Varietal Preferences of *Erythroneura* Leafhoppers (Homoptera: Cicadellidae) Feeding on Grapes in New York

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ABSTRACT Species composition of *Erythroneura* leafhoppers infesting the 3 major classes of grapes grown in New York was investigated. Eastern grape leafhopper, *E. comes* (Say), comprised 74–100% of populations collected on the native American (*Vitis labrusca* Bailey) cultivars 'Concord', 'Niagara', 'Catawba' and 'Delaware'. On interspecific hybrid (*Vitis sp.*) and *Vitis vinifera* L. cultivars, *E. comes* was largely absent, and 97–100% of leafhoppers collected were 2 cryptic species, *E. bistrata* McAtee and *E. vitifex* Fitch. On the native American variety 'Elvira', a *V. labrusca* × *V. riparia* Michaux hybrid, field populations were 24% *E. comes* and 74% the *E. bistrata/vitifex* complex. *E. vitis* (Harris), *E. tricinta* Fitch, and *E. vulnerata* Fitch were also present in commercial grapes, but never exceeded 20% of the populations sampled. Populations on wild *V. riparia* adjacent to vineyards were comprised of 24% *E. comes*, 47% *E. bistrata/vitifex*, 19% *E. vitis*, and 10% *E. tricinta*. Dissection revealed that proportions of *E. bistrata* and *E. vitifex* in field collections, varied from 97% *E. bistrata* to 61% *E. vitifex*. Oviposition of *E. comes* and *E. bistrata* on *V. vinifera*, interspecific hybrid, and native American cultivars was compared in greenhouse choice tests and field no-choice tests. In choice tests, *E. comes* laid more eggs on Concord and Elvira than on the interspecific hybrid 'Seyval blanc', or the *V. vinifera* cultivar 'White Riesling'. *E. bistrata* did not oviposit on Concord when paired with either Elvira, Seyval blanc or White Riesling. When caged to grape leaves in no-choice tests, *E. comes* laid the most eggs on native American cultivars and the fewest on *V. vinifera* and interspecific hybrids; *E. bistrata* laid the most eggs on hybrid and *V. vinifera* cultivars, and very few eggs on three native American cultivars. These results show that *E. bistrata* and *E. vitifex* are the principal pest species on *V. vinifera* and many interspecific hybrid cultivars in New York, and that *E. comes* is the principal leafhopper pest on native American *V. labrusca* cultivars.

KEY WORDS *Vitis*, *Erythroneura*, host plant resistance, oviposition preference

LEAFHOPPERS OF THE genus *Erythroneura* have been considered important pests of grapes in New York and other parts of eastern North America since the late 1800s (Slingerland 1904, Hartzell 1912, Johnson 1914). Before the postwar introduction of DDT and other synthetic insecticides, *E. comes* (Say) was considered the most important pest of grapes in northeastern North America. In the early part of the century, observers noted severe outbreaks lasting 2–3 yr, followed by several years in which leafhoppers caused little damage (Johnson 1914, Eyer 1931). Chemical control programs used in New York and Pennsylvania, which relied on 3 routine calendar-based insecticide sprays, all but eliminated leafhopper injury from vineyards from the mid-1940s throughout the mid-1980s (Taschenberg 1973, Martinson et al. 1991). Recent reductions in insecticide inputs directed at grape berry moth, *Endopiza viteana* Clemens, have led to reemergence of leafhoppers as visible pests in New York vineyards and have created a need for management recommendations specifically targeted at leafhoppers (Martinson et al. 1991, 1994).

Previous publications about grape leafhoppers in northeastern North America have cited *E. comes* as the principal leafhopper pest in New York and Pennsylvania (Hartzell 1912, Johnson 1914, Taschenberg and Hartzell 1949, Taschenberg 1973, Jubb et al. 1983). However, other *Erythroneura* species, such as *E. tricinta* Fitch, *E. vitifex* Fitch, *E. bistrata* McAtee, *E. vulnerata* Fitch, and *E. vitis* (Harris) also feed exclusively on grapes and related species in the northeast (Beamer 1938, Bierne 1956). These leafhopper species have most likely received little attention from pest managers because previous studies were conducted on Concord, *Vitis labrusca* L. (Hedrick 1908) grapes. However, Bliss (1927) reported that oviposition rates of *E. vitifex*, *E. comes*, *E. vitis*, and *E. tricinta* varied when they were placed on Concord versus 'Clinton', *Vitis riparia* Michaux, vines. This evidence suggested that we would find differences in

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Table 1. Grape cultivars used in field survey and experiments

Class	Cultivar	Abaxial leaf pubescence	Parent species (%)
Native American	Concord	Dense	*V. labrusca*[a]
	Niagara	Dense	*V. labrusca*, possibly *V. vinifera*[a]
	Catawba	Dense	*V. labrusca*, possibly *V. vinifera*[a]
	Delaware	Dense	*V. labrusca*, *V. aestivalis*, *V. vinifera*[a]
	Elvira	Glabrous	*V. labrusca*, *V. riparia*[a]
Interspecific hybrid	Baco Noir	Glabrous	*V. vinifera* (50%), *V. riparia* (50%)[b]
	Castel 196-17	Glabrous	*V. vinifera*, (25%), *V. riparia* (75%)[b]
	Cayuga white	Glabrous	*V. vinifera* (50%), *V. labrusca* (25%), *V. rupestris* (17%), *V. aestivalis* (8%)[c]
	Chancellor	Glabrous	*V. vinifera* (40%), *V. rupestris* (25%), *V. labrusca* (19%), *V. riparia* (6%), *V. aestivalis* (6%), *V. cinerea* (3%)[b]
	Dechaunac	Glabrous	*V. vinifera* (50%), *V. labrusca* (16%), *V. rupestris* (31%), *V. riparia* (3%)[b]
	Seyval blanc	Glabrous	*V. vinifera* (50%), *V. rupestris* (35%), *V. aestivalis* (15%)[b]
V. vinifera	Pinot noir	Glabrous	*V. vinifera*[b]
	Chardonnay	Glabrous	*V. vinifera*[b]
	White Riesling	Glabrous	*V. vinifera*[b]

[a] Hedrick 1908.
[b] Galet 1979.
[c] Einset and Robinson 1972.

ovipositional preferences of *Erythroneura* leafhoppers among the diverse assemblage of grape cultivars grown in New York.

Before 1970, most grape varieties grown for wine and juice production in the northeast were native American cultivars, most of which are hybrids of *V. labrusca* and other *Vitis* parents. In the late 1960s, grape growers began planting different varieties of grapes for wine production. Today, >40 grape cultivars, categorized by viticulturists into 3 major classes, are grown in the region. The first class is native American cultivars (typified by Concord) derived from *V. labrusca*, which have been grown in quantity in the northeast since the mid-1800s. A second category is the interspecific hybrid varieties, some of which are known as French-American hybrids. These hybrids are complex crosses of *V. vinifera* and up to 7 American *Vitis* species, and most were developed in Europe during the last century to enhance resistance to diseases and grape phylloxera in wine grape varieties. Many were imported and planted in New York during the early 1970s for wine production. Additional interspecific hybrid varieties have been developed by breeding programs in New York and Ontario. The 3rd category is *V. vinifera* L. cultivars, which comprise the smallest vineyard acreage in the northeast. Although *V. vinifera* cultivars only recently have been grown widely in the northeast, they represent the premium wine varieties of the world and are increasing in importance throughout the region.

In examining leafhoppers feeding on these different types of vines, we realized that *Erythroneura* species other than *E. comes* were most common on hybrid and *V. vinifera* cultivars. We hypothesized that differences in host preference among *Erythroneura* species were related to phenotypic differences among the major classes of grape cultivars. *V. labrusca* cultivars have large, thick, and leathery leaves, with dense pubescence on the lower leaf surface. *V. vinifera* cultivars, in contrast, have thinner, smaller, and glabrous leaves. Interspecific hybrids, selected for their *V. vinifera*-like characteristics often have thin glabrous leaves, but have other phenotypic characters (e.g., growth habit) intermediate between their *V. vinifera* and native American parent species.

In this article we characterize the preferences of *Erythroneura* species for different classes of grapes grown in New York. We first identify the species composition of *Erythroneura* populations on different grape cultivars in the field. We then report results of studies in which oviposition of the two predominant *Erythroneura* species on cultivars representing the different classes of grapes was compared through choice and no-choice experiments. These experiments tested the hypothesis that the observed species composition in the field was associated with host discrimination by *Erythroneura* adults among different classes of grapes.

Materials and Methods

Grape Cultivars. Names, cultivar class, and parent *Vitis* species of grape cultivars used in the field surveys and experiments are listed in Table 1. The native American cultivars (Table 1) all share *V. labrusca* as a parent. However, exact parentage of these cultivars is unknown, because most have been under cultivation since the early 1800s. In Table 1, Hedrick's (1908) listing of probable parentage is cited. Concord, 'Niagara', 'Catawba', and 'Delaware' have leaves that are densely pubescent on the abaxial leaf surface, whereas 'Elvira' has glabrous leaves and other characteristics more similar to its *V. riparia* parent. Interspecific hybrids are

Table 2. Species determination by dissection of *E. bistrata* and *E. vitifex* collected in central New York vineyards in 1992 and 1993

Year	Cultivar	Cultivar class	Date collected	No. dissected	% total dissected	
					E. bistrata	*E. vitifex*
1992[a]	Elvira	Native American	08–15 May	52	100	0
			17–25 July	26	100	0
			Total	78	100	0
1993[b]	Castel 196-17	Hybrid	30 June	13	85	15
			07 July	21	100	0
			14 July	38	97	3
			15 Aug.	21	100	0
			Total	93	97	3
	Dechaunac	Hybrid	14 July	30	60	40
			21 July	25	36	64
			12 Aug.	48	40	60
			Total	103	45	55
	Niagara	Native American	02 July	6	100	0
			23 July	24	88	12
			13 Aug.	22	91	9
			Total	52	90	10
	Chardonnay	*V. vinifera*	03 July	39	31	69
			20 July	12	33	67
			Total	51	31	69

[a] Males collected from yellow sticky traps (10 by 15 cm) in Elvira vineyard adjacent to Castel 196-17 block.
[b] Males collected via vacuum sampling.

derived from complex crosses, involving *V. vinifera* and several other *Vitis* parents, all native to North America. Probable contribution of each *Vitis* species, determined through pedigrees listed in Galet (1979) and Einset and Robinson (1972) is listed in Table 1. All interspecific hybrids and *V. vinifera* cultivars, in contrast to native American cultivars, have glabrous leaves.

Leafhopper Identification. Field-collected leafhoppers used in these experiments were first separated into 4 groups based on the pattern and coloration of their wing markings. Examination of male genitalia (Bierne 1956, Beamer 1938) confirmed that 3 of these groups were distinct species, *E. comes*, *E. vitis*, and *E. tricinta*. Identification of the 4th group was more difficult. Specimens sent to specialists for identification in 1991 were initially determined to be a possibly undescribed *Erythroneura sp.* Subsequent examination of specimens in late 1992 by another specialist revealed this group to be comprised of 2 cryptic species, *E. bistrata* and *E. vitifex* (Beamer 1938), although the adeagal structures on our *E. bistrata* specimens were somewhat different than those of *E. bistrata* illustrated in the keys (R. Gill, personal communication). Because we did not dissect individuals of this group in our 1990–1992 field collections, we will refer to it as the *E. bistrata/vitifex* complex. All of these *Erythroneura* species are native to eastern North America.

Leafhoppers of the *E. bistrata/vitifex* complex, collected in 1992 in a 'Castel 196-17' block near Dresden, NY, were used in greenhouse and field oviposition experiments (described below). We did not confirm the species identity of leafhoppers used in these experiments by dissection, because *E. bistrata* and *E. vitifex* were assumed to be one species at the time collections were made. To determine probable species identity of leafhoppers used in these experiments, we dissected samples of males collected during 1992 on yellow sticky traps from an Elvira block adjacent to the 'Castel-196-17' collection site. Fifty-two males trapped from 8–15 May and 26 males trapped from 17–25 July were removed from the sticky traps, cleared in 10% potassium hydroxide, and identified via examination of genitalic characters (Beamer 1938, Bierne 1956). All of the males dissected (n = 78, Table 2) were *E. bistrata*. To further investigate the species composition of the *E. bistrata/vitifex* complex in field populations, we made additional collections from four vineyards during the 1993 growing season. Collections were made from Castel 196-17, Niagara, Chardonnay, and 'Dechaunac' grapes 2–4 times during the growing season. Leafhoppers were collected with a gasoline-powered leaf vacuum (Homelite, Charlotte, NC) and preserved in 70% ethyl alcohol. Males from these collections were then cleared in 10% KOH and identified by examination of genitalic characters, as previously described.

Vineyard Surveys 1990–1992. Adult leafhoppers were collected on sticky traps placed in vineyards (1990 and 1992) or by vacuum sampling (1991). Vineyards were sampled in 1991 with a gasoline-powered leaf-blower (Homelite, Charlotte, NC) with a vacuum attachment. Leafhopper adults were collected at 4 locations within each of 45 vineyards at 2-wk intervals from 1 June through 15 September. The 45 vineyards were enrolled in an integrated pest management project demonstrating the use of pheromone mating disruption for grape berry moth control, and therefore, no insecticides were applied to these blocks. In 1990 and 1992, adults were collected at 5 and 14 vineyards, respectively, using yellow sticky traps (7.6 by 12.7 cm) (Olsen, Medina, OH). Fifteen to 25 traps were placed in several locations throughout the vineyards sampled and attached to vineyard posts at a height of 1–1.5 m. Traps were changed at 7- to 14-d intervals, from 1 June through 15 September. Over the 3-yr period, leafhoppers were collected from 5 native American cultivars, three interspecific hybrids, and 1 *V. vinifera* cultivar. The native American varieties (number of vineyards) were Concord (36), Catawba (4), Delaware (4), Niagara (7), and Elvira (6). The interspecific hybrid varieties were: 'Baco Noir' (1), Castel 196-17 (2), and Dechaunac (2). The *V. vinifera* variety was 'Pinot noir'(2). In 1992, leafhoppers were also collected by vacuum sampling from wild grapes, *V. riparia* Michaux, at locations adjacent to 12 of these vineyards.

Adult leafhoppers collected on the traps were returned to the laboratory, and identified by visual markings on the elytra as *E. comes*, *E. tricinta*, *E. vitis*, or the *E. bistrata/vitifex* complex. The total number of leafhoppers of each species collected during the season at each site was determined for each vineyard. Proportions of each species captured over the entire season were then calculated for every vineyard sampled. From these data, mean unweighted proportions of each group were calculated for each cultivar. The number of vineyards surveyed, cultivar, and total number of leafhoppers trapped on each cultivar and on *V. riparia* are reported.

Greenhouse Ovipositional Choice Experiment. Varietal preference of *E. comes* and *E. bistrata* were tested by pairwise comparisons of oviposition on Concord, Elvira, Seyval blanc, and White Riesling (hereafter denoted by the letters C, E, S, and R, respectively). These 4 varieties were chosen because they are representative of major classes of grape cultivars grown in New York. Concord is a native grape variety having thick, leathery leaves with dense pubescence on the abaxial surface. Elvira, though a *V. labrusca* × *V. riparia* hybrid, has many of the foliar characteristics of *V. riparia*, the most common wild grape species in Western New York. Its leaves are glabrous. White Riesling is a white *V. vinifera* variety and has no American parentage. Seyval blanc is an interspecific hybrid variety derived from *V. aestivalis* Michaux, *V. rupestris* Scheele, and *V. vinifera* (Galet 1979).

Plants used in this experiment were rooted cuttings planted in March 1992. At the time of the experiment (early July), vines were ≈40 cm tall, and had 6–10 fully expanded leaves. In this choice experiment, two plants, 1 each of 2 different cultivars, were assigned randomly to mesh-covered cages (1 by 0.5 by 0.5 m) in which either 50 field-collected *E. comes* or *E. bistrata* adults had been placed. *E. comes* and *E. bistrata* adults were collected from Concord and Castel 196-17 vineyards, respectively, near Dresden, NY, on 15 July, 1992. Plant size was standardized by removing all but 4 leaves on each plant. After 72 h, plants were removed from the cages. Leaves were removed from the plants and submerged for 24 h in 95% ethyl alcohol to clear them. Eggs were then counted using a dissecting microscope.

All 6 possible combinations of cultivars, (C × E, C × S, C × R, E × S, E × R, and S × R) were tested with both leafhopper species, for a total of 12 treatments. Treatments were replicated 4 times. After each of the 4 replicates, new pairs of plants were assigned randomly to cages and leafhoppers were added to bring the number of adults back up to 50.

Proportions of total eggs laid on each of the 2 plants in each replicate were calculated. When the total number of eggs laid on both plants in the experimental unit was <20, data from the replicate was discarded to avoid bias in calculating proportions. As a result, 3 of the 4 *E. bistrata* C × E treatments, in which <5 eggs were laid, were discarded, although the low oviposition observed may have been a treatment effect. All of the other treatment combinations had either 3 or 4 replicates. We evaluated preference by testing whether proportions of eggs laid on each cultivar were different, using paired *t*-tests on arcsine square-root transformed proportions ($P = 0.05$).

No-Choice Field Experiment. *E. comes* and *E. bistrata* adults were separately confined to leaves of nine different grape cultivars located in a mixed variety planting at the New York State Agricultural Experiment Station Farm, Geneva, NY. Oviposition of the caged leafhoppers in the leaves was measured. *E. comes* and *E. bistrata* adults were collected from a Concord or Castel 196-17 vineyard, respectively, near Dresden, NY, on 27 July, 1992, aspirated into vials (10 per vial) and transported to the experimental vineyard. Leafhoppers were then transferred to mesh-covered clip cages (6.5-cm diameter by 3.5-cm depth), and the cages were attached to individual leaves, with leafhoppers on the abaxial leaf surface. Leafhoppers were then allowed to feed and oviposit for 72 h. Each of the 18 variety × leafhopper species treatments was replicated 7 times. All treatments involving *E. comes* were established in the vineyard on 27 July. We exhausted our supply of *E. bistrata* after applying 8 of the 9 treatments and collected more *E. bistrata* on 3 August from the same vineyard to complete the 9th treatment (on Seyval blanc). Therefore the Seyval blanc × *E. bistrata* treatment was in the vineyard 1 wk later, from 3 to 6 August. After the 72 h oviposition period, leaves and cages were removed from the vines and brought to the laboratory. Leafhoppers within the cages were anesthetized with CO_2 and the number of live and dead individuals were counted and sexed. Leaves were trimmed to remove the portion that had not

Table 3. Species composition of *Erythroneura* leafhoppers collected on different grape cultivars in central and western New York from 1990 to 1992

Cultivar class	Cultivar	Vineyards sampled	No. adults collected	% adults collected[a]			
				E. comes	*E. bistrata*/ *E. vitifex*	*E. tricinta*	*E. vitis*
Native American	Catawba	4	564	80	2	17	1
	Concord	36	24,068	99	0	1	0
	Delaware	4	1,107	83	15	2	0
	Niagara	7	9,166	75	20	5	0
	Elvira	6	6,980	24	73	2	1
Interspecific hybrid	Baco Noir	1	302	0	100	0	0
	Castel 196-17	2	2,506	0	99	1	0
	Dechaunac	2	441	3	97	0	0
V. vinifera	Pinot noir	2	2,163	0	80	0	20
V. riparia	Wild	12	594	24	47	10	19

[a] Unweighted average of proportions at each vineyard.

been caged, and they were placed in 95% ethanol for 24 h to clear them. The number of eggs was then counted.

Nine grape varieties, comprising the 3 major classes of cultivars, were tested. The American cultivars were Concord, Niagara, and Catawba. The 3 *V. vinifera* cultivars were White Riesling, Chardonnay, and Pinot noir. The remaining 3 varieties were the interspecific hybrids, Seyval blanc, Chancellor, and Cayuga White.

Oviposition rates (eggs per female) were calculated by dividing the number of eggs deposited by the total number of females (live + dead) recovered from clip cages at the end of the experiment. This calculation probably underestimated the true number of eggs per female because some of the dead females may have been alive and ovipositing for only part of the 3 d that they were caged to the leaf. Nonetheless, similar numbers and proportions of females of each leafhopper species survived on all varieties tested. Because we were more interested in the relative rankings of the varieties than in absolute egg densities, we ranked the number of eggs laid in each of the 63 experimental units for each leafhopper species. The effect of grape variety on the number of eggs per female within each leafhopper species was tested by nonparametric analysis of variance on ranks of eggs per female (Kruskal–Wallis test, Conover 1980). Separate analyses were made for each leafhopper species. Mean ranks were separated using the Fisher protected least significant difference (LSD) procedure ($P = 0.05$), as recommended by Conover (1980). Mean number of eggs per female is reported. Because *E. bistrata* caged on Seyval blanc were placed on vines 1 wk later than the other treatments, results are reported, but were not included in the statistical analysis.

Results

Species Determination. Three of 4 groups of *Erythroneura* leafhoppers collected in the field were determined by dissection to represent single species. Identities of *E. comes*, *E. vitis*, and *E. tricinta*, as determined by the pattern and coloration of wing markings, were confirmed by dissection and examination of male genitalia. The 4th group distinguishable by wing markings was determined to be a mixture of 2 species, *E. bistrata* and *E. vitifex*. Dissection of males from the 1992 Elvira collection revealed that all of the 78 males dissected were *E. bistrata*, strongly suggesting that leafhoppers used in the greenhouse and field oviposition studies were *E. bistrata*. *E. bistrata* also comprised 97% of males collected from the Castel 196-17 block in 1993 (Table 2), providing further evidence that *E. bistrata* was the predominant species in the block. In other vineyards sampled, *E. bistrata* comprised 31, 45, and 90% of males collected from Chardonnay, Dechaunac, and Niagara, respectively. Although proportions of the two species varied among vineyards, proportions collected within each vineyard remained stable throughout the 1993 growing season (Table 2).

Vineyard Surveys. *E. comes* was the predominant species found on native American Concord, Catawba, Delaware, and Niagara grapes (Table 3), and comprised 75–99% of individuals captured on these varieties. On Concord, virtually all adults captured were *E. comes*. On Niagara and Delaware, the *E. bistrata/vitifex* complex comprised ≈15% of adults captured, whereas on Catawba the 2nd most abundant species captured was *E. tricinta*. On Elvira, the majority (73%) of leafhoppers captured were *E. bistrata/vitifex*, whereas 24% were *E. comes*. On the interspecific hybrid varieties, 97–100% of the adults captured were *E. bistrata/vitifex*. The single *V. vinifera* cultivar, Pinot noir, had populations composed of 80% *E. bistrata/vitifex* and 20% *E. vitis*. The wild species *V. riparia*, which grows abundantly in hedgerows, had a diverse assemblage of all 4 groups, with *E. comes* (23%), *E. bistrata/vitifex* (47%), *E. tricinta* (10%), and *E. vitis* (19%) all represented in substantial proportions.

Erythroneura vitis and *E. tricinta* comprised minor proportions of the species collected on interspecific hybrids and native American cultivars. *E. vitis* was common, however, on *V. riparia* and the few *V. vinifera* collections made. Another species, *E. vulnerata* Fitch, was not counted in these surveys, but was found to comprise roughly 10% of the adult leafhopper population on Niagara, Chardonnay, 'Castel' and Dechaunac collections made in 1993 (L. Williams III [Cornell University, Geneva, NY] and T.E.M., unpublished data). Our surveys indicate that *E. vitis, E. tricinta,* and *E. vulnerata* are minor components of the leafhopper species complex in central and Western New York vineyards.

The species composition recorded at specific sites may have been influenced by movement of leafhoppers from other varieties in nearby vineyards. In particular, all collections from *V. riparia* were made at the edges of commercial vineyards. Adults feeding on certain varieties may not have reproduced on those varieties. However, the continued presence of adults throughout the growing season at these vineyards, and striking differences in species composition found in adjacent vineyard blocks suggest that our collections reflected host preferences of the leafhoppers.

Greenhouse Choice Experiment. In the greenhouse, the number of eggs *E. comes* laid on Concord and Elvira was not statistically different (Fig. 1A). When Concord was paired with White Riesling, 75% of the eggs were laid on Concord, although the proportions were not statistically different. However, significantly more eggs were laid on Concord than on Seyval blanc. Significantly more eggs were laid on Elvira when paired with either White Riesling or Seyval blanc. Proportions of *E. comes* eggs laid on Seyval blanc and White Riesling, were not statistically different.

Results with *E. bistrata* (Fig. 1B) were different than those with *E. comes. E. bistrata* showed a consistent nonpreference for Concord (Fig. 1B). When Concord was paired with either Elvira, White Riesling, or Seyval blanc, very few eggs (6 total) were laid on Concord. In pairs that included Elvira, proportions of *E. bistrata* laid on Elvira versus either White Riesling or Seyval blanc were not significantly different, nor was oviposition on White Riesling versus Seyval blanc.

In each treatment combination, we observed feeding injury on both varieties, indicating that all varieties were fed upon by *E. comes* and *E. bistrata.* Marked differences in ovipositional preference, however, were evident. Among the varieties tested, the 2 characteristics that varied were density of pubescence on the underside of the leaf and grape species from which the cultivar was derived. Only Concord has pubescent leaves, whereas Elvira, Seyval blanc, and White Riesling have glabrous leaves. The characteristic shared by Concord and Elvira is that both are derived principally from native species, *V. labrusca* and *V. riparia,* and have very little or no *V. vinifera* parentage.

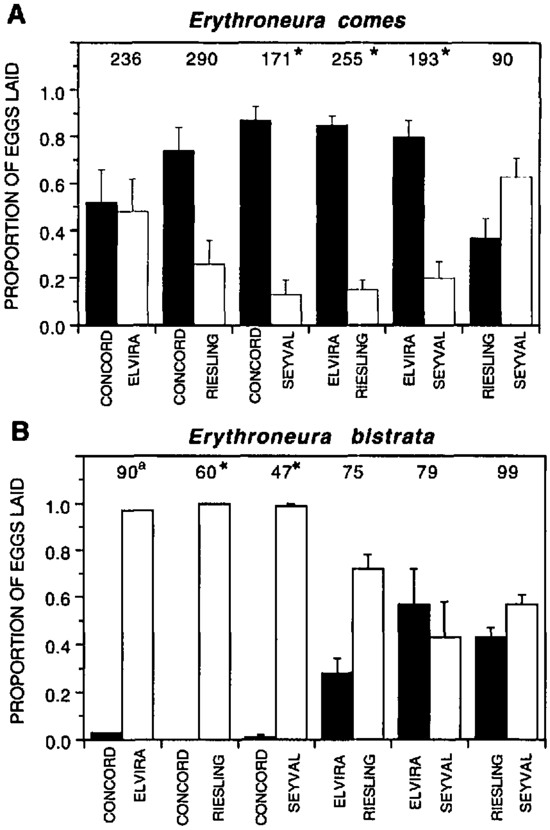

Fig. 1. Greenhouse choice experiment, showing mean proportions (±SEM) of *E. comes* (A) or *E. bistrata* (B) eggs laid on each cultivar in pairwise comparisons of two cultivars. Each pair of bars represents one pairwise comparison. Numbers above bars denote mean number of eggs per replicate ($n = 4$). Asterisk (*) by number indicates proportions were significantly different from null expectation of random oviposition (paired t-test on proportions, $\alpha = 0.05$). [a], Eggs recovered from only one replicate; results not included in statistical analysis.

Field No-Choice Experiment. Rankings of the number of eggs deposited per female in the *E. comes* and *E. bistrata* treatments (Table 4) showed clear differences in relative ovipositional preferences of these 2 leafhopper species. These differences were consistent with results from the survey and greenhouse experiments. For *E. comes,* ranking of varieties showed that native American cultivars received the highest number of eggs. Interspecific hybrid varieties Seyval blanc and Chancellor had the lowest number of eggs per female. Oviposition on White Riesling and Chardonnay was intermediate. In the *E. bistrata* treatments, native American Catawba, Concord, and Niagara grapes all had very low rates of oviposition. Other *V. vinifera* and interspecific hybrids, with the exception of Seyval blanc were at the top of the rankings. The lack of oviposition on Seyval blanc was anomalous and at odds with results of the greenhouse choice experiment, in which *E. bis-*

Table 4. No-choice field experiment measuring oviposition of *E. comes* and *E. bistrata* caged on different varieties of grapes in Geneva, NY, in 1992

E. comes			*E. bistrata*		
Variety	Class[a]	Eggs per female	Variety	Class[a]	Eggs per female
Niagara	A	14.3a	Riesling	V	6.1a
Concord	A	9.3a	Chancellor	H	4.5a
Cayuga	H	8.1ab	Chardonnay	V	4.1a
Catawba	A	5.1bc	Pinot Noir	V	3.7a
Riesling	V	4.1cd	Cayuga	H	3.1a
Chardonnay	V	3.5de	Catawba	A	0.6b
Pinot Noir	V	1.9ef	Concord	A	0.1bc
Seyval blanc	H	0.9fg	Niagara	A	0.0c
Chancellor	H	0.2g	Seyval blanc[b]	H	0.0

Ranks of means followed by the same letter are not statistically different ($P = 0.05$, Fisher protected LSD).

[a] Denotes type of variety: A, native American (*V. labrusca*) cultivar; H, interspecific hybrid cultivar; V, *V. vinifera* cultivar.

[b] Not included in the statistical analysis.

trata showed a preference for Seyval blanc. We hypothesize that *E. bistrata* adults used in the Seyval blanc treatment had entered reproductive diapause, because they were collected later than *E. bistrata* used to infest other vines in the experiment. Dissections of adult *E. bistrata* collected from the same population on 6 August showed that 40% of females carried no mature eggs (T.E.M., unpublished data) and support this conclusion.

Discussion

Results of the vineyard surveys indicated a clear dichotomy in species composition among cultivars with and without the densely pubescent leaves characteristic of most native American *V. labrusca* cultivars. *E. comes* was the predominant species only in *V. labrusca* cultivars with densely pubescent leaves. On cultivars with glabrous leaves, the *E. bistrata/vitifex* complex predominated. All *V. vinifera* cultivars, interspecific hybrids, wild *V. riparia*, and the native American cultivar Elvira fall into this category.

The most striking result of the survey was the absence of leafhopper species other than *E. comes* in extensive collections from 36 Concord vineyards. This suggests that other species present in New York do not feed or oviposit on Concord under field conditions. The historical dominance of Concord in New York and elsewhere in northeastern North America explains why other *Erythroneura* species have not been considered major pest species by previous investigators. *E. comes* was also the dominant species on the other native American cultivars, Catawba, Niagara, and Delaware. However, *E. bistrata/vitifex* was also present in these cultivars. These 3 cultivars are classified as *V. labrusca* grapes, but are thought to show some characteristics indicating hybridization with *V. vinifera* (Hedrick 1908, Galet 1979). In contrast, the cryptic species *E. bistrata* and *E. vitifex* predominated on interspecific hybrids and *V. vinifera* cultivars, where *E. comes* was largely absent. Notably, *E. bistrata/vitifex* was the predominant group captured in Elvira, a hybrid of *V. labrusca* and *V. riparia* with glabrous leaves similar to the *V. riparia* parent.

The greenhouse choice experiment demonstrated that *E. comes* and *E. bistrata* oviposit preferentially on different grape cultivars. Results of this experiment were consistent with the field composition of the 2 species in the field. In these trials, *E. comes* consistently preferred Concord and Elvira, the 2 cultivars with *V. labrusca* parentage, although Concord leaves are pubescent and Elvira leaves are not. *E. comes* consistently laid fewer eggs on White Riesling and Seyval blanc, 2 varieties without any *V. labrusca* parentage. It is noteworthy that for *E. comes* the mean number of eggs per replicate (Fig. 1) in the White Riesling × Seyval blanc pairing was one-half to one-quarter of the total oviposition of pairs with either Concord or Elvira, or both. Results obtained in the no-choice field experiment also showed consistently higher oviposition by *E. comes* on *V. labrusca* cultivars and hybrids (e.g., Cayuga White) with *V. labrusca* parents. In contrast, *E. bistrata* laid only 6 eggs in Concord leaves in any of the greenhouse choice pairings, and only 5 eggs in Concord, Catawba and Niagara in the field no-choice experiments. However, *E. bistrata* showed no preference among the other varieties tested.

Results of these experiments demonstrate host discrimination among *E. comes* and *E. bistrata* consistent with the parentage of the cultivars. Two factors may be important in mediating acceptance of *Vitis* hosts for oviposition by *E. comes* and *E. bistrata*. The 1st factor is leaf morphology. Densely pubescent leaves with thick secondary veins, characteristic of the *V. labrusca* varieties Concord, Niagara, and Catawba may deter oviposition by *E. bistrata*. *E. bistrata* eggs are invariably deposited under secondary leaf veins. *E. comes* eggs, in contrast, are laid shallowly in tissue between leaf veins on the abaxial leaf surface. The complete lack of oviposition on Concord suggests that its densely pubescent leaves may not provide the proper stimuli to ovipositing *E. bistrata*. These differences in preferred oviposition sites are similar to those reported in California with *E. elegantula* Osborn and *E. variabilis* Beamer. *E. elegantula*, like *E. comes*, deposits eggs shallowly in leaf tissue between veins, whereas *E. variabilis* deposits eggs more deeply adjacent to leaf veins (Settle and Wilson 1990). Appropriate tactile or olfactory cues releasing oviposition behavior in *E. bistrata* may be lacking in *V. labrusca* varieties. Alternatively, dense pubescence on *V. labrusca* leaves may interfere with the oviposition process. Further studies of oviposition behavior are necessary to test these hypotheses.

The second factor known to vary among grape cultivars with different *Vitis* parents is the composition of volatile constituents present in leaves and clusters. Notably, the compound methyl anthranilate, a characteristic aroma constituent in *V. labrusca* grapes, is largely absent in other *Vitis* species. Analysis of volatile constituents from Concord, Niagara, and Elvira revealed that methyl anthranilate, ethyl 3-hydroxybutanoate, ethyl 2-butenate, and 2,5-dimethyl-4 methoxy-3(2H)-furanone were found in high amounts in Concord and Niagara grapes, but only in trace amounts in Elvira grapes (Schreier and Paroschy 1981). Methyl anthranilate was absent in wild *V. riparia* (Schreier and Paroschy 1980) and in *V. vinifera* cultivars (Schreier et al. 1976). Oviposition preference of *E. comes* and *E. bistrata* in the greenhouse choice experiments was consistent with these differences in plant chemistry associated with parent *Vitis* species. Notably, *E. comes* preferentially oviposited on Concord and Elvira, both of which have *V. labrusca* parentage, when paired with Seyval blanc or White Riesling. *E. bistrata* did not oviposit on Concord, which has high levels of methyl anthranilate, but did on Elvira, which has only trace amounts, and on Seyval blanc and White Riesling. Methyl anthranilate or other compounds specific to *V. labrusca* may be associated with host recognition by *E. comes*. These same compounds may inhibit oviposition by *E. bistrata* on *V. labrusca* varieties. This hypothesis could be tested by treating non-*V. labrusca* leaves with methyl anthranilate or leaf extracts and comparing responses of *E. comes* and *E. bistrata* on treated and untreated leaves.

Ovipositional preferences of *E. vitifex* were not tested in the choice and no-choice experiments. Thus, we have no experimental evidence that ovipositional preferences of *E. vitifex* correspond to those observed with *E. bistrata*. However, the occurrence of these 2 species in mixed field populations (Table 2), and the absence or low incidence of either of these species on native American cultivars except Elvira (Table 3) suggest that the host range of *E. vitifex* probably closely overlaps that of *E. bistrata*. Further experiments with *E. vitifex* would be necessary to confirm this hypothesis.

Although differences in ovipositional preferences of *E. comes* and the *E. bistrata*/*E. vitifex* complex account, in part, for the observed species composition in field populations, other factors beside ovipositional preference may be important determinants of species composition. Laboratory and field oviposition experiments demonstrated that *E. comes* is capable of ovipositing in hybrid and *V. vinifera* cultivars (Fig. 1; Table 4). Yet, *E. comes* was absent from field collections of most hybrid and *V. vinifera* varieties, and only a minor component of collection from Elvira and Dechaunac (Table 3). Another possible explanation for the scarcity of *E. comes* on glabrous-leafed varieties may be differential parasitism by the mymarid egg parasitoid *Anagrus epos* Girault. We have found *A. epos*, long known to be an important biological control for leafhoppers in California grapes (Doutt and Nakata 1965), to be extremely common in New York vineyards. Eggs of *E. comes*, deposited shallowly in tissue between leaf veins, may be more susceptible to parasitism in the field than eggs of *E. bistrata* or *E. vitifex*, which are deeply deposited under, or adjacent to leaf veins. Differential parasitism among *E. variabilis* and *E. elegantula* in California, associated with similar differences in egg location within leaves, has been documented (Settle and Wilson 1990). The dense pubescence on *V. labrusca* cultivars may provide partial protection from *A. epos* searching for *E. comes* eggs. The influence of grape cultivar and egg location on *Anagrus* parasitism is currently under investigation in our laboratory.

These experiments demonstrate that the diversification of viticulture in New York has resulted in a more diverse leafhopper pest complex than existed when the industry was based primarily on native American cultivars. In practical terms, *E. comes* is the pest species on *V. labrusca*-based native American cultivars, but *E. bistrata* and *E. vitifex* predominate on interspecific hybrids and *V. vinifera* cultivars. Our findings have particular significance for pest management New York vineyards, because they demonstrate that growers of *V. vinifera* and French–American hybrid grapes encounter distinct problems with leafhoppers that may require different management responses in the future. *E. comes*, *E. bistrata*, and *E.vitifex* are closely related species that share similar biology and phenology. However, subtle differences in developmental rate, feeding rates, or initiation of reproductive diapause may lead to great differences in population dynamics and economic injury levels. Additionally, differences in susceptibility to insecticides may dictate different control recommendations in the future. At this time, all of the common *Erythroneura* species are highly susceptible to insecticides registered for use on grapes in New York (T.E.M., unpublished data). However, insecticide resistance could render currently available materials ineffective for one or more of the *Erythroneura* species.

Over the long term, it may be possible to exploit the ovipositional preferences we have observed in breeding programs to produce cultivars resistant to leafhoppers. We have observed heavy infestations of leafhoppers on both *V. vinifera* varieties and *V. labrusca* varieties in the field. Heavy infestations on some of the interspecific hybrid varieties such as Seyval blanc, however, seem to be rare. Further studies of host preferences of *Erythroneura* leafhoppers may reveal behavioral or chemical stimuli that are associated with differences in oviposition noted herein. Use of oviposition assays to screen selections from breeding programs may be useful in determining relative susceptibility of selections to leafhopper infestations.

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