.

To address the issue of migratory aphid habitat choice, and hence the amount of control aphids have in termination of migratory flight, we aimed to sample aphids after termination of migratory flight. The objectives of the current study were to determine if aphids exhibit a selective choice for one habitat over another and, if so, to determine what species exhibit this preference.

Materials and Methods

Suction Traps. Aphid sampling was done using a custom-built, solar-powered, adjustable-height suction trap system, in which identical, paired suction traps, drawing air at ≈3 m^3/min, were placed in adjacent habitats. One pair of traps was placed at the University of Illinois's Phillips Tract in Champaign County, 5.5 km NE of Urbana, IL (40° 08.01' N, 88° 08.98' W). One trap was put in a crop field (corn or soybean) ≈15 m from the crop-prairie boundary, and the other in a restored prairie also ≈15 m from the boundary. The two traps were therefore ≈30 m apart. Another pair of traps was placed at the University of Illinois's Rutan Tract in Vermilion County, 3.5 km SE of Ogden, IL (40° 04.26' N, 87° 54.27' W). One trap was placed in a crop field (corn or soybean) ≈3 m from the edge, and the other in a wooded plot (principally oak, maple, and shag-bark hickory), also ≈3 m from the edge. There was a small grassy area between the woods and the crop so the traps were ≈30 m apart from each other. Phillips and Rutan Tracts are 22 km apart.

The Phillips Tract traps were in place during the summers of 1995–1998, and the Rutan Tract traps during the summers of 1996–1998. Due to variation in crop planting and harvesting dates, sampling was not conducted for the same amount of time each year. At Phillips Tract, the traps were in place from 29 June to 30 August 1995, 9 August to 10 September 1996, 9 July to 6 October 1997, and 26 June to 30 September 1998. At Rutan Tract, they were in place from 2 July to 9 October 1996, 31 July to 6 October 1997, and 26 June to 8 September 1998.

The traps were short enough (average of ≈2 m) to sample well within the atmospheric boundary layer; but to minimize the effects of differing plant height, they were adjusted to be above the vegetation in the crop and prairie. The trees in the wooded plot extended much higher than the trap can be set and the effects of this difference between woods and crop will be addressed in the *Discussion.*

Aphid Collection, Preparation, and Identification. Aphids were trapped in 5 by 5-cm jars half-filled with a 1:1 mixture of propylene-glycol and water. Trap samples were removed, and the solution changed, once every week to 10 d, but occasionally following longer intervals. Aphids were sorted out of the samples, cleared in a potassium hydroxide and chloral phenol procedure (Hille Ris Lambers 1950), and preserved in 70% ethanol. They were sorted, mounted on slides in Canada balsam, and identified to species whenever possible. Determinations were made by both authors, and all specimens have been deposited in the insect collection at the Illinois Natural History Survey, Champaign, IL.

Local Versus Immigrant Aphids. We were only interested in those aphids that were leaving migratory flight and were therefore originating at some distance from the traps, but we knew we would also capture aphids in other behavioral modes, i.e., trivial flyers and aphids originating from the local habitat that were not yet migrants. To minimize the effect of trapping local aphids, we included only those species whose host plant records (Smith and Parron 1978) were for plants absent from both the crop and natural habitats (prairie or woods, for Phillips and Rutan Tracts, respectively). An inventory of the plant species in the prairie and woods was not conducted, so the aphid grouping was kept conservative by excluding aphids from plant species that might be in the natural habitats. Aphids do not generally colonize soybean in the United States (Turnipseed and Kogan 1976), therefore no species were credited to that crop. Only *Rhopalosiphum maidis* (Fitch) was noted to colonize corn to a significant degree, therefore it was the only species considered to originate from the crop. Corn was planted at Phillips Tract in 1997, and at Rutan Tract in 1996 and 1998. Soybean was planted at Phillips Tract in 1995, 1996, and 1998, and at Rutan Tract in 1997. *Rhopalosiphum maidis* was counted as a local source species when corn was planted, and as an outside source species when soybean was planted. Because *R. maidis* occurred in our traps in such high numbers (more than all other species combined), analyses excluding *R. maidis* entirely were also conducted.

Habitat Selection. The numbers of aphids of each species trapped at adjacent sites was tabulated for each trapping interval (10 d, on average). Trapping intervals were combined to give yearly and cumulative figures, and appropriate species were combined to give totals of outside-source aphids. Differential habitat selection, cumulative over the whole sampling period, was examined for all abundant species, i.e., those for which at least 10 individuals had been trapped in either of the two adjacent habitats. Differences in the numbers of aphids from the various sampling units were tested for significance ($P \leq 0.05$) by chi-square analysis. Due to the small sample sizes, individual trapping intervals were not tested.

Results

Yearly and Cumulative Results. A total of 11,530 aphids from 94 species was identified from the samples. Based on host-plant records, 60% of the Phillips Tract aphid species and 56% of the Rutan species are

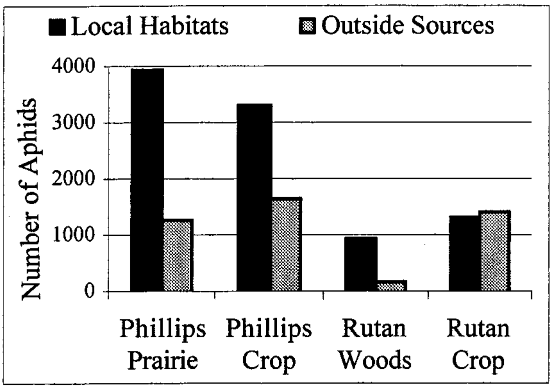

Fig. 1. Total numbers of aphids from local or other habitats trapped in the four trap locations during 1995–1998 at Phillips Tract and during 1996–1998 at Rutan Tract.

unlikely to have originated locally. These outside-source species represented only 32% of total individuals (Fig. 1).

Of the aphids that had to originate outside of the prairie/crop Phillips Tract habitats, cumulative over 4 yr, 36% flew into the prairie and 64% flew into the crop (Table 1, including *R. maidis*). On a yearly basis, a marked differential was shown for the crop in 1995 and 1998, but none was seen in 1996 and 1997. Excluding *R. maidis* gave similar results (Table 1). The differential in aphid numbers at Rutan Tract was more pronounced, where 90% of outside-source aphids flew into the crop and 10% flew into the woods, cumulative over all 3 yr (Table 1, including *R. maidis*). The rate of selection for the crop was greater during all years individually. Excluding *R. maidis* in 1997, 25% of outside-source aphids chose the woods, 75%, the crop (Table 1).

Seasonal Results. Julian date plots of the collection data indicated that outside-source aphids entered the crop in greater numbers throughout the summer (Figs. 2 and 3). Sampling period results are not shown for Phillips Tract 1996 because the traps were in place for only 1 mo. Only in 1995 (Phillips Tract) were outside-source aphids more abundant in the prairie than in the crop at peak abundance (Fig. 2a), but excluding *R. maidis* from the analysis yielded a result similar to that of other years (Fig. 2b). Omitting or including *R. maidis* in the other soybean years did not alter the general pattern; aphid peaks were similar in 1998 at Phillips Tract (Fig. 2 c and d) and in 1997 at Rutan Tract (Fig. 3 a and b).

During the corn year at Phillips Tract (1997), there was a bimodal distribution of outside-source aphids, with peaks centered around 31 July (Julian date 212) and 15 August (JD 227; Fig. 2e). The aphids trapped in the crop outnumbered those trapped in the prairie during both of these peaks, as well as during the trough between (Fig. 2e). The other 2 yr at Phillips Tract, outside-source aphids reached a single peak around or within 1 wk of 24 July (JD 205; Fig. 2). Peak abundance occurred 3–4 wk later at Rutan Tract: in 1996 and 1997, flying aphids reached their peak abundance around 13 August (JD 225; Fig. 3 a–c), and in 1998 they peaked around 23 August (JD 235) in the crop with a 10 d delay in the woods (2 September; JD 245; Fig. 3 d).

Individual Species. Twenty-two abundant (>10 individuals in any one trap) species were trapped at Phillips Tract (Tables 2 and 3). Nine (including *R. maidis* in soybean) were species from outside sources, four of which were more abundant in the crop despite the absence of potential hosts in either crop or prairie (Table 2). Four outside-source aphid species were not trapped in significantly different numbers in the two habitats, and only *Hyalopterus pruni* (Geoffroy) was trapped in greater numbers in the prairie. Fourteen species (including *R. maidis* in corn) were potentially from local sources, with seven trapped in greater numbers in the prairie, and four trapped in similar numbers in both habitats (Table 3). Three species, *Rhopalosiphum padi* (L.), *R. rufiabdominalis* (Sasaki), and *Schizaphis graminum* (Rondani), although considered local-source aphids, and hence by default prairie-source aphids, were trapped in the crop in greater numbers than in the prairie (Table 3).

Of the 17 abundant species at Rutan Tract, nine of 11 outside-source aphids (including *R. maidis* in soybean) were trapped in greater numbers in the crop. The other two outside-source aphids exhibited no differential abundance (Table 2). Three of seven local-source aphid species (including *R. maidis* in corn)

Table 1. Numbers of outside-source aphids trapped in each of the four traps, by capture site and year

Trap site	Including *R. maidis* when crop was soybean[a]					Excluding *R. maidis* when crop was soybean[a]				
	1995[b]	1996	1997	1998	All Years	1995[b]	1996	1997	1998	All Years
Phillips Tract prairie	216	121	92	468	897	29	22	92	42	297
Phillips Tract crop	301	94	119	1,047	1,561	64	21	119	90	470
Phillips Tract χ^2	13.97	3.39	3.45	221.28	179.37	13.17	0.02	3.45	17.45	39.02
Phillips Tract *P*-value	<0.0005	>0.05	>0.05	<0.0005	<0.0005	<0.001	>0.05	>0.05	<0.0005	<0.0005
Rutan Tract woods		46	98	23	167		46	55	23	124
Rutan Tract crop		104	1,276	62	1,442		104	201	62	367
Rutan Tract χ^2		22.43	1,009.96	17.89	1,010.33		22.43	83.27	17.89	120.26
Rutan Tract *P*-value		<0.0005	<0.0005	<0.0005	<0.0005		<0.0005	<0.0005	<0.0005	<0.0005

[a] Numbers do not include *R. maidis* when the crop was corn (Phillips Tract 1997, Rutan Tract 1996 and 1998) because it was considered a local-source aphid those years.

[b] No trapping took place at Rutan Tract in 1995.

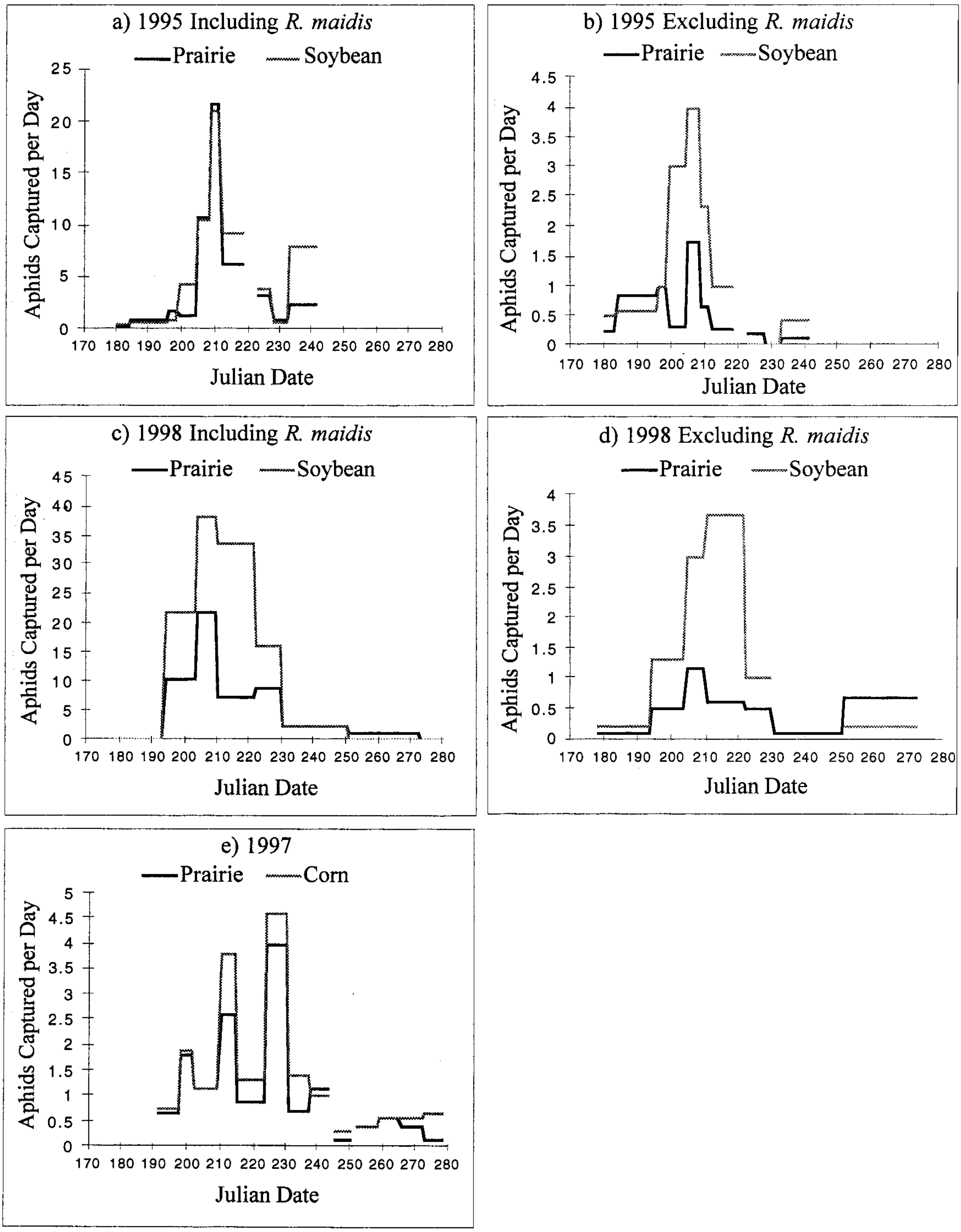

Fig. 2. Trap catches of outside-source aphids at Phillips Tract, normalized over a Julian calendar. Gaps in the curves are a result of missing data (usually due to trap failure). The abrupt, step-like nature of the curves is an artifact of capture data average over the span of several days.

were trapped in greater numbers in the crop, two showed no differential abundance, and two were trapped in greater numbers in the woods (Table 3).

Discussion

Habitat Selection. Migrating aphids arrived at differential rates in adjacent habitats that were equally

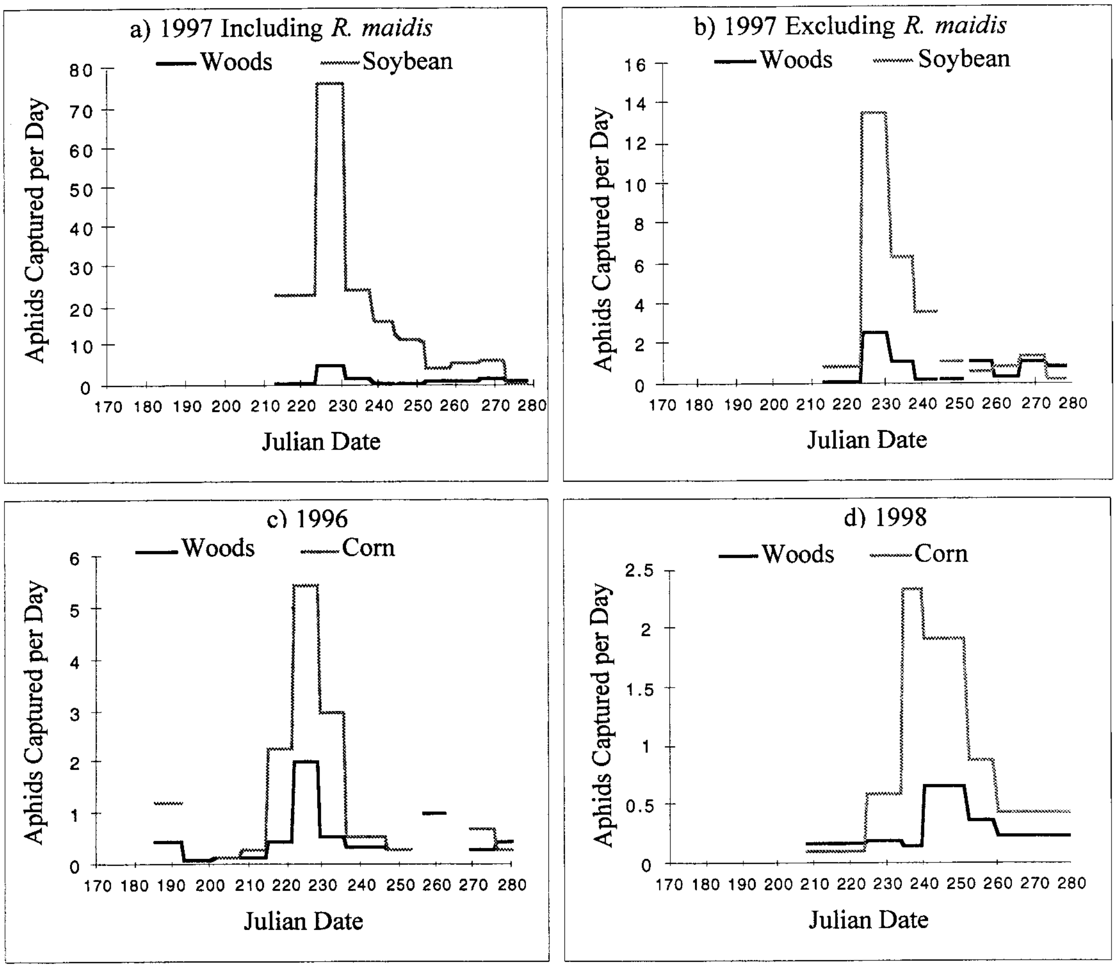

Fig. 3. Daily trap catches of outside-source aphids at Rutan Tract, normalized over a Julian calendar. Gaps in the curves are a result of missing data (usually due to trap failure). The abrupt, step-like nature of the curves is an artifact of capture data averaged over the span of several days.

devoid of suitable hosts. The choice of one habitat over the other was evident in five of seven site-years as well as in most individual collections during the summer (Figs. 2 and 3). Of the years with nonsignificant results, 1996 may have been due to small sample size (43 outside-source aphids); Phillips Tract 1997 provided a larger sample size (211 outside-source aphids), and although it did not yield significant results, the trend was in the same direction as in 1995 and 1998.

This apparent selection of one habitat over the other may be due to the aphids' response to certain, specific stimuli. Aphids can distinguish the wavelengths of various reflected light spectra, and *Brevicoryne brassicae* (L.) prefers a deep and rich green (Kennedy et al. 1961), a more prevalent color in the crop than in the heterogeneous prairie. Also, the stark contrast of green plants on a brown soil background may be more attractive to aphids than the noncontrasting landscape of the prairie or woods (Smith 1969, 1976). Crop row spacing directly affects the amount of contrasting soil that is visible from above. Studying the effect of crop canopy closure on aphid attraction, various researchers demonstrated that *Aphis craccivora* Koch, *A. gossypii* Glover, *Capitophorus elaeagni* (del Guercio), *C. hippophaes* (Walker), *Macrosiphum euphorbiae* (Thomas), and *R. maidis* were more abundant in crops with open canopies (A'Brook 1968, 1973; Iark and Smith 1976, Halbert and Irwin 1981). *Aphis spiraecola* Patch and *Myzocallis punctatus* (Monell) showed the reverse trend, however (Halbert and Irwin 1981), perhaps as *H. pruni* did in the current study. Because of highly disparate phenologies between species, it is not possible to tell from the results whether early season open canopy was more attractive than late season closed canopy.

Monocultures have long been recognized as attractive to certain species, and aphids are no exception. Increasing the diversity of a row crop, even slightly, as by intercropping, lowers the incidence of plant colonization by aphids (Bottenberg and Irwin 1992a, Ogenga-Latigo et al. 1992). It follows that if aphids are

Table 2. Abundant (10 or more individuals) outside-source aphid species whose host plants are not in the trapping habitats, their typical host plants, and the extent of their preferences for one habitat or the other

Species	Host(s)[a]	Phillips Tract				Rutan Tract			
		No. in Prairie	No. in crop	χ^2	*P* value	No. in Woods	No. in crop	χ^2	*P* value
Aphis craccivora Koch	Polyphagous, preference for legumes	8	12	0.8	>0.05				
Aphis gossypii Glover	Polyphagous, pest on many row crops	34	88[b]	23.9	<0.0005	2	23[b]	17.6	<0.0005
Aphis helianthi Monell	Dogwood (1°), sunflower, umbellifers					16	70[b]	33.9	<0.0005
Aphis nerii Boyer de Fonscolombe	Milkweed, oleander					15	39[b]	10.7	<0.005
Capitophorus elaeagni (del Guercio)	Russian olive (1°), thistles	9	37[b]	17.0	<0.0005	8	31[b]	13.6	<0.0005
Hyalopterus pruni (Geoffroy)	*Prunus* (1°), reeds	17[b]	7	4.2	<0.05				
Lipaphis erysimi (Kaltenbach)	Crucifers	5	12	2.9	>0.05				
Macrosiphum euphorbiae (Thomas)	Polyphagous					6	32[b]	17.8	<0.0005
Pemphigus populitransversus Riley	Poplar (1°), crucifer roots	3	18[b]	10.7	<0.005				
Rhopalosiphum maidis (Fitch)[c]		712	1,267[b]	155.6	<0.0005	43	1,075[b]	952.6	<0.0005
Rhopalosiphum rufiabdominale (Sasaki)	*Prunus* (1°), grass roots					4	25[b]	15.2	<0.0005
Schizaphis graminum (Rondani)	Grasses, especially cereals					5	11	2.3	>0.05
Tetraneura nigriabdominalis (Sasaki)	Elm (1°), grass roots	8	15	2.1	>0.05	4	26[b]	16.1	<0.0005
Therioaphis trifolii (Monell)	Legumes	51	65	1.7	>0.05	19	75[b]	33.4	<0.0005
Uroleucon gravicorne (Patch)	Various composites					5	12	2.9	>0.05

[a] (1°) denotes primary host(s), others are secondary hosts or hosts of monoecious aphid species.
[b] Aphid numbers significantly greater in one habitat than in the other.
[c] When soybean was the local crop.

drawn to a monoculture over a diculture crop field, they would also be drawn to a typical crop field over a natural polyculture, as per our results.

Habitat structure varied between the habitats and may have influenced the rate at which aphids arrived within them. The structure of the crop and the prairie were similar enough at Phillips Tract, but the structure of the woods at Rutan Tract was very different from that of the crop, and this difference could have biased our results. For instance, wind blows across a crop field unhindered, but is slower through the woods and might therefore carry more aphids away from the crop trap and deposit them in the woods. Conversely, the closed canopy of the woods may be an impediment to aphid penetration. The effect of plant structure on patterns of aphid deposition is contradicted by Mayse and Price (1978), who found that aerialy dispersed herbivores were concentrated leeward of windbreaks, rather than within the windbreaks themselves. The leeward position of the crop trap might explain why more aphids were caught there than in the woods (Fig. 1), but it cannot explain the variance between traps in the numbers of aphids of various species. Specifically, we would expect all outside-source species being blown in by the wind (as in Mayse and Price 1978) to show the same proportional abundance in one trap versus the other. Because consistent proportions are not observed (Table 1), and because the wind blows in many directions other than from the west, the windbreak hypothesis is unlikely to be the primary cause of the aphids' apparent selection of the Rutan Tract crop.

Because aphids typically select open canopies over closed ones (Halbert and Irwin 1981), it may be that they prefer flying above vegetation rather than through it. If this is the case, it would explain the greater numbers of most species in the crop trap, situated above the vegetation, than in the woods trap, situated well within the vegetation.

Individual Species. Examining individual species can tell us how general the crop-preference trend is across the Aphididae. All outside-source potential feeders on row crops, if they exhibited a preference, selected the crop (*A. gossypii*, *C. elaeagni*, *R. maidis*, and *Pemphigus populitransversus* Riley; Table 2). Likewise, local, prairie-source potential feeders on row crops also ended up in the crop in greater numbers (*R. padi*, *R. rufiabdominalis*, and *S. graminum;* Table 3). Of these seven species, six have near-worldwide distributions and are proven vectors of plant viruses (excepting *P. populitransversus;* Blackman and Eastop 1984). All of these species chose the crop despite the fact that few or no hosts were available. We propose that these species use the same stimuli, present in all row-crop monocultures, regardless of the actual suitability of the crop they perceive. For example, *A. gossypii* might use the same cues to choose a cotton field (a common host) as it did to choose our soybean

Table 3. Abundant (10 or more individuals) local aphid species whose host plants may be in the trapping habitats, their typical host plants, and the extent of their preferences for one habitat or the other

Species	Host(s)[a]	Phillips Tract				Rutan Tract			
		No. in Prairie	No. in crop	χ^2	*P* value	No. in Woods	No. in crop	χ^2	*P* value
Anoecia corni (F.)	Dogwood (1°), grass roots					165[b]	3	156.2	<0.0005
Anoecia cornicola (Walsh)	Dogwood (1°), grass roots	40[b]	1	37.1	<0.0005	551[b]	11	518.9	<0.0005
Aphis helianthi Monell	Dogwood (1°), sunflower, umbellifers	508[b]	161	180.0	<0.0005				
Aphis nerii Boyer de Fonscolombe	Milkweed, oleander	450[b]	108	209.6	<0.0005				
Aphis rubifolii (Thomas)	Blackberry	25[b]	2	19.6	<0.0005				
Aphis spiraecola Patch	*Spiraea* (1°), Polyphagous	10	9	0.1	>0.05				
Colopha ulmicola (Fitch)	Elm (1°), grasses					21	33	2.7	>0.05
Hyadaphis foeniculi (Passerini)	Japanese honeysuckle (1°), umbellifers	542[b]	148	225.0	<0.0005	30	145[b]	75.6	<0.0005
Macrosiphum euphorbiae (Thomas)	Polyphagous	10	19	2.8	>0.05				
Nearctaphis crataegifoliae (Fitch)	Apple, hawthorn (1°), legumes					12	18	1.2	>0.05
Rhopalosiphum maidis (Fitch)[c]	Corn, other grasses	1,625[b]	1198	64.6	<0.0005	63	863[b]	691.1	<0.0005
Rhopalosiphum padi (L.)	*Prunus* (1°), grasses, incl. cereals	23	59[b]	15.8	<0.0005	11	63[b]	36.5	<0.0005
Rhopalosiphum rufiabdominale (Sasaki)	*Prunus* (1°), grass roots	5	25[b]	13.3	<0.001				
Schizaphis graminum (Rondani)	Grasses, especially cereals	6	18[b]	6.0	<0.025				
Sitobion avenae (F.)	Grasses, including cereals and pastures	11	14	0.4	>0.05				
Uroleucon ambrosiae (Thomas)	Various composites	10	6	1.0	>0.05				
Uroleucon nigrotuberculatum (Olive)	Goldenrod	69[b]	24	21.8	<0.0005				

[a] (1°) denotes primary host(s), others are secondary hosts or hosts of monoecious aphid species.

[b] Aphid numbers significantly greater in one habitat than in the other.

[c] When corn was the local crop.

field (a nonhost). In the latter case, however, it would find itself in an unsuitable habitat.

Contradicting this proposal, however, is the case of *R. maidis* at Phillips Tract in 1997 (Table 3). Most of the disparity in differential habitat selection, *R. maidis* being in greater numbers in prairie than corn, can be accounted for in the 4 d from 29 July to 3 August 1997. During these days there were 618 *R. maidis* trapped in the prairie and relatively fewer, 260, in the corn. At the end of July and beginning of August every year, *R. maidis* leaves its local host and swamps all habitats; in 1995 it swamped soybean and prairie habitats equally (Fig. 2a). In 1997, immigrants that arrived in the corn found a host quickly and settled, but those that arrived in the prairie did not find a host and began a protracted trivial flight in search of one. These trivial flyers would thus have a greater chance of being trapped than would those aphids that had already found a host and settled (in the corn). Therefore, the high numbers of *R. maidis* in the prairie is an artifact of trivial flight, more prevalent in one habitat than in the other. This artifact highlights the importance of making habitat-choice analyses with outside-source aphids only, so that their trivial flight would not be subject to this kind of bias.

Dioecious, holocyclic aphids may have different habitat preferences, depending on the time of year. All but one (*C. elaeagni*) of the abundant cosmopolitan aphid species have no (or rarely have, in the case of *R. padi*) host alternation in our region of the world (Blackman and Eastop 1984). Therefore, it is unlikely that our results were confounded by aphids searching for an herbaceous host during the summer and a woody host during the fall.

Most habitat selection trends at Phillips Tract were mirrored at Rutan Tract, with almost all the abundant cosmopolitan pests of row crops arriving in the crop habitat in greater numbers than in the alternative habitat. The one exception was *S. graminum* that may not have been collected in sufficient numbers to reveal a difference (Table 2). *Tetraneura nigriabdominalis* (Sasaki), also a cosmopolitan row-crop aphid, although not showing a differential at Phillips Tract, did arrive in greater numbers in the crop at Rutan Tract. A feeder on roots of grasses, it would be expected to be in the prairie (hence the nonsignificant numbers at Phillips Tract), but not at all in the woods. The fact that a grassy area was adjacent to the woods only accentuates the higher numbers of *T. nigriabdominalis* in the crop.

Despite the general trend of greater numbers of aphids in the crop than in the prairie, some species had greater abundance in the prairie. The cosmopolitan, host alternating *Hyadaphis foeniculi* (Passerini) and

Aphis helianthi Monell, as well as the monoecious *A. rubifolii* (Thomas), *A. nerii* Boyer de Fonscolombe, and *Uroleucon nigrotuberculatum* (Olive) were all found in the prairie in greater abundance than in the crop (Table 3). This result was expected because all five have host plants in the prairie. *Hyalopterus pruni* also chose the prairie over the crop (Table 2), although neither its primary host (*Prunus*) nor its secondary host (*Phragmites*) is found there. Perhaps a prairie more resembles a migrating *H. pruni*'s search image, a field of reeds, than does a crop field. Similarly, perhaps *H. foeniculi* and *A. nerii*, more abundant in the prairie than in the crop at Phillips Tract, were more abundant in the crop trap than in the woods trap at Rutan because a crop field more resembles a natural herbaceous habitat, these aphids' search image, than it does a wooded plot. In a three-habitat choice test, we might expect them to preferentially select the prairie, then the crop, then the woods.

Three species of heteroecious aphids were trapped as they were migrating to their woody, primary hosts in the fall. *Colopha ulmicola* (Fitch) is a galling aphid on elm, its primary host, that migrates to grasses as its secondary host. It was trapped at all four sites in September only, the time when sexuparae migrate to their primary host (Blackman and Eastop 1994). Their equal abundance in the crop and the woods remains unexplained, but we cannot discount the possibility that the grassy area between crop and woods habitats may have been a source for this species. Alternately, perhaps this species is simply not as adept at choosing habitats as the others. Regardless of the reason, it stands in marked contrast to the situation with the dogwood aphids.

Two other tree-to-grass, host-alternating aphids, *Anoecia corni* (F.) and *A. cornicola* (Walsh), were in overwhelmingly greater numbers in the woods than in the crop at Rutan Tract; and *A. cornicola* also had greater numbers in the prairie at Phillips Tract (Table 3). Prevalent in high numbers in September and October, these were sexuparae migrating to their primary host, dogwood (Hottes and Frison 1931). There was no dogwood at the Phillips Tract prairie, however, so *A. cornicola* was selecting one habitat over the other even without potential hosts; and therefore its abundance in the woods at Rutan Tract is not just an artifact of wind and vegetation structure. That is, if these aphids really are selecting and flying into the prairie at Phillips Tract, then they are also likely selecting and flying into the woods at Rutan Tract.

Short-Term Effects. Habitat selection by outside-source aphids was not a sporadic event, but a continuous process. As seen in the Julian date analyses (Figs. 2 and 3), outside-source aphids preferred the crop almost every day of the summer, although *R. maidis* had to be removed from the analysis to achieve this result at Phillips Tract in 1995 (Fig. 2 a and b). The results from 1995 stand in contrast to those in the other soybean years during which *R. maidis* made no discernible impact on the overall pattern of habitat choice (Fig. 2 c and d, 3 a and b). The synchrony between *R. maidis* and all other outside-source aphids is noteworthy, suggesting that the conditions that attract this species also attract many others. We cannot explain the bimodal distribution of other-source aphids seen in 1997 at Phillips Tract (Fig. 2), but aphid population dynamics are very erratic and every year shows different patterns. For instance, the numbers of outside-source aphids trapped at Rutan Tract differed dramatically from year to year (Fig. 3 a, c, and d).

Why Phillips and Rutan Tracts should have consistently different timing of peak aphid abundance is unclear. Phillips and Rutan Tracts are at a nearly identical latitude and elevation and, therefore, weather is an unlikely explanation for the difference in peak timing between the two locations. This difference supports the hypothesis that aphid population effects are more of a short-range than a long-range phenomenon (Loxdale et al. 1993). Long-distance aphid migration would be expected to distribute aphids over a broad geographic area, having a homogenizing effect, and creating similar timing of abundance peaks at the two trapping locations that are only 22 km apart. The marked difference in timing indicates the importance of local factors present well within a 22-km radius of the traps.

In conclusion, aphids do discriminate between habitats, even if they are equally unsuitable. Most species selected a crop habitat rather than a natural habitat. The trend for crop selection was particularly evident in abundant, cosmopolitan aphids that are often crop pests. Aphids probably discriminate between habitats by using long-range visual cues, possibly color and contrast, and they seem to choose their habitat during migratory, not trivial flight. This pattern of habitat selection persisted throughout the summer, although certain host-alternating aphids selected different habitats in the fall.

Because crop feeders are preferentially attracted to crops, there are important implications for virus transmission. An open crop canopy may be relatively attractive to many aphids, explaining why A'Brook (1964) and Jones (1994) found a greater incidence of groundnut rosette virus and bean yellow mosaic virus, respectively, as their crop row spacing increased. Similarly, Bottenberg and Irwin (1992b) found that a mixed cropping system reduced the incidence of soybean mosaic virus. It seems the less a crop field resembles a monoculture of regularly contrasting visual stimuli, the lower the rate of virus transmission.

The results from the current study suggest that further research might be conducted on the effects of "camouflaged" crops on rates of aphid colonization and virus transmission. If aphids choose habitats that resemble row crop fields regardless of host-plant suitability, then creating a cropping system that appears more like a natural habitat from above may be a means of reducing aphid colonization and hence, virus transmission.

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