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Frassy Substrates as Oviposition/Breeding Sites for Drosophilids

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ABSTRACT

Over one thousand five hundred drosophilids have emerged from frassy fruit and nut substrates in Michigan and the mid-South (53 *D. affinis* group, 44 *D. busckii*, 38 *D. immigrans*, 554 *D. melanogaster* and *D. simulans*, 862 *Chymomyza amoena*, 5 *Scaptomyza adusta*). Both cosmopolitan and endemic species can use this niche for oviposition. Frass-breeding constitutes a fifth oviposition/larval developmental site category for temperate zone drosophilids. The evidence indicates that this may be an old niche for *C. amoena* but may be a recently invaded one for other *Drosophila*.

INTRODUCTION

Carson (1971) identified four major types of breeding sites for temperate zone drosophilids: a) fallen fruits, b) decaying bark, leaves and stems, c) slime fluxes, d) fleshy fruits. Cosmopolitan and endemic species were included in the survey. Larvae are consumers of yeast, bacteria and moulds (review: Begon, 1982). Fruits refer to typical orchard and garden fruits. Shorrocks (1982) surveyed breeding sites for temperate woodland *Drosophila* in Europe, North America and Japan. Species breeding in fermented fruits included decaying nuts, slime fluxes, decaying vegetation and fungi were listed. Intensive study of *Sorbus* berries showed flies oviposited on rotting or semirotting fruits. Use of fresh damaged berries was minimal: 3.5 flies emerging per 100 ripe berries compared to 115.3 flies emerging per 100 rotting berries. Burla and Bächli (1993) likewise bred more *Drosophila* from rotting Cornelian cherries *Cornus mas* than ripe cherries in Switzerland.

Scaptomyza are leaf miners (Carson, 1971; Collinge and Loude, 1988). *Chymomyza* larvae typically have been found under bark (Spieth, 1957; Teskey, 1976; Enomoto, 1981; Band, 1993a, 1994a; Burla, 1995).

Steyskal (1949) collected *C. amoena*, *Drosophila algonquin* and *D. paramelanica* adults on black locust (*Robinia pseudoacacia*) in Michigan; the drosophilids were feeding at fermenting frass protruding from holes in the living tree, most of which had been bored by the cerambycid beetle *Megacyllene robinia*. Frass is insect excreta. Steyskal did not report egg deposition, however Taylor (1928) bred *C. amoena*, *D. funebris*, and *Scaptomyza graminum* from weeviled pine shoots in Massachusetts. Heed (1968) reported that one *Scaptomyza* species and three *Drosophila* species emerged from frassy substrates in Hawaii. Lachaise (1977) found that fig-breeding *Lissocephala* females oviposited around the holes made by *Pyralidae* caterpillars or fig weevil larvae, if available. Band (1988a,b,c,d) found that *C. amoena* oviposited in curculio scars or holes and frass from codling moth larvae in parasitized fruits.

Carson (1971, 1974) also noted that some drosophilids become obligate commensals and in 1974 elaborated on 3 examples of drosophilids (2 *Drosophila*, 1 *Lissocephala*) living in association with land crabs, whose larvae occupy the nephritic grooves during all or part of their prepupal development. One species (*D. carcinophila*) belongs to the *mercatorum* subgroup of the *repleta* group, another (*D. endobranchia*) belongs to the *virilis* or *quinaria* group of the subgenus *Drosophila* and therefore each descends from a different lineage in the subgenus *Drosophila*.

Carson (1971) noted that some *Drosophila* were generalists, that is able to exploit a wide variety of substrates for breeding, while the examples of parallel drosophilid evolution as obligate commensals with land crabs in 3 separate phyletic lines suggested a widespread latent genetic capacity for evolutionary innovation (Carson, 1974). Parsons and Stanley (1981) included *D. repleta*, *D. virilis* and *D. mercatorum* among the cosmopolitan and geographically widespread *Drosophila* which are also ecologically versatile. Besides *repleta* and *virilis*, other cosmopolitan species include *melanogaster*, *simulans*, *hydei*, *funebris*, *busckii*, *immigrans*, and *annassee*. Wallace (1978) was able to adapt a *D. virilis* strain to a high urea environment. Schatzmann (1977) recorded over a thousand *D. busckii* emerging from English walnuts in Switzerland. Schatzmann commented that English walnuts were a firm substrate, but noted that Sturtevant (1921) reported that Shannon bred this species from butternut hulls. The only other species Sturtevant reported from nut hulls was *C. amoena*.

Spieth (1987) found that *Drosophila* in California could breed in parasitized acorns. Burla and Bächli (1991, 1992) bred *Chymomzya amoena*, *Drosophila subobscura* and *D. kuntzei* in Switzerland from parasitized nuts (chestnuts and acorns). The documented emergence of *C. amoena* and other drosophilids from frassy fruit and nut substrates in Michigan and in the mid-South (Band, 1985, 1986a, b, 1988a, b, c, d, 1991) indicates that frassy parasitized substrates constitute a fifth breeding site category for North Temperate zone drosophilids. Frassy fruits are not a recent niche for *C. amoena* (Band, 1994b).

MATERIALS AND METHODS

Emergence of North American drosophilids from frassy substrates has been compiled from published records (Tables 1 and 2): Heed (1968), Band (1985, 1986a, b, 1988a, b, c, d, 1991), Spieth (1987).

Flies emerging from collections recorded as frassy in Michigan and mid-South data have been enumerated. Records from Michigan substrates are from unripe parasitized fruits in June and July, from parasitized pears *Pyrus communis*, Bartlett variety in 1985 and ornamental crabapples *Malus pyramidus* in early autumn, 1982 and 1985. Flies emerging from black walnut husks *Juglans nigra* in autumn and winter are also given. Flies emerging from pears in autumn 1987 and apples *Malus pumilla* in autumn not scored as frassy have been excluded. Records from Eden, North Carolina are from fallen unripe apples, Delicious variety, in June and July, 1984. Records from Virginia collections in 1985 and 1986 are from multiple locations and include apples, varieties unknown, in various stages of ripeness; all retained had been parasitized from their frassy condition, from emergence of pests when apples were held long enough, and/or from dissections to score for the presence of frass (Band, 1988a). Collections in Virginia in 1987 were to obtain

TABLE 1. Year of study, location, substrate, species emerging and reference for frass breeding drosophilids in Hawaii, California and Michigan; m = male, f = female.

Year	Location	Substrate	Species emerging	no.	Source
1934	Hawaii	*Charpentiera*, Apr.	*S. crytoloba*	1	Heed (1968)
1963	Hawaii	*Freycinetia*, Dec.	*D. crucigera*	1	Heed (1968)
1963	Hawaii	*Freycinetia*, Sept.	*D. punalua*	6	Heed (1968)
1963	Hawaii	*Freycinetia*, Dec.	*D. simulans*	2	Heed (1968)
1983	California	acorns, Feb., Mar.	*D. obscura* sp.	32	Spieth (1987)
			D. immigrans	12	
	Michigan				
1981	Lansing	apples, July	*C. amoena*	58	Band (1988a)
1982	E. Lansing	apples, July	*D. melanogaster*	4	Band&Band
			D. affinis	6	(1983)
			C. amoena	25	
1985	Lansing	apples, Oct.	*D. melanogaster*	2m	Band (1986a,b)
			D. simulans	7m	
			D. mel. +*D. sim.*	8f	
			D. immigrans	3	
			C. amoena	1	
1987	E. Lansing	apples, July	*C. amoena*	130	
1991	E. Lansing,	apples, June	*C. amoena*	15	unpublished
1992	E. Lansing	apples, June	*C. amoena*	6	unpublished
1985	E. Lansing	pears, Sept.	*D. melanogaster*	194m	Band (1986b)
			D. simulans	1m	
			D. mel. +*D. sim.*	270f	
			D. immigrans	4	
1982	E. Lansing	ornamental crabapples, Oct.	*D. melanogaster*	5m	Band&Band (1983)
			D. simulans	3m	
			D. mel. +*D. sim.*	13f	
			C. amoena	5	
1985	E. Lansing	ornamental crabapples, Oct.	*D. melanogaster*	4m	Band (1986b)
			D. simulans	3m	
			D. mel. +*D. sim.*	21f	
			C. amoena	1	
1983	Lansing	blackwalnuts, Jan.,Nov	*C. amoena*	29	Band (1988a)
1984	Wmstown	blackwalnuts, Nov.	*C. amoena*	125	Band (1988a)
1985	Lansing	blackwalnuts, Oct.	*D. busckii*	4	Band (1986a)
			D. immigrans	3	
			C. amoena	2	
1987	E. Lansing	plums, June	*C. amoena*	25	Band (1988a)
1989	E. Lansing	plums, June	*S. adusta*	2	unpublished
			C. amoena	1	
1992	E. Lansing	plums, June	*D. affinis* gr.	1f	unpublished
			S. adusta	1	
			C. amoena	22	

TABLE 2. Year of study, location, substrate, drosophilid species emerging and reference for mid-south collections in the 1980s and 1990s; m = male, f = female.

Year	Location	Substrate	Species emerging	no.	Source
1984	Eden, N. C.	apples, June and July	*D. affinis*	3	Band (1985)
			D. melanogaster	4	
			D. busckii	40	
			D. immigrans	1	
			C. amoena	22	
			S. adusta	2	
1985	Rt. 700, VA	apples, July and August	*D. affinis*	35	Band (1988a)
			D. melanogaster	6	
			D. immigrans	14	
			C. amoena	48	
1986	Danville, VA	apples, June	*D. affinis* sp.	6	Band (1988c)
			D. quinaria sp.	1	
			C. amoena	68	
			diastatids	3	
1986	Blacksburg, VA	apples, July	*C. amoena*	15	Band (1988a)
1986	Rt. 700, VA	apples, June	*C. amoena*	36	Band (1988a)
1990	Blacksburg, VA	apples, July	*C. amoena*	15	unpublished
	Rt. 700, VA	apples, July	*D. immigrans*	4	unpublished
			C. amoena	38	
			Drosophila sp.	7	
	Pamplin	apples, July	*C. amoena*	23	unpublished
1991	Pamplin	apples, July	*D. immigrans*	4m	unpublished
			D. immigrans	5f	
			D. melanogaster	1m	
			D. melanogaster	4f	
			C. amoena	9	
	Danville,	apples, July	*D. robusta*	20f, 15m	unpubl.
	Blacksburg	apples, July	*C. amoena*	2	
	Rt. 700	apples, July	*D. affinis*	2	
			C. amoena	4+	
1992	Rt. 700	apples, July	*C. amoena*	14	unpublished
1989	MLBS, VA	acorns, July	*C. amoena*	74	Band (1991)
1989	MLBS, VA	acorns, Sept.	*D. melanogaster*	4	Band (1991)
			C. amoena	7	
1990	MLBS, VA	acorns, July	*C. amoena*	41	unpublished
1992	Rt. 700	oriental chestnuts, October	*C. amoena*	1	Band (1993b)

further data on aggregated oviposition (Band, 1988c, 1989); the condition of the individual apples was not recorded. In general, drosophilids emerge before any true pests: lesser apple worm *Grapholitha prunivora*, apple maggot *Rhagoletis pomonella*, codling moth *Cydia pomonella* and plum curculio *Conotrachelus nenuphar*.

Emergence of *C. amoena* from damaged acorns collected at Mt. Lake Biological Station was documented in summer and fall 1989 (Band, 1991). Acorns were again collected in July 1990; parasitized acorns were scored for the presence of eggs and larvae, and then held for adult emergence. This was done to verify that only *C. amoena* breeds in acorns despite the presence of other *Chymomyza* in the forest (Band, 1988d, 1993a, 1994a, 1995a, b). In October 1992 old oriental chestnuts (*Castanea mollissima*) that showed evidence of prior parasitism were collected at the Rt. 700 site near Mt. Lake. Newly fallen nuts from which pest larvae had not emerged were also collected (Band, 1993b).

The problem of sibling species: Sibling species occur among drosophilids and require additional tests for accuracy of identification. *Drosophila pseudoobscura* and *D. persimilis* emerging from acorns in California were not differentiated electrophoretically (Spieth, 1987). Males of *D. melanogaster* and *D. simulans* can be distinguished by their genitalia. However, progeny from *D. melanogaster* and *D. simulans* females were not grown to determine the genitalia of F_1 males. Males of the *D. affinis* group can be differentiated by sex combs. When only females emerged no species was assigned.

Microbial studies: The intestinal contents of *C. amoena* larvae were plated in December 1982 to determine they had continued feeding in a mild winter (Band and Band, 1984). Frass was plated from unripe green frassy apples with and without *C. amoena* larvae the following summer. Media used were nutrient agar and yeast-extract-Proteous Peptone (Difco)-glucose containing medium.

RESULTS

Table 1 lists the year, location, substrate, month collected, drosophilid species emerging and numbers of each species recorded from Hawaii, California and Michigan. Frass-breeding was specifically noted early among drosophilids in the western world, a *Scaptomyza* in 1934 in Hawaii (Heed, 1968), but implied by the emergence of drosophilids from weeviled pine shoots in Massachusetts (Taylor, 1928).

Spieth (1987) lists the *Drosophila* species emerging from acorns collected at Oakmont, California by Dr. William Marshall as *immigrans* and *obscura* group. Laboratory studies have demonstrated that *D. pseudoobscura*, *D. melanogaster*, and *D. immigrans* females will oviposit in holes made by emerging insect larvae or in the vascular elements at the base of the acorn, and adults will emerge.

In Michigan *C. amoena* was the only drosophilid to emerge from frassy fruits in early summer until 1989 when 2 *Scaptomyza adusta* also emerged from parasitized plums. The presence of other drosophilids in July can be variable. In September and October, parasitized fruits (apples, pears, ornamental crabapples) and black walnuts may serve as drosophilid breeding sites. Pears are typically parasitized by codling moth, ornamental crabapples by apple maggot larvae. The existence of numerous apple trees in suburban gardens suggests that ornamental crabapples are a late season oviposition niche for apple maggot but larvae in October are killed by the onset of winter.

The 1985 apples and black walnuts had fallen from adjacent trees in Lansing. The 1985 pears in September and ornamental crabapples in October were also in the same garden in East Lansing (Band, 1986a,b). Neither the adjacent apples and black walnuts at one site nor the pears and ornamental crabapples in the same

TABLE 3. Genus, subgenus (if established), species group and species having frass breeding members in the United States and Hawaii.

Genus	Subgenus	Species group	Species
Drosophila	*Sophophora*	*melanogaster*	*melanogaster*, *simulans*
		obscura	*affinis*, WestCoast species
Drosophila	*Dorsilopha*	*busckii*	*busckii*
Drosophila	*Drosophila*	*immigrans*	*immigrans*
Drosophila	*Drosophila*	'picture-wing'	*crucigera*, *punalau*
Scaptomyza	*Trogloscaptomyza*		*cryptoloba*
Scaptomyza			*adusta*
Chymomyza		*fuscimana*	*amoena*

garden at the second site contain the same complement of drosophilids. *Drosophila busckii* had earlier been bred from nut husks (Sturtevant, 1921; Carson, 1965), and was the dominant *Drosophila* to emerge from English walnuts in Switzerland (Schatzmann, 1977). As shown in Table 1, *D. immigrans* in both eastern and western North America can develop in parasitized nuts, *D. simulans* in parasitized fruits.

Drosophilid larvae, mostly *C. amoena*, were found in parasitized acorns collected in 1989 both in northern lower and mid-Michigan. However there was no emergence in the laboratory (Band, 1991).

Table 2 gives the drosophilid species emerging from unripe frassy apples 1985-1986 and from later (post-1987) collections in Virginia, when notation was made about the parasitized condition of the apples. Species in frassy fruits in June may be found in frassy substrates in Michigan later in summer.

Table 2 also shows that *C. amoena* is the only *Chymomyza* to emerge from acorns. The fact that *D. melanogaster* emerged from acorns in autumn 1989 indicates that *Drosophila* in the east have the capacity to invade and develop in this substrate as observed elsewhere (Spieth, 1987, 1988; Burla and Bächli, 1992). *Chymomyza amoena* larvae were found in old parasitized oriental chestnuts and one adult emerged. Females from laboratory stocks oviposited on and in newly fallen nuts from which weevil larvae had exited (Band, 1993b).

Frass breeding by drosophilid classification: Table 3 gives the genus, subgenus and species group, if established, for the North American species which have emerged from frassy substrates. The *Drosophila* cosmopolitan species are well represented: *melanogaster*, *simulans*, *busckii*, *immigrans*. Two endemic species now found on other Continents, *Drosophila pseudoobscura* (Millar and Lambert, 1985) and *Chymomyza amoena* (Burla and Bächli, 1992; Máca and Bächli, 1994) can exploit the frass breeding niche. European *Drosophila subobscura*, now on the west coast of Chile and California (Ayala et al., 1989), has also been found in nuts and as well as fruits.

In Hawaii, California, Michigan and the mid-South both cosmopolitan and endemic species emerge from frassy substrates. In California, Michigan, the mid-South and Switzerland, interspecies dependency is evident in the use of exit holes in firm substrates that drosophilid females enter to oviposit in the frassy interior (Spieth, 1987, 1988; Band, 1988a,b,c,d; Burla and Bächli, 1992).

Microbial content: *Chymomyza amoena* larvae from ornamental crabapples in winter 1982/83 contained fungi and yeast in their gut. Frass plated from unripe parasitized apples the following summer contained only bacteria. One culture also had a ciliate (Protozoa).

DISCUSSION

Firm parasitized nut and fruit substrates as oviposition sites for drosophilids only recently appear to have been investigated (Spieth, 1987, 1988; Band, 1988a,b,c,d, 1991, 1994b; Burla and Bächli, 1991, 1992). For *C. amoena* the nuts and fruits can serve as larval overwintering sites and summer season breeding sites (Band, 1988a,b,c,d; Band and Band, 1984).

Neither Throckmorton (1975) nor Ferrar (1987) listed *Chymomyza* breeding in fruits. Ferrar (1987) also states that *Drosophila* species breed only in fruit that is already damaged, fermented and unfit for human consumption and enumerated the same drosophilid feeding/breeding niches of his predecessors: decaying fruits and vegetation, slime fluxes, fungi, living flowers (Neotropics), specialized niches (cacti; crabs).

Given that instances of drosophilid frass feeding and breeding were noted in the 1920s, 1930s and 1940s (Taylor, 1928; Steyskal, 1949; Heed, 1968), we may ask if the frassy parasitized niche has become a new niche for *C. amoena* and for other *Drosophila*. *Chymomyza amoena*, *Scaptomyza adusta*, *D. affinis* in the East (Sturtevant, 1921), *D. obscura* group species in the West (Dobzhansky, 1937) are native North American species. *Drosophila melanogaster*, *D. simulans*, *D. busckii*, and *D. immigrans* are immigrants (Sturtevant, 1921), recognized now as cosmopolitan, associated with domestic habitats and readily attracted by fermenting fruits (Carson, 1971; Parsons and Stanley, 1981).

Prussian dipterist Hermann Loew in 1862 described *Chymomyza amoena* as *Drosophila amoena* from specimens collected in Washington, D. C., and described *D. melanogaster* as *D. ampelophila* from specimens collected in Cuba. By the 1870s *D. ampelophila* had invaded the U. S., and was spreading rapidly along the east coast. In 1882 J. H. Comstock found that the life cycle of *D. ampelophila* in decaying (fermenting) orchard apples averaged about 14 days compared to over a month for *D. amoena*. He called both pomace flies because of the attraction especially of *D. ampelophila* to crushed fruits or pomace as at wineries and cider mills (Band, 1994b). Although Sturtevant (1921) stated he bred *C. amoena* from apples, his mention of nut breeding and the later reports of Dowdy (1955), Winston (1956) and Dorsey *et al.* (1962) of *C. amoena* in acorns would suggest displacement to nuts due to competition. However, *C. amoena*'s tendency to oviposit in frass, in scars made by curculio weevils and holes made by codling moth (Band, 1988a,b,c,d) enabled its identification as the "Drosophila apple fly." This was a *Drosophila* found by A. S. Packard in 1869 to follow curculio and codling moth into early apples in Massachusetts, but was never indentified and subsequently was forgotten (Band, 1994b). Baron Osten-Sacken had been Packard's authority that the dipteran in Massacusetts apples was a *Drosophila* and Walsh's authority that the dipteran in eastern apples and Illinois haws was apple maggot (*Trypeta pomonella* = *Rhagoletis* *pomonella*). *Chymomyza amoena*'s 1869 emergence date from Massachusetts apples is earlier than the previous recorded 1891 date from Michigan apples (Band, *ibid.*).

Band (1988a,b,c) had earlier argued that *C. amoena*'s breeding in parasitized nut/fruits was likely of prehistoric vintage and the species awaited only attacking insects to enter domestic (commercial fruits). Early explorers described North America as a heavily forested land with oaks, chestnuts, walnuts, plums, grapes and other trees and shrubs (Cumming *et al.*, 1972). The colonists brought domestic plums, peaches, apples, apricots, and nectarines with them. In 1781 Jefferson listed the wild fruit and nut bearing trees native to Virginia, including crabapples (Jefferson, 1955), and noted in 1791 that weevils were attacking plums, apricots, nectarines and peaches in Philadelphia (Betts, 1944). Codling moth invaded in the late 18th/early 19th century. Winston (1956) and Dorsey *et al.* (1962) demonstrated that *C. amoena* larvae could be found in acorns as soon as exiting curculio or lepidopteran larvae made access holes enabling oviposition. No doubt, native *C. amoena* had long followed native curculio from nuts into plums and crabapples. The opportunity to follow pests into domestic (commercial) apples in Massachusetts appears to have preceded a similar opportunity in Michigan, as would be expected.

Lumme and Lakovaara (1983) have encouraged the study of northern drosophilids. As forested lands have come under cultivation, native substrates have been replaced by commercial orchards and crops. This phenomenon accelerated in the second half of the nineteenth century in states such as Michigan. In other areas, as the South, former commercial crops as tobacco, have lost their universal appeal, and replacements are needed.

Mayr (1963, see also Plotkin, 1988) argued that a shift to a new niche is usually initiated by a change in behavior. Host shifts by insects have also been argued to require a genetic change. Diether (1986) has also pointed out that different genes may control host preference, substrate suitability for larval development, and detoxification processes. Drosophila typically produce several generations during the breeding season. Monophagy is restricted to substrates which are continuously available for an extended period of time, and seems more prevalent in the Neotropics than among temperate zone drosophilids. Carson (1974) noted and Wallace (1978) demonstrated a latent capacity in drosophilids to adapt to a high urea/nitrogenous environment.

In addition to cosmopolitan *Drosophila*, which are substrate generalists and found on all continents, Parsons and Stanley (1981) recognized two other types of widespread *Drosophila*: those that are ecologically versatile and those that are ecologically restricted. The latter include *D. buzzatii* and *D. aldrichii* which breed in *Opuntia* cactus. The former include members of the *obscura* group species, *D. robusta*, and other widespread *Drosophila* that occur in domestic and natural habitats. In the east *D. affinis*, and to a lesser extent *S. adusta*, also appear to be widespread and ecologically versatile. Many species are tending to spread, as *D. pseudoobscura*, and *D. subobscura*.

Chymomyza amoena also merits inclusion in the widespread, ecologically versatile category; typical drosophilid phytophagy characterized its oviposition in nuts and wild fruits before the colonists arrived and may be a factor in its rapid spread in Europe. Larvae also appear to feed on a variety of microbes. As Winston (1956) found, larvae are not primarily yeast feeders. This may be a general *Chymomyza* trait (Carpenter, 1954; Grimaldi, 1986).

Behavioral change appears not to have been involved for *C. amoena* to have invaded domestic fruits. As an acorn breeder, it was already classified as a secondary invader (Dorsey et al., 1962) and as a fungal feeder and scavenger (Winston, 1956). Vosso (1984) studied acorn predators and associate fungi taken from a Mississippi forest (*C. amoena* was not among them) and found *Penicillium* sp. with curculio larvae, but also obtained *Fusarium solani* and *Epicoccum purpurasens*, possibly as acorn surface contaminants. Winston (1956) found that *C. amoena* fed on both *Fusarium* and *Penicillium*. Botanists argue that *Penicillium* is not insect transmitted (Rosenberg, 1990; Cipollini and Stiles, 1993). However, if drosophilids are found to transport undesirable microbes, Ferrar's (1987) claim they are of no economic importance may have to be revised.

Drosophila busckii is the only other *Drosophila* known for many decades to be capable of breeding in nuts and nut husks (Sturtevant, 1921; Carson, 1965; Schatzmann, 1977; Shorrocks, 1982), although Malloch and McAtee (1924) also bred two cosmopolitan *Drosophila* (*funebris* and *melanogaster*) from butternut hulls. In the case of *D. busckii* from Eden, North Carolina apples, larvae could not be grown on laboratory medium. Females laid eggs, which hatched, but larvae wandered around, then died. Wallace (1978) described a similar phenomenon when the *D. virilis* strain adapted to the high urea environment was transferred back to standard *Drosophila* medium. Parsons and Hoffman (1986) demonstrated that a genetic basis for habitat preference exists in *Drosophila*. From *D. busckii*'s observed reaction, it suggests that in the natural environment sufficient frassy substrates exist throughout the breeding season to permit the evolution and persistence of a resource-dependent *D. busckii* strain.

Dorsey *et al.* (1962) found the chestnut curculio was invading acorns in the absence of chestnut trees in forests. *Chymomyza amoena* may have bred in chestnuts also in this country before this once dominant tree in Eastern hardwood forests succumbed to chestnut blight introduced in the early 1900s.

Invasion of frassy substrates by *Drosophila* seems recent in time compared to *C. amoena*. Fruit odor will attract *Drosophila* (Parsons and Hoffman, 1986). The replacement of lush woodlands first by farms and orchards, then by cities and suburbs with a further cutback in land area devoted to crop and fruit production may be encouraging the *Drosophila* invasion of the parasitized ripening fruit niche. Further evidence for this comes from the finding that although endemic *D. affinis* is typically trapped in early spring in Michigan (Band, 1993b), it has rarely been bred from frassy fruits in Michigan in summer in contrast to Virginia and North Carolina.

The emergence of drosophilids from frassy substrates on other Continents and islands, as Hawaii, also suggests that it is an opportunistic invasion, whose success is due to the immense amount of genetic variation existing within populations. Existing behaviors as attraction to fruit odors and aggregation tendencies (Band, 1989; Burla and Bächli, 1993) may increase a female's chances for willingness to oviposit in a ripening parasitized fruit substrate. Shorrocks *et al.* (1984) and Parsons and Hoffman (1986) argued however than interactions among *Drosophila* species using similar resources might be unimportant. Parasitism, microbial content, the degree of fruit ripening may serve to "structure" a pool of otherwise similar substrates. Independent association between drosophilid competitors (Shorrocks, 1990) may not exist if females of one or more species choose "parasitized" to merely damaged substrates for oviposition. Interspecific aggregation of drosophilids merits further study.

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