ECOLOGY AND TAXONOMY OF LOWER RÍO GRANDE VALLEY ZETHUS^{1,2}

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ABSTRACT

Lower Río Grande Valley populations of Zethus miscogaster Saussure, Z. montezuma Saussure, Z. otomitus Saussure, and Z. aztecus Saussure vary dramatically in abundance from year to year and within each year show some differences in monthly phaenology. They are active well into winter and fly on any day when the shade temperature reaches 22C. All visit the same rather wide range of flowers. They are Neotropic taxa which approach their northern limit in Texas. Z. otomitus is recorded for the 1st time from the United States.

In a review of the Lower Río Grande Valley Zethus (Porter 1975b), I reported Z. aztecus and Z. montezuma as new for the United States, cited Z. miscogaster for the 1st time from Texas, and offered a key to all United States members of this primarily Neotropic genus. After more collecting in Hidalgo County, Texas, at the Bentsen Río Grande Valley State Park and the Valley Botanical Garden, I have obtained more specimens and ecological data on miscogaster, montezuma, and aztecus. I have established also the presence in south Texas of Z. otomitus, a species hitherto unknown north of central México.

Zethus are strong-flying vespoids that provision their nests, made in twigs or trunks or attached to twigs, with lepidopterous larvae. Of the 187 American species, 98 either enter or are restricted to the evergreen and deciduous forests of tropical South America (Bohart and Stange 1965:22). Middle America has 36 species, and all throughout its range Zethus tends to evolve forms adapted to thorn scrub or even deserts. It is thus not surprising that 4 species have reached the semiarid Lower Río Grande Valley, although remarkable that 3 of these, miscogaster, montezuma, and aztecus, often become abundant here at the northern limit of their range.

In this paper, I have summarized monthly and yearly phaenologic records accumulated since 1973, indicated those plants most often visited by Zethus, and provided a 1st report on observations of daily phaenology and activity temperatures commenced in 1977. Periods available for collection of Valley Zethus have included, in each year since 1973, 30 days in December and January, 1 week in March, 2 weeks in May, 2 weeks in June, 1 week in August, and 1 week in September, as well as 1 week each in April and November. Between 19-27 November 1977, I sampled Zethus every hour from 0900-1700 and separately labeled each hour's catch. From 18-31 December 1977 this technique was supplemented with maximum-minimum thermometers to record daily temperature ranges and small, portable thermometers

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to obtain hourly readings of both sun and shade temperatures at each collecting site.

KEY TO UNITED STATES Zethus

	KEY TO UNITED STATES Zethus
1.	Third gastric sternite with a conspicuous translucent apical lamella or flange that is truncate abruptly on each side before attaining lateral margin of sternite
1′.	Third gastric sternite with apical flange weakly to conspicuously differentiated but not abbreviated toward lateral margin of sternite
2.	Hind margin of 2nd gastric tergite evenly convex, hardly membranous; 1 well developed mid-tibial spur; interocellar area without tubercles (Texas to El Salvador)
2'.	Hind margin of 2nd gastric tergite divided into 3 sections by translucent lateral lobes; 2 mid-tibial spurs; interocellar area with broad, more or less polished tubercles separated by a narrow line of punctures (Arizona to El Salvador)
3.	Female clypeus mat with very minute regular longitudinal striae, as well as numerous large punctures; male flagellum rolled toward apex; mid-tibia with 1 well developed apical spur; gaster mostly red (Florida)
3′.	Female clypeus shining with strong punctures and/or coarse striations but without minute wrinkling; male flagellum hooked toward apex; mid-tibia with 1 or 2 apical spurs; gaster mostly black or in occasional specimens of miscogaster largely red
4.	Stem of 2nd gastric tergite definitely longer than that of 1st; notaulus weakly impressed or absent (Arizona and Texas to Argentina)
4'.	Stem of 2nd gastric tergite definitely shorter than that of 1st; notaulus distinct over at least apical 0.5 of mesoscutum
5.	Apical propodeal lamella produced into a rounded lobe above valvula; 2 well developed mid-tibial spurs; petiole slender (Texas to Colombia)
5'.	Apical propodeal lamella scarcely distinguishable from rest of submarginal carina; only 1 well developed mid-tibial spur; petiole moderately to very stout
6.	Height of petiole markedly less than 1/2 the distance from insertion of flexor muscle to apex; 1st hind tarsomere of male narrow (Texas to Panamá)
6'.	Height of petiole equal to 1/2-3/5 the distance from insertion of flexor muscle to apex; 1st hind tarsomere of male flattened beneath and conspicuously broadened (eastern United States) Z. spinipes Say
	thus (Z.) miscogaster Saussure (Fig. 1) ATERIAL EXAMINED. 81 females, 104 males: Bentsen Park, Botanical
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MATERIAL EXAMINED. 81 females, 104 males: Bentsen Park, Botanical Garden, Santa Ana National Wildlife Refuge.

MONTHLY PHAENOLOGY. 7 females and 3 males in January, 1 male in





Fig. 1. Zethus miscogaster. Triangles indicate geographic distribution in Middle and North America. Fig. 2. Zethus montezuma. Triangles indicate geographic distribution in Middle and North America.

March, 1 male in May, 2 females and 1 male in June, 10 females and 24 males in August, 25 females and 21 males in September, 24 females and 35 males in November, and 10 females and 11 males in December.

ANNUAL PHAENOLOGY. 2 females and 3 males in 1973, 2 males in 1974, 4 females and 4 males in 1975, 20 females and 16 males in 1976, and 57 females and 77 males in 1977.

TEMPERATURE AND DAILY ACTIVITY PERIOD. From 20-22 November 1977, when maxima and minima in the shade were about 18-28C and skies ranged from clear to partly cloudy, 1 *miscogaster* was taken between 0900-1000, 3 from 1000-1100, 2 from 1100-1200, 3 from 1200-1300, 6 from 1300-1400, 6 from 1400-1500, 5 from 1500-1600, and 1 from 1600-1700.

Sampling from 22-27 December, when better temperature records were kept, yielded the following data.

22 December. Minimum -0.6°C, maximum in shade 23°C; sky clear; 2 males from 1400-1500 (23°C shade, 37°C sun).

24 December. Minimum 12.9°C, maximum in shade 27.5°C; partly cloudy; 1 male from 1100-1200 (22°C shade, 29°C sun), 2 males from 1300-1400 (26.5°C shade, 39°C sun), 2 males from 1400-1500 (27.5°C shade, 32°C sun), 1 female and 2 males from 1500-1600 (22°C shade, 29°C sun).

25 December. Minimum 12.9°C, maximum in shade 25.5°C; partly cloudy; 1 female from 1400-1500 (25.5°C shade, 28.5°C sun).

27 December. Minimum 10°C, maximum in shade 22°C; partly cloudy; 1 female from 1200-1300 (22°C shade, 33°C sun).

The above data from late fall and early winter 1977 show that *misco-gaster* may be active from 0900-1700 and at a shade temperature range of 22-27.5°C and at a sun range of 28.5-39°C. It flies most abundantly during early afternoon, when temperatures are highest, and normally seeks herbs, shrubs, or trees in direct sun.

2. Zethus (Z.) montezuma Saussure (Fig. 2)

MATERIAL EXAMINED. 71 females, 25 males: Bentsen Park, Botanical Garden, Santa Ana National Wildlife Refuge.

Monthly Phaenology. 34 females and 7 males in January, 3 females and 3 males in March, 1 male in April, 2 males in August, 3 females in September, 11 females and 2 males in November, and 20 females and 10 males in December.

YEARLY PHAENOLOGY. 3 females and 1 male in 1973, 15 females and 6 males in 1974, 28 females and 7 males in 1975, 6 females and 5 males in 1976, and 19 females and 6 males in 1977.

TEMPERATURE AND DAILY ACTIVITY PERIOD. From 21-24 November 1977, when shade minima and maxima were about 10-28°C and skies ranged from clear to partly cloudy, 1 *montezuma* was netted between 1000 and 1100, 2 from 1100-1200, 2 from 1200-1300, 4 from 1300-1400, and 2 from 1500-1600.

During the December 1977 period of hourly collection and temperature recording, this species appeared only on the 24th, a warm, partly cloudy day (minimum 12.9°C, maximum in shade 27.5°C), when 1 specimen was registered from 1100-1200 (22°C shade, 29°C sun), 1 from 1300-1400 (26.5°C shade, 39°C sun), and 1 from 1400-1500 (27.5°C shade, 32°C sun).

During November and December, *montezuma* may fly from 1000-1600 and at shade temperatures of 22-27.5°C and in a sun range of 29-39°C. Most specimens are captured in bright sun and in early afternoon when temperatures are hottest.

3. Zethus (Z.) otomitus Saussure (Fig. 3)

MATERIAL EXAMINED. 2 females: Bentsen Park, 1 female, 30-VIII-77; Botanical Garden, 1 female, 27-VIII-8-IX-73.

FIELD NOTES. My Valley otomitus were netted from flowers of Baccharis in bright sun at the edge of dense woods. I have also collected many in northeast México, mostly in deep, humid forest as they flew around the dead trunks and logs in which they were nesting. Calmbacher (1977:135-7) has described the nest of this species.

DISTRIBUTION. Bohart and Stange (1965:118) cite otomitus from no farther north in México than Nayarit and Veracruz, so the Valley records provide a noteworthy range extension. I have also found it common in late May and early June every year from 1974-77 in the densely forested Cola de Caballo ravine near Monterrey, México, and only 240 km west and a little south of the Valley.

4. Zethus (Zethoides) aztecus Saussure (Fig. 4)

MATERIAL EXAMINED. 25 females and 32 males: Bentsen Park, Botanical Garden.

MONTHLY PHAENOLOGY. 1 female and 1 male in January, 1 female in May, 3 males in June, 2 females and 9 males in August, 13 females and 14 males in September, 4 females and 3 males in November, and 4 females and 2 males in December.

YEARLY PHAENOLOGY. 7 females and 3 males in 1973, 1 male in 1974, 3 females and 4 males in 1975, 8 females and 21 males in 1976, and 7 females and 3 males in 1977.

TEMPERATURE AND DAILY ACTIVITY PERIOD. On 21 November 1977, I collected 3 aztecus, of which 1 was taken between 1000 and 1100 and the

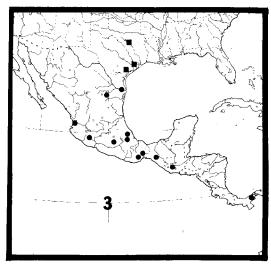




Fig. 3. Zethus otomitus. Circles indicate geographic distribution in Middle and North America. Zethus spinipes. Squares indicate geographic distribution in Texas. Fig. 4. Zethus aztecus. Rhombs indicate geographic distribution in Middle and North America.

other 2 from 1300-1400. The day was clear with a shade temperature range of 18-28°C.

Only 1 aztecus was netted during the December sampling period and this on the 31st (minimum 16.7°C, maximum in shade 25.5°C) and between 1500 and 1600, when the shade temperature was 25°C and the sun reading 27°C.

In fall and winter, *aztecus* thus may be active from 1000-1600, apparently when shade temperatures have reached at least 25°C. It almost always flies in bright sun and becomes most abundant during the warmest part of the day.

Conclusions

ZOOGEOGRAPHY. Zethus is a huge genus centered in tropical South American forests and thorn scrub. It also has a substantial endemic Middle American radiation plus some species in warmer parts of the Old World. Only 7 Zethus reach the United States, and 1 ranges north of the Mexican border area or south Florida. These wasps are well sclerotized, tolerant of bright sun and high temperatures, and seem able to fly long distances. Available information suggests that most species also can use a wide variety of caterpillars as prey. Low winter, temperatures consequently may be the major factor which keeps them from invading more successfully the deserts of the southwestern United States or the Pine-Oak woods of the northeast Gulf strip.

Valley Zethus belong to several of the major zoogeographic patterns displayed by Neotropic biota. Z. miscogaster ranges from Arizona and south Texas to Argentina and pertains to a group of 6 species, in which 4 are strictly South American and 2 extend over much of South and Middle

America. Such ichneumonids as Coccygomimus caeruleus Brullé, C. sumichrasti Cresson, and Eiphosoma dentator Fabricius, the sphecids Sphex servillei Lepeletier and Isodontia fuscipennis Fabricius, the vespid Brachygastra lecheguana Latreille, and the papilionid butterflies Papilio anchisiades Esper and P. astyalus Godart provide other examples of the same wide-ranging, endemically South American biogeographic category. Z. montezuma has been found from Texas to Colombia but pertains to a species group that ranges south to Paraguay, although centered in Middle America. The ichneumonids Coccygomimus punicipes Cresson (Texas to north Chile), Conopyge spp. (Texas to Brasil) and Eurydacus spp. (México to coastal Perú) furnish other examples of this northern South American and Middle American tropical pattern. In contrast, Z. aztecus reaches only El Salvador and forms a monotypic, predominately Middle American group but one with close relatives in South America. Ichneumonids such as Cryptanura compacta Cresson, C. lamentaria Cameron, Lymeon leucosoma Cameron, and Polycyrtidea limitis Cushman, and the sphecid Trachypus mexicanus Saussure follow a similar pattern. Finally, Z. otomitus, which ranges from Texas to Panamá, has a close relative in Colombia, while the other member of its group, Z. spinipes, occurs in the eastern United States from Massachusetts to Kansas and into Texas as far south as Victoria. Although otomitus and spinipes come within 350 km of each other in east Texas, they do not intergrade, so their geographic isolation may have been lengthy. This now mainly Middle and South American species group must have ranged far north into the eastern United States during warmer Tertiary times, so that the ancestor of spinipes survived in some Austroriparian refugium during Pleistocene glacial maxima while those populations that were to become otomitus retreated into México. Both remained forest adapted, and thus during interglacial expansion have not reestablished contact across the south Texas thorn scrub. Remnants of the eastern North American Neotropic biota are detectable among many groups of organisms. Forty Neotropic genera of Ichneumonidae, many with species restricted to the eastern United States, attain at least Maryland (Porter 1977:77-78). Among the Heteroptera of Connecticut, 33% of the genera show Neotropic affinities (Slater, 1974:153). The southeastern United States even has a few Neotropic reptiles, such as Rhadinaea flavilata Cope, Tantilla coronata Baird and Girard, and Anolis carolinensis Voigt.

Phaenology: as detailed under each species, Valley Zethus follow a uniform daily phaenologic regimen. They begin to fly when the shade temperature is 22C and the sun temperature 27C and during the cooler months peak in early to mid afternoon and rarely appear before 1000 or after 1600. All 4 species are thermophilic, but miscogaster, montezuma, and aztecus easily survive light frosts, as shown by their continued presence in December and January. I do not have quantitative data on their daily flight periods in summer, but they seem most abundant from 0900-1200 with less activity after 1300, when shade temperatures attain 34-35C.

Valley Zethus show substantial differences in monthly phaenology, as summarized in Table 1.

Z. miscogaster peaks between August and December with maximum abundance in November. The November figure is significant because I collected in the Valley during that month only in 1977; whereas the data for May, June, August, September and December derive from 1973-77 and

TABLE 1. Monthly phaenology of Zethus species from the Lower Rio Grande Valley.

Species	Jan.	Mar.	Apr.	May	June	Aug.	Sept.	Nov.	Dec.
Z. miscogaster	10	1	_	1	3	34	56	59	21
Z. montezuma	41	6	1	_		2	3	13	30
Z. otomitus	_	_	_	_	_	2	_	_	_
Z. aztecus	2		-	1	3	11	27	7	6
Total specimens/	53	7	1	2	6	49	86	79	57
Total specimens collected:	340								

those for January and March from 1974-77. Z. aztecus, always less common than the preceding, has a comparable cycle but reaches greatest abundance in September, and is relatively rare by November. Z. otomitus has been collected in the Valley only in August but is common near Monterrey, México in late May and early June. Z. montezuma is strongly invernal, with 74% of the specimens taken in December and January. Thus, although all 4 Valley Zethus may coincide at certain times of the year, each species has a different peak. When we know more about prey preferences and nesting habits, we may find that this temporal displacement helps reduce competition for resources such as prey or nesting sites, particularly since all species frequent the same habitats. However, Z. montezuma, whose optimum flight period is most out of phase with its congeners, also differs from them in being smaller (average length to apex of tergite 2 about 11-13 mm in miscogaster and aztecus and 9-11 mm in montezuma), and this size difference alone should eliminate spatial and trophic conflicts.

Valley Zethus also fluctuate in numbers from year to year, as documented in Table 2.

Yearly population density fluctuations of the type noted above are normal for most Valley insects. Probably they result from the region's unstable climate characterized in winter by occasional killing frosts and at any season by droughts which often last 2-3 months. Under these conditions, few species can be equally abundant from year to year, and some of those

TABLE 2. Annual phaenology of *Zethus* species from the Lower Rio Grande Valley.

Species	1973	, 1974	1975	1976	1977
Z. miscogaster	5	2	8	36	134
Z. montezuma	4	21	35	11	25
Z. otomitus	1	_	_	_	1
Z. aztecus	10	1	7	29	10
Total specimens/yr.	20	24	50	76	170

with strong dispersal powers may disappear from the Valley, only to be renewed in favorable periods from the more diverse and stable communities that occupy the lush eastern slopes of the Sierra Madre Oriental in nearby México.

Habitat Preferences and Plant Associations: Valley Zethus occur in all environments from open fields with scattered shrubs to dense gallery woods but almost always are found in direct sun. The species visit a variety of plants, where they feed on nectar of flowers, honeydew, or seek twigs suitable for nesting. All species seem to have about the same range of habitat and plant preferences, some of which are discussed in the following list of plants with which I have found Valley Zethus most consistently associated.

Acacia farnesiana L. (Leguminosae). Occasional Zethus, particularly miscogaster, fly around this shrub at almost any season. The flowers, which appear mostly in spring, attract a few montezuma but are not regularly visited by other Zethus species.

Acacia greggii A. Gray (Leguminosae). The flowers of this shrub, which appear sporadically in winter and last through spring into early summer, consistently attract miscogaster, montezuma, and aztecus.

Prosopis juliflora DC. (Leguminosae). In spring and early summer the flowers of this shrub are visited by an occasional *Z. montezuma* but are not commonly frequented by any *Zethus*.

Serjania sp. (Sapindaceae). I have swept a few Z. montezuma from this ubiquitous vine.

Condalia obovata Hook (Rhamnaceae). During November-January some specimens of this shrub become very attractive to Z. miscogaster, montezuma, and aztecus. At this season, C. obovata often is the best source of Zethus but during the rest of the year is not especially productive.

Bumelia sp. (Sapotaceae). Like C. obovata, this shrub may be visited by many Zethus during late fall and winter.

Labiatae (unidentified species). This small, white-flowered, scarcely aromatic mint carpets the forest floor in many areas of the Bentsen Park and Valley Botanical Garden. During fall and winter specimens in bright sun may attract numerous Z. miscogaster and montezuma.

Aster spinosus L. (Compositae). Numerous Z. miscogaster were netted from the flowers of this tall, green-stemmed herb during November 1977.

Aster sp. (Compositae). This brownish-stemmed species also attracted many miscogaster in November 1977.

Baccharis spp. (Compositae). At least 2 species of these shrubs grow in the Valley. When they are in bloom, from late August to November, they attract multitudinous Zethus and other aculeates. This is the only plant visited by all 4 Valley Zethus and the one which consistently has been most productive.

All Valley Zethus show about the same floral associations, which vary seasonally according to which species are blooming or covered with honeydew. Shrubs and small trees are the favored plants, and I have collected Zethus most often in the 2-4 m stratum of Valley woodlands, although during late fall and winter I have often taken miscogaster and montezuma from small labiates only 150-300 mm above the ground.

Collections

Material covered in this study has been deposited in the Florida State Collection of Arthropods (Division of Plant Industry, P.O. Box 1269, Gainesville, Fla. 32602) and in the author's private collection at 301 N. 39th Street, McAllen, Texas 78501.

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FIREFLY FLICKER FUSION FREQUENCY.—(Note). Flicker fusion for an adult female of Photuris versicolor (complex) (Coleoptera: Lampyridae) was found to occur at 41.6 and 45.4 flickers per second in 2 successive trials on the same insect. The stimulus had an absolute energy level of 0.602 microwatts per square centimeter and a peak intensity at 550 nanometers. The insect had been allowed to dark-adapt for 45 minutes before testing. Equipment and technique were those used by H. R. Agee (1971, Ann. Ent. Soc. Amer. 64:942). The test animal, captured as a larva, eclosed 11 days prior to the study. It has been deposited with Dr. J. E. Lloyd, Department of Entomology and Nematology, University of Florida. I thank Drs. H. R. Agee (U.S.D.A.), J. E. Lloyd (Univ. Fl.), and J. C. Davis (U.S.D.A.) for their assistance and use of facilities.—R. M. Merkhofer, Department of Botany, University of Florida, Gainesville 32611.