# Aggregated oviposition by *Chymomyza amoena* (Diptera: Drosophilidae)[1]

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*Received 7 September 1988; accepted 18 May 1989*

*Summary.* Aggregated oviposition by *Chymomyza amoena* in Virginia and Michigan has been shown to be due to egg clustering, females attracted to fruits on which *C. amoena* females have already oviposited, and to variation in fruit attractiveness. Negative binomial *k* values support behavioral similarities among females of this rarely seen species in both states. Discovery of *C. amoena* in Europe may indicate that this larval overwintering drosophilid has a Holarctic distribution.
*Key words. Chymomyza*; drosophilid; aggregation; oviposition; behavior; unripe fruits.

Aggregated oviposition was initially proposed to account for the ability of many drosophilid species to share ephemereal resources[2,3]. Independence of coexisting species was assumed. Substrate frequency was such that an inferior competitor could find unused patches where it was protected from competition. Further findings suggested that interspecific competition is not a major factor in the organization of insect communities[4].

Increasingly, however, the topic of aggregated oviposition in structuring insect communities has become controversial[5-11]. Both the nature of species' interactions and the constancy of *k*, a negative binomial parameter as a measure of aggregation, have been questioned[5,9,11]. However laboratory and natural population studies have yielded conflicting results on species' interactions.

In the initial studies on competition among drosophilid species in the laboratory, Wallace found that *Drosophila melanogaster* would outcompete all others once it entered a system[12]. More recently, Gilpin et al. found results of two-species competitions could not be translated to multispecies laboratory experiments[13]. Worthen and McGuire found positive drosophilid species' associations among emergees from mushrooms in New Jersey[9]. *Chymomyza amoena* in Michigan and Virginia and *D. pseudoobscura* in California require other species to attack firm substrates first, enabling oviposition by the drosophilid females in immature fruits and nuts[14-17].

Nevertheless, even critics acknowledge that aggregation is an interesting addition to competition theory[5] while proponents confess that there is little information on drosophilid oviposition under field conditions[8]. Atkinson and Shorrocks argued that aggregation could arise from three sources: 1) true contagion, that is, the presence of an egg or larvae could stimulate a second female of the same species to choose the same oviposition site; 2) eggs laid in clusters, and 3) variable patch attractiveness[3]. *Chymomyza amoena* is such a low density drosophilid that adults are rarely seen. Instead, substrates suspected to contain eggs are collected, inspected and those found with eggs retained. Additionally, in Michigan and in Giles County, Virginia, it is the only or the predominant drosophilid ovipositing in unripe parasitized fruits. Eggs are distinctive[14-16,18].

As part of a comparative study on oviposition behavior among populations in the two states[19], egg aggregation studies were undertaken. Aggregation has been found to be influenced by all three factors in both states. The average *k* value for the negative binomial for both Virginia and Michigan, $0.18 \pm 0.02$, is significantly lower ($p < 0.05$) than that observed in other natural drosophilid populations, $0.45 \pm 0.09$. This indication of a higher degree of aggregation is supported by distributions of egg numbers over fruits, as shown in figures 1 (Virginia) and 2 (Michigan). Other species as the lesser apple worm, *Grapholitha prunivora*, are readily able to escape competition. However, the ability of larval overwintering *C. amoena*[20,21] to have escaped detection as a breeder in unripe fruits in the United States may have implications for its presence in Europe[18,22].

## *Materials and methods*

In 1986 apple collections were made at Pamplin and Danville in the Piedmont section of Virginia and a Rt. 700 site in southwestern Virginia in June. Collections were again made in early, mid and late July in a Blacksburg orchard and at the Rt. 700 site in southwestern Virginia. The number of *C. amoena* eggs were recorded per apple, if any, and the number of lesser apple worm eggs also counted. At the southwestern Virginia sites apples containing *C. amoena* eggs in July were further categorized as brown rotting, unripe firm, ripe, frassy or non-frassy. Final determination for the latter was made by dissection in late July if no frass was visible initially. In 1987 the Rt. 700 site and the Blacksburg orchard were again sampled three times during July as were trees near Mt. Lake Hotel which had fruited in 1985 and in 1986 but were a scantly used resource in 1986. Again, numbers of *C. amoena* eggs were recorded per fruit, if any, for collections from the three 1987 sites. From laboratory experiments, *C. amoena* females have been found to preferentially oviposit where *C. amoena* eggs already exist[14]. A final collection was made in August at the Rt. 700 site to survey for the presence of 'old' (yellowed) and new unhatched *C. amoena* eggs on apples[16].

To obtain data on egg distribution over fruits in Michigan, collections of plums and apples were made in June 1987 in an East Lansing neighborhood; apples were sampled also in August 1987. In this final collection, 'old' and 'new' eggs were scored[15].

Data on numbers of fruits sampled, means and negative binomial *k* values presented elsewhere[15, 16, 19] have been based on individual collections. Here we pool all Virginia collections within years and Michigan collections for type of fruit to compare negative binomial *k* values between states and with other *Drosophila* natural population negative binomial *k* values.

For 1986 collections use of brown rotting versus unripe apples was compared at the southwestern Virginia sites; *C. amoena* females in Michigan typically oviposit on parasitized unripe apples[14, 15]. All computations have been made with the aid of the Sokal and Rohlf Stat-Pak. Sigma Plot has been used to make the graphs.

*Results*

Table 1 presents the means and negative binomial *k* values for *C. amoena* oviposition in two states. The total number of apples in Virginia in 1986 and 1987 and total number of plums and apples in Michigan in 1987, from which these statistics were determined, is also shown. Although fruit numbers were reduced in 1986 due to the southeastern drought, one site in particular – the Rt. 700 site – shows little diminution of egg clustering between years. When overall frequency distributions are compared between years, as given in figure 1, this is the site where clusters numbering over 10 eggs are frequent. Clusters of 10 or more eggs are found in Michigan apples, but are rare on plums, as is evident in figure 2. As the initially available substrate in this particular locality, the low density may be due to multiple factors: low numbers of ovipositing females, lower egg production by young females, preferential switch to apples when they become available. The average negative binomial *k* value for Michigan, 0.21 ± 0.03, is nonsignificantly higher than that for Virginia, 0.14 ± 0.01. However, the overall negative binomial *k* value, 0.18 ± 0.02, is significantly lower ($F_{1,4} = 17.55$; $p < 0.05$) than that recorded for *D. subobscura* and the Hawaiian *Drosophila*[3].

Egg clustering is evident in figures 1 and 2. Table 2 also affirms that females in nature preferentially oviposit on apples containing *C. amoena* eggs. By August, the increase in numbers of ripe damaged apples increases the numbers of unused versus previously used substrates available to *C. amoena* females. Presence of brown unripe

Table 1. Comparison of means and negative binomial *k* values for *C. amoena* oviposition on fruits in Virginia and Michigan.

| State | Year | Fruit | No. fruits | mean | *k* |
|---|---|---|---|---|---|
| Virginia | 1986 | Apples | 494 | 1.43 | 0.133 |
| | 1987 | Apples | 706 | 1.26 | 0.157 |
| Michigan | 1987 | Plums | 216 | 0.50 | 0.186 |
| | 1987 | Apples | 158 | 2.55 | 0.239 |

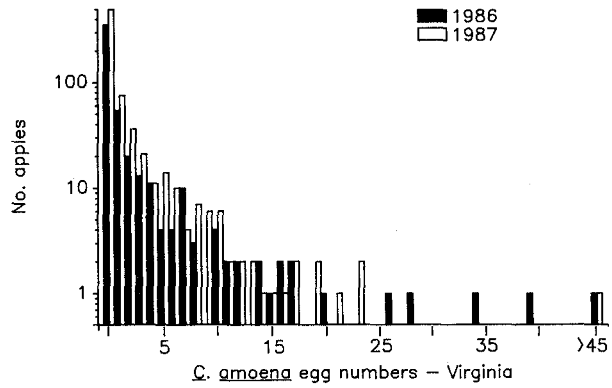


Figure 1. The distribution of eggs over fruits in two summers. The semilog plot is used to accommodate the numbers of fruits with no eggs and the number of single apples with clusters having many eggs.

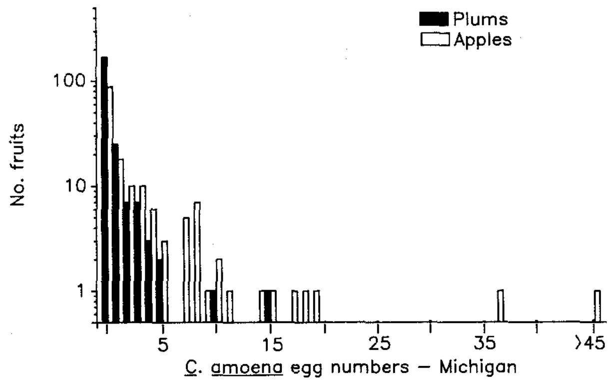


Figure 2. The distribution of eggs over plums in June and apples in June and August in an East Lansing neighborhood in summer 1987. Semilog plot has been used.

Table 2. Comparison of numbers of apples containing old and new *C. amoena* eggs collected at one site each in Virginia and Michigan in August, 1987.

| State | Apples with *C. amoena* eggs None | Old | New | Old and New | Total |
|---|---|---|---|---|---|
| Virginia | 33 | 25 | 0 | 11 | 69 |
| Michigan | 7 | 9 | 5 | 8 | 29 |
| | 40 | 34 | 5 | 19 | 98 |

d.f. = 3; G = 16.78; $p < 0.005$.

rotting apples increases diversity among available oviposition substrates. Table 3 shows that of the two types of apples available beginning in early July in Virginia, use of unripe parasitized apples agrees with Michigan usage. However, females alternately opt for a softer rotting nonparasitized substrate. The brown unripe rotting nonparasitized fruit is the predominant type of apple on which *C. amoena* females oviposit at the Hotel site, a site heavily predated by deer beginning in August. In color, texture and low density of parasitism, the brown unripe rotting apple closely resembles overwintered *Malus coronaria* fruits in Michigan. Whereas adults emerging from endemic crabapples have been fertile, there is evidence that emergees from unripe rotting apples are infertile[16]. Also, it has not been possible to establish a laboratory stock

Table 3. Categorization of oviposition substrates in southwestern Virginia in July 1986. Only apples with *C. amoena* eggs included.

| Color/type of apple | Frass | No frass | Total |
|---|---|---|---|
| Brown unripe rotting | 6 | 19 | 25 |
| Green unripe | 36 | 17 | 53 |
| Ripe | 7 | 3 | 10 |
| | 49 | 39 | 88 |

d.f. = 2; G = 14.58; $p < 0.005$. Reprinted with permission from American midland Naturalist.

Table 4. Numbers of separate and shared fruits with *C. amoena* and *G. prunivora* eggs in different Virginia areas in June and July 1986. Total number of fruits inspected is also given.

| Location | No. sites | Total No. apples | No. apples with eggs *C. a.* | *G. p.* | Both |
|---|---|---|---|---|---|
| Piedmont | 2 | 157 | 33 | 11 | 9 |
| Southwest | 2 | 337 | 91 | 4 | 6 |
| | | 494 | 124 | 15 | 15 |

d.f. = 2; G = 17.004; $p < 0.005$.

from emergees from apples collected at the Hotel site. Trees are not sprayed at any site used in this study.

Table 4 confirms that females of other insect species have available to them substrates on which *C. amoena* females have not oviposited. Furthermore, at the Danville site, *G. prunivora* had become the dominant species by mid-July. Apples collected no longer contained *C. amoena* eggs.

*Discussion*

The study on *C. amoena* demonstrates that aggregated oviposition can arise from the three causes postulated by Atkinson and Shorrocks[3]: true contagion, egg clustering and variable patch attractiveness. Where resources are abundant, other insects can escape interspecific competition, if the female so desires. Egg clustering, both from laying more than one egg at a time and attraction to sites used by females of the same species, assures intraspecific competition however. Despite the larger size of apples by late July and mid August, the low numbers of *C. amoena* adults emerging even under laboratory conditions in contrast to the numbers of eggs laid[14–16] suggests the term 'throw-away' species aptly describes this larval overwintering drosophilid. A winter mortality of over fifty percent[20], and low adult numbers in comparison to the numbers of eggs laid indicates this species remains adapted to the small population sizes that seem to typify the forest members of this drosophilid genus[19].

Controversies over increasing negative binomial $k$ values versus constant negative binomial $k$ values versus inadequacy of this measurement are not resolved by the present data. Increasing negative binomial $k$ values over serial collections of plums and apples in Michigan[15] were not realized in Virginia[16]. Computing negative binomial $k$ values from the total number of fruits collected each year in Virginia or fruit types in Michigan effects a nonsignificant reduction in their values. However, conclusions remain the same that *C. amoena* females behave comparably in both states in terms of clustered egg laying, in attraction to previously parasitized fruits including fruits still on the trees, and in attraction to substrates on which other *C. amoena* females have oviposited[19]. Taylor et al. raised the question of geographical differences[10].

To the argument that interspecific competition is not a major factor in organizing insect communities, an abandoned apple orchard or stand of untended trees continuing to produce fruits provides no single answer. Primary pests, plum curculio *Conotrachelus nenuphar* and codling moth *Cydia pomonella*, seldom co-occur in the same fruit. Ripening fruits attract later invaders. Among fallen fruits, green unripe parasitized or brown unripe rotting fruits may attract a different insect assemblage to fallen fruits available later at the same site.

Recently *C. amoena* has also been collected in the German Democratic Republic in addition to Czechoslovakia[18,22]. Arrival via infected fruits from the United States, similar to *C. procnemis*'s invasion of Japan, is suggested[18,23]. As noted, this species already possesses biological adaptation to the European climate and is capable of spreading[18].

Presumably *C. amoena* is native to North America. Freeze tolerance, use of endemic crabapples, acorns and other nuts as breeding and overwintering substrates[20,21], and ability to escape detection as a widespread invader of unripe parasitized fruits in Michigan and Virginia[14–16,19] suggest that it may have a Holarctic distribution. Oaks and many species of native crabapples are found throughout the Northern Hemisphere.

1 The research in Virginia during summer 1986, conducted at Mt. Lake Biological Station, was supported by a fellowship from the University of Virginia. Thanks are gratefully extended to all property owners in Virginia and Michigan for allowing me to collect fruits and to Blaine Cole, Director and J. J. Murray, Chairman of the Biology Dept., University of Virginia for research space in 1986 and 1987. R. N. Band constructed the figures. Comments from reviewers have been helpful.
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0014-4754/89/090893-03$1.50 + 0.20/0