

Is *Chymomyza amoena* (Loew) (Diptera : Drosophilidae) a versatile, colonizing species?

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Is *Chymomyza amoena* (LOEW) (Diptera: Drosophilidae) a versatile, colonizing species?

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Chymomyza amoena populations from the Maggia Valley, Canton Ticino, have been compared with populations from Michigan and Virginia in time to mating, duration of mating, second matings by males, and interfertility. Duration of mating differs significantly between *C. amoena* populations from the Maggia Valley and those from Michigan. Other differences between Maggia Valley populations and American populations have been noted. However, time to mating remains similar in all populations, and Swiss and American *C. amoena* are interfertile. Michigan flies emerging directly from substrates readily mate with Swiss *C. amoena*. The species may be a versatile, colonizing species. Neither Virginia nor Michigan seems likely to have been the source of European *C. amoena*.

Keywords: *Chymomyza amoena*, Switzerland, Virginia, Michigan, mating speed, duration of copulation, biological invasion, colonizing species.

INTRODUCTION

Since its discovery in eastern Europe in 1975, *Chymomyza amoena* (LOEW) has been spreading rapidly (BURLA & BÄCHLI, 1992; MÁCA & BÄCHLI, 1994). Unlike the well-studied European species *Drosophila subobscura* which invaded Chile in 1978 and western North America in 1982 and spread (PREVOSTI et al., 1989; AYALA et al., 1989), or western North America's *D. pseudoobscura* which was later found in New Zealand (PARSONS, 1983; MILLAR & LAMBERT, 1985), Nearctic *C. amoena* had been subject to few contemporary investigations (SABATH, 1974, 1975). There was initial speculation it might be either a colonizer or Holarctic in distribution (BÄCHLI & ROCHA PITÉ, 1981).

PAPP & PECSENYE (1987) raised the question if it were the same species as the North American one. Published drawings of *C. amoena*'s conspicuously banded wings from specimens captured in Berlin (SCHUMANN, 1987) suggested that European and North American species were the same. Meanwhile, studies on overwintering, coldhardy larvae in Michigan (BAND & BAND, 1984) and breeding season studies in both Michigan and Virginia (BAND, 1988a, 1988b, 1988c, 1988d, 1989a, 1991) demonstrated that *C. amoena* could breed in and overwinter in a variety of fruits and nuts. It was a broad-niched species, as suggested by SABATH (1974), pre-adapted to withstand the rigours of the European climate, as noted by SCHUMANN (1987).

Continued captures in eastern Europe, lack of reports of any *Chymomyza* breeding in fruits (FERRAR, 1987), and *C. amoena*'s widespread undetected invasion of the urban environment in the eastern United States hinted the species might have a Holarctic distribution (BAND, 1989b). However, two centuries of European forest

entomology (SCHWERDTFEGER, 1973) failed to disclose any record in Europe prior to 1975. Drosophilid collecting in Switzerland, which netted over 250,000 specimens from 1946 to 1984 (BURLA & BÄCHLI, 1991a), did not yield any *C. amoena* prior to 1988 (MÁCA & BÄCHLI, 1994). This favors a history of recent colonization.

In 1990 *C. amoena* was found to have invaded European chestnuts *Castanea sativa* and apples in the Canton Ticino (BURLA & BÄCHLI, 1991b; BAND, 1991), and in 1991 it was also bred from acorns *Quercus* sp. and cherries in addition to chestnuts and apples in the same region. It was collected over bait in September 1991 (BURLA & BÄCHLI, 1992). This has made it possible to initiate comparative laboratory investigations on European *C. amoena*, represented by two populations from the Maggia Valley, Canton Ticino, Switzerland, and American *C. amoena*, and to determine the interfertility of the European and North American populations.

MILLAR & LAMBERT (1985) demonstrated continued interfertility of New Zealand and West Coast *D. pseudoobscura* populations and argued for the stability of mate recognition systems. Chilean *D. subobscura* populations quickly began to show reproductive divergence, including divergence from European populations (BRNCIC & BUDNIK, 1984), and now show differences in mating behavior (OCHANDO *et al.*, 1991).

Comparisons of Swiss and American populations have been made for time to mating, duration of mating, male second matings as well as continued interfertility. For interfertility assessment, crosses of Swiss and American *C. amoena* have also included use of Michigan *C. amoena* emerging directly from substrates. Continued interfertility, comparable differences in duration of mating, similarities in time to mating, occurrence of the species in urban, rural, and forest settings on both continents (SCHUMANN, 1987, 1990; BAND, 1988a, 1988b, 1989a, 1991; BURLA & BÄCHLI, 1991b, 1992; PAPP, 1992) and its rapid European spread (MÁCA & BÄCHLI, 1994) suggest it is a versatile colonizing species.

MATERIALS & METHODS

Swiss *C. amoena*: A shipment of 7 flies emerging from chestnuts and acorns which had been gathered in the Maggia Valley, Canton Ticino (46° 24' N; 8° 71' E) in March, 1991, was received in East Lansing, MI on 29 April 1991; 5 more arrived on 24 May 1991. Both groups were immediately transferred to high-protein apple sauce medium. Cultures containing 18 F₁ pupae from the populations reared from nuts were received on 7 June 1991. A shipment of flies, collected over bait on 10 and 11 September 1991 at the same site, was sent in September 1991. Due to the small numbers in April and May, 1991, compared to larger number of flies realized from the June shipment, the stock established from the nut emergees is predominantly weighted by the June flies. The two stocks, emergees and baited, have been maintained separately, but are interfertile.

Virginia *C. amoena*: A stock was established from flies emerging from acorns gathered in July 1989 at the University of Virginia's MLBS Mt. Lake Biological Station (37° 10' N, 80° 30' W) at the 1200 m elevation on Salt Pond Mountain in Giles County. Flies emerging from apples collected at a farm at a lower elevation on the mountain, designated Rt. 700, constitute the second Virginia population used throughout the study.

Michigan *C. amoena*: Flies emerging from apples gathered at an East Lansing site (42° 44' N, 84° 29' W) in August 1992 were used both to establish an East Lansing stock and in direct crosses with Swiss flies. In July and August 1993 apples

gathered at a site in Iron Mountain (45° 49' N, 88° 04' W) in Michigan's Upper Peninsula yielded flies both for direct crosses with Swiss and other American *C. amoena* and for establishing a stock.

Determination of time to mating [TM] (also called mating speed in other publications) and duration of mating [DM]: Both mating behavior components in *Drosophila* have been studied via single pairs introduced into vials and multiple pairs introduced into mating chambers (see PARSONS, 1967 and SPIESS, 1970 for earlier references). BAND (1992) employed pint-size canning jars for duration of mating and interfertility studies on Virginia *C. amoena* populations to assess evidence of population differentiation and host-related (acorn/apple) or clinal speciation (mountain vs eastern). Up to three mating pairs could be observed and timed simultaneously. Single males from the Rt. 700 population, in 1989 paired with several females, had indicated that male second matings were rare.

Procedures for duration of mating studies remained similar in 1991 and early 1992. Emerging flies from a population were separated by sex and aged approximately a week prior to setting crosses between intrapopulation males and females. One to three females and males were introduced into a population bottle via aspiration. Aged flies tend to mate relatively rapidly. However, ages of flies have also varied because previous work indicated Michigan *C. amoena* become sexually active at a younger age than Virginia *C. amoena* (BAND, 1988b), and LONG *et al.* (1980) found that duration of mating increases with male age in *D. melanogaster*. Time to mating was measured from the time males and females were introduced into a population bottle to the beginning of mating, and the duration of mating from the beginning to termination of mating. With the Maggia Valley males, successful second matings by the same male began to occur. Crosses of two females x one male or three females x two males have also been used after May 1992 to obtain information on male second matings. Single pairs, multiple males and females, and single males with two females have been used. Observations continued for an hour with single pairs, an hour and a half if two or more females were used and no mating occurred within the first hour. The aim has been to achieve a comparable number of first matings in each population in a variety of culture conditions which also allows additional information about second matings by individual males.

Determination of interfertility of Swiss and American *C. amoena*: No choice reciprocal crosses were used, and crosses were made between two or three virgin males and females from the respective populations. F₁ hybrids emerging were transferred to new bottles to record the occurrence of eggs and hatching larvae of the F₂ generation.

Culture methods: All work has been carried out in pint-size glass canning jars capped with muslin and secured by an elastic band (BAND, 1988a, 1988b, 1992). Flies have been grown on high protein-apple sauce medium. To conquer a mould/mite problem, beginning in 1992 a solution of methyl parasept (1 g to 10 ml 95 % ethyl alcohol) was added to the medium after cooling. The medium was supplemented also with 35 g of sugar and 14 g of activated dry yeast which improved the flavor after the regular use of methyl parasept.

All flies have been grown at room temperature (22 °C) under constant light. A Zeiss dissecting microscope has been employed for separating the sexes following aspiration.

Data analysis: A variety of statistical procedures has been employed. ZAR (1984) can be consulted for nonparametric tests.

RESULTS

Time to mating [TM]

Tab. 1 presents the average time between transferring males and females to the same culture and the commencement of mating between males and females in each population. The range of TM and 95 % confidence limits are included. Courtship can be minimal and mating almost instantaneous. Only one culture with two females demonstrated a prolonged period before a female mated, 72 minutes. To a certain degree, TM can be compared to the South American *D. subobscura* populations (OCHANDO *et al.*, 1991); *C. amoena* males and females in all populations mate relatively more quickly. In fact, the populations do not differ significantly in average TM as demonstrated by ANOVA ($F_{5,111} = 0.7$, $P = 0.6$). Mean TM for all populations and its standard deviation is 11.6 ± 11.4 (n=117) minutes.

Tab. 1. Time to mating [TM] in minutes for *C. amoena* males in populations from Virginia, Michigan and the Maggia Valley, Canton Ticino, Switzerland. MV-E: population descended from chestnuts and acorns collected in the Maggia Valley. MV-B: population descended from flies collected over bait at the same location in the Maggia Valley. The age of mating males in days is included.

Location	No. Matings	Time to Mating [TM]		95% Confidence Limits		Male mating age Mean \pm SD
		Mean \pm SD	Min. Max.	Lower	Upper	
Mt. Lake, VA	19	8.2 \pm 7.9	0 28	4.4	12.0	7.8 \pm 2.4 days
Rt. 700, VA	14	13.6 \pm 9.5	1 32	8.1	19.1	8.9 \pm 3.4 days
E. Lansing, MI	20	10.4 \pm 9.6	0 43	5.9	15.0	5.8 \pm 1.9 days
Iron MI., MI	21	10.8 \pm 12.2	1 44	5.3	16.4	7.0 \pm 2.5 days
MV-E	20	12.5 \pm 11.2	1 4	7.2	17.7	7.5 \pm 1.4 days
MV-B	23	14.1 \pm 15.3	2 72	7.5	20.7	7.0 \pm 1.4 days

The average ages for males on mating are given in Tab. 1. Males emerging directly from apples in East Lansing have been observed to mate at three days of age, and three-day-old East Lansing males and females were successfully used. BAND (1988a) found there were fewer mating attempts among Virginia flies three to five days of age than among Michigan flies. Consequently, to optimize mating, Virginia flies tended to be older, Michigan flies younger. However, the Maggia Valley populations showed the most lek-like behavior: one male in a group of two or three males and females did all the mating, or females simply refused to mate.

The Maggia Valley-B population had the highest proportion of non-mating males (48 %) and females (39 %), although all populations contained flies which did not mate. HOSGOOD & PARSONS (1965) reported only 14 homogametic matings for the Leslie Manor *D. melanogaster* population in their studies on TM and DM in Australian *D. melanogaster* populations. OCHANDO *et al.* (1991) also encountered large numbers of non-mating *D. subobscura* males and females in Chilean populations.

Duration of mating [DM]

Tab. 2 shows the average DM, minimum and maximum DM observed and 95% confidence limits for the four American and two Swiss populations. Only first matings by males are included in the calculations for each population. Virginia populations continue to show a mean DM of 17 minutes (BAND, 1992). From non-

Tab. 2. Comparison of the duration of mating [DM] in minutes among *Chymomyza amoena* populations from Virginia, Michigan and the Maggia Valley, Canton Ticino, Switzerland. MV-E: population descended from chestnuts and acorns collected in the Maggia Valley. MV-B: population descended from flies collected over bait at the same location in the Maggia Valley.

Location	No. Matings	Duration of Mating [DM]			95% Confidence Limits	
		Mean \pm SD	Min.	Max.	Lower	Upper
Mt. Lake, VA	20	17.5 \pm 6.2	9	39	15.6	20.4
Rt. 700, VA	17	17.0 \pm 4.2	9	24	14.9	19.2
E. Lansing, MI	20	20.5 \pm 7.8	13	42	16.8	24.2
Iron Mt. MI	21	14.7 \pm 3.4	10	23	13.1	16.4
MV-E, Ticino	21	22.0 \pm 7.1	13	39	18.7	25.2
MV-B, Ticino	24	16.0 \pm 2.8	10	21	14.9	17.1

overlapping 95% confidence limits, it can be inferred that the DMs for the East Lansing, MI population and the Iron Mt., MI populations differ significantly. The DMs for the Maggia Valley-E population are also significantly longer than those of the Maggia Valley-B population, and the DM for the Iron Mt. population is significantly shorter than that of the Maggia Valley-E population.

Inspection of the standard deviations indicates that those for the Virginia populations are comparable; t-tests reveal that the standard deviations differ significantly between the two Michigan ($F = 4.6$, $P = 0.0007$) and the two Swiss populations ($F = 6.5$, $P < 0.0001$). Therefore a Mann-Whitney two-sample test between populations in each state and canton has been employed. For the Virginia populations, $U = 150$, $P = 0.6$; for the Michigan populations, $U = 93$, $P = 0.002$; for the Maggia Valley populations, $U = 97.5$, $P = 0.0005$. Hence Mann-Whitney results confirm those from the 95% confidence limits that DM differs significantly between the two Michigan and the two Maggia Valley populations. WHEELER (1947) reported a mating duration of 14 minutes for *C. amoena*, SPIETH (1952) a mating duration of 21 minutes.

In comparison with other *Drosophila* species, the mean DM in most populations is comparable to that for *D. melanogaster*, 16.5 to 21.4 minutes (HOSGOOD & PARSONS, 1965; PARSONS, 1967), 17 to 19 minutes (GROMKO, 1987, 1989), 20 minutes (HALL, 1994). Mean DMs for the Iron Mt. and MV-B populations are similar to those of 15.42 min. for South American *D. subobscura* populations (OCHANDO *et al.*, 1991), although *D. subobscura* lines, maintained in the laboratory for years, had a higher DM (GLATTHAAR & SCHENKER, 1972). All DMs are longer than those observed for *D. pseudoobscura* (PARSONS, 1967; SPIESS, 1970).

Compared to other *Chymomyza* species, the DMs among most *C. amoena* populations are generally closer to *C. aldrichii*'s 12.4 minutes than *C. procnemoides*' 32.9 minutes (BAND, 1989b, 1994).

Correlations of male age, time to mating, and duration of mating

Although LONG *et al.* (1980) found that DM in *D. melanogaster* increased with male age, no similar effect has been observed among *C. amoena* males. As shown in Tab. 3, the nonsignificant correlations indicate that male age has little effect on DM in any population. The significant difference between DMs in the two Michigan and the two Maggia Valley populations cannot be attributed to male age at the time of mating. With regard to TM, only for the Maggia Valley MV-E population was male age significantly correlated with TM. The correlations between male age and TM are also given in Tab. 3.

Duration of mating for individual males in first and second matings

Twelve of the 78 American and nine of the 45 Swiss males mated with each of two females in a culture. Tab. 4 compares the DM in first and second matings for the individual males in American and Swiss populations. American males show no difference in DM for first and second matings. DM for second matings by Swiss males is significantly shorter than for first matings. Not surprisingly, second matings for Swiss males (11.7 ± 4.0 minutes, $n = 9$) and second matings for American males (18.2 ± 6.6 ; $n = 12$) also differ significantly in duration. In investigations on *D. affinis*, *D. latifasciaeformis* and *D. littoralis*, BRESSAC *et al.* (1991) concluded that overall average copula times remained constant for males in successive matings.

The average time between first and second matings for Swiss and American males does not differ significantly. One East Lansing male and one Swiss male, when supplied with consecutive females, mated three times. More males attempt a second mating than actually achieve one, even when there is access to more than one virgin female.

Tab. 3. Correlations between male age and time to mating [TM], and male age and duration of mating [DM] for the six populations. **P = 0.02.

Population	r_{TM}	r_{DM}
Rt. 700	0.50	- 0.27
Mt. Lake	- 0.41	- 0.19
East Lansing	- 0.22	0.27
Iron Mountain	0.18	- 0.05
Maggia Valley E	0.52**	0.23
Maggia Valley B	- 0.11	0.10

Tab. 4. Comparison of individual male second matings in the population. Number, duration of first and second matings and time to second matings are shown. Time in minutes. *duration of second matings among MV flies is significantly shorter than for first matings (Wilcoxon $W = 24$, $P = 0.05$). The duration of second matings among MV flies is also significantly shorter than second matings for the combined American populations (Mann-Whitney $U = 22$, $P = 0.03$).

Location	n	First Mating	Second Mating	Time to Second Mating
Virginia	6	18.2 ± 3.2	$17.8 + 5.0$	12.5 ± 11.6
Michigan	6	17.2 ± 5.6	$18.5 + 8.4$	7.7 ± 8.0
MV, Ticino	9	16.7 ± 3.2	$11.7 + 4.0^*$	16.2 ± 10.7

A *C. amoena* female, having mated, may actually drive a continuing courting male away. Females elevate the abdomen to avoid male mating attempts (BAND, 1988a). This is characteristic of the species and does not differ between American and Swiss females. Female remating has not been studied and was not observed among a small population of males and females captured at MLBS in July 1989, although females laid fertile eggs which hatched (BAND, 1991). During the same period repeat rematings of *C. procnemoides* and *C. aldrichii* males and females occurred daily (BAND, 1989b, 1994). Pairs of *C. amoena* males and females, kept under continuous observation, also for three days have not remated.

Density and mating speed

SPIESS (1970) discussed the varied effects of density on time to mate in *D. pseudoobscura* and *D. persimilis*. Male-male interference has been inferred. *Chymomyza amoena* males and females may be aggressive. Similarities in TM among the *C. amoena* populations may result from the average effects of varied densities. Tab. 5 shows the comparisons between TM for single pairs versus first mating in cultures with multiple individuals, and cultures with single males versus multiple males. In neither case does TM differ, as demonstrated by their 95% confidence intervals. In particular, single males in cultures with more than one female mated no faster than single males in no-choice single-pair cultures.

When we look at TM for the second male to mate in cultures having two or more females and males, the delay in mating is over a quarter of an hour or twice that for single pairs, 8.8 ± 8.0 minutes. TM for a single male in a culture is also significantly more rapid than for a second male initiating a mating in a culture (Mann-Whitney $U = 329.5$, $P = 0.01$). In fact, single males achieving a second mating typically spend less time between completing one mating and initiating the second one with a different female, as shown in Tab. 4. First matings for males in cultures having an excess of males averaged $18.5 + 23.4$ minutes ($n = 10$). PARSONS (1974) argued that male mating speed is an important component of fitness. For an aggressive species, the lapsed time before a second male in a culture successfully mates may reflect his own slower mating speed, the slower acceptance response of the second female, or both. The slow response of a female can also delay mating when an excess of males is present, although data agree with SPIESS (1970) and PARSONS (1974) that male-male interference is a factor in delayed matings.

Interfertility

Cross tests show that all Swiss and American populations remain interfertile. This is reinforced by the fact that American (Michigan) flies, emerging directly from apples, will mate and produce fertile F_1 s with the populations from the Maggia Valley. Earlier, Virginia flies emerging directly from apples were also found to be interfertile with Michigan flies (BAND, 1988a).

Tab. 5. Comparisons of time to mating [TM] in *C. amoena* cultures at varying densities of male-female combinations.

Comparison	n	Time to Mating [TM]			95% Confidence Limits	
		Mean \pm SD	Min.	Max.	Lower	Upper
A. single pairs vs 3 or more flies	40	8.8 ± 8.0	1	34	6.2	11.3
	54	11.9 ± 13.6	0	72	8.2	15.6
B. single males vs multiple males	57	9.8 ± 8.1	1	34	7.6	11.9
	37	11.8 ± 15.7	0	72	6.6	17.1
C. second male to mate third male to mate	19	16.2 ± 11.0	1	44	10.9	21.4
	4	17.0 ± 9.9	4	28	1.2	32.7

DISCUSSION

The duration of mating in *Drosophila* species is regarded as species-specific though variable between species (SPIETH, 1952, 1969, 1974; SPIESS, 1968, 1970; FOWLER, 1973; OCHANDO *et al.*, 1991; PITNICK *et al.*, 1991; PITNICK & MARKOW, 1994). HALL (1994) has recently reasserted the species-specific nature of the duration of mating. Virginia *Chymomyza amoena* populations from widespread localities also had a similar DM (BAND, 1992). Other factors as genotype (KAUL & PARSONS, 1965; PARSONS & KAUL, 1965; SPIESS, 1968, 1970), temperature (PARSONS & KAUL, 1965), degree of crowding (KAUL & PARSONS, 1965), sexual activity of the males (GLATTHAAR & SCHENKER, 1972), age of males (LONG *et al.*, 1980), and size of males (PITNICK, 1991) have been shown to influence DM. MACBEAN & PARSONS (1967) demonstrated that DM, which is principally controlled by the male, could be subject to selection. GROMKO (1987, 1989) verified that DM has a significant heritability in *D. melanogaster* males. PETIT & EHRMAN (1969) speculated on the selective value for DM.

However – is DM within *Drosophila* species really constant? Individual *D. melanogaster* lines varied significantly in DM (MACBEAN & PARSONS, 1965; PARSONS, 1967). GLATTHAAR & SCHENKER (1972) found that sexually active *D. subobscura* males had a shorter DM (14 minutes) than males which did not attempt additional matings; their DM averaged 20 minutes. Yet the majority of matings for both groups occurred within 15 minutes. The DM for Chilean *D. subobscura* averaged 15 minutes, and time before mating began exceeded a half-hour for these largely sexually inactive populations (OCHANDO *et al.*, 1991). Findings of significant differences in DM among *C. amoena* populations are nonunique.

That the two populations from Maggia Valley differ in DM is unexpected, since the baited flies and the flies from the infested nuts were from the same area. Certainly the work of GLATTHAAR & SCHENKER (1972) demonstrates that a species can be variable for mating duration, which in turn can be correlated with other fitness factors. However, males in both Maggia Valley *C. amoena* populations demonstrate equal success in completed second matings although there are other differences between the two populations. It would be useful to compare other European *C. amoena* populations for mating behavior. The species had been in Europe over 10 years before it was collected in Switzerland.

The shorter DM of the Iron Mt., MI population is comparable to that obtained with Virginia *C. amoena*, grown and aged at 13 °C, then allowed to mate at room temperature. DM averaged 14.7 ± 3.9 minutes ($n=6$). This 1989 work demonstrated that temperature of the developing flies could affect DM but did not increase mating frequency at warmer temperatures. HOSGOOD & PARSONS (1965) suggested that when populations become adapted to different environments, they are likely to differ genetically with a consequent evolution in behavioral differences. The Iron Mountain, MI population is subject to an overall cooler climate. DM in other species is known to be temperature-sensitive and of shorter duration at lower temperatures (PARSONS & KAUL, 1965).

Time to mating has been the trait most variable between populations of the same species (HOSGOOD & PARSONS, 1965; PARSONS, 1967; OCHANDO *et al.*, 1991) and readily subject to selection (MANNING, 1961; KESSLER, 1968; STAMENKOVIC-RADAK *et al.*, 1992). Among both American and Swiss *C. amoena* populations, time to mating has been similar despite a positive correlation with male age in the MV-E population. Rapid mating, preceded by little or no courtship, occurred among

males and females in all populations, as is evident in Tab. 2. This may account for a lack of divergence among populations for time to mating. In nature, females approaching males are ready to mate. Courtship is minimal in *Chymomyza* (SPIETH, 1952) in contrast to *Drosophila*.

Low density, symbolized by *C. amoena*'s largely unsuspected presence in both urban and rural areas (BAND, 1988a, 1988c, 1989a), its use of varied hosts for breeding, and its widespread occurrence in North America also makes it a candidate for founder effects speciation. Evidence to date is negative (BAND, 1988a, 1988b, 1988c, 1992). The continued interfertility of Maggia Valley *C. amoena* with Michigan flies emerging directly from substrates and with Virginia populations after several years of laboratory maintenance supports the hypothesis of recent European colonization (BURLA & BÄCHLI, 1992; MÁCA & BÄCHLI, 1994). However, neither state seems likely to have contributed the founding population, although both states provide evidence that *C. amoena* was breeding in both fruits and nuts (BAND, 1988a, 1988b, 1991) prior to invading Europe and its discovery in these same niches in Switzerland (BURLA & BÄCHLI, 1991b). *Chymomyza amoena* displays the traits of a "weedy" species (DOBZHANSKY, 1965), not readily subject to speciation (CARSON, 1975). It is also ecologically versatile (PARSONS, 1983).

The date of first collection in Europe, 1975, means that *C. amoena* invaded Europe before *D. subobscura* invaded Chile in 1978 or the American Northwest in 1982 (AYALA *et al.*, 1989; PREVOSTI *et al.*, 1989), or *D. pseudoobscura* was found in New Zealand (PARSONS, 1983; MILLAR & LAMBERT, 1985). Biological invasion has been of renewed interest in the past decade. DI CASTRI (1989, 1990) noted that the Old World is more resistant to new invasions both because of a history of past invasions and species richness. Old World species are typically the more successful invaders of other ecosystems. This in part accounts for the success of European *D. subobscura* in both Chile and western North America. Among the European invaders, species from North America have had the greater success.

Echoing the role of species richness in keeping out invading species, PIMM (1989) also notes that some species are more likely to survive at low population densities than others. He also singles out the role of ecology and the nature of the community invaded in determining success. In eastern North America, *Chymomyza amoena* has been the predominant drosophilid in parasitized fruits and nuts. Europe has insect pests which attack fruits including codling moth *Cydia pomonella* (BURLA, pers. comm.). Nearctic *Chymomyza amoena* in Europe may well have entered the same unique niche it occupies in eastern North America. Its now widespread existence in Europe suggests populations may already have adaptively differentiated analogous to *D. subobscura* in the New World. Similarities and differences among *C. amoena* populations on both continents largely remain to be discovered.

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ERRATUM

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In Tab. 1, the maximum TM value for the MV-E population should be 41 minutes (instead of 4 minutes).