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On the overwintering strategy of *Chymomyza amoena* (Loew) (Diptera: Drosophilidae)

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Nearctic *Chymomyza amoena* larvae overwinter in a variety of nuts and fruits in the eastern United States; adults oviposit and larvae develop in a similar variety of nuts and fleshy fruits in summer. In Europe it has been reared from chestnuts *Castanea sativa* Miller as well as acorns *Quercus robur* L. and fleshy fruits: apples *Malus domestica* Borkh, wild sweet cherries *Prunus avium* (L.), plums *Prunus domestica* L. in summer. In the Maggia Valley in Switzerland it was reared from chestnuts in November 1990 and chestnuts and acorns in March 1991. In March 2004 overwintering studies were done. Chestnuts were collected and dissected from sites in Switzerland, Italy, and France where substrates had yielded *C. amoena* in past summers. Acorns were collected in the Bolle di Magadino, Canton Ticino and dissected. *C. amoena* larvae were found in acorns along with caterpillars (probably *Cydia splendana*); chestnuts were empty in all countries. Pest larvae in fallen chestnuts may have emerged too late in autumn 2003 for *C. amoena* females to oviposit in exit holes in the chestnuts. The niche, however, becomes an «empty niche» exploited by the species the following spring and summer until fruits, as apples, become available.

Key words: *Chymomyza amoena*, overwintering, acorns, chestnuts, France, Italy, Switzerland.

INTRODUCTION

Temperate zone *Chymomyza* Czerny are typically forest species. Both sexes are attracted to freshly damaged trees, cut wood, peeled logs. Males display and mate on such surfaces; females oviposit under bark (Wheeler 1952; Spieth 1957; Band 1988a, 1996; Burla 1995a, 1995b, 1997). Nearctic *C. amoena* (Loew) is an exception. Females oviposit in a variety of endemic fruits, e.g. native crabapples *Malus coronaria* L. (Band 1988b; Band *et al.* 2005) and nuts: acorns *Quercus* spp. L. (Sturtevant 1921;Winston 1956; Dorsey *et al.* 1962; Band 1996; Band *et al.* 2005), black walnut hulls *Juglans nigra* L. (Sturtevant 1921; Band 1988a, 1988b, see also Band *et al.* 2005) and butternut hulls *Juglans cinerea* L. (Sturtevant 1921). Males may display and mate on these fallen substrates although the species continues to be attracted to freshly damaged trees, cut wood also (Band 1988a, 1988b, 1996). Nuts have generally been attacked by primary pests whose larvae leave exit holes in which ovipositing females can lay eggs (Band, 1991, 1995).

Being principally the only Nearctic drosophilid and *Chymomyza* species breeding in native crabapples, *C. amoena* became a «domestic» species by invading domestic fruits (domestic apples *Malus domestica* Borkh., plums *Prunus domestica* L., pears *Pyrus communis* L., see Band 1988a, 1988b, 1996; Band *et al.* 2005) brought over by the colonists along with codling moth *Cydia pomonella* (L.). Host switching insects as plum curculio *Conotrachelus nenuphar* (Herbst) also aided *C.*

amoena's entry into apples. It was recorded in parasitized apples both in Michigan and Massachusetts by the late 19th century (Band 1994a, Band *et al.* 2005).

Chymomyza amoena was first recorded in the former Czechoslovakia in 1975, and was probably introduced into Europe as a domestic species via apples. However, it spread rapidly and seems to have easily reentered the forest habitat (Kekić & Bächli 1983; Máca 1985), also confirmed by its presence in both chestnuts *Castanea sativa* Miller and acorns *Quercus robur* L. in the Maggia Valley, Canton Ticino, Switzerland in 1990 and 1991 (Burla & Bächli 1991, 1992). In 1990 it was captured along with one specimen of Nearctic *C. procnemoides* Wheeler in a poplar forest in Hungary (Papp 1992). The two species are also sympatric in the Mt. Lake region of Virginia (Band 1994b), but there have been no other reports of *C. procnemoides* in Europe. Band (1994b) postulated that *C. procnemoides* was unlikely to duplicate the success of *C. amoena* as a biological invader since it must also compete with bark-ovipositing *C. caudatula* Oldenberg, *C. fuscimana* (Zetterstedt) and *C. distincta* (Egger) (Papp 1992) and *C. costata* (Zetterstedt). These four widespread, often sympatric European forest *Chymomyza* have been investigated by Burla (1995a, 1995b, 1997) in Switzerland.

Chestnut forests, apple orchards and isolated apple trees abound in southern Switzerland (Canton Ticino) and northern Italy (Valtellina and Piedmont regions). In these areas *C. amoena* is sequentially breeding in chestnuts and apples in summer. By mid/late July females are beginning to oviposit in fallen parasitized apples while 3rd instar larvae, pupae or empty pupal cases can be found in still moist, previous season's fallen parasitized chestnuts (Band *et al.* 1999, 2003, 2005). If chestnuts are too dry by July, adults can still be trapped in chestnut forests while females oviposit in available fallen parasitized apples and English walnuts *Juglans regia* L. as in southern Austria (Band *et al.* 2003).

Temperate zone *Chymomyza* typically overwinter as 3rd instar larvae. Diapause in *C. amoena* is facultative; larvae complete development and emerge as adults about 2 to 4 weeks after substrates (fruits, nuts) are placed at room temperature (Band & Band 1980; Band 1988b). In Michigan in winter larvae have been found to overwinter in a variety of substrates: black walnut husks (Band & Band 1984, 1987), domestic apples (Band & Band 1980, 1984), native crabapples and ornamental crabapples (Band & Band 1984; see also Band *et al.* 2005). The fact that Burla & Bächli (1992) reared *C. amoena* from parasitized chestnuts gathered in November 1990 and March 1991 in the Maggia Valley, Canton Ticino suggests that this species is utilizing chestnuts for overwintering. They also reared *C. amoena* from acorns gathered in March 1991.

Is this species overwintering in the larval stage in fallen parasitized chestnuts, as hypothesized in Band *et al.* (2003, 2005)? Does it also utilize acorns, since Burla & Bächli (1992) found it in acorns in March 1991? In March 2004 we therefore attempted to determine if *C. amoena* was using parasitized chestnuts for overwintering in South-Central Europe. We also investigated acorns in an oak forest in Canton Ticino in Switzerland.

Before undertaking overwintering studies on European *C. amoena*, we determined that it had arrived in France's Ardèche region, a major location of chestnut forests in that country. In summer 2003 we found that one of 27 parasitized apples at Veyras had 2 *C. amoena* eggs, one of 61 parasitized apples at Lyas had 3 *C. amoena* eggs. Chestnuts were dry, as in Austria. One *C. amoena* female was netted

Tab. 1. Drosophilids collected over banana bait at Veyras in the Ardèche region of France in July 2003. Collections were made evening only on 8 July, morning and evening on 9 and 10 July and morning only on 11 July.

Species	8 July	9 July	10 July	11 July	Total
Drosophila cameraria Haliday		8	11		19
D. deflexa Duda			3	2	5
D. funebris (Fabricus)		1	1	1	3
D. helvetica Burla		46	74	58	178
D. histrio Meigen			1		1
D. immigrans Sturtevant				1	1
D. melanogaster Meigen		4	2	1	7
D. obscura Fallén			1		1
D. phalerata Meigen		2	4	14	20
D. rufifrons Loew				1	1
D. subobscura Collin	1	777	994	706	2478
D. testacea von Roser		6	8	2	16
Amiota alboguttata (Wahlberg)		1	1	3	5
Phortica semivirgo (Máca)			4	1	5
Chymomyza amoena (Loew)			1		1
Gitona distigma Meigen		2			2
Leucophenga maculata (Dufour)		2			2
Scaptomyza pallida (Zetterstedt)				1	1
Totals	1	849	1105	791	2746

Some species are usually not attracted to bait and may have been collected «off the bait».

among 2746 drosophilids collected over fermented banana bait in a mixed forest (Tab. 1). *C. amoena* had earlier been collected in fruit orchards north of there beginning in 1994 (Withers & Allemand 1998).

MATERIALS AND METHODS

Studies were carried out under field conditions in March 2004 at localities where *C. amoena* had been found in summer in Switzerland, Italy and France. There was too much snow in Styria (Austria) to collect chestnuts. GPS coordinates and original map locations were used to return to and sample chestnuts from where substrates had been found to contain *C. amoena* in a previous summer. At the Bolle di Magadino in Switzerland acorns were also collected. All nuts were scored for the presence of holes made by departing pest larvae, dissected and inspected under a binocular microscope to determine if *C. amoena* larvae were present. Larvae were transferred to vials containing unyeasted *Drosophila* medium for shipment back to Michigan State University.

There was light snow in northern Italy and southern Switzerland in March 2004. Hand rakes were used to gather chestnuts. Chestnuts were collected at #417 trail marker outside Tirano, Valtellino region, Italy on 11 March 2004, near Cevio Hospital outside Cevio in the Maggia Valley, Canton Ticino, Switzerland on 13 March, at Purasca also in Canton Ticino on 14 March, at Bobbio Pellice, Cognetti and Villar Pellice near Torre Pellice, Piedmont area, Italy on 16 March. In the Ardèche region of France there was no snow. Chestnuts were collected at Veyras

Tab. 2. Numbers of chestnuts collected and inspected for *Chymomyza amoena* larvae in Italy, Switzerland and France in March, 2004.

Country	Region/Canton	Locality	Site	Chestnuts			
				Shells	No hole	with Hole	
						No *C. a.*	With *C. a.*
Italy	Valtellina	Tirano	#417t.m.	33	281	221	0
	Piedmont	Torre Pellice	Bobbio Pellice	2	71	80	0
			Cognetti	9	207	92	0
			Villar Pellice	14	368	117	0
Totals				58	927	510	
Switzerland	Ticino	Maggia Valley	Cevio	21	97	105	0
		Purasca		9	173	113	0
Totals				30	270	218	
France	Ardèche	Privas	Veyras	91	168	136	0
			Lyas	42	261	106	0
Totals				133	429	242	0

and Lyas near Privas on 18 March. Chestnuts were also collected near St. Pierreville in the interior of the Ardèche, a region of chestnut forests, sheep farms but no fruit trees and no *C. amoena*.

Acorns were collected in the Bolle di Magadino near Purasca, Switzerland on 14 March.

All calculations have been made using GraphPad Instat.

RESULTS

As shown in Tab. 2, no overwintering *C. amoena* larvae were found in parasitized chestnuts in March, 2004. Results were consistent over the three countries. No *C. amoena* females in the three countries appear to have used fallen parasitized chestnuts as oviposition sites in autumn, 2003. Also largely absent were *Cydia splendana* caterpillars in arrested development. In chestnuts only one *C. splendana* caterpillar per chestnut can complete development and exit to form a cocoon; the remainder that are present go into arrested development; *Curculio elephas* larvae and one *C. splendana* caterpillar can develop in the same chestnut, however (Bovey *et al.* 1978).

In fact few organisms were found in the dissected parasitized chestnuts. Small pinkish larvae were found in 3 parasitized chestnuts at #417 trail marker, in 2 parasitized chestnuts at Bobbio Pellice and in 3 parasitized chestnuts at Villar Pellice. Small ovoid eggs were present in 5 parasitized chestnuts in Lyas, France. Ants were present in a few shells in all areas.

However, *Chymomyza amoena* had been found in 13 % of the parasitized chestnuts collected at #417 trail marker outside Tirano, Italy in summer 2000 (Band *et al.* 2003, 2005). In southern Switzerland it had been reared from, collected as adults or identified in substrates, including chestnuts, in the Maggia Valley throughout the 1990s (Burla & Bächli 1991, 1992; Band *et al.* 1998) and found in both parasitized apples and chestnuts at Purasca in July 1998 (Band *et al.* 1999). In the Val-

Tab. 3. Acorns collected and inspected for *Chymomyza amoena* larvae in Switzerland in March, 2004.

Country	Canton	Locality	Shells	No hole	Acorns with Hole No *C. a.*	With *C. a.*	Number of *C. a.* larvae
Switzerland	Ticino	Bolle di Magadino	23	28	114	23	70*

*A total of 5 females emerged.

tellina region in July/August 2000 and Torre Pellice area in July 2002 in Northern Italy it had also been present in both parasitized apples and chestnuts (Band *et al.* 2003, 2005) and present in apples near Privas, France in July 2003.

Parasitized acorns collected in the Bolle di Magadino in March 2004 contained numerous third instar *C. amoena* larvae, as shown in Tab. 3. The mean number of larvae, 3.0 ± 0.5, is in good agreement with the average number of eggs found in parasitized acorns at Mt. Lake Biological Station in Virginia in summer 1990, 2.2 ± 0.4 (Band 1996). Caterpillars were also present in 28 acorns without *C. amoena* and 5 acorns with *C. amoena*. The caterpillars were probably *Cydia splendana* (Hb.), an insect pest which develops in both acorns and chestnuts in Europe (Bovey *et al.* 1978; Band *et al.* 2005). Sixty-six (4 of the 70 were dead) *C. amoena* larvae were transferred to media vials and mailed back to Michigan State University. Emergence occurred 17 and 18 days later, in good agreement with emergence data from overwintering substrates in the United States (Band & Band 1980; Band 1988a, 1988b). However, only 5 adults emerged, all females.

DISCUSSION

Burla & Bächli (1992) reared *C. amoena* from chestnuts collected in 2 places in the Maggia Valley, Canton Ticino, Switzerland in March 1991 and from acorns in one place in the same valley. This confirmed that this species could overwinter in nuts as in the United States. It had also entered a new niche on the Continent, parasitized chestnuts, where it has subsequently been found in summers elsewhere in Switzerland, in Italy or in chestnut forests in other countries. However, in March 2004, parasitized chestnuts investigated in three countries - Switzerland, Italy and France - lacked *C. amoena* larvae despite the presence of the species in those areas in previous summers.

Only acorns in the Bolle di Magadino, Canton Ticino where *C. amoena* has had an established presence for nearly a decade (Band *et al.* 1998, 1999) contained numerous *C. amoena* larvae. The acorns also contained *C. splendana* caterpillars, a species normally associated with European chestnuts; 18 % of the 23 parasitized acorns with *C. amoena* larvae also contained a *C. splendana* caterpillar. In the Valtellina region of Italy in July/August 2000, about half the *C. amoena* larvae shared chestnuts with *C. splendana* caterpillars in arrested development (Band *et al.* 2005).

Parasitized chestnuts in March 2004 from Purasca and elsewhere lacked caterpillars. The lack of caterpillars in chestnuts at Purasca compared to their presence in acorns in the Bolle di Magadino that same month is highly significant, as shown

Tab. 4. Comparison of numbers of caterpillars (*Cydia splendana*) in acorns in the Bolle di Magadino with the number in chestnuts collected in Purasca in March 2004. The acorns with *C. amoena* larvae (4 with pests and 19 without) have been included in the total number of acorns.

Locality	Substrate	Parasitized		
		With caterpillars	without	Total
Bolle di Magadino	acorns	33	104	137
Purasca	chestnuts	0	113	113
Totals		33	217	250

Fisher's exact test: two-sided P value is <0.0001

Tab. 5. Parasitized chestnuts containing arrested *Cydia splendana* caterpillars in past summers versus in March 2004.

Country	Place	Date	Number of Parasitized Chestnuts		
			With *C. s.*	No *C. s.*	Total
Italy	#417t.m., Tirano	Jul/Aug 2000	14	49	63
	Villar Pellice	July 2002	18	90	108
	Cognetti	July 2002	8	56	64
France	Veyras	July 2003	4	71	75
	St. Pierreville	July 2003	7	105	112
Totals			51	371	422
Italy	#417t.m., Tirano	March 2004	0	221	221
	Villar Pellice	March 2004	0	117	117
	Cognetti	March 2004	1	91	92
France	Veyras	March 2004	0	136	136
	St. Pierreville	March 2004	1	174	175
Totals		March 2004	2	739	741

Paired comparisons, Fisher's exact test:
- #417 t.m.: two-sided P value is < 0.0001
- Villar Pellice: two-sided P value is < 0.0001
- Cognetti: two-sided P value is 0.0036
- Veyras: two-sided P value is 0.0151
- St. Pierreville: two-sided P value is 0.0066

in Tab. 4. The fact that parasitized chestnuts in Italy and France lacked *C. splendana* caterpillars in arrested development compared to previous years is also highly significant in pair-wise comparisons ss shown in Tab. 5. Europe experienced a particularly hot summer in 2003 which may have imperiled the development of *C. splendana* eggs on the developing chestnuts, or the young caterpillar as it bored its way into the nut. *Cydia splendana* females oviposit outside the nut. *Curculio elephas* females oviposit directly into the developing chestnut. These are the two major pests of chestnuts in Canton Ticino (Bovey *et al.* 1978) and the Piedmont area of Italy (Arzone *et al.* 1993) and probably also in the Valtellina region, Italy and the Ardèche in France. Normally a *C. splendana* caterpillar that completes development exits a fallen chestnut beginning about the end of September, whereas *C. elephas* larvae do not exit until mid-October or later. This later date in autumn may be too

late for ovipositing *C. amoena* females. The Bolle di Magadino, near Gordola, is on Lake Maggiore; conditions may have been more favorable for the survival of *C. splendana* in the oak forest there.

The heat in summer 2003 also affected chestnut ripening; chestnut drop was delayed in the Piedmont region of Italy (Bounous, pers. comm.) and possibly throughout the area under study. This would also have the effect of delaying the emergence of pest larvae from the dropped chestnuts to even later in the autumn. This could also have been an additional factor in making the fallen chestnuts unavailable for ovipositing *C. amoena* females in autumn 2003.

Since *C. amoena* exploits overwintered chestnuts in the summer (Band *et al.* 1999, 2003, 2005), it would appear that this essentially empty niche is available to it as a breeding resource from spring onwards so long as chestnuts remain moist. Hutchinson (1957) argued that «the niche» was a property of the species; he defined the niche mathematically; there were as many niches as there were species. This set in motion a controversy about vacant niches that began in the last half of the 20th century. We agree with Hutchinson that the niche is a property of the species but it is behavior and physiology that enables individual members of the species to survive and reproduce in a given niche. Therefore, there can be empty niches. *C. amoena*'s preexisting adaptation to breeding in parasitized substrates in the United States enabled it to invade comparable substrates on the Continent not used by typical *Drosophila* or other *Chymomyza* species (Band *et al.* 2005). Chestnuts have rebounded in Europe following recovery from the chestnut blight which devastated *C. castanea* in the United States (see Bounous 2002). Even with *C. splendana* remaining in overwintered chestnuts, as shown in Tab. 5, more than 75 % of the fallen parasitized chestnuts in past years of sampling have been «vacant».

Conversely, there are about 30 stands of recovered chestnut trees *Castanea dentata* (Marsh.) in Michigan, some of which are mature (MacDonald & Fulbright 1991). There are also new orchard plantings. However, Michigan is too far north for chestnut curculios to survive and *C. splendana* is not in the United States. Thus, although *C. amoena* is in Michigan, chestnuts represent a niche that is closed to this species because it is «empty» for insect species attacking the nut. Mack *et al.* (2002) suggested «underused» or «unused» to replace the controversy about «empty niches». Nevertheless the data provided from the fallen parasitized overwintered chestnuts in Europe support Máca & Bächli (1994) that *C. amoena* took advantage of «empty niches» in their spread.

Oaks are more widely distributed on the Continent than chestnuts. The fact that *C. amoena* larvae can also exploit acorns may account for its widespread distribution in Northern Europe (Máca & Bächli 1994; Bächli 1999). The fact that *C. splendana* is in acorns also suggests that *Cydia* spp. may be an important insect pest series giving *C. amoena* access to acorns, chestnuts and apples throughout the year.

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ZUSAMMENFASSUNG

In den USA überwintern die Larven der nearktische Art *Chymomyza amoena* (Loew) in verschiedenen Nüssen und Früchten. Seit ihrer Einschleppung in Europa wurden einheimische Nüsse und Früchte als Entwicklungssubstrate während des Sommers nachgewiesen, unter anderem Kastanien und Eicheln. Obwohl frühe Funde im März aus Kastanien und Eicheln sowie späte Funde im November aus Kastanien bekannt sind, blieb die Überwinterung unklar. Im März 2004 sammelten wir Kastanien und Eicheln an einigen Orten in Italien, in der Schweiz und in Frankreich, an denen wir bereits während des Sommers *C. amoena* gefunden hatten. In parasitierten Kastanien wurden keine Larven gefunden; hingegen waren in Eicheln, die wir in der Bolle di Magadino, Ticino, gesammelt haben, zahlreiche Larven vorhanden. Die Befunde werden im Hinblick auf die Überwinterungsstrategie von *C. amoena* diskutiert.

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