Seasonal Activity of *Meloe americanus* (Coleoptera: Meloidae) in a Mississippi Old-field Habitat[1]

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ABSTRACT Adults and triugulin larvae of *Meloe americanus* Leach were collected by pitfall trapping and sweepnetting of foliage during 14 consecutive months at an old-field site in Washington Co., MS. Adults were captured in pitfalls from December to April, and triungulins were captured in pitfalls and attached to Apoidae (Hymenoptera) hosts on foliage only from April to May and from September through October. Several scenarios are proposed to explain this unusual pattern of disjunct triungulin seasonal occurrence. Spatial patterns of adult and triungulin occurrence are correlated with successional changes in the habitat, and attachment sites of triungulin larvae on Apoidae hosts are documented.

KEY WORDS Meloidae, *Meloe*, phoresy, old-field

The coleopteran family Meloidae occurs worldwide, with the adult instar phytophagous and larval instars predaceous or parasitic (Crowson 1981). Adults of some species in the United States can be economically important pests on such crops as alfalfa, turnips, mustard, and clover and have been recorded on plant species in at least 35 genera (Pinto and Selander 1970). Larvae of Meloidae are known to feed either on the contents of the nesting cells of bees, the eggs of grasshoppers, or the eggs of other meloids (Selander 1981).

Members of the meloid genus *Meloe* Linnaeus are flightless as adults, with the hind wings absent and elytra reduced, and are called "oil beetles" due to the release of fluid from joints of the body and legs (reflex bleeding) when disturbed (Balduf 1935). All known larvae of *Meloe* are predators of wild bee eggs and larvae, as well as consumers of the provisions in wild bee larval cells (Pinto and Selander 1970). A *Meloe* female typically lays several 1000-egg clusters in the soil in the vicinity of potential host nests. Eggs may hatch and larvae emerge within 30 days, or the emergence of larvae may be delayed for more than 130 days. Four larval stages ensue before the prepupa, with the first stage termed triungulin. This stage is very mobile and active, climbing vegetation and waiting at inflorescences for the arrival of potential hosts. Triungulins are phoretic, attaching to members of the Apoidea (Hymenoptera) for transport back to the nest where further larval development occurs in the cells of individual host larvae (Askew 1971).

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The data reported herein is the result of an attempt to determine the spatial and temporal occurrence of meloid adults and triungulin larvae in a Mississippi old-field habitat and to define various ecological parameters associated with those patterns of occurrence.

Materials and Methods

The study site was a fenced 2.5-ha old-field habitat (formerly a horse pasture) 3 km SSE of Leland, Washington Co., MS (Site 1 of Young and Welbourn 1987). Detailed descriptions of the study site, trap design, and sampling protocols are presented elsewhere (Young and Lockley 1994), as are results of other research conducted at this site (Young 1986, Young and Lockley 1990, Young et al. 1989). Briefly, the site was bordered on the east by a paved road and adjacent 32-ha cotton field, on the north by residences, on the west by a deciduous-tree-lined creek bank, and on the south by old-field habitat. The eastern third of the field had a heavy clay soil with poor drainage and no adjacent trees or structures to provide shade. The center and western portions of the field had sandy loam soil that was well drained, with shade provided by trees on the extreme western edge. The eastern and central sections contained a variety of forbs, dominated in the late summer and fall by horseweed, *Erigeron strigosus* Muhl. ex. Willd. The western third of the field contained mixed grasses, with scattered clusters of such forbs as *E. strigosus, Aster pilosus* Willd., and *Solidago altissima* L.

Three pairs of pitfall traps were placed at the site, one pair in each third of the field. Members of each pair were placed 1 m apart and connected by a sheet metal barrier 10 cm high that was embedded 2.5 cm into the soil. Each pitfall was 10 cm in diam and contained 100 ml of a 50% solution of ethylene glycol. Traps were emptied and refilled with preservative at one- or two-week intervals (depending on temperature and associated arthropod activity levels). Contents of each pair of traps were pooled as one sample. Sampling of the above-ground foliage with a sweepnet (39 cm diam, 10 sweeps per sample) was conducted mid-morning on the same day pitfall traps were processed. Material from pitfall traps and sweepnet samples were brought into the lab and refrigerated (pitfall) or frozen (sweepnet) prior to sorting and identification. Meloidae specimens were identified by the keys of Pinto and Selander (1970) and by comparison with identified material at Mississippi State University, Starkville; the Florida State Collection of Arthropods, Gainesville; and the United States National Museum, Washington, DC. Voucher material has been deposited in the Mississippi State University collections and in the collection of the author.

Results and Discussion

Between 25 March 1985 and 29 May 1986, a period of 61 weeks, 114 pitfall trap samples of the ground stratum community obtained 403 *Meloe americanus* triungulin larvae and 31 adults (Table 1). Sweepnet samples (68) of the foliage stratum community did not obtain adults or free-moving larvae of *M. americanus,* but did capture 28 Apoidea (Hymenoptera) with attached triungulin larvae (Table 2).

Temporal activity patterns. The temporal patterns of occurrence of adult and triungulin larvae documented in Tables 1 and 2 present some interesting problems

Table 1. Adults and triungulin larvae of *Meloe americanus* in pitfall traps.

	Adult				Triungulin			
Sampling Period	East	Center	West	Total	East	Center	West	Total
25 Mar-1 Apr 85		1 ♀		1				
1 Apr-5 Sep (16 sampling periods)								
5-12 Sep						8	2	10
12-19 Sep					13	4	5	22
19-26 Sep					5	7	6	18
26 Sep-3 Oct					19	7		26
3-10 Oct					55	11		66
10-17 Oct					22	4		26
17 Oct-5 Dec (3 sampling periods)								
5-12 Dec			5 ♂,3 ♀	8				
17-23 Dec			2 ♀	2				
27 Dec-3 Jan 86			1 ♀	1				
21-27 Jan			1 ♂,2 ♀	3				
7-14 Feb			1 ♂	1				
25 Feb-4 Mar		1 ♂	1 ♂,1 ♀	3				
10-17 Mar			2 ♂,1 ♀	3				
23-31 Mar			3 ♂,1 ♀	4				
9-15 Apr			2 ♂,3 ♀	5			75	75
22-28 Apr					2		81	83
5-12 May					1	9	60	70
21-29 May 86						1	6	7

Totals	Adults			Triungulin		
		East			East	117
		Center	1 ♂, 1 ♀		Center	51
		West	15 ♂,14 ♀		West	235
		Total	16 ♂,15 ♀		Total	403

Table 2. Triungulin larvae of *Meloe americanus* attached to Hymenoptera hosts.

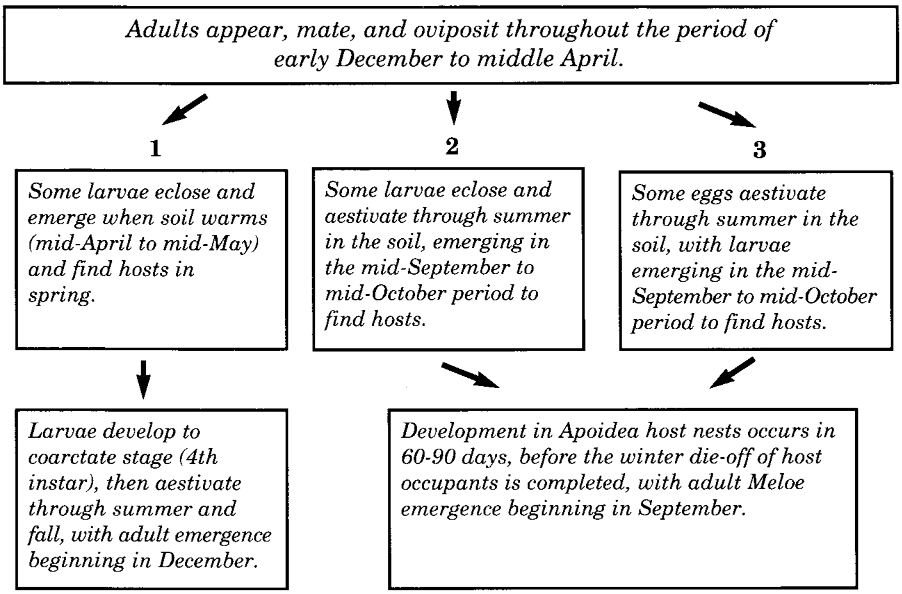
Date	Capture Site (Plant)	No. Hymenoptera Hosts Captured	No. Hosts w/Triangulins
19-Sep-85	Carduus	2 Apidae	2
26-Sep	Solidago	1 Megachilidae	1
3-Oct	Solidago	2 Sphecidae	2
3-Oct	Aster	1 Spechidae	1
		1 Anthoporidae	1
10-Oct	Aster	2 Halictidae	1
		1 Anthophoridae	1
7-Apr-86	Erigeron	1 Sphecidae	1
9-Apr	Erigeron	8 Anthophoridae	2
10-Apr	Erigeron	20 Anthophoridae	1
10-Apr	Erigeron	9 Anthophoridae	3
10-Apr	Trifolium	1 Apis mellifera	1
		5 Anthophoridae	2
10-Apr	Trifolium	1 Apis mellifera	1
		4 Anthophoridae	2
10-Apr	Erigeron	2 Anthophoridae	2
22-Apr	Erigeron	3 Vespidae	1
22-Apr	Erigeron	1 Anthophoridae	0
		2 Vespidae	2
22-Apr	Erigeron	2 Anthophoridae	1
		1 Apidae	0
	Total		28

in interpretation. The existing literature on *M. americanus,* summarized by Pinto and Selander (1970) and based primarily on studies in Illinois, indicates that the expected pattern of activity for this and several other *Meloe* species would be adult activity from fall into the early spring and triungulin activity only in late spring. The temporal pattern of occurrence in the present Mississippi study, however, indicates a winter-early spring appearance of adults and spring and fall activity of triungulin larvae. The beginning of sampling in the last week of March 1985 apparently was at the end of the adult activity period, as only one adult was captured that week. Although sampling continued throughout the summer and fall, adults were not captured again until the following winter and early spring. Triungulin larval activity was first evident in the fall of the first sampling year, disappearing several months before the winter appearance of the adults. Triungulin larvae appeared again the following mid-spring as the adults disappeared, with larval abundance much reduced when sampling stopped at the end of May. What is unusual in these observed temporal activity patterns is the presence of two disjunct periods of triungulin activity, peaking in April and October, as demonstrated by both pitfall captures and captures of hosts with attached larvae.

Within the genus *Meloe,* several seasonal activity patterns occur (Pinto and Selander 1970). Some species are active as adults only in the spring, some only in summer and fall, some only in fall, and some from fall to spring. Triungulin activity in most species occurs in the spring, coinciding with maximal foraging bee activity. Only one species, *M. laevis* Leach, is known to have triungulins active on flowers and on bees in late summer and fall. Thus, there is no evidence in the literature that a species of *Meloe* can have triungulin larvae active in both the spring and fall. The first considered explanation for this situation was that more than one species of *Meloe* was involved.

Based on known distributions of *Meloe* species in North America, only two species occur in Mississippi or the adjacent states of Alabama and Louisiana: *M. americanus* and *M. campanicollis* Pinto & Selander. Adults of these two species are easily separated by key characters, species descriptions, and by typical activity periods. Triungulin larvae of these two species are easily separated on the basis of the shape of the distal portion of the mandibles and by other features. A species that is very similar morphologically to *M. americanus*, however, is *M. impressus* Kirby. These two species can be separated by careful use of existing taxonomic keys and by geographical distribution. *M. impressus* has been recorded from the mountains of the southeastern United States and other areas to the north and west, but would be very unlikely to occur in the lowlands of west-central Mississippi. Other *Meloe* species that have a transcontinental distribution or occur to the south of the United States, and which conceivably might occur in west-central Mississippi, can also be eliminated from consideration on the basis of adult and triungulin morphological characters. Based on known biologies of the various *Meloe* species, *M. laevis* is a prime candidate for possible presence at the Mississippi site because it is the one species with triungulins active in the fall. This species, however, occurs only in arid highlands areas of the western United States and Central America and both adult and triungulin forms can be easily separated from *M. americanus* using morphological characters. The appropriate conclusion that can be drawn from the foregoing information, combined with the results of an exhaustive collection program at this site over a 14-month period, is that only one species, *Meloe americanus*, was active at the study site.

Several biological explanations are possible for the observed seasonal activity patterns of *M. americanus.* In the Mississippi study site, the occurrence of mild winters and the associated extended seasonal activity of flowering plants and adult Apoidea may have provided the opportunity in *M. americanus* for modifications of seasonal activity patterns typically displayed in the central areas of its range (i.e., in the Illinois study of Pinto and Selander, 1970). Several developmental sequences for *M. americanus* that could occur in Mississippi and that could result in the observed pattern of temporal occurrence are as follows:



The spring and fall emergence periods for triungulin larvae may merely be a function of when the egg was initially deposited: early ovipositions in December and January leading to spring emergence, and late ovipositions in March and April leading to summer aestivation of larvae and fall emergence. The absence of triungulin larvae in the first spring of the sampling period may indeed be supportive of this scenario, in that habitat conditions associated with old-field succession may have only become favorable for *M. americanus* in late winter-early spring, eliminating the early ovipositions and subsequent spring emergence of triungulins. The possibility of egg aestivation should also be considered. The sister species *M. impressus* has been documented to produce eggs in the autumn that underwent a prolonged embryonic diapause through the winter, with subsequent completion of embryo development and hatching in the spring (Pinto and Selander 1970). It would not be surprising to see such a delay of egg hatch in *M. americanus*.

Many insect species display plasticity in life history parameters, usually as an adaptation to unpredictable environmental conditions but also to climatic variations across a species' range (Denno and Dingle 1981). The documentation of such plasticity in *Meloe,* thus, would not be unexpected, particularly given the wide geographic range and diversity of climatic conditions over which some *Meloe* species occur. Information from the study site is not available to refute any of the proposed scenarios, and subsequent human-induced changes in the habitat prevent further observations.

Spatial activity patterns. Adult *M. americanus* occurred almost exclusively in the winter in the western section of the old-field, the only area of the site with afternoon shade, open grassy areas, and/or a scattering of groups of forbs. Triungulin larvae in the subsequent spring were also most abundant in the western section of the site, whereas in the previous fall they were most abundant in the eastern portion. The appearance of the vast majority of triungulin larvae in the western section 30-60 days after almost all of the adult beetles had appeared in the same section suggests that these larvae were progeny of the earlier-appearing adults. Unfortunately, sampling in this study did not begin until the end of March, and thus could not document the presence and location of the winter adults that were the putative parents of the subsequent fall triungulin larvae.

A parameter that complicates the interpretation of observed patterns of *M. americanus* occurrence at the study site is the successional changes in the habitat associated with the removal of horses 6 months prior to the start of sampling and the elimination of seasonal mowing 18 months prior (Young and Lockley 1994). These successional changes included the domination of the eastern and central sections by goldenrods (*Solidago* spp.) and fleabanes (*Erigeron* spp.) in the first season after horse removal and overgrowth of these sections by vetch (*Vicia sativa* L.) in the second season. This recent history of the study site suggests that the habitat was initially not well suited for *M. americanus,* with horse activity and mowing inhibiting the development of a flowering forb population that would be attractive to potential Apoidea hosts. One or two subsequent seasons of flowering forb dominance probably was associated with increased bee activity and the appearance of the dispersive triungulin stage of *M. americanus*. Subsequence dominance of vetch in the eastern and central sections reduced flowering forb abundance and associated Apoidea (pers. observ.), leaving the western section of the study site as the only area suitable for *M. americanus.* Further overgrowth of vetch in succeeding years might indeed have eliminated *M. aermicanus* from the site. These successional changes also impacted the spatial and temporal distribution of spiders (Young and Lockley 1994), mites (Young and Welborn 1987), beetles (Young 1995), and other arthropods (Young, in prep.).

Host attachment. Triungulin larvae of *Meloe* species have been recorded as attached to the body hairs of at least 14 potential host species of Apoidea, representing 6 genera and 4 families (Pinto and Selander 1970). Most host records, however, involve members of the genus *Anthophora* Latreille (Hymenoptera: Anthophoridae). Because sensory discriminatory abilities of *Meloe* triungulin larvae are probably limited, there is a high likelihood of either triungulin attachment to the wrong host or failure to find the correct host before starvation (Crowson 1981). One study, in fact, estimated a 99% mortality rate for triungulin larvae of a *Meloe* (Mayer and Johansen 1978). *Meloe* triungulin larvae have been recorded attached to a variety of non-host insects, including bees, wasps, flies, beetles, and butterflies (Pinto and Selander 1970).

The present study documents the attachment of triungulin larvae to 28 individual hymenopterans (Table 2). Fifteen of these individuals (Anthophoridae) could be considered likely hosts, though no host records are known for *M. americanus* (Pinto and Selander 1970). The specific attachment sites of individual triungulin larvae were recorded for five hymenopterans captured in April (Table 3). Most larvae were attached at the base of the wings or legs, attachment sites that have been documented by other investigators with other *Meloe* species (Pinto and Selander 1970).

Table 3. Attachment sites of *Meloe americanus* triungulin larvae on five hosts.

Host (Date of Capture)	Number and Location of Attached Larvae*
Anthophoridae (7 Apr)	1 left lateral head-thorax junction
	1 right lateral head-thorax junction
	1 left dorsal anterior pedicel
	1 right dorsal anterior pedicel
	1 base left dorsal anterior wing
Vespidae (22 Apr)	1 right anterior notum
	1 center propodeum
Vespidae (22 Apr)	5 left dorsal propodeum
	9 right dorsal propodeum
	2 right lateral propodeum
Vespidae (22 Apr)	1 left anterior notum
	1 right anterior notum
	1 first intercoxal segment
Anthophoridae (22 Apr)	1 under right wing at propodeum

* All attached to pile.

In conclusion, information obtained from this study in Mississippi represents a substantial addition to the body of knowledge concerning *Meloe* in the southern United States, and suggests that further research on the ecology of *Meloe* species in this region may reveal greater diversity in their ecologies than is presently known from studies in more northern areas.

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