PHENOLOGY OF EASTERN GRAPE LEAFHOPPER, *ERYTHRONEURA COMES* (SAY), AND ABUNDANCE ON GRAPE CULTIVARS, WITH NOTES ON OTHER LEAFHOPPERS OF IMPORTANCE

By

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Entomology: "...a study equally calculated for promoting the glory of God and the delight and profit of man" (Kirby, W. and Spence, W. Preface. *An Introduction to Entomology*, 1826, page xii)

"Let the glory of the Lord endure forever; let the Lord be glad in his works" (Psalm 104:31)

"And every created thing which is in heaven and on the earth and under the earth and on the sea, and all things in them, I heard saying, 'To Him who sits on the throne, and to the Lamb, be blessing and honor and glory and dominion forever and ever'" (Revelation 5:17)

Amen.

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Abstract:

Eastern grape leafhopper, Erythroneura comes (Say), is an important pest of grapes in the eastern half of the United States, capable of causing reductions in the quality and quantity of the crop. I investigated the phenology (i.e., seasonal development) of this insect using a growing degree-day (GDD) model. Growing degree days were calculated above a lower developmental threshold of 10°C (50°F) using the single sine wave method. Leafhopper nymphs were counted weekly on grape leaves from 2016 to 2018 at a vineyard in Perkins, OK. Differential abundance was observed across eight cultivars: Cynthiana, Chambourcin, Chardonel, Frontenac-Gris, Niagara, Noiret, Rubaiyat, and Traminette. The cultivars Noiret and Traminette had the highest abundance of nymphs, while Niagara and Cynthiana had the lowest abundance. In 2016, there were three peaks in population abundance, indicating three separate generations of the insect, while in 2017, there were three and possibly a partial fourth generation. In 2018, three peaks occurred. I report and discuss degree day calculations for generational peaks, as well as establish GDD-based recommendations for monitoring practices for this leafhopper in Oklahoma vineyards. The presence of the leafhoppers *Erythroneura ziczac* Walsh and *Empoasca fabae* (Harris) is also reported.

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CHAPTER I

INTRODUCTION

History of Grape Production in Oklahoma

Grapes (*Vitis* spp.) have been cultivated in the region that is now Oklahoma since the late 1800s (then divided into Indian Territory and Oklahoma Territory) (Stafne 2015). In the early days of viticulture in this region, American cultivars such as Catawba, Concord, and Delaware were grown (Stafne 2015). Oklahoma became a state of the Union in 1907. At the outset, the state constitution prohibited production and distribution of ale, beer, wine, and other alcoholic beverages, mandating a minimum penalty of \$50 and 30 days imprisonment for each offense, and this prohibition was to be in effect for at least 21 years from the establishment of Oklahoma as a state (OK Const. art. xxvii). It was not until 1959 that the prohibition article was repealed by the Oklahoma Alcoholic Beverage Control Board Amendment, State Question 386, which passed with 56% of voters in favor (Oklahoma Secretary of State 2013).

In 1908, there were 5,425 acres of this crop in Oklahoma (Stafne 2015). In 2006, the Oklahoma Grape Growers' and Wine Makers' Association surveyed grape growers in 34 counties of Oklahoma. From the results of the survey, it was estimated that Oklahoma contained about 600 acres of grapes (Stafne 2015). It was also discovered that European cultivars (i.e., *Vitis vinifera*) were the most widely grown cultivars in the state (Stafne 2015). Cabernet Sauvignon was the most widely planted cultivar with 32.4 acres; Cynthiana was the most widely planted American cultivar with 11 acres, and the hybrid cultivars Chambourcin (8.2 acres) and Chardonel (7.7 acres) were the eighth and tenth most widely planted cultivars in the state, respectively (Stafne 2015).

Grape Industry Challenges in the State

Oklahoma's grape industry has encountered a variety of challenges, apart from prohibition's negative impact in the first half of the twentieth century. These challenges range from adverse weather conditions, such as humidity, precipitation, and temperature extremes, to diseases and arthropod, avian, and mammalian pests (Stafne 2015). The state has been divided into nine climate regions, differentiated by annual precipitation and average temperatures, among other factors (Ziolkowska 2018). The climatic diversity necessitates that grape growers select cultivars appropriate to their part of the state, keeping in mind cold hardiness along with drought and heat tolerance (Stafne 2015). Climate differences also have implications for insect pests, which have particular heat and humidity requirements for their development (Zalom et al. 1983, Herms 2013, Liu et al. 2015). These requirements limit the geographic distribution of insect species (Osawa et al. 2018). Furthermore, the relationship between insect heat requirements and climate influences the number of generations to be expected and the degree of synchrony between the phenology of a pest species and its host plant(s) in a particular region; these factors, in turn, influence how severely the pest may impact a crop (Caffarra et al. 2012, Pulatov et al. 2016).

Eastern Grape Leafhopper

Eastern grape leafhopper, *Erythroneura comes* (Say), is a pest of grapes (*Vitis* spp.) in the central and northeastern United States, as well as eastern Canada (Dmitriev and Dietrich 2007). A growing degree day model has been developed to predict the phenology of *E. comes* in the northeastern U.S. for improved monitoring and pest management practices (Martinson and Dennehy 1995). This model accounts for daily high and low temperatures across time to forecast stages of population development of this pest. This involves the timing of the first appearance of the nymphs (immature stages) as well as the timing of generations throughout the season.

Objectives

The objectives of this research are as follows:

1) To characterize the phenology of *E. comes* in Oklahoma, identifying:

a) the number of generations;

b) the timing of the peaks of generations, in terms of date and growing degree days (GDD);

c) conformity to or deviation from the GDD calculations for this insect's generational peaks from the study of Martinson and Dennehy (1995);

d) the proportions of the five instars of nymphs over time

2) To set forth recommendations for:

a) the timing of monitoring practices for eastern grape leafhopper;

b) economic thresholds for treatment

3) To measure the abundance of *E. comes* on grape cultivars, analyzing:

- a) differences across cultivars;
- b) differences across time;
- c) the possible influence cultivar traits may have on leafhopper abundance

4) To identify other leafhopper pests of grapes, noting:

- a) their abundance;
- b) their population dynamics;
- c) species composition

5) To report year-to-year total abundance of the adult stage of the following auchenorrhynchan taxa:

- a) Cercopoidea (froghoppers/spittlebugs)
- b) Cicadellidae (leafhoppers)
- c) Fulgoroidea (planthoppers)
- d) Membracidae (treehoppers)

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CHAPTER II

REVIEW OF LITERATURE

Biology of Pest

Eastern grape leafhopper, Erythroneura comes (Say) (Hemiptera: Cicadellidae), is a key pest of vineyards in the central and northeastern United States and eastern Canada. This insect feeds and oviposits within leaf tissue of wild and cultivated grapes. It was first reported as a vineyard pest in Massachusetts in 1828 and in New York in 1856; in the early twentieth century, eastern grape leafhopper was "unusually numerous and destructive" in Oklahoma and several other states (Slingerland 1904). Eastern grape leafhopper overwinters as an adult under leaf litter or other debris, preferring areas with well-drained soil and avoiding low-lying land prone to flooding (Hartzell 1912). Adults disperse to overwintering sites in wooded or overgrown areas near the vineyard once grapevines have lost their leaves later in autumn (Jubb 1976, Mulder 2014). Leafhoppers may also overwinter within the vineyard, especially in clumps of dead grass or leaves along the rows (Slingerland 1904, Quayle 1908, Jubb 1976). Adults become active in spring when temperatures reach about 18 °C, feeding on various plants and colonizing grapevines when new foliage is present (Van Kirk et al. 1984). Eastern grape leafhopper enters reproductive diapause in response to shortening day length. A photoperiod of less than 13.5 hours of light is required for this change (Martinson and Dennehy 1995a). Once

the photoperiod reaches 11.6 hours of light in the spring, female reproductive organs begin to mature (Flaherty et al. 1992). The overwintering generation mates on alternative host plants before recolonizing vineyards (Hartzell 1912).

Although E. comes is only known to oviposit on grape (Vitis spp.), it feeds on the leaves of alder, alfalfa, apple, beech, blackberry, burdock, catnip, cherry, columbine, currant, dewberry, dogwood, dwarf oak, goldenrod, gooseberry, grasses, hackberry, hawthorn, honeysuckle, hornbeam, nettle, plum, raspberry, redbud, rye, strawberry, sugar beet, sugar maple, thimbleberry, and Virginia creeper; blackberry, raspberry, and strawberry are preferred among these alternative, non-grape host plants (Slingerland 1904, Hartzell 1912, Johnson 1914, Taschenberg 1973, Arnold et al. 2008). Adult females feed on newly expanded grape leaves for around 2 weeks before ovipositing first-generation eggs. Eggs are laid individually beneath the leaf epidermis on the abaxial (lower) surface (Jubb 1976, Van Kirk et al. 1984). Ovipositional activity lasts up to eight weeks and each female may lay between 100 and 140 eggs (Johnson 1914, Williams and Martinson 2000, Arnold et al. 2008). First-generation nymphs are most often found on older leaves, and therefore are unevenly distributed along the shoot; distribution of nymphs becomes more uniform along shoots as the season progresses (Elsner 1986). Eastern grape leafhopper develops through five nymphal stages before molting into an adult. The first instar is pale white, has red eyes, lacks wing pads, and measures slightly less than a millimeter. As the nymph progresses through the next four instars, its body color becomes more yellow and its eyes lose their red hue, becoming more similar to the color of the body. Furthermore, wing pads develop in the second instar and become larger

and longer with each molting event (Johnson 1914). The insect reaches a length of 2.7 - 3.0 mm as an adult (Dmitriev and Dietrich 2007).

Feeding Injury and Damage

Eastern grape leafhopper uses its piercing-sucking mouthparts to puncture mesophyll cells of the leaf and suck out the contents, leaving specks of light brown or yellowish-white tissue known as "stippling." The resulting damage may lead to a reduction in photosynthesis due to the removal of chlorophyll, ultimately reducing the quantity and quality of grapes (Johnson 1914). Elsner (1986) estimated that individual nymphs injure approximately 0.09 cm² of leaf area daily. A severe degree of stippling may occur whereby leaves become dry and nearly devoid of green pigmentation, which can lead to premature leaf drop. Heavy infestations of *E. comes* may hinder photosynthesis to the point where affected shoots become stunted. If stunting occurs over one or two consecutive seasons, the vine may be stunted for years afterward or even become permanently damaged (Johnson 1914).

Foliar damage from eastern grape leafhopper can impact harvested fruit. Hartzell (1912) reported that vines not treated with a solution of tobacco leaf extract mixed in water or Bordeaux mixture had low-quality grapes with low sugar content and high acidity. Martinson et al. (1997) found that table grapes harvested from vines with leafhopper injury had no reduction of soluble solids in juice, but numbers of berries per grape cluster and clusters per node were reduced. These reports demonstrate that stippling injury negatively affects fruit quality and quantity. Early-season feeding injury may be especially harmful because oviposition occurs primarily on leaves of the first five nodes of a shoot, which are the nodes where harvestable clusters develop (Martinson et al.

al. 1997). In contrast, Jubb et al. (1983) found no difference in bud fruitfulness between non-infested and heavily infested vines . Nonetheless, these authors concluded that earlyseason feeding injury is more deleterious than injury occurring later in the season. Feeding injury from overwintering adults may be more damaging to grape development than that inflicted by the first and second generations of leafhoppers (Jubb et al. 1983). However, the level of damage resulting from leafhopper feeding injury varies from year to year with respect to environmental conditions, such as temperature and water availability, which change the degree of stress on the vines (Martinson et al. 1997). The influence of these abiotic factors on vine health suggests that peaks in leafhopper density are not sufficient to predict levels of leafhopper damage in a vineyard.

Besides the mechanical injury eastern grape leafhopper produces via stippling, this pest may negatively impact the marketability of the fruit by facilitating the growth of unsightly saprophytic fungi. Its excrement, known as honeydew, is a sticky and sugary fluid that often covers the leaves and berries, providing a substrate and energy source for sooty molds in the genera *Capnodium*, *Fumago*, and *Scorias* among others (Van Kirk et al. 1984, UC IPM 2011). The presence of honeydew on the fruit may also impact the quality of wine (Saguez et al. 2014). Apart from grapevine injury, high densities of eastern grape leafhopper may also be a severe annoyance to workers at harvest time, as the insects fly into their eyes, mouth, and nose (Johnson 1914).

Host Plant Preference

Differential abundance of several *Erythroneura* species across grape varieties (cultivated and wild) has been well documented. Martinson et al. (1994) counted seven times more eastern grape leafhopper nymphs on the cultivar 'Diamond' than on the

cultivar 'Dutchess'. The authors concluded that this difference may be due to 'Dutchess' being less susceptible to leafhopper feeding and oviposition. Williams and Martinson (2000) report that *E. comes* more commonly attacks *Vitis labrusca* cultivars, while *E. bistrata* and *E. vitifex* mostly attack *Vitis vinifera* cultivars. *Erythroneura reflecta* and *E. vitis* are reported to prefer *Vitis riparia* (Dmitriev, 3I Interactive Keys). Runner and Bliss (1923) reported that *E. vitis* was dominant on grape cultivars having thin leaves, particularly on *Vitis vulpina*. Zimmerman et al. (1996) recorded higher numbers of *Erasmoneura vulnerata* and *Erythroneura ziczac* nymphs on certain *V. vinifera* cultivars compared to other cultivars of the same species.

Phenology and Population Dynamics

The phenology of eastern grape leafhopper has been investigated in the northeastern United States. Martinson and Dennehy (1995a) used a lower developmental threshold of 10°C (50°F) to estimate degree-day requirements for each life stage of eastern grape leafhopper based on observational studies by Johnson (1914) of their developmental times under fluctuating temperatures. These authors confirmed their estimates through field observations of eastern grape leafhopper populations.

Beginning in the late 1940s, eastern grape leafhopper populations in New York vineyards were kept at low to non-damaging levels by calendar-based chemical applications intended for management of grape berry moth, *Paralobesia viteana* (Clemens) (Martinson and Dennehy 1995a). However, increased leafhopper injury was noticed in the early 1990s as regular insecticide applications were reduced following development of a risk assessment procedure and pheromone mating disruption techniques for grape berry moth. This resulted in more detailed studies of the biology and life history

of eastern grape leafhopper as well as effective sampling methods and appropriate treatment thresholds for this pest (Martinson et al. 1994). Eastern grape leafhopper requires 623 growing degree days (GDD) to develop from egg to adult and complete post-diapause development (Martinson and Dennehy 1995a). In New York, eastern grape leafhopper usually undergoes one generation per year, but in warmer years there may be a partial second generation (Martinson et al. 1994). In Oklahoma, three generations per year are reported, with the possibility of a partial fourth generation (McCraw et al. 2005, Arnold et al. 2008). Martinson et al. (1994) used the single sine wave growing degree day model (Baskerville and Emin 1969) with a lower developmental threshold of 10°C to determine GDD for life stages of eastern grape leafhopper in New York. Calculation of GDD began on April 1 because this is generally the date by which temperatures in New York reach the lower developmental threshold of eastern grape leafhopper. The first observation of nymphs during the grape-growing season occurred on June 14 ± 4 days at 390 ± 71 GDD. The peak population of nymphs of the first generation occurred on July 6 \pm 8 days at 648 \pm 86 GDD, while the second generation peak occurred on August 26 \pm 14 days at 1190 ± 154 degree-days. In years when early-season temperatures are generally warmer, leafhopper development may be hastened and the resultant feeding injury worsened (Martinson et al. 1997).

In the early part of the twentieth century, outbreaks of eastern grape leafhopper were reported at the regional level in the northeastern U.S. for a period of two or three seasons, after which they decreased and were below damaging levels for several years until the next cycle of outbreaks (Johnson 1914). In the outbreak year of 1922, Van Dine (1923) reported an average of about 64 nymphs per leaf in a heavily infested vineyard in Pennsylvania. Predicting population density is vital to developing effective pest management techniques for eastern grape leafhopper. Martinson and Dennehy (1995a) explained that year-to-year variability in eastern grape leafhopper population density is determined by differences in temperature and photoperiod. Photoperiod, which is consistent from year to year, determines the timing of reproductive diapause, which is around late July to early August in New York. Temperature, in contrast, is variable from year to year, resulting in variable rates of population development. If the number and relative size of the second generation is to be predicted, it is necessary to track temperature over time to discover how many GDD have accumulated by the start of reproductive diapause. From these data, the proportion of the population entering reproductive diapause, and consequently the number of individuals in the next generation, may be estimated (disregarding other factors known to influence rate of development, such as host plant quality). In years with cooler temperatures, leafhoppers develop more slowly and mature to adulthood later. In such years, the proportion of the population entering reproductive diapause will be larger and fewer eggs will be laid through the course of the season. Conversely, warmer years will result in a smaller proportion entering reproductive diapause, which entails that the overall population will be larger because of an increased proportion of the population laying eggs. In this way, temperature influences the potential for both early-season and late-season leafhopper injury to the grapevines through its influence on population size. Using a probability model, Martinson and Dennehy (1995a) determined that if fewer than 760 GDD accumulated by the time of reproductive diapause on August 1, the ratio of secondgeneration to first-generation leafhoppers could be as low as 5:1, whereas if over 890

GDD accumulated by that date, the ratio could be as large as 35:1. Slingerland (1904) suggested that weather conditions during the six months of overwintering by eastern grape leafhopper may also be important in determining interannual variability in infestation levels.

In addition to temperature and photoperiod, rainfall also plays an important role in predicting population density of eastern grape leafhopper. Eyer (1931) investigated the effects of precipitation and temperature on eastern grape leafhopper populations across 5 years in multiple Pennsylvania vineyards. He concluded that above-average rainfall in combination with below-average temperatures from May through July caused a definite reduction in eastern grape leafhopper populations. Conversely, he proposed that belowaverage rainfall favors the development of large populations.

Monitoring and Treatment Thresholds

Monitoring for eastern grape leafhopper may target any of its life stages. Monitoring for eggs is not a common practice due to the difficulty of seeing them; they are smaller than a millimeter and hidden under the leaf epidermis. However, there are three methods that may be used for monitoring eggs. The first and most simple method is to inspect the surface of a backlit leaf under high magnification, recognizing the eggs as raised, bean-shaped areas on the leaf surface. This method is probably the most prone to human error, as the raised areas are easy to miss. The second method is to stain the eggs with McBride's stain (containing fuchsin dye), which makes them much easier to see under the leaf tissue (Backus et al. 1988). The third method is to use a technique known as Simplified Leafhopper Egg Detection by Autofluorescence (SLEDA), in which a blue light is shone on the leaf and the eggs fluoresce a bright green color (Herrmann and Böll 2004). This method requires special equipment for its effectiveness and is limited by the fact that the autofluorescent property of the eggs decreases over time after the egg has been deposited.

Monitoring nymphs is the standard method for growers to estimate population density of eastern grape leafhopper in their vineyards (Martinson et al. 1994). It is recommended that growers inspect at least 50 leaves for nymphs during each sampling period (Rebek 2016). Martinson and Dennehy (1995a) suggested monitoring efforts should start once 650 GDD have accumulated. This amount of heat unit accumulation corresponds to the midpoint of nymphal development of the first generation of leafhoppers in New York, which is usually when the population of first-generation nymphs reaches peak abundance. In Quebec vineyards, Bostanian et al. (2006) recommended starting leafhopper nymph monitoring efforts when 630 GDD have accumulated above a lower developmental threshold of 8° C since March 1. This amount of heat unit accumulation corresponds to the time at which the population of firstgeneration nymphs reaches 5% of its cumulative abundance across the entire season. Alternatively, rating stippling injury to leaves is an indirect way of assessing leafhopper injury in the vineyard, and it has been used in combination with monitoring of nymphs to make treatment decisions (Jubb et al. 1983).

Monitoring of adult leafhoppers does not sufficiently estimate the actual population density because sampling methods for adults are relative. Sticky traps fall in this category. A leafhopper population may be large (as seen from direct counts of nymphs), but the adults may be inactive due to cool weather and thus not fly into the traps. In this case, population density would be underestimated with this sampling

method. On the other hand, warm weather or flight associated with mating or immigration may stimulate leafhopper activity, resulting in a higher number of adults trapped and a potentially overestimated population density. Martinson et al. (1994) observed lower catches of adults on sticky card traps mid-season when compared to early-season catches, even though the population of adults was in fact increasing. The authors speculated that two factors might be responsible for the reduction in adults captured: reduced leafhopper movement and decreased attractiveness of the traps when compared with a dense canopy of foliage.

There are different treatment thresholds for eastern grape leafhopper depending on the marketable product (i.e., table grapes, raisins, or wine) and the phenology of grape cultivars (UC IPM 2015). Lower thresholds are used for vines producing table grapes as well as for cultivars ripening during mid- or late season. In the northeastern United States, some authors recommend a threshold of 5 nymphs per leaf and others a threshold of 2 nymphs per leaf, or when 15% of sampled leaves have stippling injury (Jubb et al. 1983, Martinson et al. 1997). Martinson et al. (1991) recommended using a treatment threshold of 5 nymphs per leaf in the third week of July and ten nymphs per leaf in the final week of August. Moreover, the authors recommended insecticide application if stippling injury is evident throughout the vineyard ten days after bloom because this treatment is likely to prevent feeding damage later in the season. In Oklahoma vineyards, treatment thresholds are 5 nymphs per leaf before August 1 and ten nymphs per leaf after August 1 (Rebek 2016). Van Kirk et al. (1984) reported that grapevines can tolerate a population density as high as 15 leafhoppers per leaf. Similarly, the University of California reports that grapevines can generally tolerate high leafhopper populations;

however, the geographic region where vines are planted may make them more susceptible to injury by leafhopper feeding, particularly those located in coastal areas (UC IPM 2015).

Chemical Control

From the time eastern grape leafhopper was first reported as a pest in the late 1820s to the early 1900s, treatments included applications of lime sulfur dust, fumigating vines with tobacco smoke, or spraying tobacco extract for control of nymphs (Johnson 1914). An extract of blackleaf tobacco containing 40% nicotine sulphate, mixed to a ratio of 1 gallon of extract to 1500 gallons of water (or Bordeaux mixture, a fungicidal concoction), was highly effective in killing nymphs when sprayed early in the season; specifically, when first-generation nymphs were in the fourth instar, which corresponds to the highest population density of first-generation nymphs (Johnson 1914). From 1865 to the early 1900s, it was also common for grape growers to use soaps and oils to control eastern grape leafhopper. Slingerland (1904) devised a method of managing eastern grape leafhopper in the spring prior to oviposition by overwintering adults. This involved spraying a mixture of 1 pound of whale oil soap in 6 or 7 gallons of water onto the vines to dislodge adults, then spraying an oil-in-water emulsion containing 25% kerosene onto the ground where the leafhoppers had fallen to kill them. He argued that if one-half to three-quarters of the leafhoppers were killed in the spring, this would prevent damaging levels of this pest from building up over the course of the season. This author also reported that a mixture of 1 pound of whale oil soap and 10 gallons of water sprayed on the undersides of leaves was very effective in controlling nymphs (Slingerland 1904).

From 1946 through 1970, eastern grape leafhopper was controlled with dichlorodiphenyltrichloroethane (DDT). For most of this period, the application rate was 1.5 pounds of DDT wettable powder to every 100 gallons of water (Taschenberg 1973). As early as 1954, insufficient control of eastern graph leafhopper with DDT was detected in some areas, and it was evident that this chemical was becoming largely ineffective by 1966 because much more active ingredient per acre (40 ounces vs. \leq 16 ounces) was required for the same level of control (Taschenberg 1973). When resistance to DDT became widespread, eastern grape leafhopper reemerged as a major pest in western New York (Taschenberg 1973). Once DDT was phased out by the Food and Drug Administration, carbamates and organophosphates were used for eastern grape leafhopper control. Carbaryl became the standard insecticide at an application rate of 12 to 30 ounces (AI)/acre; guthion and parathion also gave good control but were inferior to carbaryl (Taschenberg 1973). Martinson and Dennehy (1995a) suggested that routine insecticide sprays for leafhoppers are not necessary in a year with average temperatures, adding that a post-bloom spray may be warranted in years with unusually high temperatures, facilitating rapid population growth. Martinson et al. (1994) discussed the possibility of applying insecticide to the vineyard perimeter as a barrier to control eastern grape leafhopper adults as they move into the vineyard in the spring. Jubb and Danko (1981) achieved effective control of eastern grape leafhopper on Concord grapevines through monthly applications of the carbamate, aldicarb. Insecticides currently labeled for control of leafhoppers in vineyards include but are not limited to acetamiprid, azadirachtin, buprofezin, clothianidin, dinotefuran, imidacloprid, pyrethrin, and thiamethoxam. Insecticidal soaps and kaolin clay are also options for leafhopper control

(UC IPM 2015). In cases when contact insecticides are used, thorough coverage of the lower surfaces of the leaves should be ensured, especially when the foliage is dense (Arnold et al. 2008). Sulfoxaflor, in the sulfoximine class of insecticides, is a relatively new systemic insecticide approved for control of piercing-sucking insects in several crop production systems, including grapes (Watson et al. 2017).

Biological Control

Certain species of parasitic wasps in the genus Anagrus (Hymenoptera: Mymaridae) are solitary endoparasitoids of eastern grape leafhopper eggs. In New York, Anagrus wasps attacking eastern grape leafhopper include A. daanei S. Triapitsyn, A. epos Girault, A. erythroneurae S. Triapitzin and Chiappini, A. nigriventis Girault, and A. tretiakovae S. Triapitsyn. These insects generally colonize the edges of vineyards during May and June, later moving to the interior in August and September, indicating a pattern of slow dispersal for these insects (Williams and Martinson 2000). The Anagrus species present in vineyards of the northeastern USA overwinter as larvae inside diapausing leafhopper eggs laid on host plants such as sugar maple (Acer saccharum), gray dogwood (Cornus racemosa), hawthorn (Crateagus species), white ash (Fraxinus americana), eastern black walnut (Juglans nigra), apple (Malus pumila), American hophornbeam (Ostrya virginiana), black cherry (Prunus serotina), northern red oak (Quercus rubra), black locust (Robinia pseudo-acacia), Japanese rose (Rosa multiflora), black willow (Salix nigra), riverbank grape (Vitis riparia), and common prickly ash (Zanthoxylum americanum) (Williams and Martinson 2000). Refugia in which Rosa and Rubus host species are available to Anagrus wasps may increase numbers of these parasitoids in nearby vineyards, thus facilitating biological control (Prischmann et al. 2007). Moreover,

because of the overwintering strategy used by *Anagrus* spp., these insects are able to increase their population size by completing a full generation on alternate hosts before they enter vineyards in the spring to attack eastern grape leafhopper eggs (Williams and Martinson 2000). Cate (1975) found that *Anagrus* wasps may parasitize 10-20% of western grape leafhopper, *Erythroneura elegantula*, eggs of the first generation and 80-95% of second-generation eggs in California vineyards. In New York during the early part of the season, Williams and Martinson (2000) found that *Anagrus* spp. parasitize 20-41% of eastern grape leafhopper eggs on grapevines adjacent to wooded areas, while they parasitized 0-28% of eggs on grapevines in the interior part of the same vineyard. In late June, they found that the parasitism rate reached a high of 59% of eastern grape leafhopper eggs.

Eastern grape leafhopper is also attacked by nymphal-adult parasitoids in the family Dryinidae. Fenton (1918) described the parasitism of *E. comes* by *Aphelopus comesi*, which produces a visible larval sac, known as a thylacium, on the leafhopper abdomen. This parasitoid sterilizes its host by consuming its reproductive organs (Flaherty et al. 1992). Wilson et al. (1991) reported that this wasp (now *A. albopictus* Ashmead) parasitized up to one-third of western grape leafhopper adults captured in vineyards in the San Joaquin Valley of California. Furthermore, Cate (1975) discovered up to 77% parasitism of *E. elegantula* by *A. albopictus* in the same region.

Besides parasitoids, eastern grape leafhopper may be controlled by predators. Mulder (2014) recommended deploying 3,000 to 8,000 green lacewing (Neuroptera: Chrysopidae) eggs per acre. Lacewing nymphs attack and kill leafhopper nymphs. Other natural predators of eastern grape leafhopper include black hunter thrips (*Leptothrips* *mali*), brown lacewings (Neuroptera: Hemerobiidae), the dance fly *Hemerodromia superstitiosa*, *Hyaliodes vitripennis*, ladybird beetles (*Hippodamia* spp.), minute pirate bugs (*Orius* spp.), a mirid in the genus *Paraproba*, spiders (*Cheiracanthium inclusum*, *Tegenaria domestica*, and *Theridion* spp.), and the mite *Anystis agilis* (Johnson 1914; UC IPM 2015). Adult leafhoppers may become trapped in spider webs and be eaten (Johnson 1914). Under the right conditions, pathogens also contribute to the control of eastern grape leafhopper. Unusually wet growing seasons may promote infection of leafhoppers by fungi in the genus *Entomophthora* in the late fall, including *E. sphaerosperma*, which is capable of decreasing the size of the overwintering generation of leafhoppers (Dozier 1929, Jubb 1976).

Cultural Control

Wilson and Daane (2017) and Mulder (2014) suggested that there may be an advantage in managing leafhoppers via the customary practice of removing leaves from grapevines, which growers do in order to give their plants healthy and well-formed canopies. This practice may be timed immediately after the period in which leafhoppers have laid most of their eggs on the leaves, so that the population of eggs may be reduced within the vineyard (Wilson and Daane 2017).

In addition to leaf removal, pruning practices also have an effect on management of leafhoppers in vineyards. Three methods of pruning commonly implemented in vineyards are minimal pruning, balanced pruning, and pruning to a fixed number of 80 nodes per vine. Minimal pruning involves cutting off the previous year's growth at the level of the lower trellis. Balanced pruning involves following a formula set forth by Shaulis et al. (1966) designed to accomplish vegetative balance. Jubb et al. (1983) found that balanced-pruned vines did not suffer a decrease in crop weight when heavily infested as compared to lightly infested vines. However, vineyards that are mechanically hedged or undergo minimal pruning practices may be at risk of higher damage from leafhopper feeding because the resulting increase in crop load stresses the vine, leading to incomplete ripening and lower tolerance of leafhopper injury (Martinson et al. 1997). Martinson et al. (1997) found that balanced-pruned vines and vines pruned down to 80 buds experienced more leafhopper injury than minimally pruned vines.

The use of ground cover may also reduce leafhopper abundance on grapevines. Costello and Daane (2003) noted a reduction in grapevine vigor, as measured by pruning weight and nitrogen content in leaf petioles, in the presence of ground cover composed of barley (*Hordeum vulgare*) and purple vetch (*Vicia benghalensis*) until May, and afterwards an assortment of grasses (*Digitaria, Echinochloa*, and *Setaria* spp.) and common knotweed (*Polygonum aviculare*). The authors suggested that reduced grapevine vigor resulted from competition with cover vegetation for nutrients and water, which reduced the quality of the host plant for *E. elegantula* leafhoppers. Thus, there were fewer leafhoppers of the second and third generation in the treatments having cover vegetation. There was no correlation, however, between leafhopper abundance and the abundance of predatory spiders, the latter being similar between "cover" and "no cover" treatments. Nor was there any relationship found between egg parasitism and leafhopper abundance between the treatments.

Regulated deficit irrigation (RDI), a practice employed in California vineyards for improved grape quality and vegetative balance, has been shown to decrease grape leafhopper populations when implemented at the time between berry set and veraison

(Costello 2008). First-generation females of *E. elegantula* generally oviposit secondgeneration eggs during this timeframe. Costello (2008) observed a decrease in the abundance of second-generation nymphs by about one-half as a result of this practice. Abundance of leafhopper eggs was also reduced but was not consistent across the two sites monitored. Conversely, Flaherty et al. (1992) reported that well-irrigated grapevines were able to withstand heavy leafhopper infestation before losing productivity.

Sanitation and Mechanical Control

Sanitation practices are an important component of eastern grape leafhopper management. These practices may include removing debris such as pruned canes and dead leaves from the vineyard as well as burning grass strips or weedy ditches bordering the vineyard in the winter (Jubb 1976). In the past, it was recommended to spray a light coat of kerosene on overwintering sites before burning them to expedite the process (Slingerland 1904).

Slingerland (1904) noted that eastern grape leafhopper adults overwintering along vineyard rows could be controlled by running a plough close to the vines, effectively burying the insects in the soil. Tillage, used increasingly for vineyard weed management with the objective of reducing dependence on herbicides, has been shown to provide a level of control of grape berry moth when the overwintering pupae are buried at least a centimeter under the soil (Matlock et al. 2017). Thus, tillage might be a good mechanical control option for vineyards having both *E. comes* and *P. viteana*.

Another strategy for mechanical control is the use of traps coated with adhesive substances. Slingerland (1904) designed and recommended a "sticky shield" constructed

of an 8 ft X 4 ft light wooden frame overlaid with oilcloth covered in a mixture of one quart melted resin with one pint castor oil. Two of these shields, each carried by one person, could be moved along either side of a vine row while shaking the canes of the vine to dislodge the leafhoppers onto the oilcloth. This method was effective for capturing thousands of the overwintered generation of adults before they laid eggs on the foliage (Slingerland 1904).

Other Leafhoppers Occurring in North American Vineyards

Other leafhoppers in the subfamily, Typhlocybinae, which have been reported as vineyard pests in North America include the following: potato leafhopper, *Empoasca fabae* (Harris); *Erasmoneura variabilis* (Beamer); *E. vulnerata* (Fitch); *Erythroneura bistrata* McAtee; *E. coloradensis* (Gillette); *E. cymbium* McAtee; western grape leafhopper, *E. elegantula* Osborn; three-banded leafhopper, *E. tricincta* Fitch; *E. vitifex* Fitch; and Virginia creeper leafhopper, *E. ziczac* Walsh. Several other leafhoppers in the tribe Erythroneurini occur in vineyards and feed on grape leaves but have not been reported as serious pests. These include but are not limited to *Erythroneura delicata* McAtee, *E. octonotata* Walsh, *E. vitis* (Harris), and *Illinigina illinoiensis* (Gillette).

The species composition of erythroneurine leafhoppers in vineyards varies across North America. The predominant species in vineyards in the western United States, especially in California and Washington, are *Erythroneura elegantula* and *E. ziczac*; California also has *Erasmoneura variabilis* (Settle and Wilson 1990, Olsen et al. 1998). Vineyards in Michigan, New York, Ohio, and Pennsylvania are attacked mostly by *Erythroneura bistrata, E. comes, E. cymbium, E. tricincta*, and *E. vitifex* (Runner and Bliss 1923, Van Kirk et al. 1984, Martinson and Dennehy 1995b, Ellis et al. 2004). Vineyards of Colorado and Texas are primarily attacked by *Erasmoneura vulnerata*, *Erythroneura coloradensis*, and *E. ziczac* (Slingerland 1904, Paxton 1990, Zimmerman et al. 1996). Ontario, the Canadian province with the most acreage of vineyards, has *Erythroneura comes*, *E. tricincta*, and *E. vitifex*, while Quebec has *Erasmoneura vulnerata*, *Erythroneura comes*, *E. tricincta*, *E. vitifex*, *E. vitis*, and *E. ziczac* (Bostanian et al. 2006, Saguez et al. 2014). British Columbia has mostly *Erythroneura elegantula* and *E. ziczac* (Lowery 2010).

Some leafhoppers in the subfamily Cicadellinae, generally known as sharpshooters, are also pests in vineyards across North America. Glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar), for example, is responsible for transmitting the bacterium, *Xylella fastidiosa*, the causative agent of Pierce's disease of grape (Overall and Rebek 2017). Other leafhoppers in the subfamily Deltocephalinae are pests of grape, including *Scaphoideus titanus*. This leafhopper has been reported as a vector of phytoplasmas in the eastern United States as well as the Mediterranean region of Europe (Prince et al. 1993).
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CHAPTER III

PHENOLOGY OF EASTERN GRAPE LEAFHOPPER, *ERYTHRONEURA COMES* (SAY), AND ABUNDANCE ON GRAPE CULTIVARS, WITH NOTES ON OTHER LEAFHOPPERS OF IMPORTANCE

Introduction

Phenology

Phenology describes the timing of an organism's life stages and activities throughout the year, including but not limited to oviposition, migration, diapause, and the occurrence of generations (Martinson et al. 1994). Murray (2008) defines phenology simply as "biological development over time." Environmental variables, such as temperature and day length, are known to influence the phenology of various organisms. This is especially true of insects since they are poikilothermic (i.e., their internal temperature largely depends on the temperature of their surroundings). The influence of temperature on insect phenology is due to the fact that heat is necessary to sustain metabolic processes and development of the insect. Each species has a lower developmental threshold, which is the lowest temperature at which it undergoes development; temperatures below this threshold halt the organism's metabolic processes (Zalom et al. 1983). The lower threshold may be estimated by plotting development rate versus a range of temperatures and then utilizing the regression line and calculating the xaxis intercept (Zalom et al. 1983). It is possible to predict the time of occurrence of life stages of an insect with three pieces of information: the lower developmental threshold, the required amount of heat (measured in GDD) for the development of the organism through all stages, and daily high and low temperatures. Zalom et al. (1983) report that GDD requirements for a particular species are invariable, no matter what the prevailing climatic conditions are like in the geographic location of the population. Conversely, other authors have reported that GDD requirements for insect development vary depending on geographic location (Honěk 1996, Ma et al. 2019).

Growing Degree Day Modeling

Growing degree day models are used for predicting the phenology of insect populations based on formulas that sum cumulative GDD, which are heat units above a lower developmental threshold, across a range of consecutive days starting from a specified date (Zalom et al. 1983). This specified date represents the date by which temperatures reach the lower developmental threshold temperature in the region where the pest population is located. For example, in the colder regions of the northeastern United States and in Canada, the start date for summing GDD for eastern grape leafhopper, *Erythroneura comes* (Say), is March 1 or April 1 (Martinson et al. 1994, Bostanian et al. 2006), while in warmer regions it may be set as early as January 1.

There are several different growing degree day models, each with a unique formula for calculating GDD. The simplest and most commonly used is the averaging, or rectangular model (Murray 2008). However, this model is prone to underestimating degree day accumulation on certain days early in the season. On such days, the daily maximum temperature is above the lower developmental threshold, but the daily

minimum temperature is far enough below the threshold as to cancel out any GDD that would have accumulated (Zalom et al. 1983). More mathematically rigorous growing degree day models, such as the single triangulation and single sine wave models, avoid the problem of underestimating early-season GDD and, hence, are more accurate (Zalom et al. 1983). Of the three models, the single sine wave model most closely approximates fluctuation in temperatures over the course of a day.

Growing degree day models depend on intensive monitoring of the pest population and environment over time. Monitoring may be performed either by direct counts of the insect or with the use of reliable indirect sampling methods such as sticky traps or pheromone traps (Natwick et al. 2007, Akotsen-Mensah et al. 2018). Certain life stages of the organism may be more amenable to monitoring practices due to differences in visibility or mobility. The choice of which life stages to monitor may be influenced by the kinds of behaviors the insect exhibits. For example, an immature, non-flying stage may be preferred for monitoring because it is less evasive (UC IPM 2013). Monitoring efforts may target only immatures and adults, especially if the eggs are hidden under the leaf epidermis or otherwise inconspicuous (McCraw et al. 2005). For eastern grape leafhopper, the nymphs are the easiest stage to monitor by directly counting them on the surfaces of leaves. Though sometimes very active in their running movements across the leaf surface, nymphs of *E. comes* very rarely jump after being disturbed (Johnson 1914). The five instars are differentiated by size, by the depth of yellow-green coloration of the body, and by the development of wing pads; earlier instars are smaller, lighter in color, and have less developed wing pads (Johnson 1914).

Growing degree day models may be used to great advantage in the context of an integrated pest management (IPM) approach in agroecosystems as they provide growers with specific recommendations for improved precision of timing for monitoring activities and more effective control measures (Zalom et al. 1983). Growing degree day models provide growers a better understanding of the development of the pest population and, most importantly, an idea of when life stages most susceptible to control are likely to be present. As efficacy and precision of insecticide applications improve, they are used more judiciously, thus preventing their overuse (Sharma and Gavkare 2014).

Pest management recommendations based on growing degree day models have been developed for a wide variety of insects globally, including major coleopteran, dipteran, hemipteran, hymenopteran (i.e., sawflies), lepidopteran, and orthopteran pests in agriculture, horticulture, and forests (Herms 2013, Tu et al. 2014). Among these are hemipteran insects such as adelgids, aphids, kudzu bug, lace bugs, leafhoppers, plant bugs, planthoppers, psyllids, scale insects, and stink bugs (Ro et al. 1998, Herms 2013, Khlibsuwan et al. 2015, Nielsen et al. 2017, Grant and Lam 2018). Recommendations based on phenology models may provide guidance on when to monitor for the target pest, apply a pesticide prophylactically, release biological control agents, or implement cultural practices that might reduce the pest population (Welch et al. 1978).

Host Plant Preference

Preference for certain host plants is a widely reported phenomenon with regard to phytophagous insects in many orders (Cates 1981, Balusu and Fadamiro 2011). There are complex interactions between insect host selection behavior (e.g., host location, acceptance, and use) and host plant cues – whether gustatory, olfactory, tactile, or visual

(Heard 2000). Host preference may be considered from two vantage points of insect behavior: feeding and oviposition. Such preference may be strict, as in the case of a monophagous insect that specializes on a particular host species (e.g., *Bombyx mori* on mulberry, Zhang et al. 2019), or more lax, as in the case of an oligophagous insect that will feed or lay eggs on several plant species within a single genus (e.g., *Cactoblastis* cactorum on Opuntia spp. cacti, Zimmermann et al. 2004). Hopkin's host selection principle (HHSP) proposes that an adult insect herbivore will prefer to breed on the plant species it utilized during its life as an immature (i.e., its natal host), rather than choosing to breed on an equally available, alternative suitable host plant species as an adult (Hopkins 1916). The earlier host selection principle of Walsh (1864) states that a female insect herbivore will select her natal host species for oviposition over other host plants. Thorpe and Jones (1937) proposed the idea of "pre-imaginal conditioning," in which the nervous system of the preimago (i.e., immature form) is conditioned to respond to the natal host plant odor, and this conditioning persists beyond metamorphosis into an adult. These authors suggest pre-imaginal conditioning as a mechanism for the origin of biological races (viz. non-interbreeding populations within a species that prefer different hosts).

In addition to herbivores, Hopkin's host selection principle has also been applied to insect parasitoids and their choice among available suitable hosts (Smith and Cornell 1979). The literature has demonstrated that HHSP does not apply to every insect specialist feeder (Barman et al. 2012), and there is continuing debate as to the principle's validity for herbivores and parasitoids alike (Monteith 1962, Barron 2001, Mader et al. 2012). On the other hand, there has been a growing body of literature exploring the

concept of host preference determination via adult learning of host plant volatiles, especially in flower-foraging insects (Cunningham et al. 2004, Riffell 2011, Anderson and Anton 2014). It is now known that a multitude of factors may influence host choice, including the biology of the feeder or that of the host (Frey and Bush 1990), maternal and paternal effects (Mousseau and Dingle 1991, Futuyma et al. 1993), and environmental conditions (Sabtu and Majid 2018) to name a few.

Host Plant Preference among Leafhoppers

Leafhopper host plant preference has a long history of investigation, especially among pest species that transmit plant pathogens or otherwise harm crops. In a three-year field study, Wallis (1962) observed variable abundance of the leafhopper, Macrosteles *fascifrons* (Stål), a vector of aster yellows, in sweep net samples taken across 38 plant species, from which he concluded that bindweed, carrot, celeriac, and celery were preferred. In choice tests, the polyphagous potato leafhopper, *Empoasca fabae* Harris, exhibits a preference for a smooth-stemmed alfalfa variety over a variety possessing glandular trichomes on the stems (Ranger and Hower 2002). Bullas-Appleton et al. (2004b) determined that leaf color serves as a visual cue explaining bean cultivar preference in potato leafhopper; namely, a cultivar with higher percent reflectance of green light and lower reflectance of blue and yellow light was preferred. Chuche et al. (2016) found that nymphs of Scaphoideus titanus Ball, a vector of yellows diseases of broadbean and grape, were more attracted to yellow than to green squares; furthermore, S. titanus nymphs preferred diseased, yellowed grapevines over healthy, green grapevines. However, the nymphs chose healthy grapevines over diseased, yellowed broadbean plants. From these results, the authors suggest that a combination of color cues

and volatile cues from diseased plants are responsible for the preference of *S. titanus* for diseased grapevines. Another example of a leafhopper showing host plant preference is the beet leafhopper, *Circulifer tenellus* (Baker). This vector of curly top virus exhibited a preference for sugar beet over tomato in caged choice studies (Thomas 1972).

Leafhoppers in the genus *Erythroneura* (tribe: Erythroneurini) are known to prefer certain grape species or cultivars over others. A cultivar is defined in the U.S. Fish and Wildlife Service's Code of Federal Regulations as "a horticulturally derived plant variety that: has been selected for a particular character or combination of characters; is distinct, uniform, and stable in these characters; and when propagated by appropriate means, retains these characters" (e-CFR 2019). Such cultivar-specific characters might be expected to influence host plant preference among leafhoppers feeding on grape. Indeed, preference for particular grape species has been linked to leaf thickness in some cases (Runner and Bliss 1923).

Martinson et al. (1994) reported counting seven times more eastern grape leafhopper nymphs on the leaves of the cultivar 'Diamond' than on those of the cultivar 'Dutchess' from late June through September. The authors suggested that the leafhoppers prefer to oviposit on the former cultivar over the latter. It is also reported that eastern grape leafhopper prefers cultivars having *Vitis labrusca* heritage over those with *Vitis vinifera* heritage (Williams and Martinson 2000). The former species is native to the American continent and the latter is of European origin. Dmitriev (3I Interactive Keys) reported that *Erythroneura reflecta* McAtee and *E. vitis* (Harris) prefer riverbank grape, *Vitis riparia*, while Runner and Bliss (1923) observed *E. vitis* mostly on frost grape, *Vitis vulpina*.

Materials and Methods

Vineyard Sites

I conducted weekly sampling of leafhopper nymphs and adults from late spring to early fall of 2016, 2017, and 2018. Sampling for leafhopper nymphs was performed at one vineyard in 2016 through 2018 and at two additional vineyards in 2017 and 2018. The site sampled all three years was an experimental wine grape vineyard measuring 1.33 acres of planted rows at the Cimarron Valley Research Station (CVRS) in Perkins, Oklahoma. This vineyard contained several cultivars having European (*Vitis vinifera*) and/or American parentage (*V. aestivalis*, *V. labrusca*, *V. riparia*, and *V. rupestris*). These included Chambourcin, Chardonel, Cynthiana (also called Norton), Frontenac-Gris, Niagara, Noiret, Rubaiyat, and Traminette. The other two vineyards sampled in 2017 and 2018 were commercial wine grape vineyards located in Bristow, Oklahoma and Norman, Oklahoma. The Bristow vineyard measured 0.6 acres of planted rows containing a mix of cultivars with European and/or American parentage, including Lambrusco, Léon Millot, Merlot, and Muscadine. The Norman vineyard, measuring 1.46 acres of planted rows, had only cultivars of European parentage, Cabernet and Muscat.

Sampling protocols

Sampling began when nymphs were first detected on the leaves in the spring and lasted until the population dipped below 0.2 nymphs per leaf in October. I recorded the numbers of each of five instars as they appeared throughout the season. In the course of sampling, I gently removed each leaf where the petiole meets the shoot. In this way I could easily hold the petiole and turn it to view the top and bottom surfaces of each leaf. I

ensured that I did not count the same nymph twice by removing it from the leaf with an ink pen. This method worked well as nymphs readily stuck to the point of the ink pen when it came in contact with their dorsum. The focus of this study was eastern grape leafhopper, Erythroneura comes (Say) (Figure 1), but I also counted other species such as Erasmoneura vulnerata (Fitch) (Figure 2) and Virginia creeper leafhopper, Erythroneura *ziczac* Walsh (Figure 3), as well as other erythroneurines (species belonging to the tribe Erythroneurini). Sampling selecting leaves from a random position anywhere from the third basal to third apical node of a randomly selected shoot on a randomly selected plant. For sampling leafhopper adults, I deployed yellow sticky card traps measuring 20 x 13.75 cm (Alpha Scents, Inc., West Linn, OR; henceforth referred to as cards) throughout the vineyard (Figures 4 and 5), securing them at mid-canopy level to the vine support cables with two clothes pins. These remained in place for approximately 72 hours. The number of cards deployed weekly for each year is reported below. A second method for adult leafhopper sampling involved the use of a handheld, gasoline-powered leaf blower (model BG 56 C-E, Stihl, Inc. USA, Virginia Beach, VA) operated in suction mode to take vacuum samples. For this method, a mesh bag (124 holes per cm^2) measuring 30.48 x 15.24 cm was inserted three-quarters of the way into the leaf blower extension tube, and four thick rubber bands were stretched around the excess material to secure the bag to the tube. For each sample, the leaf blower was run at full throttle for 30 seconds, targeting all levels of the canopies of two or three grapevines (the number depending on the density of the foliage). Once 30 seconds elapsed, the bag was taken out of the tube and immediately tied at the end to prevent any insects from escaping. Bags were then placed in a cooler to slow the activity of the captured arthropods, as to prevent predators

from eating the leafhoppers. Upon returning to the lab, the samples were placed into a freezer.

In 2016 I began sampling on May 31 at the Perkins vineyard. This was a late start, as I likely missed the first appearance of first-generation nymphs of *E. comes*. My sampling methods involved inspecting 50 leaves throughout the vineyard two days out of the week (separated by three days), counting all nymphs present on a total of 100 leaves per week. I preferentially sampled leaves with stippling injury, an approach recommended by Flaherty et al. (1992). This is the conventional sampling method for grape growers, as it allows them to estimate the populations in areas of the vineyard that have the highest densities of the pest, thus informing their treatment decisions (Daane et al. 2013). Nymph sampling in 2016 lasted until October 6. Adult sampling began the week of May 10. For the first four weeks, twelve cards were deployed weekly among exterior grapevines, and for the remainder of the season five cards were added to interior grapevines for a total of seventeen cards weekly through September 30. The number of vacuum samples equaled the number of cards deployed throughout the season and corresponded to their locations in the vineyard.

In 2017, I began sampling at the three vineyards on May 8, when first-generation nymphs began appearing on leaves. Nymph sampling methods at the Perkins vineyard were identical to those of the previous season, with the exception that I sampled 100 leaves on a single day of the week rather than sampling 50 leaves on each of two days. In addition, I deployed sixteen cards throughout the Perkins vineyard (two in each of the eight cultivars), the Bristow vineyard (five in Merlot and seven in Léon Millot) and eight throughout the Norman vineyard (four each in Cabernet and Muscat). Vacuum samples

corresponded to the locations of the cards. Both nymph and adult sampling lasted until October 13.

In 2018, I began sampling at the three vineyards on May 17, when first-generation nymphs began appearing on leaves. Nymph sampling methods were identical to those of 2017, except that I modified my criteria of selection so that I did not preferentially select leaves with stippling injury. Both nymph and adult sampling lasted until October 11.

Temperature Data Collection and Growing Degree Day Calculation

I obtained daily temperature data from Mesonet weather stations located near the Perkins and Norman vineyard sites. The Perkins Mesonet station is located 0.56 km (0.35 miles) west of the Perkins vineyard, while the Norman Mesonet station is located 13.05 km (8.11 miles) northwest of the Norman vineyard. Mesonet, a partnership between Oklahoma State University and the University of Oklahoma, is a network of 121 weather stations located throughout all counties of the state which record weather variables such as air and soil temperature, barometric pressure, humidity, rainfall, solar radiation, and wind direction and speed (Mesonet.org, Ziolkowska 2018). For the Bristow vineyard site, I collected temperature data with an onsite weather station (Vantage Pro2, Davis Instruments, Hayward, California). I used the single sine wave model to calculate GDD above a lower developmental threshold of 10°C (50°F) starting on January 1 each year, as these are the model and threshold used in the eastern grape leafhopper phenology work of Martinson et al. (1994) in New York. However, these authors started accumulating GDD on April 1, which they explained is the date by which temperatures generally reach the lower threshold in New York. Furthermore, the single sine wave model is more accurate

than the averaging model in terms of calculating early-season degree day accumulation (Zalom et al. 1983).

Differential Abundance across Cultivars

To compare abundance of nymphs across the eight cultivars at the Perkins vineyard, one way repeated measures analysis of variance (SAS 9.4) was performed with the response variable being the number of nymphs per leaf. Two class variables were time (by month) and cultivar. Tukey's mean separation tests were used for both class variables ($\alpha = 0.05$).

Data Reporting

I only report and discuss data from the Perkins vineyard for 2016 through 2018. The Bristow vineyard, sampled in 2017 and 2018, is excluded from analysis for two reasons: 1) the diversity of nymphs of similar-looking species on the leaves presents a high probability that I regularly misidentified the individuals; and 2) the low number of eastern grape leafhopper adults caught by sticky card traps and vacuum samples likely implies that a majority of the nymphs I counted were other species. In fact, when I brought nymphs from the Bristow vineyard back to the lab and reared them to adults, most specimens were *Erythroneura amanda* McAtee (Figure 6), which were also much more numerous than eastern grape leafhopper on the sticky card traps and in vacuum samples. For these reasons, it would be inappropriate to use nymph data from Bristow for analyzing eastern grape leafhopper phenology. I did not use nymph data from Norman because of the use of insecticides for insect pest control in 2017, and there was little to no leafhopper activity in 2018.

Identification of *Erasmoneura*, *Erythroneura*, and *Hymetta* adult specimens was based on photographs in a publication by Dmitriev and Dietrich (2007). Identification of all other Auchenorrhyncha adult specimens was based on photographs from either university extension websites or bugguide.net, a website hosted by the Iowa State University Department of Entomology.

Results

Phenology in Perkins, Oklahoma

In 2016, I counted a total of 1,073 eastern grape leafhopper nymphs. There were three peaks in *E. comes* abundance on June 3, July 22, and August 26. These dates corresponded to 756 GDD, 1,632 GDD, and 2,263 GDD, respectively (Figure 7 shows population curve and instar proportions). Adults caught on cards and in vacuum samples numbered 24,336. Total abundance of all adults belonging to the suborder Auchenorrhyncha was 39,155 individuals (Figure 8; see Appendices A through E for a more detailed breakdown of taxa).

In 2017, I counted a total of 576 eastern grape leafhopper nymphs and there were four peaks in *E. comes* abundance on May 15, July 25, September 1, and September 30. These dates corresponded to 531 GDD, 1,717 GDD, 2,307 GDD, and 2,696 GDD, respectively (Figure 9 shows population curve and instar proportions). Adults caught on cards and in vacuum samples numbered 6,614. Total abundance of all adults belonging to the suborder Auchenorrhyncha was 13,828 individuals (Figure 10; see Appendices F through J for a more detailed breakdown of taxa).

In 2018, I counted a total of 1,219 eastern grape leafhopper nymphs. There were three peaks in *E. comes* abundance on May 17, July 12, and September 13. These dates corresponded to 525 GDD, 1,434 GDD, and 2,474 GDD, respectively (Figure 11 shows population curve and instar proportions). Adults caught on cards and in vacuum samples through September 15 numbered 64,229. Total abundance of all adults belonging to the suborder Auchenorrhyncha was 190,126 individuals (Figure 12; see Appendices K through O for a more detailed breakdown of taxa). The samples from the remainder of the season were not processed due to time constraints. Voucher specimens were deposited in the K.C. Emerson Entomology Museum at Oklahoma State University, Stillwater, Oklahoma.

Differential Abundance across Cultivars

In 2016, the mean number of nymphs per leaf was significant for the cultivar class variable, but not for the time (by month) class variable. The cultivar variable separated into three significant groups (Figure 13). In 2017, mean nymphs per leaf was not significant for either class variable. In 2018, the relationship between the response and class variables was the same as in 2016 (Figure 14). The cultivars Noiret and Traminette had the highest mean nymphs per leaf for 2016 and 2018, while Cynthiana and Niagara had the lowest mean nymphs per leaf for these years.

Although there were no significant differences in mean nymphs per leaf across cultivars in 2017, Noiret and Traminette still had the highest total numbers of nymphs among the cultivars. Figure 15 shows the total abundance of eastern grape leafhopper nymphs across all eight cultivars for each year. It can be seen in this figure that Cynthiana had fewer than twenty-five nymphs in each of the three years, while both Noiret and Traminette frequently had more than 150 nymphs per season. The former had in excess of 400 nymphs in 2018, the highest total abundance of any of the cultivars in any of the years of the study.

Discussion

Leafhopper Populations

For all three years of my study, pooled across all eight cultivars at the Perkins vineyard, the population of eastern grape leafhopper nymphs did not exceed a conservative economic threshold of five nymphs per leaf. The season-high nymph densities were as follows: 1.36 nymphs per leaf the week of August 26, 2016; 0.94 nymphs per leaf on September 30, 2017; and 1.23 nymphs per leaf on September 13, 2018. When including all erythroneurine nymphs present on the leaves, an early-season economic threshold of five nymphs per leaf was still not exceeded in any of the years. Season-high densities were 1.96 nymphs per leaf the week of August 26, 2016 (including *Erasmoneura vulnerata, Erythroneura comes*, and *E. ziczac*); 1.69 nymphs per leaf on September 1 and 30, 2017 (including *Erasmoneura vulnerata, Erythroneura comes*, *E. cymbium, E. delicata, E. rubra, E. vitis*, and *E. ziczac*); and 3.98 nymphs per leaf on August 24, 2018 (including *Erasmoneura vulnerata, Erythroneura comes*, and *E. ziczac*).

Cultivar-specific Leafhopper Populations

Considering the density of eastern grape leafhopper nymphs on each cultivar, a threshold of five nymphs per leaf was surpassed only on two cultivars in two years of the study (Table 1). During the week of August 26, 2016, there were 5.2 nymphs per leaf on Traminette; on September 13, 2018, there were 7.75 nymphs per leaf on Noiret.

However, the economic threshold for late-season population densities (i.e. after 2200 GDD have accumulated) is ten nymphs per leaf. Therefore, no treatment measures would be necessary in either of these cases. Table 2 reports the dates of the first and last observation of *E. comes* nymphs on each of the cultivars for each year of the study.

When including all erythroneurine species counted, the season-high density for Traminette rose from 5.2 to 6.5 nymphs per leaf during the week of August 26, 2016 (including Erasmoneura vulnerata, Erythroneura comes, E. delicata, and E. ziczac). In 2017, season-high densities across cultivars did not exceed a threshold of five nymphs per leaf; however, the density rose as high as four nymphs per leaf on Noiret (including Erasmoneura vulnerata, Erythroneura comes, E. cymbium, and E. ziczac) and 4.17 nymphs per leaf on Traminette (including the same species, as well as *E. delicata*) on September 1 of that year. In 2018, nymph population densities exceeded a threshold of five nymphs per leaf for three cultivars. On Chardonel, there were 9.33 nymphs per leaf on July 26. Since by this date, only about 1700 GDD had accumulated, a treatment would be deemed appropriate. On Noiret, there were 7.08, 5.92, 7.92, 18.42, 14.75, 14.92, and 14.92 nymphs per leaf on July 19, August 9, 17, 23, and 30, and September 6 and 13, respectively. In all these cases, a treatment would be deemed appropriate, since both the early-season economic threshold of five nymphs per leaf and the late-season threshold of ten nymphs per leaf were surpassed. On Traminette, there were 5.42 and 7.33 nymphs per leaf on July 12 and September 6, respectively. Treatment would be deemed appropriate only on the first of these dates, as the early-season threshold was then surpassed, but the late-season threshold was not exceeded on the latter date. In all instances of the economic threshold being surpassed in 2018, the species composition was limited to Erasmoneura

vulnerata, Erythroneura comes, and *E. ziczac*, except on August 17 on Traminette when *E. delicata* was also present.

Virginia Creeper Leafhopper, Erythroneura ziczac Walsh

The species composition of erythroneurine nymphs at the Perkins vineyard for all three years is shown in Figure 15. An interesting result is the abundance of *E. ziczac* nymphs was 12% higher than that of *E. comes* nymphs in 2018. In contrast, the abundance of *E. ziczac* represented only 12% and 13% of the abundance of *E. comes* in 2016 and 2017, respectively. Additionally, there were more *E. ziczac* adults caught in 2018 than *E. comes* adults (see Appendix K). The dramatic increase in Virginia creeper leafhopper in the last year of this study was unanticipated. Large outbreaks of *E. ziczac*, a species native to the midwestern U.S., have been occurring in California since 2011 when the species invaded vineyards of the northern part of the state (UCCE 2019). Outbreaks of this leafhopper, *E. elegantula*, for four reasons: 1) *E. ziczac* lays eggs earlier in the season, 2) *E. ziczac* produces more eggs per female, 3) *E. ziczac* lays eggs later into the season, and 4) biological control by *Anagrus* spp. egg parasitoids is not occurring in some areas of the state (UCCE 2019).

Feeding injury by this leafhopper is similar to that of *E. comes* and may result in similar damage to grapevines, which includes loss of photosynthetic capacity, reduced sugar content in fruit, premature leaf drop, and vine stunting (UC IPM 2019). As *E. ziczac* can attain high populations and is possibly a vector of grapevine red blotch-associated virus (GRBaV) (Poojari et al. 2013), it would be beneficial to continue

studying the biology and ecology of this pest in Oklahoma. The GRBaV was first detected in Oklahoma grapevines in 2015 and subsequently confirmed through a 2016 Cooperative Agricultural Pest Survey to be present in 8 counties (Wallace 2018). The status of *E. ziczac* as a potential GRBaV vector is disputed, as there have been studies that have not confirmed its ability to transmit the virus (Zalom and Sudarshana 2017). In addition, this geminivirus is phloem-limited, while *E. ziczac* feeds on mesophyll, so it is not likely that it is capable of transmission of this particular pathogen (Zalom and Sudarshana 2017). Figures 17 through 19 show the population curves of *E. ziczac* nymphs for the three years of the study. Figures 20 through 22 show the population curves of nymphs of *Erasmoneura vulnerata*, which was the second most abundant species found completing development on grape leaves in 2016 and 2017 and the third most abundant in 2018.

Potato Leafhopper, Empoasca fabae (Harris)

Potato leafhopper (Figure 23) was the fifth most abundant leafhopper species counted on cards and in vacuum samples in 2016 and 2017 at the Perkins vineyard, numbering 613 and 806 adults, respectively. In 2016, the majority (380) were captured during the weeks of May 27 and June 3. In 2017, the majority (493) were captured during the weeks of May 25 and June 2. In 2018, *E. fabae* was the fourth most abundant leafhopper species, numbering 1,460, with the majority of these (1,246) being captured during the weeks of May 29 and June 6. The between-year consistency of timing for potato leafhopper's migration into the Perkins vineyard (i.e., the last week of May and the first week of June) may be useful for Oklahoma grape growers to anticipate this pest and apply any necessary control measures. High populations are potentially very

damaging in wine grape vineyards; if uncontrolled, this insect may lead to leaf chlorosis and cupping, cause a decrease in shoot growth, result in the condition known as hopperburn, and negatively impact fruit ripening, especially in certain wine grape cultivars with European (i.e., *Vitis vinifera*) heritage (Isaacs and van Timmeren 2010). These cultivars – which include Cayuga White, Chardonnay, and Pinot Gris – exhibit a hypersensitive response to the saliva of *E. fabae*, possibly leading to closure of the stomata with reduced carbon assimilation and leaf transpiration (Isaacs and van Timmeren 2010, Lenz et al. 2012). Their saliva is also capable of impeding flow within the vascular tissue (Growing Grapes in Minnesota 2016). Given that in 2006, seven of the top ten cultivars grown in Oklahoma were European and two were hybrids with some *Vitis vinifera* heritage (Stafne 2015), it behooves Oklahoma grape growers to be wary of this pest, particularly because leafhopper feeding injury occurring early in the season has the potential to interfere with photosynthesis at a crucial stage in the development of the vine (Jubb et al. 1983).

Historically, grapes have not been reported as a reproductive host for *E. fabae*; however, Lamp et al. (2011) verified with growth chamber experiments that the European cultivar Cabernet Sauvignon is a suitable reproductive host for this leafhopper. Furthermore, Isaacs and van Timmeren (2010) recommended weekly scouting for potato leafhopper nymphs in Michigan vineyards. These authors also report that eggs laid in grape leaves eclose in mid- to late June. However, in the entire timeframe of nymph sampling, I counted only one *E. fabae* nymph on Traminette on June 16, 2018. This result suggests that in central Oklahoma this leafhopper rarely lays eggs on the cultivars involved in the present study. Control strategies for potato leafhopper in wine grapes

include cultural and chemical measures. Thick-leaved interspecific hybrids have a level of host plant resistance to this insect (Isaacs and van Timmeren 2010). Systemic neonicotinoids such as Actara, Assail, Clutch, Provado, and Scorpion, applied as foliar sprays, are an option for control of this pest in vineyards (Isaacs and van Timmeren 2010).

Phenology

The number of generations of eastern grape leafhopper at the Perkins vineyard was usually three (in 2016 and 2018), but there may have been a partial fourth generation in 2017. The majority of the individuals of a partial generation die before maturing to adulthood (Howard 1903). The literature supports these observations, as *E. comes* undergoes three or four generations in Oklahoma (McCraw et al. 2005). The interpretation of the abundance data for the nymph population operates on the assumption that peaks represent separate generations. This assumption alone, however, is insufficient for confidently interpreting the data in terms of the procession of generations. A more detailed data set including the abundance and proportion of the instars over time assists in the confirmation of this assumption. If the rise in abundance is correlated with an increase in first instar nymphs, then it can be reasonably concluded that the population increase is due to the commencement of a new generation.

In 2016, the peaks in abundance of first instar nymphs coincided with the second and third peaks in the abundance of all instars combined (Figure 7). Since instar data was not collected at the time of the first peak of all instars combined, no conclusion may be drawn as to whether they are correlated. In 2017, peaks in first instar abundance coincide

with the first and third peaks of all instars combined (Figure 9). The second peak of first instars occurred three weeks later than the second peak of all instars combined, but the difference between first instar nymph abundance on these two dates is not large (13 vs. 16 first instar nymphs on July 25 and August 15, respectively). Instar data for the fourth peak of all instars combined was not collected, so no conclusion as to correlation between the two may be drawn. In 2018, the first instar peaks coincided with the first and third peaks of all instars combined, but not with the second peak of all instars (Figure 11). In fact, abundance of first instars was higher a week before and two weeks following the peak in abundance of all instars combined.

The difference in number of generations between New York and Oklahoma was expected, as insect populations at higher latitudes generally have fewer generations per year (Buckley et al. 2017). I found some differences between Oklahoma and New York when using growing degree day calculations to compare peaks in *E. comes* nymph populations. While GDD accumulations were similar between Oklahoma and New York for the first peak of nymphs (632 versus 648 GDD, respectively; Figure 24), accumulated GDD for the second peak were much higher in Oklahoma (1,190 versus 1,594 GDD). This dissimilarity may be due to differing lower developmental thresholds between leafhopper populations, a possibility mentioned by Wells and Cone (1989) in their work with *Erythroneura elegantula*.

A difference in lower developmental thresholds between populations has been reported in China for the tephritid fly *Bactrocera minax* (Ma et al. 2019). Moreover, Honěk and Kocourek (1990) demonstrated across several insect orders, including Hemiptera, that a decrease in the lower developmental threshold corresponds to an

increase in the number of GDD required for development. This possibility as it relates to leafhopper populations in the United States will be discussed in more detail later.

Recommendations for Monitoring Eastern Grape Leafhopper

Given the phenological differences between populations of *E. comes* in Oklahoma and New York, new guidelines are needed for monitoring populations of this leafhopper pest in Oklahoma vineyards. This is particularly true with regard to the second generation of this insect pest. I recommend that Oklahoma grape growers adhere to the following guidelines for monitoring *E. comes* in their vineyards. Once 500 GDD have accumulated above a lower developmental threshold of 10°C (50°F) (likely to occur in early or mid-May), start scouting for first-generation nymphs. Scouting involves selecting two leaves from each of 25 vines, one leaf from either side of the vine, ensuring that the selected vines are reasonably distributed throughout the vineyard. Though there is no precise spatial pattern for sampling recommended in the literature, walking along an "M" or "X"shaped pattern will suffice for representing both the exterior and interior rows of the vineyard. This is a customary sampling approach with regard to other leafhopper pests (e.g. Shields and Specker 1990). Repeat this procedure one week later. Treat the vineyard with a registered insecticide if an economic threshold of five nymphs per leaf is exceeded. Resume monitoring for second-generation nymphs when 1,400 GDD have accumulated (likely to occur in early or mid-July), again repeating scouting one week later and using the same economic threshold for making treatment decisions. Resume scouting for third-generation nymphs when 2,200 GDD have accumulated (likely to occur in mid- to late August), following the same protocol but using a modified economic threshold of ten nymphs per leaf to make treatment decisions. The use of a higher

treatment threshold during the later part of the season follows current scouting recommendations for this pest in Oklahoma vineyards (Stafne 2010). When scouting, I advise grape growers to pay special attention to the cultivars Chardonel, Noiret, and Traminette, as these at times harbored mean populations of eastern grape leafhopper nymphs that exceeded an early-season economic threshold of five nymphs per leaf; Noiret also exceeded a late-season threshold of ten nymphs per leaf.

Developmental Thresholds

If it is assumed that degree day requirements for an insect species do not vary across its range (UC IPM 2016), then higher degree day accumulation for its development in one area compared to another may suggest that an upper developmental threshold temperature exists in warmer climates. For example, the potato leafhopper, *Empoasca fabae*, has an upper developmental threshold of 30°C (86°F), and this threshold is incorporated into the GDD model when daily temperatures exceed this temperature (Kouskolekas and Decker 1966). In the case of *Erythroneura comes*, however, an upper developmental threshold has not been reported. If temperatures in Oklahoma exceed an upper threshold for eastern grape leafhopper, then GDD may be overestimated on days warmer than this temperature. When an upper developmental threshold exists for an insect species (as may be the case in southern climates), it is important to incorporate it into the GDD model for more accurate calculation (Herms 2013).

Differences in GDD requirements for development time from egg to adult have been reported for *Erythroneura elegantula*, particularly between populations in California

and Washington (Cate 1975; Jensen and Flaherty 1982; Wells and Cone 1989). Growing degree day accumulations were more than double in California compared to Washington. Wells and Cone (1989) suggested that these regional differences may result from local adaptation at the population level to variable lengths of growing seasons. Further, these authors suggested that such adaptations may be mediated by a change in the lower developmental threshold of the population, which is to say that these thresholds may differ from region to region.

Honěk (1996) demonstrated variation of lower developmental thresholds for insect populations, concluding that the lower developmental threshold of a species generally varies inversely with latitude. On the other hand, it may be that western grape leafhopper has the same lower threshold temperature in California and Washington, but an unreported upper developmental threshold may be surpassed by California's warmer temperatures, resulting in overestimated growing degree day accumulation in this state. This phenomenon may explain the differences I observed for *E. comes* between Oklahoma and New York. In any case, it would be advantageous to conduct experiments to verify the lower developmental threshold and developmental time from egg to adult (measured in GDD), and to determine whether there is an upper developmental threshold for Oklahoma populations of *E. comes*. This might be achieved by rearing them on their host plant in environmentally-controlled growth chambers across a range of temperatures, as has been done with many hemipteran pest species (Kouskolekas and Decker 1966, Varikou et al. 2010, Ju et al. 2015). Exploring these temperature thresholds under laboratory conditions would certainly help to clarify population trends observed in the field.

Leaf Microclimate

Another factor potentially impacts the accuracy of predicting the development of leaf-feeding insects. This is the difference that may exist between ambient air temperature (which is usually what is measured in GDD models) and the actual leaf surface temperature. Such differences have been demonstrated with reference to grapevines. Namely, the leaf surface temperature may be higher than the ambient temperature during the day, while the opposite may be true during night; there are also seasonal differences, including the minimum daily leaf surface temperature being cooler than the minimum daily air temperature from late spring through early autumn (Peña Quiñones et al. 2019). The leaf surface temperature may have an effect on rates of physiological processes of leaf-dwelling insects (Pincebourd and Woods 2012). In some cases, insect feeding has been shown to change the leaf surface temperature via its effect of lowering transpiration rates, as in the case of the green apple aphid, Aphis pomi (De Geer); this is thought to result from the closure of stomata in response to feeding (Cahon et al. 2018). Closure of the stomata as well as any loss of functionality incurred from damage to these organs by insect feeding might be expected to make the leaf microclimate drier and warmer (Pincebourd and Woods 2012).

As grapevines have the majority of their stomata located on the abaxial (i.e. lower) surface of the leaves (Keller 2014), and this is the surface where *E. comes* and *E. ziczac* nymphs generally feed (Dozier 1929, Zimmerman et al. 1996), it may be useful in the future to investigate the effects of these species' feeding on grape leaf stomata opening or closing. In this way, the effects of leafhopper feeding on microclimatic variables such as leaf temperature and humidity – which are influenced by transpiration –

might be predicted from nymph population density. This in turn would provide data that might supplement the findings of this study for the more efficient prediction of the phenology of these organisms in vineyards. For example, if the nymph population density can be used to predict the impact of feeding on these leaf microclimatic variables, the rate of development might be more precisely tracked over the course of the season. This, admittedly, would involve an understanding of complex interactions between abiotic and biotic factors – and perhaps is more complicated by the fact that leaf surface temperatures may be considerably heterogeneous (Saudreau et al. 2017) and arthropods may engage in thermoregulatory behavior by moving to cooler areas of the leaf (Caillon et al. 2014).

Interannual Variability in Leafhopper Abundance

Year-to-year variability in seasonal abundance of eastern grape leafhopper was evident, specifically with lower numbers of adults and nymphs in 2017 compared to 2016 and 2018. Interannual variability in abundance of *E. comes* is not a novel observation. Johnson (1914) observed in 1903 "an apparent sudden disappearance" of eastern grape leafhopper from certain vineyards in Westfield, New York, which had been severely infested the two previous seasons. A possible explanation for low numbers of eastern grape leafhopper at the Perkins vineyard in 2017 may be that heavy rainfall (4.14" on April 29) killed a proportion of the overwintering generation before they had the chance to lay their eggs. Quayle (1908) observed high mortality of overwintering *E. elegantula* adults under continuously rainy conditions. Another explanation might be that entomopathogenic fungi in the genus *Entomophthora* could have caused high mortality of the leafhoppers, which has been reported during growing seasons with high precipitation (Jubb 1976). However, I did not observe any indications of fungal development on leafhoppers.

The high abundance of both *E. comes* nymphs and adults in 2018 (1,219 and 64,229, respectively) was surprising, in contrast to the observation of Johnson (1914) that eastern grape leafhopper populations usually build up slowly over several years to reach high levels. One reason for the high numbers of this insect in 2018 might be that the weather during the first half of the year (January through June) was dry. Dry conditions have been reported to favor *E. comes* population development, leading to large numbers of the pest (Eyer 1931). Relative to the 15-year average of total rainfall over this sixmonth period obtained for the Perkins Mesonet weather station (mesonet.org), total rainfall over this period in 2018 was 2.14" less. The second generational peak of 2017 occurred the latest out of the three years (i.e., in late July). This observation aligns with the findings of Hartzell (1912) and Eyer (1931) that years with low eastern grape leafhopper populations, known as "years of repression," may show a delay in the phenological events of this insect. The same cannot be said, however, with reference to the third generational peak of 2017, which occurred nearly two weeks earlier than that of 2018. These results highlight the fact that calendar dates by themselves are an insufficient means of prediction for insect phenology.

Season-high densities of eastern grape leafhopper nymphs across all eight cultivars occurred later in the season in 2017 (most of them in September) compared to the other years, during which the season-high densities usually occurred from May through August (Table 1). The cultivar Noiret was unique in its relative consistency of the timing of season-high densities of *E. comes* nymphs, which occurred in early to mid-September of all three years.

Differential Abundance across Cultivars

Factors influencing high abundance of eastern grape leafhopper nymphs on the cultivars Noiret and Traminette are unknown. Daane et al. (2013) reported that lateseason grape cultivars may develop high densities of leafhoppers, as these cultivars are generally vigorous and "produce a continuation of newly matured leaves that are favored by leafhoppers for depositing eggs." Noiret is a mid-season, moderately vigorous, interspecific hybrid red wine grape cultivar, while Traminette is a late mid-season, moderately vigorous, interspecific hybrid white wine grape cultivar (Reisch et al. 1996, Reisch et al. 2006).

Interspecific hybrids have a mix of American and European heritage. Neither heritage nor time of ripening seem to account for the high densities of leafhopper nymphs present on Noiret and Traminette. Chambourcin and Chardonel, for example, are lateseason interspecific hybrids, Frontenac-Gris is a mid-season interspecific hybrid, and Cynthiana and Niagara are largely American, originating from *V. aestivalis* and *V. labrusca*, respectively (Motioike et al. 2002, Parker et al. 2007) and having some European heritage (Smiley and Cochran 2016). Cynthiana and Niagara had the lowest mean number of nymphs per leaf in 2016 and 2018. This finding, especially with respect to Niagara, was not expected, as Williams and Martinson (2000) have reported that *E. comes* prefers cultivars with *Vitis labrusca* heritage.

The low abundance of nymphs on Cynthiana raises the question of whether this cultivar may express an antibiotic or antixenotic mode of resistance to eastern grape leafhopper. It may be that since *Vitis aestivalis* and *V. labrusca* have historically shared a large part of their geographic range with *E. comes* (primarily in the eastern U.S.; USDA NRCSa, b), these native grape species may have evolved biochemical or physical resistance mechanisms as they have been under selection pressure from this insect's feeding. It is difficult to draw conclusions as to the role heritage may play in the differential abundance of *E. comes* on the cultivars involved in this study.

Choice and no-choice tests under controlled conditions, along with studies of host suitability, might help elucidate the factors affecting the abundance of eastern grape leafhopper across these cultivars. Such studies may eventually be helpful in providing grape growers with recommendations for which cultivars they may select for resistance to this pest when establishing new vineyards or expanding existing ones. Furthermore, they may provide insight as to whether some cultivars (e.g. Chardonel, Noiret, or Traminette) could be used as trap cultivars for eastern grape leafhopper. Experiments have demonstrated the successful use of trap cultivars for management of potato leafhopper in bean crops (Bullas-Appleton et al. 2004a) and of scarab beetles in soybean (Talekar and Nurdin 1991). Phenological events (e.g. flowering) of successful trap cultivars may occur earlier than those of the cash cultivar (Ruck et al. 2017). This allows the pest population to build up on the trap cultivar early in the season so that a treatment can be applied for control of the pest before the cash cultivar can be attacked. Therefore, it would be important in the investigation of potential grape trap cultivars for *E. comes* to consider

cultivar phenology, as this may prove a determining factor of its efficacy as a management strategy.

Conclusions

Oklahoma grape growers will benefit from improved prediction of eastern grape leafhopper populations as it relates to more effective monitoring and timing of insecticide applications when warranted. To this end, I have improved on the ability to track leafhopper phenology using a single sine wave model for calculating GDD. However, more data will need to be collected across the grape-growing areas of Oklahoma to develop a more robust phenological model. Several factors limit the strength of the conclusions I present here. First, I was only able to use weather and nymph abundance data from one vineyard site, which means my data do not capture any regional variation that may exist between eastern grape leafhopper populations in Oklahoma. The second limitation is the short duration of my study, encompassing only three growing seasons. Finally, population peaks were not easily discernible in some cases. This may have been due to environmental variables affecting leafhopper populations, such as precipitation events or the presence of biological control agents including fungi, parasitoids, and/or predators.

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TABLES AND FIGURES

Figure 1. *Erythroneura comes* fifth instar nymph (left; on leaf surface) and adult (right; point-mounted specimen). Not to scale.



Figure 2. *Erasmoneura vulnerata* fifth instar nymph with mite attached to dorsal abdomen (left; on leaf surface) and adult (right; point-mounted specimen). Not to scale.



Figure 3. *Erythroneura ziczac* fourth instar nymph (left; on leaf surface) and adult (right; point-mounted specimen). Not to scale.





Figure 4. Placement of 17 sticky card traps (yellow rectangles) along vine rows (numbered on left) at the Perkins, Oklahoma vineyard starting June 9, 2016. Rows are labeled by cultivar and rootstock (Own = on its own rootstock).



Figure 5. Placement of 16 sticky card traps (yellow rectangles) along vine rows (numbered on left) at the Perkins, Oklahoma vineyard in 2017 and 2018. Rows are labeled by cultivar and rootstock (Own = on its own rootstock).

Figure 6. *Erythroneura amanda* last instar nymph (left; on leaf surface) and adult (right: pin-mounted specimen). Not to scale. Note the faint red lines running longitudinally along the wing pads of the nymph; this feature distinguishes the nymphs of this species from those of *E. comes*. The bold red forewing markings of the adult are also characteristic of this species.





Figure 7. Mean *Erythroneura comes* nymphs per leaf (n = 100 leaves) plotted with the proportions of the five instars over calendar proportions for June 3 through July 1 were not recorded. Total number of nymphs for each sampling date is shown above each date and cumulative growing degree days (GDD) calculated since January 1 in 2016 at the Perkins, Oklahoma vineyard. Instar stacked bar. Error bars represent standard error of the mean.

Таха	Abundance
Cercopoidea	32
Cicadellidae	39083
Fulgoroidea	28
Membracidae	17

Figure 8. Total abundance of the adult stage of 4 taxa belonging to the suborder Auchenorrhyncha captured on sticky card traps and in vacuum samples at the Perkins, Oklahoma vineyard in 2016.



Figure 9. Mean *Erythroneura comes* nymphs per cultivar (n = 96 leaves; 12 leaves per cultivar) plotted with the proportions of the Oklahoma vineyard. Instar proportions for September 30 and October 9 were not recorded. Total number of nymphs for each five instars over calendar date and cumulative growing degree days (GDD) calculated since January 1 in 2017 at the Perkins, sampling date is shown above each stacked bar. Error bars represent standard error of the mean.

Таха	Abundance
Cercopoidea	5
Cicadellidae	13796
Fulgoroidea	26
Membracidae	1

Figure 10. Total abundance of the adult stage of 4 taxa belonging to the suborder Auchenorrhyncha captured on sticky card traps and in vacuum samples at the Perkins, Oklahoma vineyard in 2017.





Таха	Abundance	
Cercopoidea	3	
Cicadellidae	190102	
Fulgoroidea	9	
Membracidae	12	

Figure 12. Total abundance of the adult stage of 4 taxa belonging to the suborder Auchenorrhyncha captured on sticky card traps and in vacuum samples at the Perkins, Oklahoma vineyard in 2018.







Perkins 2018: mean nymphs/leaf by cultivar

Figure 14. Mean nymphs per leaf on each of 8 cultivars at the Perkins vineyard in 2018; three statistical groups (A, B, and C). Error bars represent standard error of the mean.





Perkins: Total erythroneurine nymphs for each of three years



Figure 16. Total abundance of erythroneurine nymphs in 2016, 2017, and 2018 (left to right) at the Perkins, Oklahoma vineyard; lightest gray: Erythroneura comes, light gray: Erasmoneura vulnerata, medium gray: Erythroneura ziczac, dark gray: other erythroneurine species.











Oklahoma vineyard. Total number of nymphs for each sampling date is shown above each stacked bar. Error bars represent standard Figure 19. Mean *Erythroneura ziczac* nymphs per cultivar (n = 96 leaves; 12 leaves per cultivar) plotted with the proportions of the five instars over calendar date and cumulative growing degree days (GDD) calculated since January 1 in 2018 at the Perkins, error of the mean.







Figure 21. Mean *Erasmoneura vulnerata* nymphs per cultivar (n = 96 leaves; 12 leaves per cultivar) plotted with the proportions of the Oklahoma vineyard. Total number of nymphs for each sampling date is shown above each stacked bar. Error bars represent standard five instars over calendar date and cumulative growing degree days (GDD) calculated since January 1 in 2017 at the Perkins, error of the mean.



Figure 23. Empoasca fabae adult (point-mounted specimen).







Cultivar	Season-high	2016	2017	2018
Chambauris	Density (nymphs/leaf)	1.3	0.25	1.5
	Date	22-Jul	9-Oct	31-May
	Density (nymphs/leaf)	1.2	1.92	1.83
	Date	19-Aug	25-Jul	8-Jun
Cunthiana	Density (nymphs/leaf)	0.6	0.5	0.33
	Date	15-Jul	15-Sep	25-May
Erontonac Gric	Density (nymphs/leaf)	1.4	0.75	2
	Date	12-Aug	15,30-Sep	25-May
Nicercia	Density (nymphs/leaf)	1	0.67	0.67
INIdgala	Date	9-Jun	30-Sep	25,31-May, 15-Jun, 6-Sep
Noicot	Density (nymphs/leaf)	2.5	3.25	7.75
	Date	9-Sep	21-Sep	13-Sep
Purbainat	Density (nymphs/leaf)	2	0.58	2
nubaiyat	Date	9-Jun	1-Sep	17-May
Traminotto	Density (nymphs/leaf)	5.2	2.83	3
	Date	26-Aug	1-Sep	17-May

Table 1. Density (nymphs/leaf) and date of season-high counts of eastern grape leafhopper on 8 cultivars for 2016, 2017, and 2018.

Cultivar	Observation of nymphs	2016	2017	2018
Chambaurcin	First	31-May	22-May	17-May
	Last	16-Sep	9-Oct	4-Oct
	First	3-Jun	8-May	17-May
	Last	20-Sep	13-Oct	20-Sep
	First	6-Jun	15-May	17-May
	Last	30-Sep	30-Sep	20-Sep
Erontonac Gric	First	3-Jun	15-May	17-May
	Last	6-Oct	30-Sep	4-Oct
	First	3-Jun	15-May	25-May
INIdgal d	Last	6-Oct	9-Oct	4-Oct
Noirot	First	31-May	3-Jul	25-May
NOILEL	Last	6-Oct	13-Oct	4-Oct
+cvicd.10	First	31-May	30-May	17-May
nubaiyat	Last	30-Sep	13-Oct	4-Oct
Traninatto	First	31-May	6-Jun	17-May
	Last	6-Oct	13-Oct	11-Oct

 Table 2. Dates of the first and last observation of eastern grape leafhopper nymphs on each of 8 cultivars for 2016, 2017, and 2018.

CHAPTER IV

SUMMARY

Eastern grape leafhopper populations on all eight cultivars combined at the Perkins, Oklahoma vineyard did not exceed either the early-season economic threshold (i.e. before 2200 GDD have accumulated since January 1) of five nymphs per leaf or the late-season threshold (i.e. after 2200 GDD since January 1) of ten nymphs per leaf. However, when considering all erythroneurine species present on the leaves, the earlyseason economic threshold was exceeded once on the cultivar Chardonel in late July, 2018; once on Traminette in mid-July, 2018; and four times on Noiret in mid-late July through August, 2018. The late-season economic threshold was exceeded three times on Noiret in late August through mid-September, 2018.

Eastern grape leafhopper undergoes three generations – and possibly a partial fourth generation – per year in Oklahoma. This differs from populations of this insect in the northeastern U.S., where one generation and sometimes a partial second generation per year are observed. Moreover, the accumulated GDD at the second generation peak abundance of nymphs differs between Oklahoma and New York, with Oklahoma having much higher GDD totals. These differences demonstrate that the GDD recommendations for monitoring practices and treatment decisions for this pest in New York vineyards may not apply to Oklahoma. Rather, we advise grape growers in Oklahoma to use the growing

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degree day-based monitoring and treatment recommendations set forth in the present study.

Among all eight cultivars at the Perkins vineyard, Noiret and Traminette had the highest densities of leafhopper nymphs during 2016, 2017, and 2018. Cynthiana had the lowest nymph densities, followed by Niagara, in 2016 and 2018. There was not a significant effect of time (by month) on nymph abundance among any of the cultivars. Possible mechanisms of host plant resistance to *E. comes*, especially with regard to Cynthiana, have yet to be explored.

The presence of the leafhoppers, *Empoasca fabae* and *Erythroneura ziczac*, at times in high densities, is noted. As these species have the potential to be serious pests, it is here suggested that future investigations should be geared toward characterizing their phenology and population dynamics in detail for the state of Oklahoma.

APPENDICES

Appendix A. Numbers of adult individuals of the erythroneurine genus *Erythroneura* caught on sticky card traps and in vacuum samples at a vineyard in Perkins, Oklahoma over the sampling season of 2016.

Genus							Er)	ythroneura							
species	comes	cymbium	delicata	diva	elegans	festiva	infuscata	kanwakae	octonotata	ontari	reflecta	rubra	tricincta	vitis	ziczac
13-May	199	2	0	1	0	0	0	0	0	0	0	0	0	1	50
20-May	48	1	0	1	0	0	0	0	0	0	0	0	0	0	11
27-May	17	2	0	0	0	0	0	0	2	0	0	0	0	0	12
3-Jun	72	4	0	0	0	0	0	0	0	0	0	0	0	0	10
9-Jun	110	0	0	0	0	0	0	0	0	0	0	0	0	0	22
17-Jun	170	11	0	7	0	0	0	0	0	0	0	0	0	0	20
24-Jun	231	27	1	1	0	0	0	0	9	1	0	1	1	1	20
1-Jul	354	69	7	-	£	0	0	0	9	0	0	0	0	2	36
8-Jul	443	84	10	0	1	0	0	0	20	0	0	2	0	1	33
15-Jul	479	99	6	7	0	0	0	0	29	0	0	Ч	0	ŋ	39
22-Jul	448	124	18	4	£	0	0	0	34	ŝ	0	ε	0	6	58
29-Jul	602	113	19	£	1	0	0	1	20	4	1	4	0	7	74
5-Aug	1059	246	34	4	0	0	0	0	26	œ	1	9	0	17	187
12-Aug	1298	245	31	m	0	0	1	0	10	œ	ß	2	0	13	205
19-Aug	1573	276	21	4	0	1	0	0	19	1	2	£	0	14	230
26-Aug	1678	269	18	1	0	0	0	0	18	ŝ	2	ε	0	œ	403
2-Sep	1852	298	11	S	0	7	0	0	21	Υ	2	£	0	7	548
9-Sep	2040	305	32	4	0	ß	0	0	28	0	2	1	0	9	379
16-Sep	4890	223	10	1	0	5	0	ſ	20	0	1	1	0	9	942
23-Sep	2653	66	7	2	0	4	0	0	10	0	0	0	0	4	400
30-Sep	2965	86	9	0	0	9	0	0	6	0	2	0	0	4	430
6-Oct	405	8	0	0	0	0	0	0	1	0	0	0	0	0	82
14-Oct	115	2	0	0	0	0	0	0	0	0	0	0	0	0	19
21-Oct	575	5	0	0	0	0	0	0	0	0	0	0	0	0	33
Total	24336	2588	234	37	8	26	1	4	279	26	16	30	1	105	4243
Genus	Erasmor	neura		Erato	neura		Hymetta	Illinigina							
---------	---------------	-----------	-----------	---------	-------	---------	---------	--------------							
species	atra or nigra	vulnerata	basilaris	carmini	era	unknown	unknown	illinoiensis							
13-May	0	13	0	0	0	0	1	0							
20-May	0	8	0	0	0	0	1	0							
27-May	0	8	0	0	0	0	0	0							
3-Jun	0	10	0	0	0	0	1	0							
9-Jun	0	16	0	0	0	0	2	0							
17-Jun	0	18	0	0	0	0	1	0							
24-Jun	0	52	0	0	0	0	2	9							
1-Jul	0	06	0	0	0	0	6	S							
8-Jul	1	59	1	0	0	0	5	2							
15-Jul	0	103	1	0	1	0	7	'n							
22-Jul	0	124	0	0	1	0	6	Ū							
29-Jul	1	246	0	0	0	0	7	6							
5-Aug	0	465	0	0	0	0	17	30							
12-Aug	0	454	0	0	0	0	19	30							
19-Aug	0	503	0	0	0	2	24	43							
26-Aug	0	368	0	1	0	0	36	19							
2-Sep	0	469	0	0	0	0	27	37							
9-Sep	0	390	0	2	0	0	27	36							
16-Sep	0	538	0	0	0	0	30	23							
23-Sep	0	302	0	2	0	0	24	12							
30-Sep	0	271	0	1	0	0	43	14							
6-Oct	0	22	0	1	0	0	3	M							
14-Oct	0	12	0	m	0	0	5	1							
21-Oct	0	52	0	0	0	0	7	0							
Total	2	4593	2	15	2	2	304	278							

Appendix B. Numbers of adult individuals of various erythroneurine genera caught on sticky card traps and in vacuum samples at a vineyard in Perkins, Oklahoma over the sampling season of 2016.

Subfamily	Aphrodinae		Cica	Idellinae			lassi	nae	Megophthalminae	Typhlocybinae
Genus	Xestocephalus	Cuerna	Draeculocephala	Graphoce	sphala	Paraulacizes	Gyponana	Stragania	Agallia	Empoasca
species	unknown	costalis	unknown	coccinea	versuta	irrorata	unknown	unknown	unknown	fabae
13-May	T	0	0	0	1	0	0	0	0	4
20-May	0	0	0	0	0	0	0	0	1	16
27-May	0	0	0	0	£	0	3	0	0	177
3-Jun	7	0	0	0	Υ	0	1	0	ĉ	203
9-Jun	2	0	0	0	8	0	2	0	10	84
17-Jun	1	0	0	0	25	1	0	0	61	9
24-Jun	0	0	0	1	31	0	2	0	18	4
1-Jul	0	0	0	2	32	1	0	0	21	2
8-Jul	0	1	0	2	22	0	1	0	12	4
15-Jul	1	0	1	2	50	0	0	0	12	3
22-Jul	0	0	0	0	50	0	1	0	5	2
29-Jul	0	0	0	2	79	1	1	0	5	8
5-Aug	0	0	0	0	38	0	1	0	6	2
12-Aug	0	0	1	0	12	0	2	0	4	1
19-Aug	0	0	0	0	26	0	0	0	14	4
26-Aug	0	0	0	0	7	0	2	0	1	ĉ
2-Sep	0	0	0	0	0	0	7	0	13	4
9-Sep	1	0	0	0	1	0	6	0	8	ĉ
16-Sep	0	0	0	0	0	0	S	0	4	15
23-Sep	0	0	0	0	0	0	12	2	2	7
30-Sep	0	0	0	0	1	1	0	30	0	46
6-Oct	0	0	0	0	0	1	æ	8	0	9
14-Oct	0	0	0	0	0	0	0	9	0	C
21-Oct	0	0	0	0	0	0	0	181	1	6
Total	13	1	2	6	389	5	52	227	201	613

Appendix C. Numbers of adult individuals of various cicadellid subfamilies caught on sticky card traps and in vacuum samples at a vineyard in Perkins, Oklahoma over the sampling season of 2016.

Subfamily			Ď	eltocephalinae			
Genus	Deltocephalus	Graminella	Macrosteles	Norvellina	Scaphoideus	Scaphytopius	Stirellus
species	unknown	nigrifrons	unknown	chenopodii	titanus	unknown	bicolor
13-May	0	0	5	0	0	0	0
20-May	0	0	1	0	0	Ο	0
27-May	0	0	1	F	0	0	0
3-Jun	0	0	1	0	0	0	0
9-Jun	0	0	1	0	0	0	1
17-Jun	-	2	0	0	0	0	1
24-Jun	0	0	0	H	1	0	0
1-Jul	0	0	0	0	0	0	0
8-Jul	0	0	0	0	0	2	0
15-Jul	0	0	0	-	0	1	0
22-Jul	0	0	0	-	0	1	0
29-Jul	0	0	0	ñ	0	9	0
5-Aug	0	m	0	7	0	7	0
12-Aug	1	4	0	-	0	2	0
19-Aug	0	2	0	2	0	ſ	0
26-Aug	œ	F	0	0	0	1	0
2-Sep	0	1	0	Т	1	1	0
9-Sep	0	15	0	0	T	2	0
16-Sep	0	0	ĉ	0	0	1	0
23-Sep	0	T	1	0	0	2	0
30-Sep	0	0	26	0	0	4	0
6-Oct	0	0	1	0	0	C	0
14-Oct	0	0	2	0	0	0	0
21-Oct	0	0	6	0	0	6	0
Total	5	29	51	18	3	45	2

Appendix D. Numbers of adult individuals of the cicadellid subfamily Deltocephalinae caught on sticky card traps and in vacuum samples at a vineyard in Perkins, Oklahoma over the sampling season of 2016.

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neihilariuae	Liburniella		0	0	0		0																			
	unknown	0	0	0	0	C	>	> 0	00			> 0 0 0 0 0	> 0 0 0 0 0 0	> 0 0 0 0 0 0 m	> 0 0 0 0 0 m H	> 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	> 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	> 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	> 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	, 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	, , , , , , , , , , , , , , , , , , ,	, , , , , , , , , , , , , , , , , , ,	> 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	> >	0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
Clastontera	シーションションション		5	5	J	J																F				
	Genus	13-May	20-May	27-May	3-Jun	9-Jun	17-lun	11NC_ /T	24-Jun	24-Jun 1-Jul	24-Jun 1-Jul 8-Jul	24-Jun 24-Jun 8-Jul 15-Jul	24-Jun 24-Jun 8-Jul 8-Jul 15-Jul 22-Jul	24-Jun 24-Jun 1-Jul 8-Jul 15-Jul 22-Jul 29-Jul	24-Jun 24-Jun 1-Jul 8-Jul 15-Jul 22-Jul 29-Jul 5-Aug	24-Jun 24-Jun 8-Jul 15-Jul 22-Jul 29-Jul 5-Aug 5-Aug	24-Jun 24-Jun 1-Jul 8-Jul 15-Jul 22-Jul 29-Jul 5-Aug 5-Aug 12-Aug	24-Jun 24-Jun 1-Jul 8-Jul 25-Jul 29-Jul 5-Aug 12-Aug 12-Aug 26-Aug	24-Jun 24-Jun 1-Jul 8-Jul 15-Jul 22-Jul 29-Jul 5-Aug 12-Aug 19-Aug 26-Aug 26-Aug	24-Jun 24-Jun 1-Jul 8-Jul 15-Jul 22-Jul 29-Jul 5-Aug 12-Aug 12-Aug 26-Aug 2-Sep 9-Sep	24-Jun 24-Jun 8-Jul 8-Jul 15-Jul 5-Aug 12-Aug 12-Aug 19-Aug 26-Aug 2-Sep 9-Sep 9-Sep	24-Jun 24-Jun 1-Jul 8-Jul 25-Jul 22-Jul 29-Jul 5-Aug 12-Aug 12-Aug 26-Aug 2-Sep 9-Sep 9-Sep 23-Sep	24-Jun 24-Jun 1-Jul 8-Jul 15-Jul 22-Jul 29-Jul 29-Jul 19-Aug 19-Aug 26-Aug 2-Sep 9-Sep 9-Sep 30-Sep 30-Sep	24-Jun 24-Jun 8-Jul 8-Jul 15-Jul 22-Jul 5-Aug 19-Aug 19-Aug 26-Aug 26-Aug 26-Aug 23-Sep 30-Sep 6-Oct 6-Oct	24-Jun 24-Jun 1-Jul 8-Jul 15-Jul 22-Jul 29-Jul 29-Jul 12-Aug 12-Aug 12-Aug 26-Aug 26-Aug 23-Sep 30-Sep 6-Oct 14-Oct	24-Jun 24-Jun 1-Jul 8-Jul 15-Jul 22-Jul 29-Jul 19-Aug 19-Aug 26-Aug 26-Aug 23-Sep 9-Sep 9-Sep 9-Sep 16-Oct 6-Oct 14-Oct 21-Oct

Appendix E. Numbers of adult individuals of the superfamilies Cercopoidea, Fulgoroidea, and Membracoidea caught on sticky card traps and in vacuum samples at a vineyard in Perkins, Oklahoma over the sampling season of 2016.

Genus						Ъ	ythroneu	ra					
species	bistrata	comes	corni	cymbium	delicata	diva	elegans	fraxa	octonotata	ontari	reflecta	rubra	vitis
27-Apr	0	37	0	4	0	0	0	0	0	0	0	0	0
4-May	0	11	0	0	0	0	0	0	0	0	0	0	0
11-May	0	14	0	0	0	0	0	0	0	0	0	0	1
18-May	0	4	0	0	0	0	0	0	0	0	0	0	0
25-May	0	1	0	0	0	0	0	0	0	0	0	0	0
2-Jun	0	4	0	2	0	0	0	0	0	0	0	0	0
9-Jun	0	17	0	1	0	1	0	0	1	0	0	0	0
16-Jun	0	17	1	4	0	0	0	0	0	0	0	7	0
23-Jun	0	25	0	C	0	0	0	0	0	0	0	0	1
30-Jun	0	24	0	S	0	0	0	0	0	0	0	e	ß
7-Jul	0	26	0	7	æ	0	0	0	0	0	0	ĥ	1
14-Jul	0	17	0	0	3	0	0	0	0	0	0	0	0
21-Jul	0	28	0	13	0	0	1	0	2	0	1	2	9
28-Jul	0	107	0	21	7	1	0	0	5	0	0	2	ß
4-Aug	1	323	2	62	13	1	0	0	6	2	0	9	22
11-Aug	0	644	0	81	7	2	0	0	18	1	0	17	23
18-Aug	0	93	0	22	2	0	1	1	0	1	0	7	9
28-Aug	0	633	0	78	9	0	0	0	15	1	0	7	11
1-Sep	0	359	0	72	ß	0	0	0	9	1	0	6	m
11-Sep	0	1439	0	118	9	1	0	0	13	0	0	10	21
15-Sep	0	669	0	40	2	0	0	0	ſ	0	0	5	4
25-Sep	0	919	0	105	16	1	0	0	7	0	0	10	31
2-Oct	0	1173	0	29	2	1	0	0	3	0	0	0	З
Total	1	6614	ŝ	665	72	8	2	1	82	9	1	76	139

Appendix F. Numbers of adult individuals of the erythroneurine genus *Erythroneura* caught on sticky card traps and in vacuum samples at a vineyard in Perkins, Oklahoma over the sampling season of 2017.

Genus	Erasmor	neura		Eraton	eura		Erythridula	Hymetta	Illinigina
species	atra or nigra	vulnerata	basilaris	carmini	era	unknown	unknown	unknown	illinoiensis
27-Apr	0	11	0	0	0	0	0	0	0
4-May	Ο	6	0	0	0	0	0	0	0
11-May	0	7	0	0	0	0	0	0	0
18-May	0	2	0	0	0	0	2	0	0
25-May	0	2	0	0	0	0	0	0	0
2-Jun	0	1	0	0	0	0	0	0	1
9-Jun	0	9	0	0	0	0	0	0	0
16-Jun	0	7	0	0	0	0	0	0	2
23-Jun	0	19	0	0	0	0	0	0	0
30-Jun	0	19	0	0	0	0	0	0	1
7-Jul	0	17	0	0	0	0	0	0	1
14-Jul	0	18	0	0	0	0	0	0	2
21-Jul	Ο	45	0	0	0	0	0	0	ß
28-Jul	1	81	0	0	0	0	0	1	0
4-Aug	0	278	0	0	1	0	1	2	11
11-Aug	0	389	1	0	0	0	2	1	12
18-Aug	Ο	19	1	7	0	0	0	1	1
28-Aug	0	270	0	0	0	0	0	1	12
1-Sep	0	128	Г	0	0	0	0	0	0
11-Sep	Ο	708	0	0	1	1	2	1	10
15-Sep	0	172	0	0	0	2	0	0	10
25-Sep	0	814	0	0	0	IJ	4	2	20
2-Oct	0	394	1	0	2	4	2	0	2
Total	1	3416	4	2	4	12	13	9	88

Appendix G. Numbers of adult individuals of various erythroneurine genera caught on sticky card traps and in vacuum samples at a vineyard in Perkins, Oklahoma over the sampling season of 2017.

Subfamily	Aphrodinae		Cicadellinae		lass	inae	Megophthalminae	Typhloc	ybinae
Genus	Xestocephalus	Graphocephala	Oncometopia	Paraulacizes	Gyponana	Stragania	Agallia	Alebra	Empoasca
species	unknown	versuta	orbona	irrorata	unknown	unknown	unknown	unknown	fabae
27-Apr	0	0	0	0	0	1	0	0	5
4-May	0	0	0	0	0	0	1	0	59
11-May	0	0	7	0	0	0	1	0	22
18-May	0	0	0	0	0	0	0	0	27
25-May	0	0	0	0	0	0	0	0	222
2-Jun	1	0	7	0	1	0	0	0	271
9-Jun	0	2	T	0	0	0	2	0	78
16-Jun	0	16	0	0	0	0	2	2	10
23-Jun	0	13	2	0	7	0	22	0	5
30-Jun	0	15	0	1	0	0	10	0	8
Jul-7	0	44	15	F	0	0	29	0	25
14-Jul	0	S	7	0	0	0	4	0	2
21-Jul	0	C	3	1	0	0	1	0	9
28-Jul	0	1	0	0	1	0	0	0	9
4-Aug	0	23	4	0	2	0	1	0	9
11-Aug	0	32	0	0	1	0	8	0	15
18-Aug	0	4	0	0	0	0	0	0	7
28-Aug	0	56	2	0	7	0	8	0	9
1-Sep	0	29	T	0	12	0	8	0	5
11-Sep	0	1	æ	0	4	0	8	0	7
15-Sep	0	1	0	0	29	0	4	0	2
25-Sep	0	0	0	0	3	0	1	0	7
2-Oct	0	1	0	0	0	0	0	0	5
Total	1	544	40	3	61	1	103	2	806

Appendix H. Numbers of adult individuals of various cicadellid subfamilies caught on sticky card traps and in vacuum samples at a vineyard in Perkins, Oklahoma over the sampling season of 2017.

Subfamily				Deltocepl	halinae			
Genus	Macrosteles	Norve	llina	Paraphlepsius	Penthimia	Scaphoideus	Scaphytopius	Stirellus
species	unknown	chenopodii	seminuda	irroratus	americana	titanus	uwouyun	bicolor
27-Apr	0	2	0	0	0	0	0	0
4-May	0	0	æ	2	2	0	1	0
11-May	0	1	1	7	0	0	0	0
18-May	0	1	0	10	0	0	0	0
25-May	1	F	0	1	0	0	0	0
2-Jun	0	0	0	1	0	0	0	0
9-Jun	0	0	0	1	0	0	Т	0
16-Jun	0	0	2	0	0	1	7	0
23-Jun	0	0	0	0	0	0	0	0
30-Jun	1	0	0	2	0	0	0	0
Jul-7	0	0	2	0	0	1	1	0
14-Jul	0	0	0	æ	0	0	0	0
21-Jul	0	7	0	0	0	0	1	0
28-Jul	0	0	0	1	0	1	0	0
4-Aug	0	0	0	1	0	0	1	0
11-Aug	0	7	0	1	0	1	3	0
18-Aug	0	0	1	0	0	0	0	0
28-Aug	0	0	0	0	0	0	Ч	0
1-Sep	0	0	0	0	0	1	0	0
11-Sep	0	0	0	1	0	0	0	0
15-Sep	1	0	0	4	0	0	0	0
25-Sep	0	0	0	0	0	0	0	0
2-Oct	0	0	0	0	0	0	1	1
Total	3	7	6	40	2	5	10	1

Appendix I. Numbers of adult individuals of the cicadellid subfamily Deltocephalinae caught on sticky card traps and in vacuum samples at a vineyard in Perkins, Oklahoma over the sampling season of 2017.

							_												0		0	0		0		
Membracoidea	Membracidae	Micrutalis)	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	
	Other	uwouyun	0	0	0	0	0	ñ	1	0	T	0	0	0	0	0	0	0	0	0	0	Г	0	0	0	9
	idae	uwouyun	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
ulgoroidea	Flat	Metcalfa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Fi	Delphacidae	Liburniella	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	2
	Cixiidae	unknown	0	0	0	0	0	0	0	1	0	0	æ	0	0	0	ŵ	2	Û	1	2	1	0	0	0	16
opoidea	Clastopteridae	Clastoptera	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	3
Cerco	Cercopidae	Prosapia	0	0	0	0	0	0	H	0	H	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Superfamily	Family	Genus	27-Apr	4-May	11-May	18-May	25-May	2-Jun	9-Jun	16-Jun	23-Jun	30-Jun	7-Jul	14-Jul	21-Jul	28-Jul	4-Aug	11-Aug	18-Aug	28-Aug	1-Sep	11-Sep	15-Sep	25-Sep	2-Oct	Total

Appendix J. Numbers of adult individuals of the superfamilies Cercopoidea, Fulgoroidea, and Membracoidea caught on sticky card traps and in vacuum samples at a vineyard in Perkins, Oklahoma over the sampling season of 2017.

Genus							Ł	Erythroneur	ä						
species	amanda	comes	cymbium	delicata	diva	elegans	fraxa	infuscata	octonotata	ontari	reflecta	rubra	tricincta	vitis	ziczac
27-Apr	0	3164	0	T	0	0	0	0	0	0	0	0	0	0	1576
4-May	1	1509	5	0	0	0	0	0	2	0	0	0	0	4	1215
11-May	0	352	2	0	0	0	0	1	0	0	0	0	0	1	317
18-May	0	790	9	0	0	0	0	0	5	0	0	0	0	S	689
29-May	0	791	12	0	0	0	0	0	S	0	0	0	0	11	513
5-Jun	0	650	6	Η	0	0	0	0	3	0	0	0	0	9	334
9-Jun	0	710	6	0	0	0	0	0	2	0	0	7	0	4	510
18-Jun	0	1416	6	ß	0	0	0	0	4	1	0	2	0	9	811
25-Jun	0	1334	14	4	0	1	0	0	1	0	0	1	0	S	608
2-Jul	0	1640	27	9	7	0	0	0	S	0	0	2	0	9	824
6-Jul	0	430	8	9	0	0	0	0	0	0	0	1	1	ß	379
16-Jul	0	3362	42	16	2	7	0	0	8	0	0	4	0	4	3063
20-Jul	0	697	11	0	0	0	0	0	1	0	0	1	0	5	691
27-Jul	0	1319	16	2	0	0	0	1	4	1	7	S	0	S	2234
3-Aug	1	7673	44	10	7	0	0	0	10	0	0	m	1	27	10909
10-Aug	0	3003	21	ſ	0	0	0	0	œ	0	2	4	0	14	4559
17-Aug	0	3101	31	H	0	0	0	0	2	0	0	1	0	8	6429
24-Aug	1	3429	32	Η	0	0	0	0	2	0	0	0	0	7	6295
1-Sep	0	7584	30	m	0	0	0	0	18	1	0	0	1	9	14226
8-Sep	1	10933	23	4	0	1	1	0	28	0	0	0	0	6	17444
15-Sep	0	10342	19	2	0	0	0	0	22	0	1	1	0	3	2278
Total	4	64229	370	73	4	S	1	2	129	e	4	24	3	153	75904

Appendix K. Numbers of adult individuals of the erythroneurine genus *Erythroneura* caught on sticky card traps and in vacuum samples at a vineyard in Perkins, Oklahoma over the sampling season of 2018.

	10	0	0	0	0	0	0	0	Ч	Ч	7	Ч	Г	0	Ч	4	2	m	7	7	8	4	
Illinigina	illinoiensis																						3
Hymetta	unknown	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	2	1	0	2	0	0	8
Erythridula	unknown	3	3	0	1	0	1	0	0	1	0	0	0	0	0	2	0	2	0	0	2	0	15
	unknown	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1	5
ura	era	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	1
Eratone	carmini	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	2	0	9
	basilaris	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	1	0	5
neura	vulnerata	476	356	68	216	296	310	252	829	774	1341	196	3016	355	748	6269	2232	2465	1490	1984	2750	20341	46764
Erasmoi	atra or nigra	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	3
Genus	species	27-Apr	4-May	11-May	18-May	29-May	5-Jun	9-Jun	18-Jun	25-Jun	2-Jul	6-Jul	16-Jul	20-Jul	27-Jul	3-Aug	10-Aug	17-Aug	24-Aug	1-Sep	8-Sep	15-Sep	Total

Appendix L. Numbers of adult individuals of various erythroneurine genera caught on sticky card traps and in vacuum samples at a vineyard in Perkins, Oklahoma over the sampling season of 2018.

Subfamily	Aphrodinae		C	icadellinae		Eurymelinae		lassinae		Megophthalminae	Typhlo	cybinae
Genus	Xestocephalus	Grapho	cephala	Oncometopia	Paraulacizes	ldiocerus	Gyponana	Ponana	Stragania	Agallia	Dikrella	Empoasca
species	unknown	coccinea	versuta	orbona	irrorata	unknown	unknown	unknown	unknown	unknown	maculata	fabae
27-Apr	0	0	0	0	0	0	0	0	0	0	0	5
4-May	0	0	0	1	0	0	0	0	0	2	0	20
11-May	0	0	0	0	0	0	0	0	0	0	0	8
18-May	0	0	0	0	0	0	1	1	0	0	0	40
29-May	0	0	0	0	0	0	4	1	0	1	0	949
5-Jun	0	0	1	0	0	0	0	0	0	1	0	297
9-Jun	0	0	4	0	0	0	5	0	0	0	0	13
18-Jun	0	0	13	0	0	0	1	1	0	2	0	16
25-Jun	0	0	22	0	0	0	1	0	0	3	0	17
2-Jul	0	0	51	1	1	1	2	0	0	12	0	15
lul-9	0	0	29	2	3	0	0	0	0	4	0	5
16-Jul	0	1	12	0	1	0	2	0	0	3	0	4
20-Jul	0	0	ĉ	0	0	0	æ	0	0	0	0	3
27-Jul	1	0	13	1	0	0	17	0	0	1	0	3
3-Aug	0	0	20	1	0	0	20	0	0	5	0	4
10-Aug	T	0	37	0	0	0	15	0	0	43	0	S
17-Aug	0	0	24	0	0	0	51	0	0	6	0	2
24-Aug	0	0	14	0	0	0	24	0	0	1	0	0
1-Sep	0	0	9	0	0	0	45	0	1	2	0	4
8-Sep	0	0	23	0	0	0	63	0	0	0	0	11
15-Sep	1	0	41	0	0	0	65	0	6	1	1	41
Total	8	1	313	9	5	1	319	3	7	90	1	1460

Appendix M. Numbers of adult individuals of various cicadellid subfamilies caught on sticky card traps and in vacuum samples at a vineyard in Perkins, Oklahoma over the sampling season of 2018.

mily						Delto	ocephalinae					
	Deltocephalus	Japananus	Macrosteles	Menosoma	Norve	llina	Paraphlepsius	Penthimia	Scaphoideus	Scaphytopius	Spangbergiella	Stirellus
	unknown	hyalinus	unknown	cincta	chenopodii	seminuda	irroratus	americana	titanus	unknown	unknown	bicolor
	0	0	1	0	0	2	0	0	0	0	1	0
~	0	0	0	0	0	7	7	4	0	0	0	0
~	0	0	0	0	0	0	S	0	0	0	0	0
~	0	0	0	0	0	0	3	1	0	1	0	0
~	0	0	0	0	0	0	2	0	1	0	0	0
-	1	0	1	0	0	0	1	0	1	4	0	1
-	0	0	0	0	0	0	0	0	0	1	0	0
c	0	0	0	0	1	0	1	0	0	0	0	0
c	0	0	0	0	0	0	0	0	0	0	0	0
=	0	1	0	0	0	0	2	0	1	0	0	0
=	0	0	0	0	0	0	1	0	1	0	0	0
	0	0	0	0	0	0	0	0	0	9	0	0
_	0	0	0	0	0	0	0	0	1	5	0	0
	0	0	0	0	0	0	1	0	0	7	0	0
60	0	0	0	0	0	0	0	0	0	3	0	0
00	1	0	0	0	0	0	1	0	0	-	0	0
60	0	0	0	1	0	0	2	0	1	2	0	0
60	0	0	0	1	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	1	0	0	0	1
0	0	0	0	0	0	0	-	0	1	m	0	0
0	0	0	2	0	0	0	5	0	2	43	0	0
	2	1	4	2	1	6	30	9	6	26	1	2
Fotal	2	1	4	2	1	6	30		9	6 9	6 9 76	6 9 76 1

Appendix N. Numbers of adult individuals of the cicadellid subfamily Deltocephalinae caught on sticky card traps and in vacuum samples at a vineyard in Perkins, Oklahoma over the sampling season of 2018.

<u> </u>			-	-	-	-	•	-	-	-	-		-	-	-	-	-	-	-	-	•	-	-	<u> </u>
		unknown	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
		Telamona	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
mbracoidea	embracidae	Spissistilus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Me	W	Micrutalis	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	4
		Cyrtolobus	0	0	0	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
	Other	unknown	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	4
	tidae	unknown	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
goroidea	Flat	Metcalfa	0	0	0	0	0	0	0	0	0	Η	0	0	0	0	Н	0	0	0	0	0	0	2
Ful	Derbidae	Anotia	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
	Acanaloniidae	Acanalonia	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Cercopoidea	Clastopteridae	Clastoptera .	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	F	0	0	1	3
Superfamily	Family	Genus	27-Apr	4-May	11-May	18-May	29-May	5-Jun	9-Jun	18-Jun	25-Jun	2-Jul	6-Jul	16-Jul	20-Jul	27-Jul	3-Aug	10-Aug	17-Aug	24-Aug	1-Sep	8-Sep	15-Sep	Total

Appendix O. Numbers of adult individuals of the superfamilies Cercopoidea, Fulgoroidea, and Membracoidea caught on sticky card traps and in vacuum samples at a vineyard in Perkins, Oklahoma over the sampling season of 2018.

VITA

Kevin Ross Jarrell

Candidate for the Degree of

Master of Science

Thesis: PHENOLOGY OF EASTERN GRAPE LEAFHOPPER, <u>ERYTHRONEURA</u> <u>COMES</u> (SAY), AND ABUNDANCE ON GRAPE CULTIVARS, WITH NOTES ON OTHER LEAFHOPPERS OF IMPORTANCE

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