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BEHAVIOR AND TAXONOMY OF A CHYMOMYZID FLY *(CHYMOMYZIA AMOENA)*

Henretta Trent Band

ABSTRACT: Molecular genetics studies on the chymomyzids have produced divergent results on their relation to the genus *Drosophila*. Behavior has been used to assess the appropriateness of their inclusion in the genus (MacIntyre and Collier, 1986) or off the drosophilid main stem (Beverley and Wilson, 1984). Laboratory and natural population studies on *Chymomyza amoena* in Michigan and Virginia and observations on multiple species aggregations at natural sites in 1986 and 1987 in Virginia's Allegheny Mountains have been carried out. Wing-waving and foreleg splaying are characteristics of both sexes. In nature, females do not approach males until sexually mature. All population sizes seem small. Studies on *C. amoena* indicate that behavioral phenotypic plasticity exists for all stages: larval feeding substrates, pupation site choice, mating system, egg deposition and oviposition site selection. Behavioral traits shared with the lek *Drosophila* (Hawaiian and Australian), genus *Scaptomyza*, subgenus *Scaptodrosophila*, subgenus *Sophophora* and genus *Lissocephala* among the drosophilids, and the tephritids, otitids and hymenopterans outside the family Drosophilidae suggest that chymomyzids retain characteristics of primitive drosophilids that have undergone selective modification in the evolution of different drosophilid lineages. Significant differences in aggression between Michigan and Virginia *C. amoena* populations support this conclusion. Throckmorton (1962, 1966) anticipated the chymomyzid relation to the drosophilid stem from external and internal anatomical studies. A wood breeding habitat of most forest chymomyzids is also in agreement with recent molecular genetics evidence that fermented fruit breeding evolved later in drosophilid evolution.

The status of the chymomyzids within the family Drosophilidae has become controversial. Systematics based on morphological and behavioral data treats them as a separate genus (Wheeler, 1952, 1981; Hackman et al., 1970; Okada, 1976; Bachli & Rocha-Pite, 1981, 1982; Grimaldi, 1986). Molecular systematics places them in the genus *Drosophila* (Collier & MacIntyre, 1977; MacIntyre & Collier, 1986) or considerably distant from this genus (Beverley & Wilson, 1982, 1984). Molecular systematics is not without critics (Throckmorton, 1977, 1978) or cautionary interpreters (Wilson, Carlson & White, 1977).

The phylogenetic position of the chymomyzids underwent revision earlier in the 1970s. Chromosomally, the group is related to the subgenus *Sophophora* of the genus *Drosophila* (Clayton & Ward, 1954; Hackman et al., 1970; Clayton & Guest, 1986). Comparative internal morphological studies also suggested affinities to the Sophophoran and Hawaiian drosophilids (Throckmorton, 1962, 1966). The separate genus status

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was retained. Hackman et al. (1970) agreed on the chromosomal relationships but suggested deriving the chymomyzids as a separate lineage between the *Sophophora* and the *Scaptodrosophila*, with which larvae share morphological traits. Throckmorton (1975) adopted this proposal.

Behavior is a component of taxonomy for chymomyzid species (Wheeler, 1952; Okada, 1976; Grimaldi, 1986). Adults wing-wave; males are aggressive and use their front feet like boxers; matings are of the assault type (Wheeler, 1952). Grimaldi (1986) describes foreleg splaying for a South American chymomyzid. Behavior may provide clues to the taxonomic status of the group, bearing on old and current controversies. Summaries of drosophilid behavior have been provided in recent books or reviews (Spieth, 1975, 1982; Ehrman, 1978; Grossfield, 1978; Ehrman & Parsons, 1981; Barker & Starmer, 1982; Parsons, 1982; Parsons, 1983; Brncic, 1983; Lachaise & Tsacas, 1983; Lumme & Lakovaara, 1983; Mueller, 1985). They contain little behavioral information on the chymomyzids for which only scattered reports exist (Wheeler, 1952; Watabe, 1985; Band, 1986; Grimaldi, 1986).

Laboratory and natural population studies on *Chymomyza amoena* in Michigan and Virginia and other chymomyzids at higher elevations in Virginia's Allegheny Mountains provide comparisons with other drosophilids. It also enables a beginning behavioral comparison to other insect groups (Alcock, 1979; Thornhill & Alcock, 1983). The relationship of the family Drosophilidae to other insect families has also come into question (Beverley & Wilson, 1982; MacIntyre & Collier, 1986)

MATERIALS AND METHODS

Study Sites

A detailed description of study sites for *C. amoena* has been given in Band (1988a). Behavioral studies made use of the East Jordan, Michigan (lat. 45. 10 ° N), mid-Michigan (lat. 42. 43 ° N) and mid-South (Lats. 36.29 ° N to 37.24 ° N) populations. Additional information has been derived from St. Louis, Missouri (lat. 38.38 ° N) populations collected and shipped to East Lansing by the late Harrison Stalker. All photographs made in the laboratory have been made with a Nikon camera; all photographs at Mt. Lake Biological Station (MLBS) have been made with a Pentax.

Briefly, populations for East Jordan, Michigan derive from apples collected from a group of old trees summer 1978 through summer 1981. Mid-Michigan populations for mating, oviposition, breeding season and laboratory studies since 1981 primarily derive from farms west of Lansing (site A) having apple and walnut trees, an East Lansing neighborhood (site B) having a variety of fruit trees, a farm east of East Lansing (site D) with walnut and other nut and apple trees, a thicket of *Malus coronaria* of unknown age which existed until spring 1987 when it was cleared away. Mid-South Virginia sites for *C. amoena* summer behavioral work include Danville orchard and city sites, a Blacksburg orchard, sites along Rt. 700 near the Biological Station and the apple tree at the Station. Other populations have also come from the MLBS vicinity in Giles County, and Eden, North Carolina.

Additional chymomyzid species have been studied also at the Station (1985) and two other localities near the Station in 1986 and 1987, respectively. Observations followed by collection and identification provide information on species aggregation, niche attractiveness and inter-species interactions. If and when present, *C. amoena* is the only banded wing species. Laboratory work provided further information on *C. aldrichii*.

EXPERIMENTS AND OBSERVATIONS

For *C. amoena*, larval and adult behavior will be treated separately, where appropriate.

Substrate Utilization

Carson (1971) recognized four breeding sites for temporal woodland drosophilids: a) fleshy fruits and fungi; b) sap fluxes; c) decaying vegetation; d) flowers. Cosmopolitan species are typically associated with rotting fruits and vegetables (Ehrman, 1978). Throckmorton (1975) notes that generally *Scaptodrosophila* like substrates in a fresher state. *Chymomyza amoena* as a breeder in multiple fruit and nut substrates and in frass is covered in Band (1988a, b, c), as a larval overwinterer in fruits and nuts in Band & Band (1982, 1984, 1987). Re-creation in the laboratory, using fresh commercial apple, of the lengthy emergence from any one apple/native crabapple collection (Band, 1988a) provides data both on an F_1 and F_2 ability to breed in fresh apple, and lengthy prefertile period. Other oviposition work also provides information on larval ability to develop in unripe frassy and ripe fruits.

Larval Behavior and Pupation Site Choices

Grossfield (1978) presents information on drosophilid larval migratory behavior and puparition. *Scaptodrosophila* larvae skip when leaving the substrate, as do some Hawaiian *Drosophila* (Carson et al., 1970). *Drosophila melanogaster* larvae typically migrate but may pupate in a variety of locations, on the surface or away from the substrate. Many Hawaiian *Drosophila* pupate in the soil; some scaptomyzoids pupate on the substrate surface, others in situ.

To study pupation site choice, individual crabapples (MI) and apples (VA) having *C. amoena* eggs in 1985 and 1986 were placed over potting soil (vermiculite) and numbers of larvae leaving the substrate versus numbers of larvae remaining with the substrate for pupation were determined by transferring the soil to a beaker of water; numbers of pupal cases floating in the water versus total numbers of adults emerging from the culture were compared (Band, 1988a). To determine the tendency for larvae to pupate on the surface, the 12 walnuts yielding many *C. amoena* adults in November 1984 were later inspected; 33 walnuts gathered at the same time, but kept in an unheated shelter and held overwinter, were inspected in spring 1985 (Band & Band, 1987).

Other species are known to migrate following disturbance. Necessity to transfer *C. amoena* larvae to fresh media due to mold, mites or both stimulates migration, followed by pupation, usually within 24 hours. A photograph of this phenomenon was made in summer 1987.

Natural and Laboratory Populations of C. amoena

Carson et al. (1970), Ehrman (1978), Ehrman & Parsons (1981), Spieth (1975, 1982) and Parsons (1982, 1983) provide information on mating behavior in different drosophilid genera and subgenera. Wheeler (1952) and Grimaldi (1986) give descriptions of some chymomyzid behaviors. Observations for a week at East Jordan and sporadically in mid-Michigan enabled comparison of natural population and laboratory observed behaviors. Apples on which adults were displaying in 1981 and 1982 were collected and inspected. Males and females on apples in 1981 were transferred to laboratory medium and time to oviposition determined. A pair captured in 1982 was transferred to apple and time. to oviposition determined. To determine that fallen apples on which flies were displaying were not feeding substrates, 150 adults were distributed in 3 population bottles, supplied with immature unbroken apples and numbers alive after two days determined. By contrast, 179 apples were collected 13 June 1985, inspected for eggs and all were dissected and scored for presence of internal frass. A windstorm blew down many in May.

To determine that some movements occur in both sexes, females were transferred to a population bottle and their manner of walking observed. To date, attempts to photograph some behaviors (e.g. fighting, foreleg splaying) have been unsuccessful. Other behaviors include simple courtship (if any) prior to assault type mating attempts, capture-in-the-air type matings, female avoidance of "courting" males (Band, 1988a).

Time To Oviposition, Laboratory Data

For both intra- and interpopulation crosses, matings were made with nonaged females and males. Time to oviposition was compared with data from interpopulation crosses made with aged flies and pairs captured in nature (Band, 1988a). In 1986 crosses between Michigan *C. amoena* emerging from apples and Virginia *C. amoena* also emerging from apples were carried out on apples + frass (Band, 1988c). Time to oviposition were compared with interpopulation crosses carried out on laboratory medium.

Oviposition Preference, New Versus Used Substrates:

Females of some species produce pheromones that inhibit others of their species from ovipositing on the same piece of fruit (Thornhill & Alcock, 1983). *Drosophila* females commonly lay eggs where others of their species have oviposited (Mueller, 1985). *Chymomyza amoena* females emerging from native crabapples in May 1985 were allowed to choose between two immature firm apples, matched for size, on one of which two *C. amoena* eggs had been placed. A dish of medium assured continued fertility. Four pairs (females and males) were used in three replicates over a seven-day period (Band, 1988a).

Egg Aggregation in Nature

Two sites near MLBS produced apples in summer 1986 and 1987. Collections were scored for the presence of *C. amoena* eggs and negative binomial k values determined (Band, 1988c). Collections of plums and apples were also recorded for *C. amoena* eggs in Michigan in 1987 (Band, 1988b). Egg aggregation were compared in the two states.

Egg aggregation, for an unknown or little known species, is a compound measure of females to oviposit where others of their species have oviposited and for females to lay more than one egg at a time. Behavioral oviposition diversity exists among drosophilids (Carson et al., 1970; Grossfield, 1978; Mueller, 1985). The numbers of substrates with one versus more than one egg were also compared in 1987.

Aggressive Behaviors

The frequency of aggressive events determined by half-hour observations of small populations (7-12 individuals with at least 3 males present) were compared for Michigan and Virginia populations at one-two days after emergence versus 3-6 days after emergence. The number of encounters between individuals (orienting toward one another), number of fights and number of mating attempts were recorded. If population bottles were moved prior to the timed observations, populations were given a half-hour to equilibrate before observations were made. At least two localities for each state were included in the replicates.

For crowded cultures, Virginia populations of 15-20 adults were used. Glass population bottles were supplied with a dish of laboratory medium.

For more serious consequences of aggression, a clear plastic box was used into which an apple was placed having one or more holes. A small population (3 males, 2 females) was aspirated into it and timed experiments carried out. Again, adults were of comparable ages.

Other Chymomyzid Species

Single male aggregations have been recorded for a number of insect species, including Hawaiian *Drosophila* (Thornhill & Alcock, 1983). Males of different species share the same lek in Australia (Ehrman & Parsons, 1981; Parsons, 1982, 1983). *Drosophila melanogaster* males have demonstrated lek behavior in Yugoslavia (Taylor & Kekic, 1988). Other *Drosophila* species are attracted to the same site year after year (Carson & Stalker, 1951). Attraction of chymomyzids to fresh cut fire wood was noted in 1985 at MLBS. A chymomyzid species aggregation was observed at a natural site in 1986. Species coming were determined over a two-week period in July. Attraction to old versus fresh damaged trees and observations on species present were extended into August in 1987 until no more were attracted to the site.

RESULTS

Substrate Utilization

A single *C. amoena* pair from an October 1978 EJ apple collection produced 34 F_1 on fresh commercial apples. Mass matings among sequential emergees had an average emergence-to-oviposition interval of 8.7 ± 1.4 days and produced 81 F_2, again on fresh apples. The four pairs emerging from native crabapples produced 52 adults on unripe apples and 51 adults on ripe apples after being transferred to this substrate. The following year adults presented simultaneously with unripe frassy apples and ripe apples supplied with frass oviposited on both but 76 adults emerged from the unripe frassy apples, 32 adults from the ripe frassy apples ($\chi^{22}_{1} = 17.0$; $P < 0.005$). Data are the pooled results of three replicates which are similar.

Larval Behavior and Pupation Site Choices

In 1985, 46 larvae pupated in soil and 76 pupated in situ among the 122 *C. amoena* adults emerging from 9 native crabapples collected in May. In 1986, 49 migrated to the soil, 127 pupated in situ among the 176 adults from 20 native crabapples. In 1985, 11 larvae pupated in soil and 30 in situ among the five apples from the initial mid-July collections from which *C. amoena* adults emerged. Both *Drosophila* and *C. amoena* adults emerged from the later July 1985 collection (Band, 1988a), complicating determination of behavioral polymorphism for pupation site choice. In 1986, 13 of 16 adults emerging from the initial apple collection migrated to the soil; only three remained with the substrate. Our interest here is not in the effects of the 1986 Southeast drought on numbers surviving but in the persistence of variation for migrating versus remaining with the substrate at the time of puparition. Overall figures for both years indicate that 32% of the Michigan and 42% of the Virginia larvae pupariated in soil.

The 33 walnuts inspected in spring 1985 had 2 pupae on the outside, 27 inside and 3 still larvae after being held overwinter in an unheated shelter; the 12 walnuts yielding a November 1984 population showed 12 pupae on the outside.

Mass migration typically results from disturbing a culture. Plate I.c shows pupae on tissue following larval migration 24 hours previously.

Natural and Laboratory Populations of C. amoena

Mating pairs of *C. amoena* were not observed at East Jordan, Michigan. Battles between adults, presumably males, were lengthy, wide-ranging, but inflicted no damage. Larger aggregations of adults at site A Lansing seemed not to diminish the intensity of fights between any two individuals, just the scope of the territory covered in chasing. Aggression is present in a variety of insects, including Hawaiian drosophilids (Thornhill & Alcock, 1983). Seven adults, all males, captured at site A in early July 1981 were on immature fallen apples. Kept on them in the laboratory, all died within 24 hours. Five adults (3 females, 2 males) captured the next day on the same substrates were transferred to medium + apple and produced eggs in 3 days. A pair captured in 1982 also produced eggs in 3 days, given commercial apple only.

In 1981, 18 of the 22 immature fallen apples on which flies were displaying (wingwaving) at site A had *C. amoena* eggs. In 1982, 17 of 21 immature fallen apples at site B had *C. amoena* eggs. There is a significant probability ($\chi^2_2 = 15.72$, $P < 0.001$) that a displaying adult will be on an apple on which a *C. amoena* female has already oviposted. In *Drosophila* both sexes can be attracted to sites where gravid females

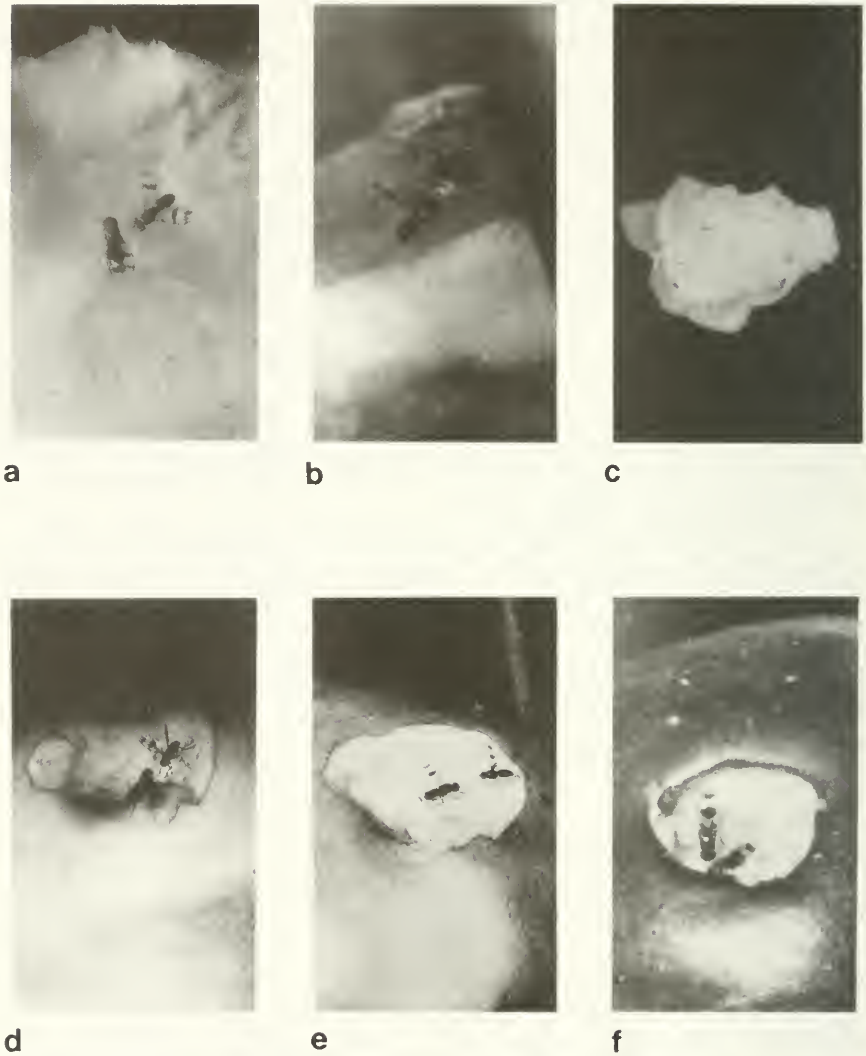

Plate 1. a) A *C. amoena* male approaches a female; b) A female with uplifted abdomen, the male mating avoidance position; c) Pupation in tissue following larval mass migration; d) Forelegs uplifted; in "splaying" both forelegs are extended outward, then sidewise simultaneously as in a swimmer's breaststroke; e) A hostile encounter showing single wing elevation by each individual; the fly on the right is a female; f) Two individuals (two females or a male and a female) may share a feeding site.

have been (males: Spence et al., 1984; females: Mueller, 1985). When adults were placed in population bottles with unripe fallen apples comparable to those on which adults had been captured, all died within two days. However, 31 of the 179 fallen apples collected 13 June 1985 contained internal frass and 7 had 23 *C. amoena* eggs on the exterior.

Laboratory observations reveal that females elevate the abdomen to avoid "courting" males, as shown in Plate 1.b. Females may also rotate their wings to 90° angles to the body in such a position, and continue feeding. Ehrman & Parsons (1981) describe the uplifted abdominal position in other *Drosophila* females but to date this has not been seen in natural populations of *C. amoena*. Females in nature do not approach males until past their prefertile period.

Capture-in-the-air-type matings have been observed among Michigan, Missouri and Virginia populations in laboratory cultures; here a male on the top or side of the population bottle leaps on the departing female and the two glide to the bottom of the population bottle where mating may or may not occur. The assault-type mating system (Wheeler, 1952) is also inefficient as practiced in this species since a male mounted on a female may not be "in copula." Courtship is simple when practiced and consists of tapping the female from any direction. In laboratory culture, males may approach females, as seen in Plate 1.a, or females approach males. A mating pair continues to be mobile, the female carrying the male. Although rape has received some attention among other animal species (Alcock, 1979; Thornhill & Alcock, 1983; Krebs & Davies, 1987), only one possible incidence to date has been noted among laboratory *C. amoena;* this was among the slowest emergees in the October 1978 F_1 cultures where a female fled after mating. Females usually struggle free or dislodge a male by kicking. Similar behavior is described for *Scaptomyza* females (Carson, Hardy, Spieth & Stone, 1970).

Both sexes have the capacity to move sidewise, to wing-wave, to splay the front feet while wing-waving, to pulsate the abdomen by rapidly depressing it downward, to "rush" an opponent. Females are also aggressive but are less pugilistic than males; female-female encounters are marked by much wing-waving and rapidly depressing the abdomen. Plate 1.d shows an individual with uplifted forelegs. Plate 1.e shows a hostile encounter between two, one of which is a female. Plate 1.f shows that individuals, two females or a female and a male, will share a limited feeding site. Photographs also depict attraction to fresh damaged apple.

Time to Oviposition, Laboratory Data

Table 1 shows the comparisons of oviposition rates among intra-and interpopulation matings on medium and on apples. The latter includes both crosses between populations within states and between states. Typically when flies are not aged, mating and oviposition appear to take

TABLE 1
Comparison of emergence (e) to oviposition (o) in days for *Chymomyza amoena* in a variety of crosses

Type of Cross	*Number*	*e to o (MEAN ± SEM)*	*F*
On Medium			
Not aged			
MI	7	6.42 ± 0.75	
MO	2	4.50 ± 0.50	
Mid-South	5	8.40 ± 2.25	$F_{2,11} = 1.07$
MI x MI	8	9.25 ± 0.77	
MI x MO	6	10.20 ± 1.01	
MI x Mid-South	6	7.33 ± 1.02	
VA x VA	4	9.75 ± 3.09	$F_{3,20} = 0.87$
Hybrids			
Walnuts	7	9.75 ± 0.82	$F_{1,10} = 5.96$
Crabapples	4	6.50 ± 0.48	$(P < 0.05)$
Aged			
MI x MI, MO	12	3.40 ± 0.29	
On Apples, not aged			
1978 MI	3	8.67 ± 1.45	
1986 MI x VA*	4	5.25 ± 0.25	
1986 VA x VA*	4	7.50 ± 1.50	$F_{2,8} = 2.13$

* on frass

place faster when males and females come from the same culture. Interestingly, laboratory grown flies mated with walnut emergees show an oviposition delay comparable to interpopulation crosses; crabapple emergees are more readily accepted. Aged males and females have the same oviposition time as males and females captured together in nature, 3 days. The 1986 crosses using apples + frass demonstrate that Michigan and Virginia flies readily mate and produce eggs in about the same time as intraMichigan cultures on medium. However the use of frass does not significantly speed laboratory oviposition on apples.

Oviposition Preference, New Versus Used Substrates

Females presented with immature apples, matched for size, laid 87 eggs on the ones that had been "seeded" with two *C. amoena* eggs, 42 on the ones that lacked eggs ($\chi^2_1 = 22.2$; $P < 0.005$). Of the 42, 21 were laid in frass deposited by a pest larva that broke the surface (Band, 1988a). In August 1987, 12 apple collected in Virginia had a total of 134 eggs of which 29 looked new; 33 collected had no *C. amoena* eggs readily evident. In Michigan, 7 apples collected in August at site B contained 35 eggs of which 16 looked new; again 16 other apples lacked eggs (Band, 1988b). All apples had been damaged. Thus natural population results confirm earlier laboratory data that females are attracted to sites of prior *C. amoena* oviposition.

Egg Aggregation In Nature

Negative binomial *k* values indicating egg aggregation demonstrated no significant differences between Virginia populations (Band, 1988c) or between Michigan populations on different fruits (Band, 1988b). Virginia values for 1986 were 0.26 ± 0.05 ($N = 9$) for 1987, 0.18 ± 0.02 ($N = 9$). Michigan values were 0.24 ± 0.09 for eggs on plums ($N = 3$) and 0.29 ± 0.12 for eggs on apples ($N = 3$). The similarity of values between the two states is supported statistically. The average *k* value for Virginia is 0.22 ± 0.03, and for Michigan is 0.26 ± 0.07.

It is however, possible to compare numbers of apples with zero, one or more than one egg. This is shown in Table 2 for 1987 data. Significant heterogeneity becomes apparent in both Virginia (d.f. = 4; $G = 20.75$; $P < 0.005$) and Michigan (d.f. = 1; $G = 8.41$; $P < 0.05$) regarding substrates with one versus more than one egg, although again most substrates collected lacked any eggs.

Individually scattered eggs occur on media surface in the laboratory. For instance, 53% of 60 eggs on medium in a Virginia culture and 79% of 88 eggs in a Michigan culture did not touch another egg. Eggs are also oviposited on the surface and are not buried into the medium. In nature females lay significantly more eggs in holes, scars or breaks in the surface (Band, 1988a).

Aggressive Behaviors

Table 3 shows the average number of encounters, fights and mating attempts for 4 populations from Virginia and Michigan at different ages (0-2 days after emergence and 3-6 days after emergence). Table 4 gives the 3-way comparisons a) between age categories within states and b) between states within age categories. Older populations in both states have an increased frequency of mating attempts. Michigan populations in both age categories are more aggressive than Virginia populations, both in number of fights and number of mating attempts. Two Michigan females etherized and dissected at 2 days were immature despite male mating attempts.

Two large Virginia populations assessed for fights and mating attempts at 2 days past emergence had a mean number of 2.5 ± 0.5 fights

TABLE 2
Number of fruits with zero, one or more than one *C. amoena* egg in 1987

State	*Location*	*Number of fruits*	*Zero*	*One*	*> One*
VA	MLH	269	160	30	47
	Mid-700	200	132	13	55
	Blacksburg	237	160	30	47
MI	plums	216	169	25	22
	apples	158	88	18	52

1 vs > 1: VA: d.f. = 2, $G = 15.86$, $P < 0.005$; MI: d.f. = 1, $G = 9.13$, $P < 0.05$

TABLE 3
Comparison of *C. amoena* aggression by state and age, small populations, half-hour observations, four replicates (MEAN ± SEM)

State	*Age*	*Encounters*	*Fights*	*Mating Attempts*
VA	0–2 days	37.2 ± 7.92	0.25 ± 0.25	0.5 ± 0.5
	3–5 days	35.0 ± 8.80	1.5 ± 0.96	4.25 ± 2.36
MI	0–2 days	40.5 ± 4.55	1.25 ± 0.25	4.5 ± 1.19
	3–6 days	23.8 ± 2.29	1.75 ± 0.85	12.0 ± 1.47

and 6.5 ± 2.5 mating attempts. They did not differ significantly from small Michigan populations in the same age categories in these two measures. Only one actual mating was observed during these timed observations.

Small populations given a single apple with one hole cut into it and with three holes nevertheless supported only one male of the three aspirated into the container. Females, as expected, laid eggs in the exposed apple flesh.

Other Chymomyzid Species

In 1985 chymomyzid aggregations appeared on fresh cut (oak) firewood at the Station. Morning and evening assemblages occurred. As the only banded wing species, *C. amoena* could be observed courting interspecifically. Other chymomyzids captured fell into two groups, and contained previously unknown species. A larger species no. 1 was

TABLE 4
ANOVA Statistical comparisons of aggression data by state and age

State/Age	*Comparisons*	*d.f.*	*G*	*P*
VA	RxCxA Independence	17	79.45	< 0.005
	AxC Independence	2	17.41	< 0.005
	RxA Independence	3	19.57	< 0.005
	RxC Independence	6	22.63	< 0.005
	RxCxA Interaction	6	19.84	< 0.005
MI	RxCxA Independence	17	54.30	< 0.005
	AxC Independence	2	33.39	< 0.005
	RxA Independence	3	7.93	< 0.025
	RxC Independence	6	7.74	n.s.
	RxCxA Interaction	6	5.25	n.s.
A = age, R = replicates, C = behaviors				
Younger	RxCxA Independence	17	37.24	< 0.005
	AxC Independence	2	14.94	< 0.005
	RxA Independence	3	8.98	< 0.05
	RxC Independence	6	2.75	n.s.
	RxCxA Interaction	6	10.57	n.s.
Older	RxCxA Independence	17	79.47	< 0.005
	AxC Independence	2	23.61	< 0.005
	RxA Independence	3	14.86	< 0.005
	RxC Independence	6	11.04	n.s.
	RxCxA Interaction	6	29.96	n.s.
A = state, R = replicates, C = behaviors				

captured initially, a smaller species later. A pair of large chymomyzids included a species no. 1 male and another chymomyzid, now retrospectively, a *C. caudatula* male from its posterior anatomy (Band, 1986), after the capture of this species in 1986 and a species no. 1 female in 1987.

Species aggregations for 1986 and 1987 are shown in Table 5. Both occurred on damaged trees at elevations comparable to the Station grounds. The 1986 tree was wild cherry *Prunus* sp. (Plate 2.a); the wound measured 12.7 x 38 cm and was ringed by sap but no eggs or larvae were found in samples taken. Chymomyzids were captured between July 15 and July 25. Trapping and identification demonstrate a maximum of four and a minimum of two species were present, as shown in Table 5. Dark and light forms of both *C. procnemoides* and *C. aldrichii* were present. *Chymomyza caudatula* was captured only over the first three days but fighting between unequal sized males demonstrated

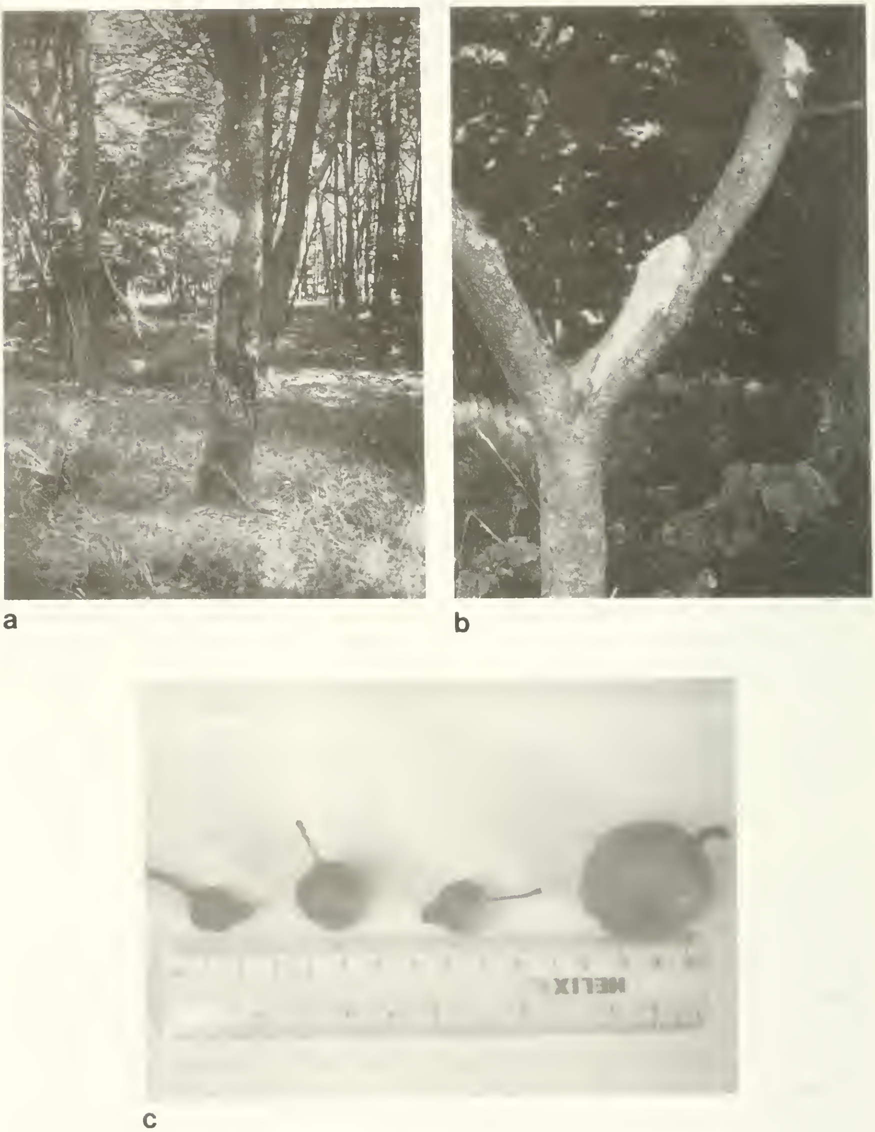

Plate 2. a) The 1986 lek chymomyzid tree, a wild cherry *Prunus* sp.; b) The 1987 lek chymomyzid tree, a striped maple *Acer pensylvanicum;* c) Size range of fallen apples used by *C. amoena* females for oviposition in Southwestern Virginia in early July 1987.

TABLE 5
Occurrence of chymomyzid species in Virginia's Allegheny Mountains in July 1986 and July and August 1987.

Species	*Dates*					*July 1986*					
	15	*16*	*17*	*18*	*19*	*20*	*21*	*22*	*23*	*24*	*25*
C. caudatula	—	—									
sp. no. 2			x								
C. procnemoides	—	—	—	—	—	—	—	—	—	—	
C. aldrichii			—	—	—	—	—	—	—	—	
C. amoena	x		x								

	July and August 1987															
	18	*19*	*20*	*21*	*22*	*23*	*24*	*25*	*26*	*27*	*28*	*29*	*30*	*31*	*1*	*2*
C. procnemoides	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
C. aldrichii	—	—	—	—	—	—	—	—	—	—	—					
sp. no. 1 female	x															

interspecific aggression. Mating pairs were observed beginning on July 16. Mating interference was also observed. Thornhill and Alcock (1983) argue that mating interference is a cost of male aggregation.

The 1987 tree was a striped maple *Acer pensylvanicum;* the wounds were extensive and there was no evidence of accumulated sap exudate (Plate 2.b). Both *C. procnemoides* and *C. aldrichii* shared the site and a single species no. 1 female was also captured. In these more shaded 1986 and 1987 locations, aggregations could be observed throughout the day. At a lower elevation on a lot being cleared, both *C. procnemoides* and species no. 2 chymomyzids were captured.

In 1986 of the 37 individuals trapped, 76% were males (Band, 1987). In 1987 22 individuals were trapped and 70% were males. The excess males to females at chymomyzid leks is as expected (Watabe, 1985; Band, 1986) and found by Parsons (1982, 1983) at the lek sites of Australian lek *Drosophila*.

A captured *C. aldrichii* male was placed with a *C. aldrichii* female, collected a day earlier, on Stalker's potato medium in the laboratory. Mating was observed the next day. However, both died within four days; the female was dissected and had two eggs ready for oviposition. Again, this supports evidence from *C. amoena* that females in nature only approach males past a lengthy prefertile period.

TABLE 6
Behavioral comparison of preadult traits

Chymomyza	*Also observed in*	*Reference*
Larvae		
cold-hardy	Tephritidae	Storey & Storey (1986)
	Otitidae	Band (1988a)
	Hemiptera, Hymenoptera	Somme (1982)
	Coleoptera, Lepidoptera	Somme (1982)
	Diptera	Somme (1982)
	Drosophila deflexa	Basden (1954)
Puparia		
in situ	Tephritidae	Storey & Storey (1986)
on surface	some drosophilids	Grossfield (1978)
in soil	Tephritidae	Dean & Chapman (1973)
	many Hawaiian *Drosophila*	Grossfield (1978)
Breeding substrate		
firm fruits	many insect groups	
	Lissocephala	Lachaise (1977)
fleshy fruits	*Scaptomyza*	Brncic (1983)
	s-g* *Scaptodrosophila*	Parsons (1983)
	s-g *Sophophora*, *Drosophila*	Parsons (1983)
	Tephritidae, Otitidae	Borror et al. (1981)
fresh fruits	s-g *Scaptodrosophila*	Throckmorton (1975)
	Tephritidae	Borror et al. (1981)
nut husks	Tephritidae	Borror et al. (1981)
acorns	Coleoptera	Borror et al. (1981)
frass	some *Drosophila*	Heed (1968)
wood	many insect groups	

*s-g = subgenus of the genus *Drosophila*

DISCUSSION

Tables 6 and 7 summarize behavioral comparisons of chymomyzids to well studied drosophilid genera, subgenera and other insect groups. Larval traits are surveyed in Table 6, adult traits in Table 7. Chymomyzids display a mixture of drosophila-like, nondrosophila-like and non-drosophilid behaviors. They span preadult, adult, male and female behaviors. Larval overwintering, wing-waving, male aggregations, capture-in-the-air or assault-type mating, and the use of firm substrates or decaying wood are primarily nondrosophila, nondrosophilid or found among the Hawaiian drosophilids. Foreleg splaying (Grimaldi, 1986;

TABLE 7
Behavioral comparison of adult traits

Chymomyza	*Also observed in*	*Reference*
Both sexes		
wing waving	Otitidae	personal observation
	Tephritidae	Borror et al. (1981)
	Hawaiian *Drosophila*	Spieth (1982)
	Drosophila tetraspilota	Grossfield (1978)
Males		
aggressive	Otitidae	Thornhill & Alcock (1983)
	Tephritidae	Thornhill & Alcock (1983)
	Hawaiian *Drosophila*	Spieth (1982)
lek behavior	Otitidae	Thornhill & Alcock (1983)
	Tephritidae	Bush (1975)
	Hawaiian *Drosophila*	Thornhill & Alcock (1983)
shared leks	Australian *Drosophila*	Ehrman & Parsons (1981)
aggregations	Otitidae	Thornhill & Alcock (1983)
	Tephritidae	Thornhill & Alcock (1983)
	Hymenoptera	Thornhill & Alcock (1983)
	Hawaiian *Drosophila*	Spieth (1982)
	Australian *Drosophila*	Parson (1983)
	Drosophila melanogaster	Taylor & Kekic (1988)
assault-type mating	Tephritidae	Thornhill & Alcock (1983)
	Scaptomyza	Carson et al. (1970)
capture-in-air	Hymenoptera	Thornhill & Alcock (1983)
Females		
mating avoidance	s-g *Sophophora*	Ehrman & Parsons (1981)
aggressive	Hymenoptera	Thornhill & Alcock (1983)
	Hawaiian *Drosophila*	Spieth (1975)
eggs on surface	*Scaptomyza*	Grossfield (1978)
eggs singly	s-g *Antopocerus*	Grossfield (1978)
(one per site)	some Hawaiian *Drosophila*	Grossfield (1978)
eggs not clustered	*Scaptomyza*, some	Grossfield (1978)
	Hawaiian *Drosophila*	Grossfield (1978)
eggs clustered	some Hawaiian *Drosophila*	Grossfield (1978)
	s-g *Sophophora*	Grossfield (1978)
aggregation	s-g *Sophophora*	Grossfield (1978)

Band, 1988a) not described among *Drosophila* or other groups, may be unique to *Chymomyza*.

Larval overwintering by *C. amoena* in exposed substrates is both a physiological, and a morphological difference from cosmopolitan drosophilids that can share fruit substrates in summer (Band, 1988a, c).

Among the forest chymomyzids, *C. costata* is known to breed and overwinter in decaying wood (Enomoto, 1981). The fat body is the most conspicuous organ in a chymomyzid larva. Its overdevelopment protects the brain and other internal organs. Possibly all insect species overwintering in the larval stage have overdeveloped fat bodies, suggesting in this case that behavior is strongly correlated with morphology and development, all of which have undergone radical modifications within the insects, especially with regard to nonlarval overwinterers (Somme, 1982; Zachariassen, 1985).

The single most typical adult chymomyzid trait, wingwaving, is also typical of otitids captured displaying on wood near Mt. Lake. Otitids are also aggressive and have male aggregation hormones (Thornhill & Alcock, 1983). One otitid, *Euxesta notata* larvae, overwinters with *C. amoena* larvae in Michigan orchard apples in winter (Band, 1988a); adults wing wave. Tephritids called "peacock flies" also wing wave (Borror et al, 1981). Recently, Spieth (1982) described this behavior among the primitive picture-wing Hawaiian *Drosophila*, the *planitiba* group, which are also the most pugnacious.

Rhagoletis species, which also are tephritids as is the cold hardy larval overwintering gall-forming *Eurosta solidagenis*, display capture-in-the-air, assault-type matings, and are aggressive (Bush, 1975; Thornhill & Alcock, 1983). Citing Prokopy and Heindrich (1979), Thornhill & Alcock (1983) note that Mediterranean fruit fly males may be attracted to fruits used by ovipositing females. Thus the fact that *D. melanogaster* and *D. simulans* males are attracted to sites where gravid females of their species have been (Spence et al., 1984), is also found in *C. amoena* and possibly distantly related tephritids. Gravid females, whether their hormones encourage or discourage others of their species from using the same oviposition site, announce the location of acceptable substances for larval development. The *Scaptomyza* have assault-type mating.

Male aggregations for the purpose of attracting mates, as displayed especially by the forest chymomyzids, is of more limited occurrence (Thornhill & Alcock, 1983, Table 6.2), although reasons for lekking continue to be controversial (Krebs & Davies, 1987). However, tephritids, otitids and hymenopterans are among those having males that track olfactory signals and aggregate. Possible differences among chymomyzids in display postures and prancing have been suggested (Watabe, 1985). Sympatric occurrence of mating pairs of *C. procnemoides* and *C. aldrichii* near MLBS in 1986 (Band, 1987) supports this conclusion. However, size, foreleg color and its extent (Wheeler, 1952) distinguish a majority of the males in the MLBS vicinity. Multiple species' male aggregations occur for relatively brief periods in Virginia's Allegheny Mountains. Chymomyzid adults are attracted only to fresh cut wood or fresh damaged trees.

The relationship of the Hymenoptera to the other insect orders is still debated (see Hennig, 1981). Hymenoptera recognize colony odor, have aggressive females, matings in the air, and react as a colony to disturbance. Some species have queens which overwinter, which enter into burrows or tunnels for protection as well as oviposition (Thornhill & Alcock, 1983). Parasitized apples frequently have to be dissected to demonstrate that *C. amoena* females have oviposited inside.

The use of firm substrates for oviposition probably hindered the discovery that *C. amoena* invasion of apples and other fruits has been widespread (Band, 1988a, b, c). Adult females, however, display the drosophilid need for a damaged surface (Carson and Heed, 1983: Band, 1988a, b). Bract oviposition, practiced by the fig-breeding lissocephalids (Lachaise, 1977) is rare in *C. amoena*. Previously, the fig-breeding African lissocephalids were the only drosophilids known to oviposit in unripe fruits. *Lissocephala* breeding in the nephritic gills of crabs have a high tolerance for a nitrogenous environment (Carson, 1974), similar to that imposed by frass breeding.

Therefore, despite being a drosophilid, *Chymomyza amoena* in particular displays undrosophila-like affinities while the multiple species' male aggregation of the forest group has been reported only for Australian *Drosophila* (Ehrman & Parsons, 1981; Parsons, 1982, 1983). It may be atypical for other species with aggressive males. *C. amoena* males distributed individually on a group of fallen apples may represent a male aggregation, although apples chosen have typically already been used for oviposition.

Comparing chymomyzids to other drosophilid genera and subgenera, again behavior demonstrates multiple affinities. *C. amoena* and *Scaptodrosophila* association with fresh fruits supports Hackman et al. (1970) that these two taxa are related. Unknown at that time was the range of adult and preadult traits shared with the *Scaptomyza* and the lek *Drosophila* in addition to the *Sophophora* as shown in Tables 6 and 7.

Observational data on behavior, emphasized by Ehrman (1978), confirm affinities of the *Chymomyza* to the Sophophoran subgenus but are more in agreement with Throckmorton's (1966) suggested association of the chymomyzids to the *Scaptomyza* and Hawaiian *Drosophila*. Chymomyzids could have diverged early from the Sophophoran lineage or alternately be at or near the drosophilid stem. The latter is suggested by Beverley & Wilson (1984), but anticipated by Throckmorton (1962, 1966).

Small population size and a predominant forest nature of the chymomyzids (Okada, 1981; Bachli and Rocha-Pite, 1981; Grimaldi, 1986 and here) including the wood breeding habitat (Enomoto, 1981; Grimaldi, 1986) again refocuses on the question of the origin of the drosophilids. African high altitudes would have promoted cold hardiness (Somme & Zachariassen, 1981) while retaining an African origin of the chymomyzid stem group (Wheeler, 1963). The feeding habits of *C. procnemis* remain unknown despite its presence in Hawaii and Japan (Wheeler, 1981). Ethanol concentration affects host selection in "secondary" bark beetles (Klimetzek et al., 1986). Nevertheless, this agrees with Throckmorton (1975) that adaptation to alcohol in the environment and exploitation of the fermenting fruit niche (Parsons, 1982, 1983; Mueller, 1985) came later in drosophilid evolution. Molecular studies on the alcohol dehydrogenase polymorphism (Aquadro et al., 1986) and comparative molecular data of *D. simulans* and *D. mauritania* to the *D. melanogaster Adh*^{4} allele (Cohn and Moore, 1988) support this conclusion.

The phenotypic plasticity manifested especially in all stages of *C. amoena* life cycle suggests chymomyzids retain traits from the primitive drosophilid ancestor which have undergone differential evolution in the drosophilid radiation. Certainly behavior gives little support to MacIntyre & Collier's (1986) inclusion of the chymomyzids in the genus *Drosophila* while linking them to otitids and tephritids more strongly than suggested by LSP-2 analysis (Beverley & Wilson, 1982, 1984). It also indicates that parallel evolutionary divergence has occurred in both families regarding behavior associated with feeding, breeding, development and overwintering.

The significant geographic difference between *C. amoena* populations in aggressive behavior indicates that aggression is a trait that has also been subject to divergent selection and parallel evolution both in the Drosophilidae and the superfamily Tephritidae. Although much attention has been focused on males in the evolution and speciation in Hawaiian *Drosophila*, both male and female behaviors have been subject to evolutionary modification in other lines. Wing-waving and aggressive behavior shared by chymomyzids and primitive picture-wing Hawaiian *Drosophila* females reveal unexpected affinities, paralleling the assault-type mating system shared between chymomyzids and scaptomyzids. Behavior therefore argues for a stem position of the chymomyzids to the genus *Drosophila*. Behavioral affinities to the otitids and tephritids, in particular, support an acalypterate origin, as postulated by Borror et al. (1981).

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