

**THE ARACHNID ORDER SOLPUGIDA
IN THE UNITED STATES
(SUPPLEMENT 2, A BIOLOGICAL REVIEW)**

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NOVEMBER 21, 1988

**Printed By
Southwest Offset
1008 Pope Street
Silver City, New Mexico 88061**

THE ARACHNID ORDER SOLPUGIDA IN THE UNITED STATES
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INTRODUCTION

Taxonomic investigations by Muma (11, 12, 13, 20, and 28), Brookhart (4 and 5), Rowland (32), Brookhart and Muma (6 and 7), and Muma and Brookhart (29) have fixed the identity of most common solpugid species in southwestern United States. These studies have also outlined the ranges of many common species. As a result, biological, behavioral, and ecological studies can now be conducted on our solpugids with reasonable assurance of valid species identification.

Prior to these publications most biological observations and studies were suspect because of questionable identity of the observed species. However, the notes and observations of Fichter (8) were unquestionably on *Eremobates pallipes* (Say). Brookhart (3 and 5) also studied *E. pallipes* and significantly added to our knowledge concerning the biology of this species. Muma (14) reported on the egg masses and eggs of 5 species of Eremobatidae and the egg deposition and incubation of *Eremobates durangonus* Roewer. He also reported on the mating behavior of 3 species of the genus *Eremobates* Banks, Muma (15), made comparative studies of the feeding behavior of 18 species representing 7 genera and 2 families, Muma (16), outlined the general burrowing habits of North American solpugids and cited the specific burrowing habits of 11 species representing 6 genera and 2 families, Muma (17). Muma (18) also recorded a 3 year laboratory and field investigation into the life cycle and growth stages of *E. durangonus*. Muma (19) summarized our knowledge concerning the basic behavior of North American solpugids.

Muma (13), in his study of solpugids from the Nevada Test Site, included biological notes on the 12 most common species, representing 5 genera and 2 families. These notes included information on sex ratios, abundance, longevity, life cycle, and plant associations in which species were found. Allred and Muma (1) reported similarly on a collection of eremobatid solpugids from the National Reactor Testing Station, Idaho. Muma (21) examined geographical and seasonal distributions of adults of 26 common North American solpugids, and speculated on the effect of sexual maturity on reproductive isolation of solpugids. Muma (22, 23, 24, 25, 26, and 27) reported on a series of studies designed to determine the locations, levels, and dynamics of specific solpugid populations in southwestern New Mexico. Altogether 11 species were recorded in these studies but only 5 including 1 *Arenotherus* Brookhart and Muma and 4 *Eremobates*, were sufficiently abundant to produce meaningful data.

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We have accumulated a number of biological notes and records on various species of North American solpugids over the past 20 years. Rather than publish these in a series of small notes, we have decided to integrate them with previously published data, and summarize current biological knowledge of each studied family, genus, and species. Some biological information is now available for both North American families, 10 genera and 37 species.

The references cited at the beginning of each specific summary are not intended as indications of synonymy. They represent the original description, and one or two more complete recent descriptions for purposes of identification.

METHODS

Since these investigations were conducted over an extended period of time, 25 years, both with and without financial and institutional support, our methods have been too varied to record concisely. The following are general statements concerning methodology.

Observations and experiments on living solpugids were made under field conditions with the use of visible, infrared, and ultra-violet light. Studies were made before and shortly after dawn, shortly after sunset, and at varying hours throughout the night. Solpugids were observed both in areas of high visible light concentration, where insect prey was abundant, and where the only available light was that produced by the observer and prey was scarce. In a few cases solpugids were studied under direct sunlight, usually before 10:00 A.M.

Live solpugids in the laboratory were confined primarily in terraria varying in size from 10.2-20.4 cm. diameter and 15.33-25.6 cm. depth. Early instar specimens and eggs were occasionally placed and held in petri dishes to facilitate microscopic examination. Substrates varied in composition from crumpled paper toweling and sawdust, to sand and clay, and in depths from 0.6 cm. to 20.4 cm. Laboratory temperatures varied from those regulated within plus or minus 2°C. to the normal fluctuations experienced in laboratories and basements, i.e. 21 to 29°C. In some studies solpugids were examined and fed daily; in others they were observed only once or twice a week.

Special procedures or extenuating conditions were reported separately in the paragraphs dealing with individual species.

We have cited all pertinent previous publications that include biological information in order to assure that our family, genus, and species summaries are as complete as possible. They include taxonomic, biologic, behavioral, and ecologic studies. We are aware that most, if not all, of the summaries are incomplete or fragmentary, but they all include biological information that may be of interest and use to future students, workers, and specialists of this order of arachnids.

BIOLOGICAL AND BEHAVIORAL SUMMARIES

Certain facets of solpugid biology have proved to be

relatively consistent for the species studied. Not surprisingly, these include the major aspects of the life of any invertebrate animal. They are longevity and activity of the sexes and immatures, mating behavior, egg deposition, incubation and hatching, food, water and feeding behavior, burrowing, young protection, and life cycle. In addition there are several behavioral phenomena that seem to be common to most species, either of a given species-group, genus, or family of the order in North America or possibly of solpugids throughout the world. They are eliminating, investigating, fighting, autotomy, clustering, taming, huddling, drowning, and climbing.

These biological and behavioral activities are summarized in the following paragraphs.

Longevity

Males of six eremobatid, and two ammotrechid species, of which adequate live material was available, lived a shorter period of time than females. On an average males lived 11 days, females 21 days. Although the exact times are not significant, the consistency is indicative that males are probably much shorter lived than females under natural conditions. Comparable data for females and immatures are available for only four eremobatid and two ammotrechid species. In this case, the females lived an average of 28 days and the immatures averaged 36 days. Again, the exact times are not significant, but indicate that females may be shorter lived even than those immatures that do not survive more than one or two ecdyses. Some eremobatid immatures must, of course, survive the entire 365 day annual cycle.

Mating

The mating behavior of North American Eremobatidae has been observed and recorded, either partially or completely, for 7 species representing 3 genera and 4 species-groups. The major aspects are quite similar to those recorded in (15) for 3 species of *Eremobates*. Mating generally consists of three phases including an attack phase, a contact phase, and a release phase. In the attack phase, the female either accepts the male and submits, combats the male, or rejects him and retreats. During a successful contact phase, the pair achieves three different positions: A, in which the pair are oriented in the same direction with the female's abdomen bent forward over her peltidia and the male has his fixed cheliceral fingers imbedded in the female's vulvular area which he chews lightly; B, in which the male slides forward along the female's abdomen until his genital opening is opposite and in contact with hers and emits a globule of seminal fluid; and C, a repeat of position A but with the male's fixed cheliceral fingers not as quickly or as deeply imbedded, but accompanied by a chewing in of the seminal package. The release phase is a separation of the pair which results in mutual retreat or combat. Males making contact with a combative or retreating female seldom complete copulation. During either the attack phase or early stages of the contact phase, aggressive females may eat the male or males may wound and eat the female. It is believed that females who do not signal acceptance and submission during the attack phase have been

previously mated. This belief is fortified by the fact that aggressive, combative, or retreating females are usually released by the male after position A of the contact phase. This indicates that the male has encountered evidence of a completed mating. An aberrant mating of a field collected male of *Eremobates durangonus* with a virgin laboratory reared female also seemed to confirm the belief. In this observation, positions B and C were repeated 50 times without the emission of sperm, indicating that the male may have to make contact with seminal fluid in position C before accepting completion of the mating. Males will often attempt and complete copulation with several females, but only 2 females have been induced to mate twice. A spermatophore has not been observed for Eremobatidae (19). The mating behavior of Ammotrechidae has not been observed. The mating behavior of Near East and African Galeodidae reportedly involves a spermatophore and indirect transfer of the sperm package with the chelicerae.

Eggs

Details on egg deposition, incubation, and hatching are known for only one species, *Eremobates durangonus*, (14 and 18).

It would appear that egg deposition occurs mainly at night, during late evening, or early morning hours. Egg masses are most often deposited in burrows so observation is difficult. Actual deposition lasts 40 to 60 minutes. Eggs may slip from the female when she is absolutely quiescent or may be preceded by labor-like contractions or tremors.

Eggs of all species are spherical and glistening, opalescent to white when laid. Fertile eggs dry quickly to a grainy off white color. Sterile eggs generally develop a yellow color when dry and within a day or two shrivel or collapse. All solpugid eggs presently known also have a microscopic sculpturing of the shell (14).

Feeding

The behavioral pattern involving location of prey and possibly that of a mate is highly varied. Many species seemingly search, stalk, or lie in ambush for prey, but do not sense it until touched. Others apparently "see" it at a distance of several centimeters. Still others seemingly hear, feel, or otherwise sense prey, enemies, or mates approaching from the rear at a distance of several centimeters (16). A similar variance in prey location behavior has been reported for Asian and African solpugids. Some facets of feeding and drinking are relatively similar among solpugid species. Food searching involves random running or congregating at high density prey locations such as night lights, or at prey nests. Prey are located by tactile, visual, or substrate vibration stimuli. Capture is by chase, stalk, or ambush. Actual capture may involve use of either or both palpi or chelicerae. Ingestion is similar with variations caused mainly by prey size, form, or sclerotization. Most species survive without food for 1 to 3 weeks. All species drank water readily from standing droplets but shunned rain or simulated rain (16).

Burrowing

There is broad similarity in burrowing habits of North American solpugids. All species use the chelicerae to bite at

the substrate, pith, wood, or soil. The 2nd and 3rd pair of legs are used to rake loosened particles back under body between the 4th pair of legs. The chelicerae are often used to assist the legs in removal of excavated material such as small stones and bits of wood. The palpi are often used as probes or to tamp material after it is dumped outside the burrow.

Variations occur in substrate, burrow angle, burrowing time, biting, raking, plowing, probing, and tamping but may be related to specific, generic, and perhaps familial behavior (17).

Young Protection

North American solpugid eggs are deposited in nests at the end of deep burrows. The female then abandons the eggs, plugging and concealing the burrow entrance. This action protects the eggs from predation and cannibalism and provides relatively uniform incubation temperatures (19).

Life Cycle

When the adjusted mean figures for egg incubation time and developmental times of active stages at 80-90 degrees F are added together for *Eremobates durangonus*, a total of 321 days is obtained. This total along with an allowance for a 30% increase in developmental time for four late nymphal stadia during the four cold winter months, produces a figure closely approximating the number of days in a year (18). This indicates that species of the genus probably have an annual life cycle. This cycle is also indicated because the adults of this species and other eremobatids suddenly appear and are active at approximately the same time each year. Comparable data are not presently available either for other genera of Eremobatidae or Ammotrechidae. However, adults of two species of ammotrechids, *A. stimpsoni* Putnam and *A. peninsulana*, are not seasonally cyclic in their appearance. These, and possibly other species of that family, may have either partial or multiple year life cycles, greater variations in stadia developmental time, or variation in either the number or duration of developmental stadia. The same may also be true for unique eremobatid species such as *Hemerotrecha californica* Banks and *Hemerotrecha denticulata* Muma. Both annual and multiple year life cycles have been reported for Asian and African solpugids.

Elimination

Solpugid behavior in eliminating provides avoidance of contamination by waste products. The anus is terminal and liquid fecal matter was ejected forcibly 1 to 3 centimeters behind end of abdomen. This ejection is followed by a forward surging of the solpugid which provides an even greater distance from contamination. See reference (19).

Investigating

Solpugids have a tendency to explore and examine their immediate environs. Such investigative behavior has been noted both in the field and in laboratory terraria. It was noted that investigation may be readily interrupted by ingestive, agonistic, or sexual behavior (19).

Fighting

Some species of solpugids are highly antagonistic to large moving objects or shadows. Others exhibit avoidance, seldom

showing antagonism. *Eremobates* and *Eremopus striatus*-group, and some *Eremochelis* species are consistently antagonistic. *Arenotherus magnus*-group, some *Eremochelis*, and most ammotrechids commonly avoid or flee from major disturbance (19).

Autotomy

Ammotrechids readily drop appendages by autotomy, especially palpi, which are regenerated. Eremobatids seldom drop palpi or legs unless tightly restrained.

Clustering

First instar nymphal solpugids of the genus *Eremobates* do not feed, but exhibit a behavioral pattern termed "clustering" by Muma (19). Second instar sibling nymphs, both in and shortly after emergence from the egg chamber, are similarly oriented in a loose, often several-layered cluster. Slight natural or induced movement of one or two individuals of such clusters causes a shift or progression of the cluster away from the disturbance. High intensity stimulus causes dispersion, which if not complete and wide spread may not be permanent with some small clusters reassembling. A similar behavior has been reported for Galeodidae in Asia and in Africa.

Taming

North American solpugids of both families exhibit a series of distinctive behavioral patterns some of which have also been reported for Asian and African forms. Perhaps the most puzzling and universal is that of "taming" recorded by Muma (16 and 19). Solpugids confined in laboratory terraria commonly become tame, they cease to feed, burrow, fight, or mate, develop a lassitude, and eventually die.

Huddling and Drowning

Several genera and species of both North American families of solpugids exhibit two unique, possibly related, behavioral patterns reported in (19) as "huddling" and "drowning". Both patterns involve a flexing and retracting of the appendages to a position near the body, an elevation of the peltidia, especially in drowning, and a general almost trance-like quiescence. Individuals in nests and burrows frequently are huddled. Huddling can also be induced by a thin gentle stream of air. Drowning of solpugids does not result in death although the animals appear to be dead. After immersion in water for a few minutes to 1 to 2 hours, solpugids upon drying out recover and appear to be unharmed. Huddled solpugids can often be gently touched several times or even rolled over before they respond to the stimulus. It has been hypothesized that huddling and drowning may be two ramifications of the same survival behavior. Huddling in a nest or burrow may involve a protective, reduced metabolism to permit survival during winter, drought, or a period of low prey density. Drowning may also involve reduced metabolism to permit survival during flash floods or periods of high rainfall (19).

Climbing

Eremobatidae readily climb smooth vertical surfaces such as glass, utilizing the adhesive palpal organs. Some, possibly all, species of Ammotrechidae are capable of running freely over glass surfaces (19). Some small eremobatids can also climb in this manner.

FAMILY, GENUS, AND SPECIFIC SUMMARIES

Eremobatidae Roewer, 1934

Some biological information is available on 30 of the 166 eremobatid species known to occur in the United States. Three are in the genus *Arenotherus* Brookhart and Muma, 3 in the genus *Eremopus* Roewer, 12 in the genus *Eremobates* Banks, 5 in the genus *Eremochelis* Roewer, 3 in the genus *Chanbria* Muma, and 5 in the genus *Hemerotrecha* Banks.

This family contains both the largest and the smallest known solpugids in the United States. Fully fed or gravid females of several species of *Arenotherus* will measure over 50 mm. in length. Males of several species of *Hemerotrecha* are 10 mm. or less in length. Most of the species are restricted to the deserts and arid grasslands of the southwest, but several range eastward into eastern Texas, Oklahoma, Kansas, and Nebraska, and several northward into Montana, Idaho, and Washington. Both species diversity and population size or density are highest in the valleys and plains, decrease significantly on the rises and ridges near and in the foothills, and are lowest in the mountains.

Arenotherus Brookhart and Muma, 1987

With a few exceptions representatives of this genus are large, varying from 30 to 50 mm. in length. Most are distinctively patterned species. All known species primarily inhabit sandy, rocky or gravelly ridges, some in or near mountain foothills, and others in the valleys. Most of the species that mature in the spring to early summer are members of the *magnus* species group. Those that mature in the summer are usually members of the *pulcher* species group.

Although adults and partly grown immatures are known to feed on a wide variety of invertebrates, see Muma (16), the primary food of early instar immatures is not known.

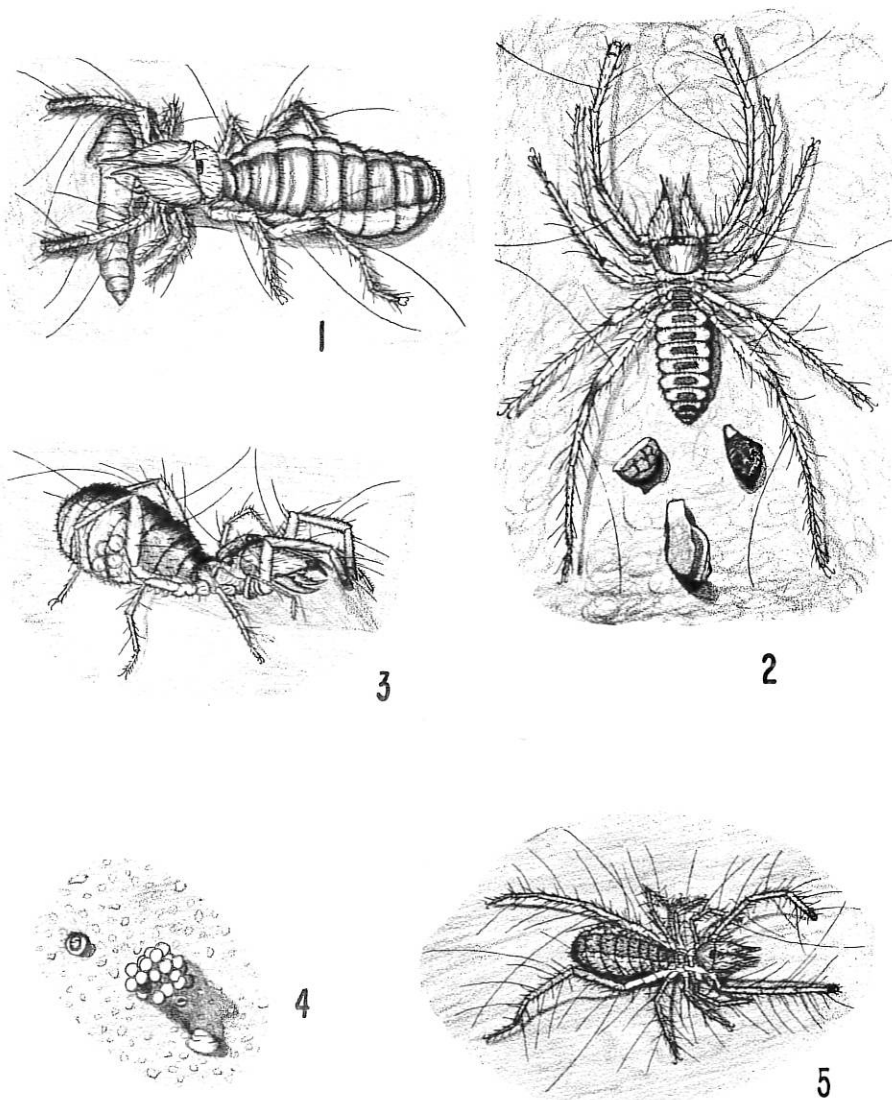
This genus occurs in the Coahuilan, Chihuahuan, Sonoran, Mojave, and Great Basin Deserts. Three species also extend into the warm, arid grasslands and cold, high plains of New Mexico, Colorado, and Nevada.

Arenotherus magnellus Brookhart and Muma

Arenotherus magnellus Brookhart and Muma, 1987, p. 5.

Published biological information on this species was recorded as that of *Eremorhax magnus* (Hancock) in references (14, 16, 17, 19), as that of *Eremorhax* undescribed species in (21), as that of *Eremorhax* n. sp. in (22, 25, 26), and as that of *Eremorhax* species #1 in (27).

This large species is known from southwestern New Mexico and southeastern Arizona. It matures in the spring and early summer. Males appear in April and females live through July. Biological



studies have been conducted from June through September and have involved 24 specimens, 7 females, and 17 immatures. Specimens have been collected from nests under cow dung, rocks, and boards, dug out of burrows, and captured around incandescent lights (75% at lights).

Males apparently mature during April and May but do not survive into June (25) according to recent April-May collections in southeastern Arizona. Nothing is presently known about the biology of this sex.

In the laboratory, immatures lived 8 to 72 days, mean 36. Females lived 22 to 49 days, mean 25.

Nothing is known concerning the mating of this species.

Data concerning the eggs of this species are cited in (14). One female laid 2 masses of eggs that did not hatch. Therefore, nothing is known about egg incubation or development of early instars.

Specific information on prey search, location, capture, and preference, and food and water ingestion is cited in (16), and Fig. 1.

Specific burrowing variables are listed in (17). In the laboratory, immatures burrowed and were in burrows 68% of the observation time, they remained burrowed for 1-10 days, mean 3. Earlier instars were in burrows less time and for fewer days. Females were in burrows 61% of the observation time, they remained burrowed for 1-9 days, mean 3.

Three field collected immatures molted in 31-48 days, mean 38, with ecdysis requiring 6-15 days, mean 11.

Females did not exhibit antagonistic behavior unless cornered or irritated. When threatened they turned and ran.

Field data on this species in southwestern New Mexico (21, 22, 25, 26, and 27) indicate that it may be common in the arid grasslands, on the gravelly bajadas, and in the pinyon-juniper life zone of the montane foothills.

Arenotherus pimanus Brookhart and Muma

Arenotherus pimanus Brookhart and Muma, 1987, p. 8.

One female, collected east of Tucson, Arizona at combined ultra violet and strong incandescent lights, showed little or no antagonism, but turned and ran to avoid capture. She ate termites and killed and buried termites, but readily fed on *Gryllus* sp., *Ceuthophilus* sp., *Pelidnota* sp., and slender green, red, and white-winged katydids.

Figures 1 to 5, *Arenotherus*, *Eremopus*, and *Eremobates*. 1. *Arenotherus magnellus* Brookhart and Muma, female eating mealworm larvae, about 3.0 times life size. 2. *Eremopus striatus* (Putnam), female resting on gravel ridge, about 1.5 times life size. 3. *Eremobates durangonus* Roewer, gravid female, slightly more than 2.5 times life size. 4. *Eremobates durangonus* Roewer, egg mass on soil, about 2.0 times life size. 5. *Eremobates bajadae* Muma and Brookhart, male at rest on sand, about 1.3 times life size.

Arenotherus pulcher (Muma)

Eremorhax pulcher Muma, 1963, p. 2 and Muma, 1970, p. 6.

Arenotherus pulcher (Muma); Brookhart and Muma, 1987, p. 7.

Published biological information on this species is cited in references (13, 16, 27, and 21).

This species is presently known only from Nevada. Adults are active in June and July but living males and females have not been available for biological study.

In the laboratory, two immatures captured in dry can traps lived for 30 and 53 days.

These immatures accepted 8 kinds of prey offered, 5 of them readily (16). Observations on systematic capture and ingestion were not made.

The two immatures remained in burrows 41% of the observation time for 1-22 days at a time, mean 5. Both specimens burrowed readily with the usual biting, raking, plowing, and carrying. Specific variables are discussed in (17).

Neither specimen moulted.

The only field data available are those in (13). Since dry pitfalls were used in the study and solpugids are now known to be capable of climbing smooth vertical surfaces utilizing their palpi (pedipalps), the deductions concerning adult longevity, sex ratios, and fertilization requirements of the species must be considered incorrect. Even the maturity period, June and July with peak adult activity in June, is open to question. Males maturing in May and females still laying eggs in August could have avoided or escaped from the traps. It seems probable, however, that the species is most frequently found associated with *Salsola*, Russian thistle, on rocky or wasteland bajadas, as stated in (13).

Eremopus Roewer, 1934

Representatives of this genus are variable in size. The *montezuma*-group, presently known only from Mexico is moderate to moderately large in size, 25-30 mm., but the *striatus*-group is large in size, 30-50+ mm.

Four out of 7 of the known species of the *striatus*-group of the genus are known from the United States, and some biological and ecological data are available for 3 species. However, except that they are known to mature during the early summer, our data are fragmentary.

Eremopus striatus (Putnam)

Datames striatus Putnam, 1883, p. 255; Muma, 1951, p. 45; Muma, 1988.

No previous biological information has been published on this species. That cited in references (16 and 17) should be referred to *E. gigasellus* Muma.

This large Sonoran species matures in June, July, and August. It has been recorded from California but this record may be erroneous. Our records are from southeastern Arizona and

northeastern Sonora, Mexico. Nine males and 2 females have been available for biological studies. Most of our specimens were collected on gravelly ridges at lights and one under a board. See Fig. 2.

In the laboratory, males lived only 7 to 14 days. They either did not burrow or made only shallow nests under rocks. They accepted termites and noctuid moths as prey, lifting the termites to the chelicerae with the palpi.

Two females burrowed extensively for egg deposition. One laid an egg mass in a soil chamber at a depth of 8 cms. Two masses varied from 90 to 117 in number of eggs, mean 103. Although one mass was from a recently mated female, neither mass hatched and were presumed sterile. One female lived 28 days, the other 35.

Nine males and two females were recently taken at incandescent and U/V lights in southeastern Arizona. The males were found running rapidly over the soil surface. The females were running or feeding noisily, crushing the exoskeletons of beetles, crickets, and grasshoppers. One pair was observed mating. This behavior was similar to that reported for *Eremobates* spp. (15).

Eremopus gigasellus (Muma)

Eremorhax gigas, Muma, 1951, p. 48; Muma, 1970, p. 8; Muma, 1988.

Published biological information on this species may be found in reference (16 and 17). The data were erroneously referred to *E. striatus* (Putnam).

This large Chihuahuan species matures in June, July, and August. It has been recorded from southeastern New Mexico and extreme western Texas. Muma (11) recorded two females of this species as *E. striatus* (Putnam). Only 2 females and 2 immatures have been available for biological studies. They were collected under rocks and "cow pies" in surface nests.

Females lived 20-35 days, mean 28, in the laboratory. They remained mainly in shallow nests under rocks for 1-4 days at a time, mean 2. Immatures lived 28-35 days in the laboratory, mean 31. They burrowed extensively, remaining in the burrows for 1-13 days at a time, mean 4. See reference (17) for burrowing variables. No males of this species have been available for study. The male cited in (17) refers to an immature.

Data on feeding behavior and offered and accepted prey are cited in reference (16). The preferred prey was not determined.

In the laboratory, one immature moulted in 30 days with ecdysis requiring 7 days.

Eremopus titania (Muma)

Eremorhax titania Muma, 1951, p. 48; Muma, 1970, p. 9; Muma, 1988.

Published biological information on this species is cited in (16).

This large, long-legged Mojave species matures in June, July, and August. Most of the study specimens were seen in truck headlights crossing roads at night. Seven males and two females

were available for biological study.

In the laboratory, males lived 6-16 days, mean 10. Two females lived 12-27 days.

Both females were gravid when collected but never laid eggs.

Males drank water and accepted 8 of 9 kinds of offered prey. They refused only myremeleontid adults. Females accepted all 7 kinds of offered prey. Both males and females readily accepted termites, often refused by *E. striatus*. Males did not see non-moving prey but saw both shadows and objects at distances of 10-20 cms. (16). Females responded only to tactile stimuli. Prey were captured by both sexes at the end of a short lunge, with the chelicerae. Termites were lifted to the chelicerae with the palpi and then supported by the first legs.

Males remained on the soil surface over 83% of the observation time. When burrowed, they remained in the burrows only 1 or 2 days, mean 1. Only one female burrowed once for one day.

Males and females in the field were both observed in apparent random cursorial searching.

Eremobates Banks, 1900

Representatives of this genus are variable in size, both within the genus and within certain species. Adults of some species are as large as or nearly as large as species of the genus *Arenotherus*. Others are moderate to small in size, one-half or less the size of most species of the latter genus. On the other hand, large males of certain species may be nearly twice the size of small males of the same species. All species are distinctively structured, but some species are well patterned while others are pale and indistinctly marked.

Most species of the genus inhabit the valleys, plains, flats, and bajadas between the mountain ranges. A few are found on the buttes, plateaus, and in the foothills of the mountains. Individuals of any of the forms may be occasionally found in the washes, arroyos, and canyons of the mountains and even on the mountains.

Species of the *pallipes* species group usually mature in June, July, and August with females living into September and October. Those of the *palpisetulosus* species group, with the exception of *E. nodularis* Muma, mature from March through June with females living into July and August. Those of the *scaber* species group mature from May through July with females living into August and September.

Adults and large immatures feed on a wide variety of invertebrates, (16), though early instars feed almost exclusively on termites. Large immatures and adults also feed readily on termites, both in the laboratory and in the field. Termites are most certainly the primary food of the genus.

This genus is known to occur in the Coahuilan, Chihuahuan, Sonoran, Mojave, and Great Basin Deserts. It is also known from the warm, arid grasslands and cold, high plains throughout the western third of the country.

Eremobates septentrionis Muma

Eremobates scaber (Kraepelin), Muma, 1951, p. 522; Muma, 1970, p. 12.

Published biological information on this species occurs in reference (1).

The species is apparently common in the Great Basin Desert and surrounding cold, high plains. In Idaho the species was collected in June, July, and August with adults more active in July. The Idaho specimens were found most commonly on sandy and gravelly flats with *Chrysothamnus* and *Artemisia*, but the optimal habitat has not been determined.

Eremobates zinni Muma

Eremobates zinni Muma, 1951, p. 58; Muma, 1970, p. 14.

Published biological information on this species occurs in references (13) and (16).

This moderate sized Mojave species is the only species of the *scaber* group of which live specimens were available for study. It is mature in June, July, and August and relatively common in the Mercury-Las Vegas, Nevada area, but only one male and one female were available for biological study.

The male lived 14 days in the laboratory and never burrowed but frequently climbed the glass wall of the terrarium and ran rapidly over the soil surface. The female lived 7 days in the laboratory and never burrowed but frequently ran over the soil surface and hid under cow dung.

The male readily accepted termites and lifted them to the chelicerae with the palpi to form a ball of termites which rotated with the masticatory actions of the chelicerae. The female also readily accepted termites which she ate in the same manner as the male. She refused mealworm larvae.

Deductions concerning the fertilization requirements of the species are probably erroneous (13). It is far more probable that males avoid or escape from dry pitfall traps. However, it is known that the species is associated with Russian thistle in the Grayia-Lycium plant community at Mercury, Nevada (13).

Eremobates nodularis Muma

Eremobates nodularis Muma, 1951, p. 69; Muma, 1962, p. 4; Muma and Brookhart, 1988.

Published biological information on this species is cited in references (14, 15, 16, 17, and 18) under the above name. However, in (21, 22, 25, 26, and 27), it is cited under the name *E. hessei* (Roewer).

This small to moderate sized Chihuahuan-Sonoran representative of the *palpisetulosus* group is found in west Texas, southern New Mexico, southern Arizona, southern California, and Chihuahua, Mexico. We have not seen specimens from Sonora or Baja California, Mexico. Most of the specimens presently known are from southern New Mexico. It matures in June, July, and August with both males and females often still active in September.

Specimens have been collected from nests under cow dung and rocks, in houses, running on ground at night, around lights at night, and in killing-preserving can traps. More than 50% have been collected in can traps. Twenty-three live specimens, 12 males, 6 females, and 5 young, have been available for study and observation.

In the laboratory, males lived 9-17 days, mean 13. Females lived 12-40 days, mean 25. Immatures lived 9-94 days, mean 34.

Details of the mating behavior of this species are in (15). They were similar to but slightly different from those of *E. durangonus*.

Two females deposited egg masses. One was in the soil and one on the soil surface. They did not hatch (14).

Males drank water and accepted all 7 kinds of prey offered, 3 of them readily, but ate termites most readily. They cleaned their chelicerae in the same manner as *E. bajadae*. Females drank water and accepted all 8 kinds of prey offered, 3 readily. Male, female, and immature laboratory specimens were observed apparently in ambush, saw moving prey and apparently sensed prey approaching from the rear, at a distance of 4 to 5 cm. Small prey such as termites were captured with the palpi, large prey with the chelicerae. Palpi were held down and to the side during ingestion. Females also cleaned chelicerae in the same manner as males. Immatures drank water and accepted 5 of 6 kinds of offered prey, 4 readily, refusing only *Tenebrio* adults, (16).

Males were in burrows 40% of the observation time, remaining there for 1-2 days at a time, mean 2. Females were in burrows only 19% of the observation time, remaining there for 2-3 days at a time, mean 2. Specific burrowing variables of males and females are cited in (17). Immatures burrowed more extensively but in the same manner as adults. Immatures were in burrows 40% of the observation time, remaining there for 1-5 days at a time, mean 3.

Although many immatures have been available for study since 1971 and have lived reasonably well, none of them moulted.

This species exhibited huddling and drowning (19).

Eremobates palpisetulosus Fichter

Eremobates palpisetulosus Fichter, 1941, p. 179; Muma, 1951, p. 61; Muma and Brookhart, 1988.

This species, as restricted in reference (29), ranges from Colorado into western Nebraska, western Kansas, western Oklahoma, and extreme northern Texas. From collection records it may be deduced that it matures in May, June, and July.

We have biological notes on only 2 males and 1 female collected in Colorado in June of 1970.

Two incomplete matings of these 2 males with the same female were recorded for this species. The attack phase and engagement were similar to those recorded (15) for *E. bajadae* and *E. durangonus*. Variations included male stroking of female abdomen during contact, intertwining of palpi while in position A, and the female not becoming quiescent during contact, and in position A. The female may have been previously impregnated since both

males released her after chewing in position A.

Eremobates bajadae Muma and Brookhart

Eremobates bajadae Muma and Brookhart, 1988.

Published biological information on this species is cited in references (14, 15, 16, 17, 19, and 21) under the name *Eremobates palpisetulosus*. In these references this species was also confused with *E. texanus* Muma and Brookhart which was collected from west Texas. References (25, 26, and 27) referred to this species as *Eremobates* sp. #2. These published findings are sorted and corrected here.

This large, distinctive species is common in the arid grasslands of southwestern New Mexico and southeastern Arizona. It matures in late spring and early summer, May to July, with both sexes still active in mid to late summer, July and August. This indicates that both sexes may mature at or nearly at the same time during the season. Twenty-six males and 20 females have been available for study and observation. Comparative studies of immatures of this species, *E. nodularis*, and *E. norrisi* Muma and Brookhart are suspect since the 3 are sympatric and morphologically similar. Specimens have been collected from nests under cow dung and boards, at lights at night, and in killing-preserving can traps. Greater numbers were taken at lights and in can traps on gently sloping bajadas near mountains. Male/female ratios at lights varied from 2/1 to 4/1.

In the laboratory, males lived 2-72 days, mean 12. They were in burrows or nests only 26% of observation time, remaining for only 1-4 days at a time, mean 2. Females lived 20-25 days, mean 15. They were in burrows or nests only 27% of observation time, remaining for only 1-4 days at a time, mean 2.

The mating behavior of this species except for certain details was similar to that of *durangonus* (15).

Two females deposited eggs, in both cases a single mass of 12 to 21 eggs. This number of eggs per mass is probably atypical for this large species. The eggs had a mean length of 1.69 mm., a mean width of 1.59 mm., and a chorion ornamentation of moderately spaced, rounded, microscopic papillae. None of these eggs hatched.

Feeding habits of 8 immatures of this species were cited in (16) but now are believed to be suspect, see statement on immatures in above introduction. Males and females both accepted readily, *Tenebrio* sp. adults and larvae, *Gryllus* sp., *Melanoplus* sp., small Noctuidae, Pyralidae, and *Reticulitermes* sp. Males and females often apparently cleaned their chelicerae of food particles by standing high on the tarsi and jittering their deflected chelicerae back and forth over the soil surface. Recently, 1974, early and late instars believed to be this species have been observed entering termite galleries in cow dung. Several have been collected by breaking up the dung.

This species exhibited drowning (19).

As its name implies, this species is most common on the ridges of the gravelly, rocky bajadas, but invades both the grassy flats and foothills. See Fig. 5. It competes

successfully with 3 other species of the genus, (22, 24, 25, 26, and 27).

Eremobates norrisi Muma and Brookhart

Eremobates norrisi Muma and Brookhart, 1988.

There is no published biological information on this species prior to 1988.

This species is relatively common in the pinyon-juniper life zone in southwestern New Mexico and is also found on the ridges and bajadas adjacent to mountains. References (25) and (27) refer to this species as *Eremobates* sp. #1. Males are mature in early spring (March and April) and females may still be active in early summer (June). Specimens have been collected in houses, and in dry and killing-preserving can traps. Since the species has only recently been recognized, only 2 live females were available for study and observations.

One female lived 16 days. The other lived for 18 days.

Both females deposited a single mass of eggs, one a mass of 50 eggs at a depth of 5.5 cms., the other an estimated mass of 35 eggs at a depth of 10 cms., mean 43 eggs at 7.7 cms. One mass hatched in 53 days and the other in 58 days at about 70°F, mean 56 days.

Both females accepted termites, *Ceutophilus* sp., and *Gryllus* sp. as prey. Termites were captured and lifted by the palpi. Both genera of crickets were captured by chelicerae and palpi simultaneously. Although second instar nymphs often rested side by side and fed 2 to 4 at a time on a single termite, cannibalism was also observed.

In the laboratory, both of the females burrowed extensively, completely churning the gravelly, sandy-clay substrate of their terraria. The burrowing habits and times were not recorded.

One set of postembryos moulted to first instar nymphs in 23 days, the other in 21 days at 70°F., mean 22 days. The first instar nymphs moulted to second instar nymphs in 16 days. All second instar nymphs gang fed, 2 to 4 at one time, on termites. All specimens died in the second instar. All stadia took considerably longer to complete development than those reported for *E. durangonus* at 80° by Muma (18). One egg mass was left undisturbed for observation of early instar behavior. Postembryos after hatching remained on or near the egg mass. First instars moved around the egg chamber to some extent, but remained quiet for long periods of time. Second instars burrowed upward to the substrate surface 5 days after ecdysis.

First instar nymphs exhibited clustering as reported by Muma (19).

Eremobates texanus Muma and Brookhart

Eremobates texanus Muma and Brookhart, 1988.

Biological information on this species was combined with that of *E. bajadae* Muma and Brookhart in references (16, 17, and 19) under the name *E. palpisetulosus*. Published findings are sorted, corrected, and supplemented here. The mating behavior

(15) and egg information (14), cited for *palpisetulosus* should be referred to *E. bajadae*.

This moderate sized to large, probably Chihuahuan, species matured from April through July. It has been recorded from extreme western Texas. All of our records are from the Alpine-Van Horn area. It has been collected from nests under cow dung, running on the ground at night, in houses, and in can traps. Six live males and 5 females from Van Horn and Alpine, Texas were available for study and observation. Since two or more species of the *palpisetulosus* group of *Eremobates* Banks are known to be sympatric in west Texas, immatures could not be positively identified or studied.

In the laboratory, males lived 1-18 days, mean 6. They were in burrows only 26% of the time remaining for 1-6 days, mean 3. Females lived 1-43 days, mean 17. They were in burrows 60% of the time and remained for 1-8 days, mean 3.

Males accepted all offered prey readily including mealworm larvae and adults, crickets, grasshoppers, and termites. They cleaned their chelicerae in the same manner as *E. bajadae*. Prey capture and ingestion by this species seemed to be the same as those of *E. bajadae*. Both males and females were observed in random cursorial searching in the field, but were not observed feeding. A ground beetle (*Harpalus* sp.) was, however, observed eating a male of this species.

The burrows and burrowing habits differed in no important respects from those of *E. bajadae*.

Eremobates kraepelini Muma

Eremobates mormonus (Roewer), Muma, 1951, p. 76; Muma, 1970, p. 18; Muma and Brookhart, 1988.

Muma (13) reported on this species under the name of *E. mormonus*. It seemingly is widespread through the Sonoran, Mojave, and Great Basin Deserts in southwestern United States. In Nevada, it matures from March through June, with May apparently the month of greatest adult activity. In that area, it was also found most abundantly on the salt flats and near wastelands around the playas. Muma's (13) statements concerning overwintering, sex ratio and fertilization requirements are probably erroneous, owing to the use of dry can traps in that study.

Eremobates scopulatus Muma

Eremobates scopulatus Muma, 1951, p. 67; Muma, 1970, p. 20; Muma and Brookhart, 1988.

Notes on the biology of Nevada specimens of this species were published in (13). Adults were collected in May, June, and July with peak adult activity in May. Conjecture concerning overwintering, sex ratio, and fertilization requirements may be erroneous, but the species is probably associated with *Salsola* in *Grayia-Lycium* communities in southern Nevada (13).

This apparently is a Great Basin form.

Eremobates durangonus Roewer

Eremobates durangonus Roewer, 1934, p. 557; Muma, 1951, p. 78; Brookhart and Muma, 1981, p. 297.

Published biological information on this species occurs in references (14, 15, 16, 17, 18, 19, and 21).

This moderate sized Sonoran representative of the *pallipes* group is common in extreme southeastern Arizona and extreme southwestern New Mexico. It has been found as far south as Durango, Mexico. The species matures from May through August. Males may be found in May and June, but attain peak population in July. Some females are still alive in September and October. It has been collected from nests under cow dung, rocks, and boards, running on the ground at night, in houses, around lights at night, and in dry and killing-preserving can traps. Of 250 specimens collected from 1963 through 1965, over 75% were taken in nests or burrows under cow dung. From 1963 through 1965 many live males (100+), females (50+), and immatures (100+) have been available for study and observation.

In the laboratory, mated males lived from 2-36 days, mean 11. Unmated males lived up to 49 days. Males occasionally burrowed, but most frequently made nests under cow dung, stones, and boards. Females lived from 1-73 days, mean 33. Unmated females lived up to 70 days. They burrowed 40 to 60% of the observation time, often remaining burrowed for more than two weeks at a time.

Details of the mating behavior of this species are outlined in (15).

Egg deposition behavior, egg incubation, and egg hatching data are presented in (14). See Figs. 3 and 4.

In the laboratory, males drank water readily and accepted 10 of 15 kinds of offered prey, 5 readily. They refused roaches, earwigs, ground beetles, *Dinotrombium* sp., *Schizocosa* sp., and occasionally *Phylliphaga* adults. Females drank water and accepted 13 of 17 kinds of offered prey, 5 readily, but refused roaches. Immatures accepted 16 of 17 kinds of prey offered, 7 readily, refusing only roaches, see (16).

Burrows were constructed at an angle of 30° or less to the soil surface. General burrowing habits and specific burrowing variables are included in (17).

The calculated and estimated annual life cycle of the species and details on the development and behavior of the immatures are given in (18).

Most of the basic behavioral patterns recorded in (19) refer to this species. These included young protection, fighting, mating, clustering, investigating, taming, eliminating, huddling, drowning, and climbing.

The only population data available on this species is presented in reference (21).

Eremobates pallipes (Say)

Galeodes pallipes Say, 1823, p. 3; Fichter, 1940, p. 355; Brookhart and Muma, 1981, p. 290.

Biological information on this species was cited in reference (3) and published in references (5) and (8).

This small to moderate sized cold, dry plains representative of the *pallipes* group is common in Nebraska, eastern Colorado, western Kansas, northeastern New Mexico, and northwestern Texas. The center of its distribution appears to be Nebraska, Colorado, Kansas, and possibly Oklahoma.

Say (33) found his male and female under buffalo chips. Fichter recorded 13 specimens from houses, 4 in shallow burrows under stones and 3 similarly under "cow chips". He also reported cannibalism and that grasshopper nymph prey was located by contact (touch) with the pedipalps (palpi) functional in this respect. The burrowing recorded by Fichter, translated into our terminology, included biting, raking, and plowing. He mentioned two specific burrowing variables. Large pieces of gravel were carried out of the burrows in the chelicerae and plowing was accomplished with the chelicerae spread laterally, the palpi and first legs preventing lateral scatter. Brookhart (3) reported this to be the most prevalent species in southern Colorado, attaining largest populations in over-grazed pastureland. His studies showed that the males suddenly appeared in July but few adult females were found prior to August. Brookhart found no consistence in the kind of prey accepted by the species, except that it did not eat beetles or lycosid spiders. It accepted or refused termites, noctuid moths, milkweed bugs, grasshoppers, and adult flies, and accepted crickets, clubionid spiders, and mealworms. He also recorded cannibalism and the fact that black widow spiders, crab spiders, and centipedes could subdue and eat solpugids. Brookhart also mentioned a mass of 25-50 eggs deposited 7.5 cms. below the surface of the soil, that failed to hatch, and the fact that the solpugid in the laboratory became sluggish, Muma (19) referred to this latter behavior as "taming".

Mating behavior, previously unrecorded, is nearly identical with that reported by Muma (15) for *E. durangonus*. Specific variations of mating included that males imparted vibratory motion to females in position A before insemination and position C before release, males exhibited a peristaltic-like motion of the abdomen prior to insemination, in two matings the pair rolled completely over in position A, and position C lasted less than one minute in most matings. Altogether five complete matings and four incomplete matings have been observed. Elapsed time during mating varied from 4-22 minutes.

One laboratory mated female laid a mass of 50-60 white eggs in a small burrow within 7 days of matings. These eggs were incubated at 25°C on water soaked cotton in a culture dish. They hatched in 21 days. The newly hatched postembryos were similar to those described by Muma (18) with a translucent outer covering, and a pale yellow interior mass that appeared to be separated from each other. Two days later the postembryos were a non-translucent, shiny white with the layers not visible.

Eremobates arizonica (Roewer)

Eremostata arizonica Roewer, 1934, p. 572; Brookhart and Muma, 1981, p. 295.

Published biological information on this species in references (21, 22, and 24) was erroneously referred to *E. pallipes*; that published in references (25, 26, and 27) was referred to *Eremobates* sp. #3.

This small to moderate sized warm to hot, arid grassland representative of the *pallipes* group is common in eastern Arizona from Mexico to Utah and western New Mexico from Mexico to Colorado. It may range into Mexico, southeastern Utah, and southwestern Colorado. The species matures in July, August, and September with occasional males and females found a month or two earlier or later. It has been collected from nests and burrows, under cow dung, rocks, boards, and yucca logs on the ground, in houses, running on the ground at night, around lights at night, in dry pitfalls, and in killing-preserving can traps. Most of our specimens were taken in killing-preserving can traps in New Mexico. Previously unpublished data were obtained by study of 8 live males, 9 females, and 1 immature.

Studies on this species in southwestern New Mexico have demonstrated that females and young feed readily on termites, *Gryllus* sp. and *Ceuthophilus* sp. Males accepted termites but neither of the two genera of crickets.

Males seldom burrowed except to build surface nests under cow dung, rocks, and boards. Females and young, both in the laboratory and field, burrowed at an angle of 30° or less to the soil surface and frequently completed the burrows only 2 to 5 cms. below the surface.

Data from killing-preserving can traps in southwestern New Mexico indicated that this species was most common in over-grazed arid grasslands where it apparently competes successfully with 3 other species of termite feeding *Eremobates*, (21, 22, 24, 25, 26, and 27.

Eremobates barberi (Muma)

Eremothera barberi Muma, 1951, p. 83; Brookhart and Muma, 1981, p. 302.

Biological information on this species has not been previously recorded.

It is a small to moderate sized Chihuahuan or Coahuilan representative of the *pallipes* species group and is common in south central to southwestern Texas. The species matures in June, July, and August. In the field, all specimens were collected at night on the ground, at light, or in nests under termite infested cow dung. One male, 1 female, and 10 immatures were collected from west Texas in 1974 for biological study.

Males, females, and immatures all readily accepted and ate termites. This prey was lifted to the chelicerae with the palpi and the resultant "ball of termites" was supported by the palpi and first legs during ingestion. Other prey offered to and accepted by the species included mealworms and small lycosids.

Late instar immatures burrowed readily and frequently into a

gravelly, sandy, clay soil in the laboratory and remained burrowed most of the time. Some specimens also burrowed into yucca logs. Longevity of immatures was not accurately recorded but all specimens died within six weeks without moulting to maturity.

Eremochelis Roewer. 1934

Representatives of this genus are primarily small, less than 20 mm. in length, but several species measure 20 to 30 mm. and would have to be considered moderate-sized. Most species are strikingly colored and marked.

Most of the species inhabit bajadas, usually in thorn thicketed areas, canyons, and foothills of mountains. Certain species seem to be restricted to pure or mixed stands of *Prosopis*, *Larrea*, *Cassia* and *Acacia* in these areas.

We have made insufficient collections and studies of most species to determine the periods of maturity. For common species, however, they are known, and are cited in the specific summaries.

This genus is known from central Texas to California along the Mexican border and northward into Colorado, Utah, and Nevada, but we have more biological information on the species in the Chihuahuan, Sonoran, and Mojave Deserts, and adjacent arid grasslands.

Eremochelis bilobatus (Muma)

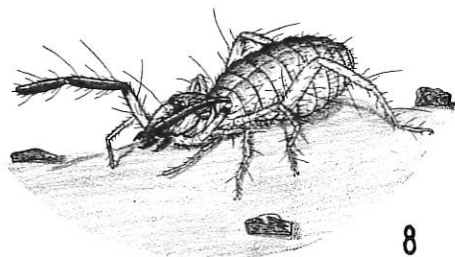
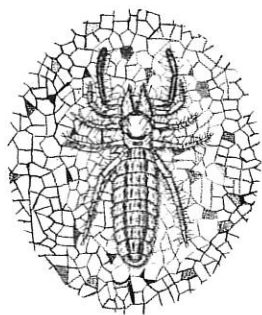
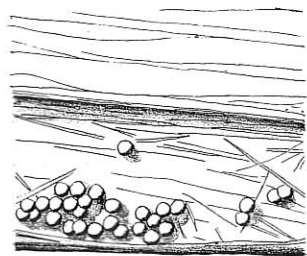
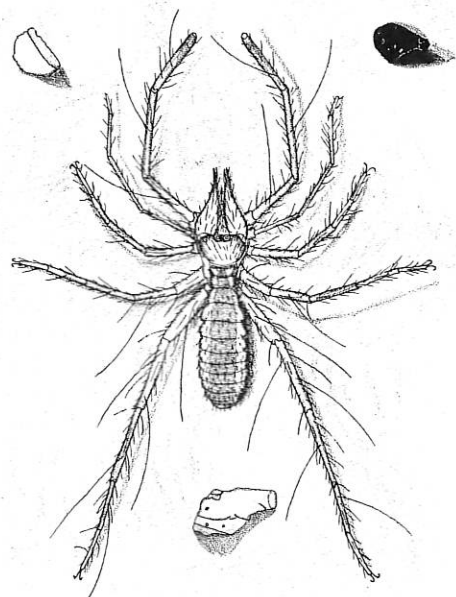
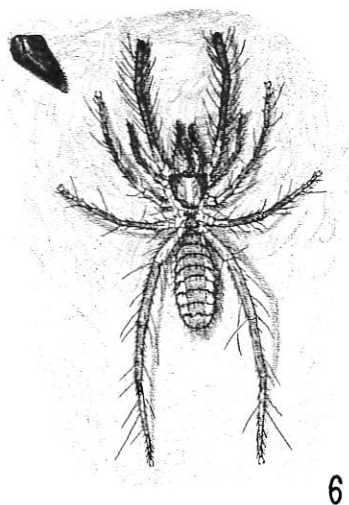
Therobates bilobatus Muma, 1951, p. 922; Muma, 1970, p. 33.

Published information on this species is referred to *Therobates bilobatus* Muma (14, 16, 17, and 19), and to *Eremochelis bilobatus* (5, 21, 22, and 25).

Although this species was recorded from California by Muma (20), the specimen was labeled a variant female, and probably belongs to another species. Most of our specimens are from eastern Arizona, Colorado, New Mexico, and western Texas, in or near the eastern edge of the Sonoran and western edge of the Chihuahuan Deserts, and adjacent arid grasslands. The species matures in June, July, and August with occasional males and females collected in May and September. It has been collected from nests under cow dung, around lights at night, in dry pitfalls, and killing-preserving can traps. Over 90% have been collected around lights at night. Most specimens were taken in brushland or thorn thickets. See Fig. 6. The ratio of males to females for all collecting is 12 to 1. At lights the ratio has varied from 22 to 1 in 1964 to 30 to 1 in 1965. Many live males (150+), a few live females (10), and a few immatures (11) have been available for study and observation.

In captivity males have lived 6-47 days, mean 14. Females lived 7-41 days, mean 22.

Recent observation of mating behavior in one complete and two incomplete matings indicated that it is similar to that reported by Muma (15) for *E. durangonus*. Specific variations included contact in the meso-metapeltididal area, a quiescent period between position A and position B, female abdomen contracted rhythmically during quiescence, and an elapsed mating time of



about 25 minutes. The males also seemed to impart vibration to the female abdomen during vulvular chewing, and may not have inserted the fixed cheliceral fingers as deeply into the vulva as the males of *Eremobates*. One female ate a male during the attack phase.

Three females laid 6 egg masses (3 laid 1 mass, 1 laid 2 masses, and 1 laid 3 masses), 4 were on the soil surface and 2 were partly or completely eaten. None of these eggs hatched (14). Recently, May 1984, 2 females laid undisturbed egg masses in laboratory terraria. One mass contained 46 eggs, and 1 had 35 eggs, mean 40. Neither of these masses hatched. They were also suspected of being sterile.

Prey capture was accomplished with either or both the palpi and the chelicerae. The palpi were not used to assist ingestion (16). Males seemed to prefer adult crambids and pyralids as prey. Females preferred termites and immatures ate ant larvae and termites.

Under laboratory conditions males seldom burrowed except immediately preceding death. Females burrowed primarily for egg deposition. Young specimens burrowed only 14% of the observation time and remained in the burrows 1-11 days at a time, mean 5 days. Reference (17) gives details on burrowing.

This species exhibited both huddling and drowning in the laboratory (19).

Eremochelis insignitis Roewer

Eremochelis insignitis Roewer, 1934, p. 570; Muma, 1951, p. 90; Muma, 1962, p. 13; Muma, 1970, p. 31.

The only published biological information on this species is in references (13) and (16), under the name *T. cameronensis* Muma. The species was mature from May through July with the greatest adult activity during July in that area. Over 85% of the specimens were taken on the flats near the playas.

The species has been reported from the Sonoran, Mojave, and Great Basin Desert areas.

In (16) Muma reported that the one living female available was repelled by and refused a coccinellid larva. It frantically cleaned its chelicerae after each contact with the larva. It did capture an unidentified fly with the chelicerae, held the palpi back and to the side during ingestion, and consumed all but the body exoskeleton, wings, and legs.

Figures 6 to 10. *Eremochelis*, *Hemerotrecha*, *Annotrechula* and *Branchia*. 66. *Eremochelis bilobatus* (Muma), male resting on gravel in thorn thicket, nearly 3.0 times life size. 7. *Hemerotrecha serrata* Muma, female resting on rocky hillside, about 2.5 times life size. 8. *Annotrechula peninsulana* (Banks), female in "ambush" on rocky hillside, about 3.5 times life size. 9. *Annotrechula peninsulana* (Banks), egg mass laid in corn stalk, about 1.5 times life size. 10. *Branchia brevis* Muma, female resting on coarse sand, slightly more than 2.0 times life size.

Several (10) males and some (5) females were collected in a *Larrea* thicket near the Yuma dunes north of Glamis, California in June 1975 with a combination of strong incandescent light and an ultra violet light. Males moved very rapidly but only slightly faster than females. The species appeared early at the lights often within minutes after the lights were turned on. Most specimens were not feeding but one female was observed feeding on a small moth (probably a pyralid). In laboratory terraria, males and females readily ate termites but refused small tenebrionids and tiny gnats.

Eremochelis bidepressus (Muma)

Hemerotrecha bidepressus Muma, 1951, p. 105; Muma, 1962, p. 13; Muma, 1970, p. 30.

This Great Basin Desert species was reported on by Muma (13) under the name *Therobates bidepressus*. The species was mature during April and May but exhibited no distinct peak of adult activity. It was collected near the playas on the flats.

Eremochelis imperialis (Muma)

Therobates imperialis Muma, 1951, p. 94; Muma, 1963, p. 4; Muma, 1970, p. 35.

Muma (16) published the only previous biological information on this species.

One male and 1 female of this species from Mercury, Nevada have been available for study. Both sexes readily accepted and ate termites. Capture and ingestion behavior were not recorded. Neither the male nor the female burrowed but the male climbed the wall of the terraria easily and frequently. Both specimens lived 11 days in the laboratory. The faunal affinities and habitat are unknown.

Eremochelis plicatus (Muma)

Therobates plicatus Muma, 1962, p. 11; Muma, 1970, p. 33.

Muma (13) reported on the maturity and adult activity period as extending from May through August with adults most abundant in July. The species probably overwinters as a mid to late instar nymph. Muma's speculations on adult longevity and sex ratios may be erroneous, since dry pitfalls were used in the study.

Muma (16) erroneously recorded the food habits of this species as those of the male. Only 1 live female from Mercury has been available for study and observation. It drank water, ate a grasshopper and a *Tenebrio* pupa, but lived only 7 days in the laboratory. It remained burrowed for one 2 day period. Prey capture, ingestion, and burrowing were not recorded.

Chanbria Muma, 1951

Representatives of this genus are moderate sized, 20 to 30 mm. in length, slender, long-legged, and either pale or distinctively marked. They are sand inhabiting forms that may be found

either in extensive wind dune areas, or along limited arroyo and intermittent stream dunes.

We have made insufficient collections and studies to determine the maturity and adult activity periods, but to date most specimens have been collected in June and July. One female was taken in September.

The food habits are unknown. All collected specimens have eaten termites.

The genus is definitely known only from the Sonoran Desert, but immatures have been identified from the Great Basin Desert.

Chanbria regalis Muma

Chanbria regalis Muma, 1951, p. 96; Muma, 1962, p. 28; Muma, 1970, p. 36.

There are no previously published notes on the biology of this species.

In early June 1975, 8 males and 3 females of this species were collected at a combination of strong incandescent lights and an ultra violet light on the Yuma Desert south and east of Yuma, Arizona, on the Yuma dunes, in a *Larrea* thicket near Glamis, California, and at Twenty-nine Palms, California. All specimens were taken on open dune sands or on flats adjacent to the dunes. Living specimens varied from pale yellow to light tan in body color with light brownish appendages. No feeding specimens were collected, but both males and females fed readily on termites and refused tiny gnat-like flies. Males and females also accepted or readily accepted termites, sand roaches, sand crickets, and *Ceutophilus* sp. while in terraria.

Chanbria serpentinus Muma

Chanbria serpentinus Muma, 1951, p. 98; Muma, 1971, p. 37.

There are no previously published notes on the biology of this species.

Five males and 3 females of this species were collected at strong incandescent lights on low sandy ridges beside 10 Mile Wash north of Ajo, Arizona in early June 1975. Living specimens are pale yellow to tan with distinctively marked legs and palpi. A female was observed in the field eating a sand roach. Captured males and females still in the collecting tubes readily accepted individual termites. They apparently oriented the termites to their body lines before ingestion. In laboratory terraria, they fed readily on termites, sand roaches, sand crickets, and *Ceutophilus* sp. They accepted small black tenebrionids and refused tiny gnat-like flies.

Chanbria rectus Muma

Chanbria rectus Muma, 1962, p. 30; Muma, 1971, p. 36.

There are no previously published notes on the biology of this species.

In early June 1975, 4 males and 3 females of this species were collected at a combination of strong incandescent lights and

an ultra violet light on sand dunes, 20 miles due east of Palmdale, California. Living specimens are pale yellow to light tan with legs 3 and 4 lightly to distinctly dusky at femoral-tibial unions. They readily accepted termites as food, but refused gnat-like flies.

Hemerotrecha Banks

Representatives of this genus are mainly small in size, varying from 10 to 15 mm. in length, but a few range into moderate size, 20 to 25 mm. All are unique in structure and many are dark colored, well marked species.

Many species are known from only 1 to a few specimens, and their habitats are unknown. A few species are common enough to evaluate, and are known to inhabit brushland, thickets, or forested areas near or in the foothills and mountains.

Most known common species mature between April and September. The *banksi* species group achieves peak maturity in May, June, and July, the *serrata* species group in July and August, and the *simplex* species group in April and May. The *denticulata* species group seems to achieve peak maturity in the early spring and/or late fall.

The food habits of neither immatures nor adults are known. The greatest population density of this genus presently appears to occur in the Great Basin Desert and environs, but species are known from central Texas, southern California, and Canada.

Hemerotrecha californica (Banks)

Cleobis californica Banks, 1899, p. 314; Muma, 1951, p. 100; Muma, 1970, p. 38.

Muma (13) and (21) reported on this west coast species. In Nevada it was mature from April through August with a strong peak of adult activity in June. The species is known from collectors and collection records to be both arboreal and diurnal. Muma's (13) comments on overwintering and sex ratio may be erroneous owing to dry can trap trapping bias.

Hemerotrecha serrata Muma

Hemerotrecha serrata Muma, 1951, p. 102; Muma, 1970, p. 39.

Two live males and 3 live females of this Mojave or Great Basin Desert species from Mercury, Nevada were available for study and observation in 1965. See Fig. 7. See also references (13) and (16).

Males lived 8-10 days, mean 9 in the laboratory. Females lived 5-19 days, mean 10. Males did not burrow and only one female burrowed, once for 2 days and once for 3. Burrowing behavior was not recorded. Males drank water and accepted pyralid moths, but refused termites. Females drank water, reluctantly accepted termites, and *Tenebrio* larvae and pupae, and readily accepted pyralid moths, but refused *Tenebrio* adults, Muma (16).

At Mercury, Nevada, Muma (13) found that this species was

mature from June through September and attained peak adult activity in July and August. Since the species has been collected only in southern California and southern Nevada, it is believed to be a Mojave or Great Basin Desert form. Muma's conclusions concerning overwintering, sex ratio, and fertilization requirements are probably erroneous, owing to trapping bias.

Hemerotrecha denticulata Muma

Hemerotrecha denticulata Muma, 1951, p. 105; Muma, 1970, p. 39.

Muma (13) and Allred and Muma (1) have published on this species. In Nevada the species did not exhibit a distinct peak of adult activity, but was mature from October through May. This demonstrates that it overwinters as an adult, at least in the male sex. Allred and Muma, in Idaho, corroborated this finding with the periods of adult activity confined to September and October in the fall and April and May in the spring. Since the species has also been recorded from Colorado, Utah, and Washington as well as other areas in Nevada and Idaho it probably lives in and around the Great Basin Desert. Muma's statements about the sex ratio and fertilization requirements of the species must be considered erroneous pending population estimates with methods other than dry pitfalls.

Hemerotrecha proxima Muma

Hemerotrecha proxima Muma, 1963, p. 4; Muma, 1970, p. 41.

This Mojave or Great Basin Desert species has been reported only from Mercury, Nevada by Muma (13). Nine specimens were taken in October and November, 6 representing 3 males and 3 females in October which indicates a probable peak of adult activity in the fall. Muma's speculation that the species overwinters as an egg or early instar may be true, but on the bases of limited collections in dry pitfalls his sex ratio and fertilization requirement statements must be viewed with suspicion.

Hemerotrecha fruitana Muma

Hemerotrecha fruitana Muma, 1951, p. 106; Brookhart, 1965, p. 154; Muma, 1970, p. 39.

Biological data on this species have been published by Brookhart (5) and Muma (21 and 22). Both workers stated that the species is a foothills or mountain form that matures and attains peak adult activity in the spring; May in southern Colorado and March, April, and May in southwestern New Mexico. The habitat is unknown. Collections from California, Colorado, Nevada, New Mexico, Utah, and Wyoming indicate it may be a montane species around the arid or desert areas of southwestern North America.

Ammotrechidae Roewer, 1934

In the United States, this family includes 15 small to moderate sized species, measuring about 10 to 20 mm. in length.

We have some biological information on 5 species, 1 of the 3 known species of *Ammotrechella* Roewer, 1 of the 7 known species of *Ammotrechula* Roewer, and all 3 of the known species of *Branchia* Muma. Unlike the Eremobatidae this family is not restricted to the arid grasslands and deserts. One species is known only from Florida and one species is known from Louisiana as well as Texas. Although collections of all species have been made on the ground and/or under ground surface litter, there are strong indications that the two common species may be arboreal.

Ammotrechella Roewer, 1934

Representatives of this genus, with the exception of *Ammotrechella pilosa* Muma, have a coastal distribution in North America, and are distributed throughout the West Indies. In the United States, they are found in Florida and coastal California. The holotype of the exception was from Eagle Pass, Texas which is also less than 200 miles from the coast of the Gulf of Mexico.

The distribution of the species suggests most of what we know about the most common species in this country. They all exist in xeric microhabitats involving water worked sands, often referred to locally as "ball bearing sand". Precipitation over these sands, even when heavy at 12.7 to 25.4 cm. per day, disappears immediately because of the nature of the substrate.

Both adults and immatures may be found in any month of the year with populations higher during the spring and summer. Food habits are incompletely known but immatures can live and develop on termites in the laboratory.

Ammotrechella stimpsoni (Putnam)

Galeodes (Cleobis) stimpsoni Putnam, 1883, p. 261; Muma, 1951, p. 127; Muma, 1970, p. 47.

Biological information on this species has been recorded in references (16 and 17).

Although this small species is not associated with any specifically named desert, it is found almost exclusively on both coastal and inland, white, water worked sand dunes in peninsular Florida in the United States and in Chiapas, Mexico. Such dunes in Florida represent xeric habitats under mesic conditions. Maturity dates for the species are not known. Mature specimens have been collected in every month of the year and matures are often found in association with both early and late instar immatures. Both adults and immatures are more common from March through July and are equally common on the ground and above the ground on plants. Seven males, 2 females, and 22 immatures were available for biological study and observation in 1963-1965. These specimens were mainly collected from nests under the loose bark of dead standing pines from 1 to 3 feet above the ground and in dead, rotten, and termite infested mangrove and sweet bay limbs from 1 to 4 feet above the ground. They were also collected on the walls and floors of houses. Males were most frequently collected under the latter conditions.

In the laboratory, males lived from only a few hours to 18

days with a mean of 10 and a mode of 15. They were never observed to burrow. One of the 2 females lived 18 days, the other 62. They burrowed in rotten wood, corn stalks, and sand, the former two media from 11 to 18 days, the latter from 50 to 62 days. Immatures lived from 5 to 169 days with a mean of 51. They remained burrowed 82% of the time; 53% of burrowed time they were in wood and 47% in sand.

A single mass of eggs was laid in a sand burrow by 1 of the 2 field collected females. These eggs did not hatch and fungus overgrowth prevented an egg count.

Males fed readily on termites, females drank water and fed readily on termites but refused *Drosophila* maggots and small *Tenebrio* larvae (16). Other prey were not offered to this small species. Prey were located at a distance of several cms., apparently by sight, and were captured almost exclusively with the palpi which were held aloft and to the side during ingestion.

Females and immatures burrowed in sand by biting, raking, and plowing with biting and raking predominating. They burrowed in pith and rotten wood by biting and raking with biting predominating.

Nests in rotten wood and termite burrows were smaller than those built in sand. Females and immatures may or may not close such burrows or nests. When an opening was left the specimen remained just inside of the entrance from which it extended the palpi for prey.

Seven immatures moulted. They were in a stadium from 25 to 40 days, mean 32, and required from 3 to 10 days for ecdysis, mean 7. One immature moulted into an adult male form in 25 days, requiring 9 days for ecdysis.

Males, females, and immatures all readily dropped a leg or palpus (autotomy) when captured or injured.

Females and immatures also exhibited huddling and drowning. Immatures climbed smooth vertical surfaces such as glass without using the palpi.

Ammotrechula Roewer, 1934

Although only one species is common and well known, populations of this genus appear to be restricted to the brushland and thorn thickets of the arid grasslands and deserts, and on the upper bajadas in the foothills. Species of the genus have been found in the Coahuilan, Chihuahuan, Sonoran, Mojave, and Great Basin Deserts as well as the intervening grasslands.

The only common species in the United States has been collected as adults and immatures from March through December, but is more abundant from April through September.

Food habits are incompletely known.

Ammotrechula peninsulana (Banks)

Cleobis peninsulana Banks, 1898, p. 290; Muma, 1951, p. 130; Muma, 1970, p. 54.

Biological information on this species is recorded in references (16, 17, and 19).

This small, widespread species is recorded from Baja California, Chihuahua and Sonora in Mexico, and California, Arizona, New Mexico, and Texas in the United States. Mature specimens have been collected from March through December, and early and late instar immatures are often associated with adults. Both matures and immatures are more common in the warm months, April through September. Although nearly 70 specimens were available for biological study and observation, we have laboratory notes on only 24 males, 18 females, and 12 immatures, mostly from eastern Arizona and western New Mexico. This discrepancy is because the species, males particularly, often lives less than a day in captivity. The species has been collected from inside a soft ground surface stick, from nests under cow dung and boards on the ground, on walls in houses, in killing-preserving can traps, and around lights at night at a ratio of 3 males to every female or young. Females and immatures were more frequently collected under cow dung and boards on the ground. Most of our specimens were also collected in brushland, Fig. 8, or thorn thickets.

In the laboratory, males, on which records were kept, lived from 1 to 26 days, mean 8. Only one of the 24 observed males constructed a subterranean burrow and it emerged from same daily during the daylight hours. Males either constructed surface nests or rested in hollows under rocks or wood. Only 8 of the 18 females constructed burrows in which they remained only 18% of the time for 1 to 13 days at a time, mean 4. Eight of the 12 immatures constructed burrows in which they remained only 13% of the time for 1 to 24 days at a time, mean 5.

Females in the laboratory laid eggs on and in soil and in cornstalks, Fig. 9. Seven females produced 9 egg masses. Two females produced 2 masses. The masses varied from 4 to 65 eggs per mass, mean 36. None of these eggs hatched and several masses were scattered over the surface of the sand which indicates either sterility, atypical deposition, or egg destruction. It is probable that the mean obtained is low for the species.

Under laboratory conditions males drank water and accepted all 3 kinds of prey offered, termites most readily. Females drank water and accepted all 7 kinds of prey offered, *Gryllus* sp., pyralid moths, and termites most readily. Immatures drank water and accepted 7 of 9 kinds of prey offered. Pyralid moths, unidentified flies, ant larvae, and termites were accepted most readily. They refused earwigs and pardosid spiders. Because of its small size the species was not offered large or heavily sclerotized prey. The species oriented to, and located distant prey which indicates sight recognition or some other sense. Prey were captured with the palpi which were held aloft and flexed during ingestion. Males, females, and young were all observed feeding at night lights, but the prey was too mascerated to recognize.

Females and immatures constructed surface nests, subterranean burrows, and burrows in cornstalks. Details of the behavior with specific variables are cited in reference (17).

Five late instar immatures moulted in the laboratory, one of them twice. The nymphal instar stadia varied from 20 to 37 days,

mean 26, requiring 4 to 15 days for ecdysis, mean 9.

Several unique behavior patterns were recorded for this species. Males emerged from nests daily and during daylight hours. Males and females dropped palpi and legs by autotomy when captured or injured. Females and immatures exhibited drowning (19).

Gore and Cushing (9) published a short term behavioral study of this species in southwestern Arizona. Although they were primarily interested in energetics, return to burrows, and foraging areas, they did record the facts that males constructed nests (depression burrows) to which they frequently returned, and females constructed burrows (tube burrows) to which they often did not return. They also recorded an egg (brood) chamber and predation of second instar juveniles by silverfish (*Thysanura*: possibly *Thermobia* sp.).

Branchia Muma 1951

Representatives of this genus are found in the Coahuilan-Chihuahuan Desert region, the western part of the Sonoran Desert, and the Mojave-Great Basin Desert area.

Adults mature from March through August and immatures are often collected with adults.

Food habits are incompletely known, but all known species, both adults and immatures, readily accept termites as food.

Branchia brevis Muma

Branchia brevis Muma, 1951, p. 137.

Four males and 3 females of this Chihuahuan species were available for study in 1964 (16 and 17). All were collected in west Texas from surface nests under cow dung.

Males lived 6 to 12 days, mean 10, in the laboratory. Females lived 16 to 29 days, mean 23. Only termites were offered as prey. Both sexes readily accepted or refused the offering. All four males burrowed but emerged each day during the daylight hours. Females burrowed 30% of the time for 4 to 5 days at a time, mean 4. Both sexes constructed subterranean burrows. They did not burrow in pith or cornstalks. Burrowing was accomplished by biting, raking, and plowing with no noted unusual variations.

In late April of 1980 this species was common under cow pies at windmills, stock tanks, and in dry pastures from Dryden, Texas east to Roma Las Saenz, Texas. We collected and preserved 23 males and 15 females. Four females and 1 immature were kept alive for biological studies.

Both sexes were active until 10:30 A.M. on warm mornings, but not active on cool mornings in the field. All specimens were in surface nests or running, Fig. 10.

Both females and immatures in the laboratory readily accepted termites as food. All specimens burrowed but surfaced at 1 to 5 day intervals and fed on termites. One female built a surface nest similar to those found in the field. The last specimen died 25 days after collection. The immature did not

moult and none of the females laid eggs.

Branchia potens Muma

Branchia potens Muma, 1951, p. 138.

Biological information on this species is cited in references (13, 16, and 19).

Only 1 male and 3 immatures of this Mojave-Great Basin Desert species were available for study and observation. Muma (16) reported on the feeding habits of the female, but this is an error. The reported habits refer to the male and immatures. Muma (13) recorded maturity dates of June, July, and August for the species at Mercury, Nevada.

The male only lived 5 days in the laboratory. It accepted and ate a mealworm pupa and drank water. No other food was offered. The immatures lived 10 to 59 days, mean 27, accepted all 4 kinds of prey offered but readily accepted only termites. One immature moulted in 28 days and required 10 days for ecdysis. All immatures remained burrowed most of the time. The process of burrowing was not observed.

One immature of this species exhibited drowning as described by Muma (19).

Branchia angustus Muma

Branchia angustus Muma, 1951, p. 135; Muma, 1970, p. 56. (males and females).

There are no previously published biological notes on this species. It has been found only in the western portion of the Sonoran Desert.

Three males and 3 females of this species were collected alive at a combination of strong incandescent lights and ultra violet light in a *Larrea* thicket north of Glamis, California in June, 1975. The species appeared early at the lights, within minutes after the lights were turned on. None of the specimens were observed feeding under field conditions, but in laboratory terraria females both accepted and rejected termites. The males died before the availability of food.

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