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Predation and cannibalism of lady beetle eggs by adult lady beetles

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Abstract

The introduced lady beetle *Harmonia axyridis* now occurs across much of North America. This species is a strong intraguild competitor that may negatively impact local populations of native Coccinellidae. A laboratory examination of coccinellid egg predation, including cannibalism, revealed that eggs of two native species, *Coleomegilla maculata* and *Olla v-nigrum*, had significantly higher egg predation than did *H. axyridis* eggs. The addition of an alternative food source reduced egg cannibalism and predation. However, in the absence of an alternative food source, both native species attacked exotic eggs less than native eggs whereas, the exotic *H. axyridis* attacked all egg species similarly. This laboratory study shows that under conditions of low food availability, native coccinellid eggs would suffer from both cannibalism and predation whereas, cannibalism would be the larger threat to *H. axyridis* eggs.
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1. Introduction

The introduced multicolored Asian lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae), has established in many habitats over much of North America (Chapin and Brou, 1991; Coderre et al., 1995; Colunga-Garcia and Gage, 1998; Krafsur et al., 1997; LaMana and Miller, 1996; Tedders and Schaefer, 1994). Many different traits could have facilitated establishment of *H. axyridis* in North America and may include high fecundity (Michaud, 2002), aggressive behavior (Kajita et al., 2000; Michaud, 2002; Yasuda and Ohnuma, 1999), high mobility (With et al., 2002), large body size (Michaud, 2002), low susceptibility to a parasitoid (Hoogendoorn and Heimpel, 2002), low susceptibility to pathogens attacking native coccinellids (Cottrell and Shapiro-Ilan, 2003), and a polyphagous diet (Hodek and Honék, 1996).

This polyphagous predator can be important as an aphid predator (Fox et al., 2004; Tedders and Schaefer, 1994) or potentially harmful through a variety of ways (Koch, 2003; Koch et al., 2003). One potentially harmful impact of *H. axyridis* is intraguild predation upon native lady beetles. Intraguild predation among coccinellids in natural situations has been documented when aphid prey become scarce (Hironori and Katsuhiro, 1997; Musser and Shelton, 2003; Schellhorn and Andow, 1999a). In fact, most studies that have examined the interactions of *H. axyridis* with other coccinellids have shown *H. axyridis* to be a strong intraguild competitor (Kajita et al., 2000; Sato et al., 2003; Takahashi, 1989; Yasuda and Ohnuma, 1999; Yasuda et al., 2001). Although unlikely that a coccinellid, i.e., *H. axyridis*, would subsist entirely on other coccinellid species, it is likely that *H. axyridis* would be favored when encountering other species. For example, a laboratory study by Cottrell and Yeargan (1998c) showed that

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H. axyridis was capable of completing development on a diet consisting of *Coleomegilla maculata* eggs. In that study, larval interactions also were examined and typically found to favor *H. axyridis*. Furthermore, Musser and Shelton (2003) reported that *H. axyridis* does prey upon the native *C. maculata* in corn fields. Negative impacts upon native coccinellids by established exotic coccinellids is not unprecedented as Elliot et al. (1996) suggested that the exotic *Coccinella septempunctata* may have reduced populations of certain native coccinellids in the US.

Egg predation may play a role as to how *H. axyridis* could impact native coccinellids. Laboratory data by Cottrell (2004) showed that larvae of the exotic *H. axyridis* were capable of completing development solely on eggs of the native *C. maculata* or *O. v-nigrum* whereas, larvae of those native species did not complete development on *H. axyridis* eggs. In addition, when native larvae attacked an *H. axyridis* egg cluster, many eggs within the cluster were only partially consumed. That data would suggest that eggs of the native *C. maculata* and *O. v-nigrum* would be susceptible to both egg cannibalism and egg predation whereas, *H. axyridis* eggs would be more susceptible to cannibalism in the field.

Although the occurrence of egg cannibalism and predation most often focuses on larvae, adults also come into contact with coccinellid eggs. However, less is known about egg cannibalism and predation by adult Coccinellidae, especially native egg predation by exotic adults. In addition, even less is known about egg cannibalism and predation by adult male and female coccinellids although it could be expected that males would feed less. Obata and Johki (1990) documented that male *H. axyridis* spent more time moving and at a faster rate than did female *H. axyridis*. Those males appeared to be preoccupied with mate finding and commonly passed over encountered aphid prey. Therefore, the objective of this laboratory study was to examine egg cannibalism and egg predation by the exotic *H. axyridis* and two native species, *C. maculata* and *O. v-nigrum*, that overlap spatially and temporally in various habitats. This was done using male and female adults of each species in no-choice tests and again for adults of each species when provided with, or without, an alternative food supply.

2. Materials and methods

2.1. Insect colonies

Laboratory colonies of *O. v-nigrum* and *H. axyridis* originated from adult beetles collected from pecan orchards at the USDA, Agricultural Research Service, Southeastern Fruit and Tree Nut Research Laboratory at Byron, GA, USA. The *C. maculata* colony originated from overwintering adult beetles collected near Lexington, KY, USA. Field-collected adults of each species from the USDA laboratory at Byron, GA were added intermittently to the colonies. Each species was housed in 9-cm diameter petri dishes in an environmental chamber at 25 ± 1 °C and a photoperiod of 14:10 (L:D) h. *Olla v-nigrum* and *H. axyridis* were fed pecan aphids (*Monellia caryella* and *Monelliopsis pecanis*), frozen lepidopteran eggs (*Helicoverpa zea* and *Ephestia kuhniella*), supplemented with a beef-based diet (Cohen, 1985), and water provided with a moistened cotton dental wick. The polyphagous *C. maculata* was fed the beef diet and supplemented with lepidopteran eggs (Cottrell and Yeargan, 1998a). Aphids were reared on foliage of greenhouse-grown seedling pecans (Cottrell et al., 2002). Green florist's paper was used to line lids of petri dishes containing adult female coccinellids (Cottrell and Yeargan, 1998a). The paper provided an ovipositional substrate for the lady beetles that could be easily removed and replaced. Egg clusters used in all studies were from mated, laboratory-reared coccinellids. Egg clusters were collected daily and stored at 10 ± 1 °C. The quantity of egg clusters needed usually required collection of eggs for several days; eggs used in studies were $\leqslant$7-day-old.

2.2. Adult feeding assays

Feeding assays were done using laboratory-reared *C. maculata*, *O. v-nigrum*, and *H. axyridis* adults against eggs from each of those species. Male and female beetles were assayed separately. For each sex, similar-aged beetles (i.e., 2- to 3-week-old) were starved for 18 h and then individuals of each species were randomly assigned to a plastic dish containing a single cluster of *H. axyridis*, *O. v-nigrum* or *C. maculata* eggs (on an approximately 5 cm^2 piece of green florist's paper) and a moistened cotton dental wick. All eggs used in feeding assays were from laboratory-reared beetles maintained for egg production and never from beetles used in these feeding assays. Numbers of eggs per cluster were counted before the assays began and only clusters with similar numbers of eggs (within and between species) were used. Mean numbers of eggs per cluster (± SE) for *C. maculata*, *O. v-nigrum*, and *H. axyridis* were 19.4 ± 0.3, 20.7 ± 0.7, and 21.1 ± 0.4, respectively, for the assay using females and 18.7 ± 0.3, 20.4 ± 0.8, and 20.4 ± 0.7, respectively, for the assay using males. Assays were done in an environmental chamber using a completely randomized design. Environmental conditions were 25 ± 1 °C and a photoperiod of 14:10 (L:D) h. Numbers of eggs attacked (i.e., partially consumed + entirely consumed) were determined with the aid of a dissecting microscope at 3, 6, 12, and 24 h after the assay began. Each adult species × egg species combination was replicated 13 times for the female group and 9 times for the male group. Before the assay was begun, females had been provided an opportunity to mate, placed singly into plastic dishes (with food and water), and selected based upon an observed oviposition event within 10 days. Selection of male beetles for use in the assay was based upon observed copulation attempts with female beetles. In addition, dissection for confirmation of male genitalia was done following the conclusion of the feeding assay.

2.3. Alternative food assay

Adults of each species were reared in the laboratory as previously described. Consumption of each coccinellid species' eggs by each species of adult lady beetle was measured when adult beetles were presented only the coccinellid eggs or the coccinellid eggs in the presence of an alternative food source (i.e., live pecan aphids for *O. v-nigrum* and *H. axyridis* or frozen *E. kuhniella* eggs for *C. maculata*). Adult beetles were placed singly into a plastic dish that contained a single coccinellid egg cluster on green florist's paper (placed in the center of the plastic dish) or a single coccinellid egg cluster plus the alternative food source (provided ad libitum) scattered throughout the dish. The mean number (± SE) of *C. maculata*, *O. v-nigrum*, and *H. axyridis* eggs per cluster provided to each adult species was 20.2 ± 0.1, 20.3 ± 0.2, and 20.2 ± 0.2, respectively, for *C. maculata*; 23.1 ± 0.1, 23.9 ± 0.2, and 23.8 ± 0.2, respectively, for *O. v-nigrum*; and 19.9 ± 0.2, 20.4 ± 0.3, and 20.0 ± 0.2, respectively, for *H. axyridis*. The experimental design was a completely randomized design for each species using 12 beetles per treatment. Beetles were assayed for 4 h and then the percentage of attacked eggs per cluster was determined.

2.4. Statistical analyses

A factorial repeated measures MANOVA was used to analyze the percentage of eggs attacked (i.e., partially + entirely consumed) across sample periods (JMP, 2002). The model included main effects for time, sex, adult species, egg species, and their interaction terms. When significant interactions ($P < 0.05$) were detected, ANOVA was used to test main effects (JMP, 2002). Tukey's HSD was used for mean separation when $P < 0.05$. When beetles were tested with or without an alternative food source, the percentage of eggs per cluster attacked after 4 h was arcsine transformed (Zar, 1999) and separately analyzed for each predating species using a factorial ANOVA and testing for an egg species × alternative food availability interaction. If the interaction was not significant ($P \leqslant 0.05$), one-way ANOVA of the main effects (i.e., egg species and alternative food availability) was examined separately for each adult species. When $P \leqslant 0.05$, mean separation was done using Tukey's HSD (JMP, 2002). All data is presented as non-transformed means (± SE).

3. Results

3.1. Adult feeding assay

Repeated measures MANOVA did not reveal any significant 4- or 3-way interactions ($P > 0.05$) although the interaction of 'time × sex × egg species' was nearly significant ($F = 2.13$; $df = 6,350$; $P = 0.0506$). The 2-way interactions of 'time × sex' and 'time × adult species' were not significant ($F = 1.18$; $df = 3,175$; $P = 0.3190$ and $F = 2.03$; $df = 6,350$; $P = 0.0615$, respectively) (Figs. 1A and B). However, 'time × egg species' was significant ($F = 3.73$; $df = 6,350$; $P = 0.0013$) (Fig. 1C). The ANOVA on the main effect 'egg species' was significant at 3 h ($F = 6.97$; $df = 2,189$; $P = 0.0012$), 6 h ($F = 13.07$; $df = 2,189$; $P < 0.0001$), 12 h ($F = 21.28$; $df = 2,189$; $P < 0.001$), and 24 h ($F = 23.10$; $df = 2,189$; $P < 0.0001$) (Fig. 1C).

3.2. Alternative food assay

Two-way ANOVA revealed a significant interaction of 'egg species × alternative food availability' for the percentage of eggs attacked by *O. v-nigrum* ($F = 6.64$; $df = 2,66$; $P = 0.0024$) (Fig. 2). A significantly higher percentage of *O. v-nigrum* and *C. maculata* eggs were attacked by adult *O. v-nigrum* in the absence of an alternative food source than in the presence of an alternative food source. Percentage attack on *H. axyridis* eggs by adult *O. v-nigrum*, regardless of an alternative food, was similar to attacks on *C. maculata* and *O. v-nigrum* eggs without an alternative food (Fig. 2).

Two-way ANOVA did not reveal an interaction of 'egg species × alternative food availability' for the percentage of eggs attacked by *C. maculata* ($F = 2.20$; $df = 2,66$; $P = 0.1194$) or *H. axyridis* ($F = 2.84$; $df = 2,66$; $P = 0.0654$). Analysis of the main effect 'alternative food availability' for each adult species revealed that *C. maculata* attacked significantly more *C. maculata* eggs without an alternative food present ($F = 7.32$; $df = 1,22$; $P = 0.0129$) but no significant difference was detected for percentage attack by adult *C. maculata* on *O. v-nigrum* eggs ($F = 1.70$; $df = 1,22$; $P = 0.2058$) or *H. axyridis* eggs ($F = 2.61$; $df = 1,22$; $P = 0.1206$), regardless of alternative food availability (Fig. 3A). *H. axyridis* adults attacked significantly more *C. maculata* eggs ($F = 8.48$; $df = 1,22$; $P = 0.0081$) and *O. v-nigrum* eggs ($F = 27.39$; $df = 1,22$; $P < 0.0001$) but not *H. axyridis* eggs ($F = 2.58$; $df = 1,22$; $P = 0.1222$) in the absence of an alternative food source (Fig. 3B).

Analysis of the main effect 'egg species' revealed that adult *C. maculata* attacked a lower percentage of *H. axyridis* eggs than eggs of either *C. maculata* or

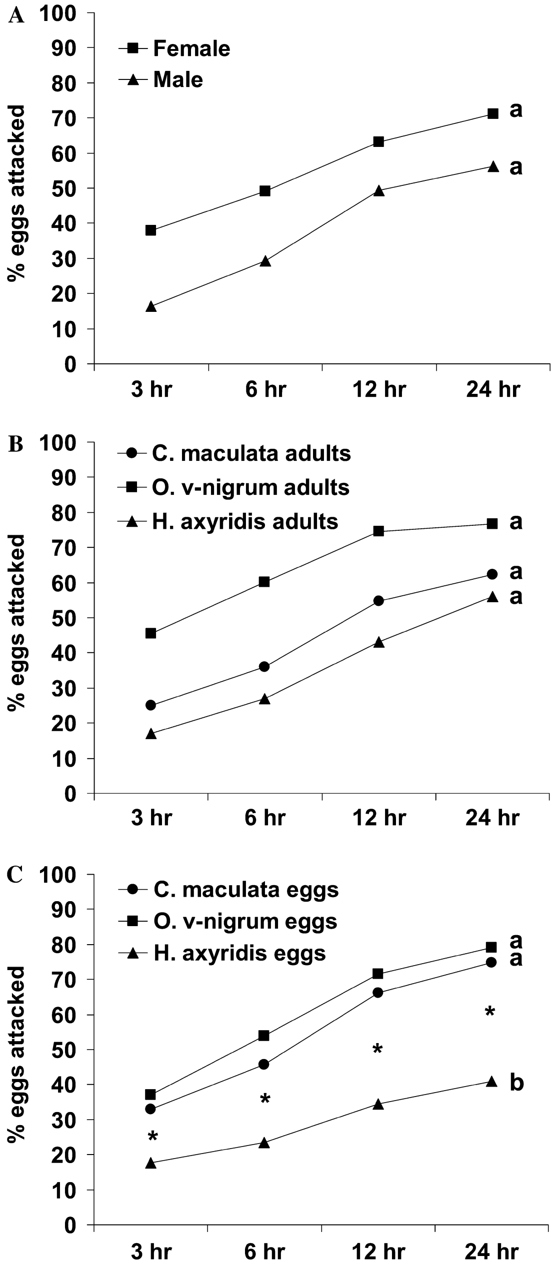

Fig. 1. Percentage of all coccinellid eggs attacked across sample periods by (A) males vs. females, (B) adults of each species tested, and (C) the percentage of eggs from each species that was attacked. For each graph, significant treatment effects ($P < 0.05$) across sample times are indicated by unlike letters. Mean separation at each sample time was done using Tukey's HSD test when $P < 0.05$. Unlike means ($P < 0.05$) at a single sample time are vertically separated by an asterisk.

O. v-nigrum in the absence of an alternative food source ($F = 7.26$; $df = 1, 33$; $P = 0.0024$) whereas, in the presence of an alternative food source, adult *C. maculata* attacked a similar percentage of eggs of each species ($F = 3.06$; $df = 1, 33$; $P = 0.0602$) (Fig. 3A). Adult *H. axyridis* attacked a similar percentage of eggs of each species regardless of the presence or absence of an alternative food source ($F = 0.27$; $df = 1, 33$; $P = 0.7646$ or $F = 3.03$; $df = 1, 33$; $P = 0.062$, respectively) (Fig. 3B).

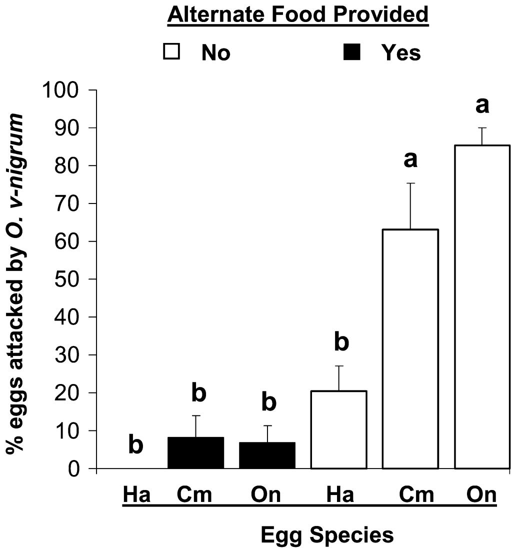

Fig. 2. Percentages (± SE) of *C. maculata*, *O. v-nigrum*, and *H. axyridis* eggs attacked after 4 h by adult *O. v-nigrum* when an alternative food source, i.e., *E. kuhniella* eggs was, and was not, provided. Cm, *C. maculata*; On, *O. v-nigrum*; and Ha, *H. axyridis*. Unlike letters above vertical columns indicate significant difference ($P < 0.05$).

4. Discussion

Coccinellid eggs are most likely protected from predation by defensive alkaloids, pyrazines and quinolenes. The alkaloids are synthesized de novo by coccinellids and are reported to be found in all developmental stages (Agarwala and Yasuda, 2001; Ayer and Browne, 1977; Hemptinne et al., 2000a,b,c). This would help to explain why their eggs are attacked by a low number of predator species compared with eggs of pest species (e.g., *H. zea* [Lepidoptera: Noctuidae]) even in the same habitat (Cottrell and Yeargan, 1998a,b). Thus, the introduction of a new predator, capable of feeding on coccinellid eggs, may negatively impact native coccinellid species through resource competition and intraguild egg predation. Although this impact will not be fully understood without adequate field experimentation, results from this laboratory study suggest that eggs of two native North American coccinellids will suffer increased predation compared with the established exotic species.

In addition to resource availability, spatial and temporal factors affecting overlap of lady beetle species will determine the incidence of intraguild predation. Musser and Shelton (2003) suggest that *C. maculata* and *H. axyridis* will not overlap on corn enough, either spatially or temporally, to affect one another. They reported that adult *H. axyridis* occurred higher on corn plants than did adult *C. maculata* but it is interesting that field observations have documented *H. axyridis* attacking *C. maculata* but not vice versa (Cottrell and Yeargan, 1998c; Musser and Shelton, 2003). Musser and Shelton (2003) also reported

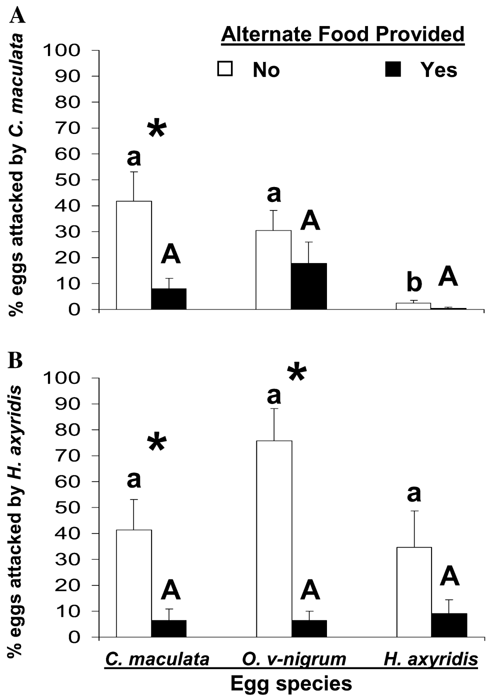

Fig. 3. Direct comparison of percentages (± SE) of *C. maculata*, *O. v-nigrum* or *H. axyridis* eggs attacked after 4 h by (A) adult *C. maculata* and (B) adult *H. axyridis* when an alternative food source (i.e., *E. kuhniella* eggs for *C. maculata* or yellow pecan aphids for *H. axyridis*) was or was not provided. In both (A) and (B), an asterisk indicates significant difference ($P < 0.05$) between paired columns. Unlike lowercase letters above white columns indicate a significant difference ($P < 0.05$) in the percentage of different egg species attacked by adult *C. maculata* (A) and *H. axyridis* (B) when an alternative food source was not provided. Unlike uppercase letters above black columns indicate a significant difference ($P < 0.05$) in the percentage of different egg species attacked by adult *C. maculata* (A) and *H. axyridis* (B) when an alternative food source (i.e., *E. kuhniella* eggs for *C. maculata* or yellow pecan aphids for *H. axyridis*) was provided.

that *H. axyridis* larvae had a distribution on corn plants that was lower (i.e., where most *C. maculata* eggs occur) than adult *H. axyridis*. Other native coccinellid species, such as *O. v-nigrum* and *Adalia bipunctata*, heavily reliant upon aphidophagy will have substantial spatial and temporal overlap with *H. axyridis*. On pecan, adult *H. axyridis* overlap spatially and temporally with *O. v-nigrum* and eggs of both species are commonly found on foliage (Cottrell, 2004). In the case of *A. bipunctata*, females oviposit on upper portions of corn plants (Schellhorn and Andow, 1999b) and it has been suggested that *A. bipunctata* eggs suffer higher mortality because they are exposed to more predators attracted to aphids on the upper portions of corn plants (Schellhorn and Andow, 1999b). It is likely that adult *H. axyridis* would encounter *A. bipunctata* eggs on upper portions of corn plants and encounters between *H. axyridis* and *A. bipunctata* would favor the former because Sato and Dixon (2004) found that *A. bipunctata* larvae could not survive on *H. axyridis* eggs but *H. axyridis* larvae could survive on *A. bipunctata* eggs. Burgio et al. (2002) also showed that adult and late instar *H. axyridis* could feed on *A. bipunctata* eggs. In fact, most studies have found *H. axyridis* to be a strong intraguild competitor with other lady beetle species (Kajita et al., 2000; Takahashi, 1989; Yasuda and Ohnuma, 1999; Yasuda et al., 2001).

Even when coccinellid species do overlap spatially and temporally, abundant prey could discourage egg cannibalism and intraguild egg predation. Thus, a strong indicator of the propensity for one species to attack the eggs of another species is whether the eggs are attacked in the presence of alternative food. In this study, alternative prey were chosen based upon laboratory observations that indicated which available alternative prey would be acceptable to the coccinellids tested. Pecan aphids were considered highly palatable to *H. axyridis* and *O. v-nigrum* and lepidopteran eggs for *C. maculata* thus preventing coccinellid eggs from being the favored choice. With a palatable alternative food source available, the percentage of eggs attacked was lower than without an alternative food source. This is similar to results from Burgio et al. (2002) where egg cannibalism and egg predation by adults and larvae of *H. axyridis* and *A. bipunctata* decreased when aphid prey were provided. In fact, Cottrell and Yeargan (1998b) showed that egg cannibalism by the native *C. maculata* in sweet corn plantings was reduced during anthesis when abundant corn pollen was available. Nonetheless, it is important to note that the exotic *H. axyridis* fed similarly on eggs of all coccinellids in the absence of alternative prey and some potential food sources (i.e., corn pollen) may not prevent *H. axyridis* predation on coccinellid eggs. In stark contrast, the two native species attacked a significantly lower percentage of *H. axyridis* eggs, compared with native eggs, when no alternative food was available.

The eggs of the native *C. maculata* and *O. v-nigrum* are likely to suffer more total predation when encountered by adult Coccinellidae as they are more susceptible to attack from the exotic and native species whereas, exotic *H. axyridis* eggs are more susceptible to cannibalism. A direct field assessment of the impact *H. axyridis* may have upon native species is needed. The laboratory results presented here suggest that *H. axyridis* is capable of negatively affecting native species but extrapolation of these results to the field will not be entirely accurate.

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(University of Kentucky, Lexington, KY, USA). This article reports the results of research only. Mention of a proprietary product does not constitute an endorsement or a recommendation for its use by the United States Department of Agriculture.

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