

Reproductive Development of Female Plum Curculio (Coleoptera: Curculionidae) in the Mid-Atlantic: Presence of Multivoltine Populations¹

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Abstract The plum curculio, *Conotrachelus nenuphar* (Herbst), is a key pest of pome and stone fruit throughout eastern and central North America. There are two strains of plum curculio, the univoltine 'northern' strain and the multivoltine 'southern' strain. Voltinism associated with populations located in the mid-Atlantic region has been unclear from historic records, with recent studies suggesting multivoltine populations. In studies conducted in West Virginia, female plum curculios obtained from emergence and screen traps and from samples of host tree canopies strongly indicate the presence of at least some multivoltine populations, based on an ovarian development bioassay. Two periods of active oogenesis were detected. The first occurred in early spring between late April and early May and represented overwintered females reaching sexual maturity. A second period of oogenesis was detected beginning in late June and continuing through early August. Based on degree day accumulations and known developmental rates of plum curculio, the mid-Atlantic is comprised, at least in part, of multivoltine populations. Fruit growers, therefore, must consider that plum curculio can pose a threat to tree fruit throughout the active growing season.

Key Words weevil, ovarian development, oogenesis, voltinism, monitoring

The plum curculio, *Conotrachelus nenuphar* (Herbst), is a key pest of pome and stone fruit throughout eastern and central North America (Racette et al. 1992, Vincent et al. 1999) and is considered a major pest of both apples and peaches in the mid-Atlantic region (Hogmire 1995). Broad-spectrum insecticides, particularly the organophosphate insecticides, have been the preferred materials for plum curculio control for 5 decades although several new materials, notably indoxacarb on apples, have proven effective. With the exception of phosmet, the use of organophosphates has been cancelled or is slated for cancellation which will lead to greater reliance on pyrethroids and on newer limited-spectrum compounds. As these limited-spectrum chemistries supplant broad-spectrum materials for control of key insect pests like the plum curculio, it is imperative that insecticide treatments be triggered by detection of increases in plum curculio abundance or activity and the mode of action of these newer chemistries (Wise et al. 2006) be well understood.

One of the critical questions for plum curculio management in the mid-Atlantic is

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the uncertainty surrounding voltinism and associated period of risk posed by this key pest. In a map produced by Chapman (1938), plum curculios in locations north of Virginia including much of the mid-Atlantic region were identified as univoltine. Univoltine populations undergo an obligatory, reproductive winter diapause, whereas multivoltine populations have a facultative diapause (Smith and Salkeld 1964). In the mid-Atlantic region, however, Leskey and Wright (2004) reported that female plum curculios obtained from trapping samples taken from the eastern panhandle of West Virginia indicated a strong likelihood of multivoltine populations based on an ovarian development bioassay, although this study was conducted for only a portion of the fruit growing season and the number of females available for dissection was relatively small. Here, a much more robust data set is presented based on trap and host tree canopy samples taken throughout the entire season (prebloom to harvest) to establish the presence and phenology of multivoltine populations, and the period of risk of plum curculio injury to fruit in orchard ecosystems in the mid-Atlantic.

Materials and Methods

A mixed fruit orchard planted in 1997 at the Appalachian Fruit Research Station (Kearneysville, WV, USA) in a 4 × 4 partial Latin Square replicated 3 times was used for this study. Eight species of fruit trees were planted in each square and repeated twice. They included: apple, *Malus domestica* Borkh, cultivars 'Granny Smith' and 'Empire'; pear, *Pyrus communis* L., cultivars 'Beurre Bosc' and 'Seckel'; peach, *Prunus persica* Batsch, cultivar 'Loring'; apricot, *Prunus armeniaca* L., cultivar 'Deatrick'; sour cherry, *Prunus cerasus* L., cultivar 'Montmorency'; sweet cherry, *P. avium* (L.), cultivars 'Ulster' and 'Emperor Francis'; European plum, *P. domestica* L. cultivar 'Stanley'; and Japanese plum, *P. salicina* Lindl., cultivars 'Santa Rosa' and 'Formosa'. The orchard consisted of 4 rows of 12 trees, planted with 6 m between rows and 6 m between trees. Surrounding the orchard were 2 unmanaged apple orchards (~30 m to the east and ~20 m to the west), a hedgerow (~20 m to the north), and an open field to the south (Leskey and Wright 2007). Throughout this study in 2004, the orchard received no insecticide applications and 1 fungicide application of fenbucanazole on 17 May to control brown rot.

Emergence traps (1 × 1 m at the base using the specifications of Piñero et al. [2004]) were deployed within and adjacent to the orchard to monitor timing and duration of emergence of plum curculio. Seven traps were placed within each replicate, with a single trap positioned beneath the outer edge of the dripline (1 m from the trunk) of the canopy of 2 apple, 2 peach, and 2 European plum and 1 Japanese plum. Six emergence traps were deployed in the hedgerow, and 2 emergence traps were deployed in the open field. These sites were chosen as locations for monitoring emergence of overwintering adults because adults are known to overwinter outside the orchard in areas with thick layers of fallen leaves, grass and/or duff (Smith and Flessel 1968, LaFleur et al. 1987) and within the orchard (Piñero et al. 2005), likely near highly used host trees (Brown 2005). Emergence traps within the orchard were moved from their original location under a specific host tree to a new position 90° counterclockwise around the tree on 4 June 2004 to detect newly-eclosing summer generation adults from the soil.

Screen traps (Mulder et al. 1997) consisting of folded vinyl screen (New York Wire Co., Mt. Wolf, PA) sized to encircle the tree trunk and attached at the base of tree trunks and modified according to the specifications of Leskey and Wright (2004) were

deployed within each replicate, 1 on each host tree type including apple, peach, apricot, sour cherry, sweet cherry, European plum, and Japanese plum. Screen traps were deployed on pear trees in replicates 1 and 3 only because a pear tree had been lost in replicate 2. All remaining trees within each replicate were not subject to a trap directly attached to the tree itself.

Beginning on 6 April, each screen trap was sampled for the presence of plum curculios. All adults were removed from traps, placed in individual vials, and taken to the laboratory. Traps were checked twice weekly through 28 July and weekly thereafter until 30 September. A final sample was conducted on 28 October. Beginning on 16 April (based on captures in screen traps indicating adults were moving into host fruit trees), the remaining trees without screen traps in each replicate were sampled by using a beating stick to tap branches in the canopy. A large circular collection sheet (3.36 m diam) was positioned directly beneath the tree canopy to capture falling adults. This sampling regimen involved moving around the entire tree and tapping all large limbs (>10 cm diam). Sampled trees included 1 apple, pear, peach, apricot, sour cherry, sweet cherry, European plum, and Japanese plum each per replicate. Sampling was conducted between 1600-1900 h during the same sampling dates as those for screen traps. All adults recovered from the sheet were placed in individual vials and taken to the laboratory.

The sex of all adults captured over the entire season from emergence traps, screen traps, and from tapping host tree canopies was determined based on the characteristics described by Thomson (1932) using a Leica GZ4 dissecting scope at 30 $\times$. Subsequently, all females were dissected to determine the stage of ovarian maturity based on descriptions of Smith and Salkeld (1964). Three classifications for ovarian maturity were used: (1) no development, sexually immature females incapable of oviposition due to lack of oocytes in the vitellarium; (2) developing, females rapidly becoming sexually mature based on the presence of numerous developing oocytes in the vitellarium; and, (3) mature, females capable of oviposition based on mature eggs in the calyx and numerous developing oocytes in the vitellarium. The mating status of each female also was determined; the spermatheca was removed, positioned on a microscope slide with a few drops of deionized water, topped with a cover slip, and examined for the presence of sperm using an Olympus BX41 light microscope at $\sim$ 100 $\times$.

The total number of adult females exhibiting no ovarian development, developing ovaries, or mature ovaries are presented for each sampling method (emergence and screen traps and tapping host tree canopies) over the entire season. The total number and percentage of females exhibiting each stage of ovarian development during 5 phenological development periods of Japanese plum, the preferred host of plum curculio (Leskey and Wright 2007) are also presented. These stages include: white bud-bloom (6-13 April), petal fall-shuck split (14-30 April), $\leq$ 24 mm fruit (1 May-15 June), 25-30 mm fruit (16-28 June), and fruit drop (29 June-30 September). Temperature data used to estimate developmental time of plum curculio life stages under field conditions were collected in Kearneysville, WV, every 10 min (Spectrum Technologies, Inc., Plainfield, IL).

Results

Adult females were captured from 16 April-30 September 2004. Throughout the entire study, 81 females captured in emergence traps, 351 females captured in

screen traps and 405 females obtained from tapping samples of host tree canopies were dissected for ovarian maturity and mating status.

No captures were recorded in emergence or screen traps, and no individuals were recovered from host tree canopies between white bud and bloom (6-13 April). From petal fall to shuck split (14-30 April), active oogenesis (indicative of imminently sexually-mature females) was detected in 33% of females in emergence traps, 34.2% in screen traps, and 10.4% from host tree canopies. Most females in emergence traps (66.6%) showed no signs of ovarian development during this phenological period, whereas most females captured in screen traps (57.1%) and recovered from host trees (84.1%) were sexually mature (Table 1). Mated females comprised 33.3%, 79.7%, 92.6% of the sample from emergence traps, screen traps, and host tree canopies, respectively.

When fruit was ≤ 24 mm (1 May-15 June), 10.2% of females in screen traps and 1.8% from host tree canopies exhibited active oogenesis whereas $\geq 89\%$ were sexually mature (Table 1). No females were captured in emergence traps between 1 May-4 June. After emergence traps were repositioned on 4 June, 4 sexually-mature females were captured between 5-15 June. Mated females comprised 75.0%, 98.3%, 99.3% of the sample from emergence traps, screen traps, and host tree canopies, respectively.

Active oogenesis was detected in 13.3% of females captured in emergence traps, 11.1% in screen traps, and 3.3% recovered from host tree canopies (Table 1) when fruit was between 25-30 mm diam (16-28 June). In samples from emergence traps and host tree canopies, 86.7% and 73.7% of females, respectively, showed no sign of ovarian development. Mated females comprised 20.0%, 77.8%, and 56.7% of the sample from emergence traps, screen traps, and host tree canopies, respectively.

After fruit had dropped to the ground (29 June-30 September), active oogenesis was detected in 2.0% of females in emergence traps, 2.3% in screen traps, and 10.4% recovered from host tree canopies. Mated females comprised 8.0%, 31.8%, and 58.3% of the sample from emergence traps, screen traps, and host tree canopies, respectively.

Throughout the entire season, females undergoing active oogenesis were observed from 23-27 April, 22-28 June, and on 28 July in emergence traps, from 20 April-4 June, 28 June, and 17 August in screen traps, and from 23 April-11 May, and from 28 June-6 July, and 10 August from host tree canopies (Fig. 1).

Discussion

The presence of developing oocytes in ovaries of adult females indicates that females are undergoing active oogenesis and rapidly becoming sexually mature (Smith and Salkeld 1964, Leskey and Wright 2004). Here, the presence of females with developing oocytes was detected during roughly 2 periods, 20 April to 4 June and from 28 June to 17 August 2004. The first detection period in early spring represented those females who had successfully overwintered. Smith and Salkeld (1964) stated that ~50% of all females have begun oogenesis upon emergence. Ovarian development from females captured in emergence traps (16-30 April 2004) in studies reported here revealed that 66% of all females showed no sign of ovarian development upon emergence; whereas, 33% had begun oogenesis.

The second detection period likely represents the presence of at least 1 additional reproductively active generation of adults in the mid-Atlantic. Females recovered from

Table 1. Total number and percentage (%) of adult females from emergence traps, screen traps, or from host tree canopies exhibiting no ovarian development, developing, or mature ovaries from 6-13 April (white bud-bloom), 14-30 April (petal fall-shuck split), 1 May-15 June (≤ 24 mm fruit), 16-28 June (25-30 mm fruit), and 29 June-30 September (fruit drop)

Sampling Dates	Emergence Traps			Screen Traps			Tapping Host Tree Canopies		
	None	Developing	Mature	None	Developing	Mature	None	Developing	Mature
6-13 April	—	—	—	—	—	—	—	—	—
14-30 April	6 (66.6)	3 (33.3)	—	10 (8.7)	39 (34.2)	64 (57.1)	9 (5.5)	17 (10.4)	137 (84.1)
1 May-15 June	—	—	4 (100.0)	—	19 (10.2)	166 (89.8)	1 (0.6)	3 (1.8)	160 (97.6)
16-28 June	13 (86.7)	2 (13.3)	—	3 (33.3)	1 (11.1)	5 (55.6)	22 (73.3)	1 (3.3)	7 (23.4)
29 June-30 September	52 (98.0)	1 (2.0)	—	34 (76.7)	1 (2.3)	9 (21.0)	37 (77.0)	5 (10.4)	6 (12.5)

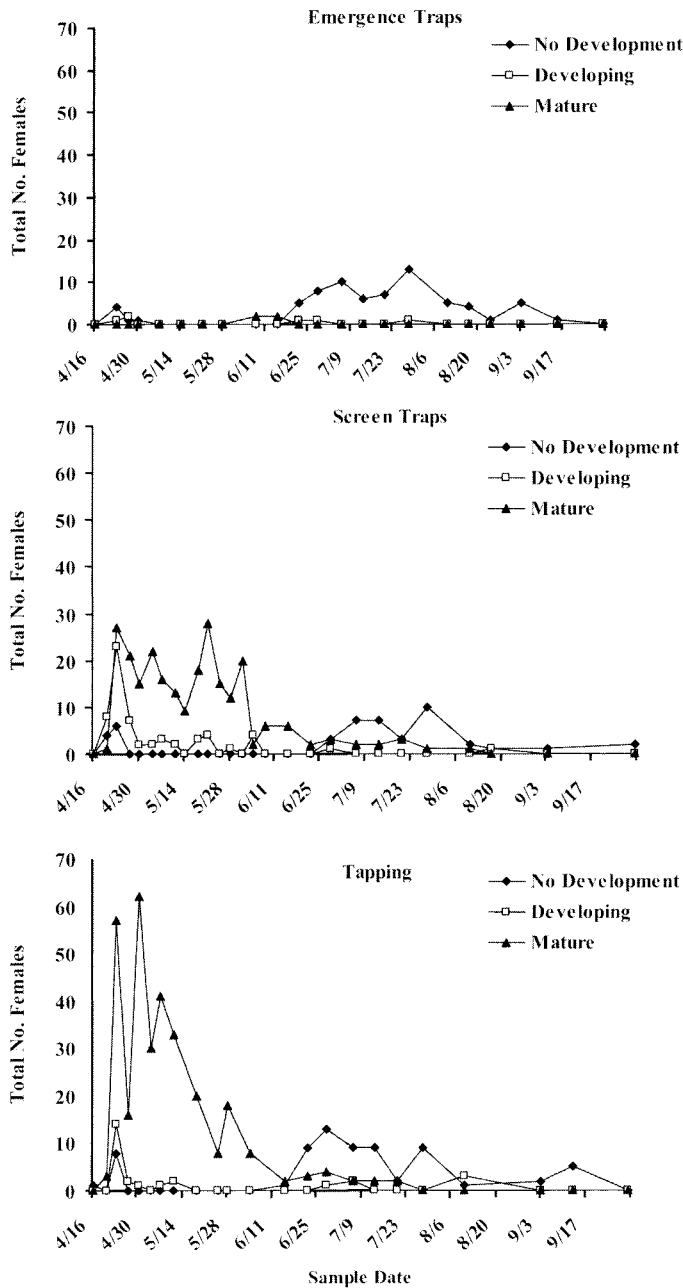


Fig. 1. Total number of females captured in emergence traps, screen traps, and from tapping samples of host tree canopies with mature ovaries, developing ovaries, and no ovarian development based on laboratory dissections and descriptions by Smith and Salkeld (1964).

samples taken in late June through August had obvious signs of oogenesis and were rapidly becoming sexually mature. Because their appearance was over 3 months after emergence of the wild population was first detected (8 April 2004), and a 2-month period in which nearly all females that were dissected were reproductively mature, it is reasonable to assume that these females did not overwinter, but instead are the progeny of the overwintered generation and represent the newly-emerged reproductively active summer generation. These results are strengthened by degree day models generated by Lan et al. (2004) on temperature-dependent development of the multivoltine summer generation of plum curculio found in the southeastern United States. They reported that the lower temperature thresholds for larval and pupal development were 11.1°C and 8.7°C, respectively, with thermal time requirements for peak larval emergence occurring at 215.5 DD and adult emergence at 442.4 DD thereafter. Based on significant oviposition occurring beginning on 21 April 2004 in these studies (Leskey, unpubl. data), peak larval emergence could have occurred as early as 10 May 2004 (over 220 DD accumulated), with over 300 DD accumulated by 15 May 2004. Adult emergence was reached by 14 June 2004 based on an accumulation 442.4 DD beginning on 16 May 2004. Developmental results predicted by these degree day models align to field data closely as newly-eclosed adults were present in emergence traps beginning on 22 June 2004.

These results are further supported by developmental data based on the timing of oogenesis. Hoffman et al. (2004) reported that oocyte development in newly-eclosed multivoltine populations reared at 25°C and 16:8 (L:D) was detectable in less than 200 DD₁₀ with the total numbers of oocytes peaking by ~278 DD₁₀. In results reported herein, females with developing oocytes were identified from screen and tapping samples collected between 28 June-17 August; therefore, they likely emerged from 18 June-6 August 2004 based on accumulations of greater than 225 DD₁₀ on 28 June 2004. These dates based on timing of oogenesis are in close agreement with emergence dates predicted by larval and adult emergence models developed by Lan et al. (2004), and on field data reported herein. In the mid-Atlantic, it appears that a summer generation of reproductively active adults occurs and is capable of damaging fruit by late June. This reproductively active generation is detected approximately 1 month earlier in more southerly locations, such as Georgia (Yonce et al. 1995).

Females captured in emergence and screen traps and those recovered from tapping samples of host tree canopies in September (along with most females recovered in late August) revealed no signs of oogenesis (Fig. 1) and likely reflected those individuals that overwinter in a state of reproductive diapause based on the descriptions of Smith and Salkeld (1964). However, unlike univoltine populations which enter an obligatory reproductive diapause, multivoltine populations have a facultative diapause (Smith and Flessel 1968) and can reproduce under favorable conditions. Indeed, Leskey and Wright (2004) were able to colonize and continuously rear plum curculio in the laboratory at 25°C (14L:10D) from larvae collected from infested fruit in the region, again providing strong biological evidence for the existence of multivoltine populations in the mid-Atlantic.

Recently, molecular-based efforts to separate morphologically identical univoltine and multivoltine populations have revealed differences in the strains of the *Wolbachia* bacterium present in (McClanahan et al. 2004, Zhang 2007) and in the partial mitochondrial cytochrome oxidase gene subunit I (mtCOI) obtained from (Zhang 2007) adults from different geographic populations. These differences corresponded roughly with known northern-location univoltine and southern-location multivoltine

populations and should help better define where the so-called 'northern' and 'southern' strain populations are located. In the mid-Atlantic, ovarian development data presented here and genetic data based on mtCOI (Zhang 2007) support the presence of multivoltine populations, which is in contrast to the map generated by Chapman (1938). For tree fruit growers in the mid-Atlantic, this means that fruit is at risk to damage by plum curculio from fruit set until near harvest, and highlights the importance of establishing an effective management program for this destructive pest.

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