DEVELOPMENT AND BEHAVIOR OF A SNAKEFLY, *RAPHIDIA BICOLOR ALBARDÁ* (NEUROPTERA: RAPHIDIIDAE)

Peter W. Kovarič, Horace R. Burke and Charles W. Agnew

**ABSTRACT**

The ontogenetic development and behavior of larvae, pupae and adults of a snakefly, *Raphidia bicolor* Albardá, are described. Adults of *Raphidia bicolor*, the only species of snakefly known to occur in Texas, are active from early spring to mid-summer in central and western Texas. They are mainly associated with *Juniperus ashei* Buchholz. Immature stages are described and the differences in larval instars are compared. There are usually 10 larval instars with a 11th occurring occasionally. Readily observable aspects of ontogenetic development of the immature stages are described. Duration of the egg stage ranges from 7 to 9 days, combined larval instars 255-458 days, and pupa 10-19 days. The behavior of the various stages is discussed in detail and compared with published observations on other species.

**INTRODUCTION**

*Raphidia bicolor* Albardá is the most widely distributed snakefly in North America. This species has been recorded from British Columbia southward into Baja California and eastward to central Texas (Aspöck 1975). Despite being widely distributed and fairly common, little is known about its biology except for observations on behavior made by Acker (1966) (as *Agulla bicolor*; *Agulla* is presently considered as a subgenus of *Raphidia*). Nearctic snakeflies as a whole are poorly known. Immature stages and general biologies have been studied for only two of 21 North American species: *Raphidia bractea* (Carpenter) (Woglum and McGregor 1958), and *Raphidia astuta* Banks (Woglum and McGregor 1959). Both species are associated with citrus trees in California.

Ecological data are available for many Old World species, primarily due to the studies of Aspöck (1974) and Aspöck et al. (1974, 1975). While the larvae of most species of *Raphidia* (sensu lato) live under bark, many develop in the soil, usually in detritus at the base of trees and shrubs (Aspöck 1974, 1975). Larvae of the two North American species of *Raphidia*, for which the biologies have been investigated, live beneath tree bark (Woglum and McGregor 1958, 1959).

Plant associations for species of snakeflies are often quite variable within a genus, a subgenus or even a species. While some species are associated with relatively few plants, or specifically with either angiosperms or gymnosperms, many others associate with a diverse array of plant species. *Raphidia bicolor* has been collected from species of 15 families of plants (Aspöck 1974).

*Raphidia bicolor* is the only species of snakefly known to occur in Texas. The species was not listed from Texas by Carpenter (1936) in his revision of Nearctic snakeflies, but later collecting added numerous records from the state (Aspöck 1974, 1975). Most records of the species are from central Texas with a few from the Trans-Pecos and Panhandle regions. Adults of *R. bicolor* are most active in central Texas during the spring (March-May), but they have also been collected in early July in the Trans-Pecos region. Adults are most frequently collected in the field in central Texas during April after

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1 Department of Entomology, Ohio State University, Columbus, OH 43210.
2 Department of Entomology, Texas A&M University, College Station, TX 77843.
3 414 Maple St., West Lafayette, IN 47906.
which time their numbers decrease considerably.

The present study was conducted to contribute to the knowledge of this little known, but fairly frequently collected, species. Information presented here deals mostly with ontogenetic development and behavior of the larval, pupal and adult stages.

MATERIALS AND METHODS

Adults used to initiate this study were collected by sweeping *Juniperus ashei* Buchholz at Inks Lake State Park, Burnet Co., Texas, 14 April 1985. Individuals were confined in the laboratory in clear plastic containers (9 x 10 cm) with a small branch of juniper and a piece of corrugated paper as an ovipositional substrate. The insects were provided with distilled water and either freshly-killed caterpillars or an artificial diet of the type used to feed adult chrysopids (Hagen and Tassen 1970). Eggs collected during daily inspections of the containers were counted and measured. The temperature and relative humidity of the rearing room were maintained at 23 ± 3°C and 58%, respectively.

Eggs of *R. bicolor* were held for incubation in 3.5 x 7 cm plastic containers enclosed in sealable plastic bags. Eggs of *Sitotroga cerealella* (Oliver) were provided as food for larvae with fresh eggs being added approximately every three days. After attaining the 3rd instar, larvae were individually confined to 1/4 dram glass shell vials with cork stoppers. A disk of paper was placed in the bottom of each vial to provide concealment for the larva. When larvae reached the 8th instar, they were transferred to 1/2 dram shell vials. Larvae were held in the dark and checked daily for evidence of molting, at which time exuviae were removed and molts recorded. Pupae were transferred to 250 ml plastic cups to be held until adult emergence. Newly emerged adults were paired and placed in 38 x 19 x 37 cm cages for mating. Food was provided as described above.

Representatives of each larval instar were preserved for measurements of head capsules, description and as voucher specimens. The length of the head capsule was measured from the base of the antennae to the point of constriction near the occiput, while width was measured across the widest part of the head capsule. The various developmental stages are described here as part of the general biology and ontogeny of the species. A more detailed analysis of the larval and pupal chaetotaxy and distribution of sensilla is in progress and will be published later. Voucher specimens of the material studied here have been deposited in the Insect Collection of the Department of Entomology, Texas A&M University (voucher # TAMU 558).

DESCRIPTION OF IMMATURE STAGES

**Egg** (Fig. 1). The shape of the egg of *R. bicolor* is similar to that described for two other species of raphidiids (Woglum and McGregor 1958, 1959). Length of 29 eggs measured was 1.56 ± 0.05 mm (X ± SD) and the width was 0.3 ± 0.03 mm. Eggs are oblong-ovoid, usually slightly curved, and pale green in color. The chorion is uniformly dimpled. A prominent micropyle, consisting of a nipple-shaped structure approximately 0.05 mm in length, is located at one end of the egg. The opposite end of the egg is bluntly rounded.

**Larva**. Larvae of *R. bicolor* are morphologically similar to those described for other species of raphidiids (Williams 1913; Woglum and McGregor 1958,1959). Although the chaetotaxy is not described in detail here, the following descriptions of the larval instars of *R. bicolor* are sufficiently complete to aid in distinguishing the various instars. Head capsule measurements of each instar are presented in Table 1. First Instar (Fig. 5): Integument unpigmented, smooth, nearly transparent. Tagmata bearing numerous short, fine setae. Head capsule soft, nonpigmented; ecdysial suture absent. Antenna four segmented; numerous sensilla, including pegs and setae, occur on apices of third and fourth segments. Mandibles dark, each bearing four sharply pointed teeth. Maxillary palpi bluntly conical, apparently four segmented, bearing cluster of sensilla at apex. Maxillae quadrate, bearing several sensilla on apical third. Labial palpi short, apparently three segmented, otherwise similar to maxillary palpi. Apex of labium broadly rounded. Eyes consist of pale orange pigmented areas visible beneath integument. Six or more red maculae located caudad of antennal bases. Legs five segmented; pair of claws and clavate organs (as described by Woglum and McGregor 1958,1959) occur distally on unsegmented tarsus. Anteriormost
TABLE 1. Larval Head Capsule Measurements, *Raphidia bicolor* \( (n=30) \)

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spiracles located between pro- and mesothorax, borne on prominent cone-shaped tubercles. Meso-, meta- and abdominal spiracles relatively inconspicuous; borne on flattened, circular lobes. Small, posteriorly directed tooth-like cuticular projections occur on meso- and metanota and all abdominal segments; larger and medially clustered on thorax; smaller on abdomen; evenly distributed on all tergites, sternites 7-10, and pleural regions of segments 9-10. Similar structures restricted to abdomen of subsequent instars. Terminal abdominal segment with fleshy lobes surrounding anus. Second Instar (Fig. 6): Second instar larvae strongly resemble 1st instar larvae in general appearance. The following differences distinguish the two: some setae on body of 2nd instar longer; head capsule lightly pigmented; ecdysial suture present; mandibles darker; eyes appear as cluster of maroon pigmented spots; projections absent on thorax. Third Instar (Fig. 7): Differs from preceding instar as follows: body considerably more slender and elongate; cuticle lightly pigmented; most setae longer; head capsule moderately and pronotum lightly pigmented; antennae more elongate and slender; eyes solid mass of purple pigment; circle of seven stemmata on head capsule behind antennal bases. Stemmata become more prominent in later

Instar larvae. Fourth to Tenth Instars: Morphological changes in 4th through 10th instar larvae are slight. Each successive molt results in a larva more closely resembling the final instar. The most obvious change is an increase in pigmentation and establishment of patterns characteristic of each stage. Fourth Instar: Sub-cuticular eyes clearly visible beneath moderately pigmented head capsule, appearing as dark purple ellipses. Faint cuticular patterns visible on meso- and metathorax and last three abdominal segments. Fifth Instar: Mandibles more elongate than in preceding instars. Subcuticular eyes appear circular. Cuticular pigmentation present on legs. Sixth Instar (Fig. 8): Head capsule dark brown. Eyes located more laterally directly behind antennal bases in this and subsequent larvae. Maculations more apparent with distinct W-shaped markings on abdominal segments 2 through 5. Seventh Instar: W-shaped markings on all abdominal segments. Faint lateral and ventral maculations discernible. Eighth Instar (Fig. 3): W-shaped markings more prominent. Lateral and ventral markings distinct. Ninth Instar: All markings darker and more distinctly defined. Lateral and ventral patterns more extensive. Tenth Instar (Fig. 9): Some additional maculations present. Otherwise resembling preceding stage. Eleventh Instar: Non-prothetelous 11th instar larvae are slightly larger that 10th instar larvae but otherwise the two are indistinguishable.

Pupa (Figs. 2, 10). The following discussion includes some of the more distinctive aspects of the pupa. The ovipositor is composed of a large and a small pair of annulated tubular appendages. The large pair arises from abdominal segment 9 and each appendage appears to be two segmented. The largest portion of each appendage is the basal segment to which is attached apically a short, knob-like segment. The smaller pair, consisting of one segmented appendages, arises from segment 8. The prothorax of the pupa is shorter and broader than that of the adult and the margins are not expanded to cover the prosternum as in the adult. The maculations on the pupal abdomen are similar to those found on larvae; adults lack these maculations. The pupal abdomen is also larva-like. Long, hairlike setae are present on the pupal head, thorax, wing pads and abdomen.

DEVELOPMENTAL BIOLOGY

Embryogenesis. A pattern of reticulation is visible at high magnification just beneath the chorion of the egg. Developing structures become obvious 3 days after deposition. The first indication of the developing embryo is the appearance of a translucent yellow band. Within a day before eclosion, the banding pattern disappears and the egg becomes off-white in color with red eyespots being discernible near the micropylar end. Duration of the egg stage, as determined for 16 eggs, was 8.25 ± 0.94 days.

Hatching. Observations on the hatching of 1st instar larvae of R. bicolor agree well with those of Williams (1913) on Raphidia maculicollis Stephens. Immediately before eclosion, the 1st instar larva is visible through the chorion of the egg. The larva is oriented so that its thoracic region lies against the micropylar end of the egg. The head is directed caudally and is tightly appressed to the ventral surface of the body. Oblique upward and downward movements of the head usually indicate hatching is imminent. Movement of the head is generally accompanied by small, infrequent contractions of abdominal and thoracic regions beginning posteriorly and progressing anteriorly. Subsequently, a reduction of egg turgor occurs, superficially indicated by the loss of the swollen, shiny appearance of the egg. The chorion continues to contract, eventually conforming to the body of the larva. The next phase of eclosion is the onset of successive, anteriorly directed contractions of the abdomen and thorax. These contractions are sporadic at first but eventually occur at regular intervals of every 2 to 3 minutes. The thorax swells and the abdomen shrinks during contractions. Contractions eventually cease and the larva becomes quiescent. This inactive period is terminated by a major body contraction causing expansion of the thorax and rupture of the chorion. Air bubbles may be seen moving through the pharynx immediately following rupture of the chorion, possibly indicating that the larva ingests egg fluid up to and including the point of rupture of the chorion. The larva extricates itself from the chorion principally by abdominal contractions. Legs are not used for this purpose until the larva is almost completely free from the chorion. Four or 5 minutes are required for the larva to free itself after the egg shell is ruptured. The entire process of eclosion takes 15-20 minutes.

Molting. The first molt usually occurs within 24 hours after hatching. Prior to ecdysis the larva fastens its caudal end to the substrate with an anal secretion. It then raises off the substrate, twists the body and flips over so as to lie on the back or side. After lying
motionless in this position for about 10 minutes, a series of abdominal contractions begin. These contractions are accompanied by a gradual swelling of the thorax. The abdomen gradually shrinks and becomes partially separated from the old cuticle while the thorax continues to expand until the cuticle ruptures. The larva extricates itself from the old cuticle mostly via abdominal contractions. The molting process is similar for subsequent instars except that attachment of the caudal end to the substrate is not practiced. The exuvia of the 1st instar larva appears as a shriveled white strand with an elliptical anterior opening. The exuvia of 2nd and subsequent instars have well defined head capsules.

Larval Development. Normal Development: Seventy-six percent of 41 larvae developing in the laboratory completed 10 instars, while the remainder attained the 11th instar. Durations of the various larval instars are summarized in Table 2. During larval development, there is the general trend of steady increase in the durations of the various instars. Durations of the final instar were highly variable, ranging from 197-308 days ($\bar{x}$ = 235.0, $n$ = 31) for 10th and 187-258 ($\bar{x}$ = 214.5, $n$ = 10) for 11th instar larvae. Although Aspöck (1975) reported that exposure to low temperature is critical for pupal development in some snakeflies, chilling was not necessary to initiate pupation in R. bicolor. Unlike most European snakeflies which have two year life cycles (Aspöck et al. 1974), Nearctic species, which have been studied, complete their development in one year (Woglum and McGregor 1958,1959) under normal conditions.

Abnormal Development: Several prothetelous 11th instar larvae were observed in laboratory cultures after the majority of the F1 larvae had completed their development. These larvae, with an odd combination of pupal and larval characters, may be distinguished from normal larvae in several ways. The most obvious characteristic of the prothetelous larva is the presence of large eyes. Less apparent is the occurrence of membranous outgrowths, which appear to be wing pads, extending laterally from the meso- and metanotal margins. According to Aspöck et al. (1974), the wing pads of Palaearctic prothetelic larvae are often well developed and may have veins. Well developed wing pads were not observed in larvae of R. bicolor. Two specimens examined during this study possessed paired appendages on the ventral surface of segments 8 and 9. One specimen had a pair of partially fused, annulated, three segmented appendages on the venter of segment 9. The basal segments were fused, the middle segments angled toward the midline, and the terminal segment knob-like. A pair of small protuberances, ringed basally with a thin dark line, was located on the preceding segment. Appendages on segment 9 of this specimen are similar to the pupal ovipositor in having the annuli and a knob-like apical segment. Appendages of segment 9 of the second specimen were not fused and appeared to be

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a Larvae in penultimate instar.
b Larvae in final instar.
composed of two segments. The distal segment had two partially fused finger-like lobes, one in front of the other. Protruberances on segment 8 were pronounced in this specimen. Abdominal appendages of this specimen are similar to those shown in a photograph in Aspöck et al. (1974) of a prothetelous larva of *Raphidia major* Burmeister. The latter authors identified the appendages as primordial genital organs.

**Pupal Development.** Pupation observed in the laboratory was preceded by a period of larval quiescence lasting 6.45 ± 1.37 days (n = 35). As in larval ecdysis, this period of inactivity is terminated by the onset of successive contractions of the abdominal segments. The resultant swelling of the thoracic region causes the larval cuticle to split along the pronotum. Splitting of the cuticle continues posteriorly as the pupa begins to extricate itself. Wing pads are eventually exposed by lateral tearing of the cuticle. At this stage the pupal head remains within the old cuticle of the larval head capsule. The pupa then works itself forward through the split in the exuvium, primarily by contractions of the abdomen, after which only the head and posterior abdominal segments remain in the old larval cuticle. The pupal abdomen is then used to pull against the strand of exuvium which connects the head and abdomen, eventually freeing the head. The extricated pupal head is narrow at first but eventually expands to normal size. Once the head is free, the remainder of the exuvium is gradually shed by abdominal contractions. The next step in the process is the shedding of the gut lining. Shedding of the external larval cuticle usually requires ca. 15 minutes while the gut lining is eliminated in ca. one hour. The newly eclosed pupal head is transparent and the tracheae within are clearly visible. The anterior 3/4 of the eye is light brown while the remainder is unpigmented. Mouthparts are light brown except for the dark apices of the mandibles. Wing pads, legs and ovipositor are initially transparent. Color patterns similar to those of the last larval instar are present on the abdomen. Within eight hours the mandibles darken, wing pads become light fuscous, and legs begin to show signs of pigmentation. After 24 hours, further darkening of the eyes, mandibles and ovipositor occur. A faint pattern of pigmentation also begins to emerge on the prothorax. The mandibles are functional and this destichous pupa is capable of biting at this time. Following about six days of development, the mandibles appear black and there is further evidence of color patterns on the prothorax. The head has usually darkened considerably by the ninth day with the darkened areas appearing deep metallic green. Several symmetrically arranged transparent regions are present on the posterior half of the developing pupal head. These areas eventually darken prior to adult eclosion. Similar markings occur in the adult stages of the species studied by Woglum and McGregor (1958, 1959). By the tenth day short black setae are visible along the veins of the wing pads of the pharate adult. Eyes turn a vivid metallic green, especially in males, and black setae on the legs and margins of the prothorax are visible through the transparent cuticle by day 11. The mandibles are fully hardened with their apices nearly black. Coloration of the meso- and metathorax is nearly adult-like by day 12. Further development occurs rapidly so that the ovipositor has lengthened and there is an increase of activity involving movement of legs, mouthparts, and abdomen by day 13. By day 14 the pupa has begun to walk, indicating that adult eclosion will occur within a 24-hour period. An active pupa bites if provoked; on foliage it responds to disturbance by tucking in its legs and head and dropping to the ground.

Pupae required 14.67 ± 4.81 days (n = 21) to complete development. Although 46% of 93 laboratory-reared snakeflies reached the active pupal stage, only 23% of the total cohort survived to the adult stage. Twenty-five percent of the total mortality occurred in the active pupal stage. Active pupae which do not molt within 24 hours usually die before attaining the adult stage. Water and food were offered in an effort to induce some of these persistent pupae to eclose. Although accepted, molting did not occur. Aspöck et al. (1974) reported similar mortalities in the pupal stage of laboratory-reared European species. These authors also reported that active pupae on tree trunks are often eaten by birds.

**Prior to adult eclosion.** The exarate pupa wanders about for an indefinite period. As in chrysopids (Smith 1922), proper orientation of the pupa on a vertical surface appears to be critical to successful ecdysis. When supplied with such a surface the pupa stops and remains motionless with the head and prothorax directed upward and slightly reflected when molting is imminent. When the pupa cannot orient itself in this way the wings fail to expand properly. Duration of the quiescent period is variable but generally exceeds one hour. An active pupa was occasionally observed to move a short distance from its former resting spot and then resume a motionless state.
Adult Development. Emergence of the adult begins with successive anteriorly-directed waves of contraction of the abdominal, meta-, and mesothoracic segments. As the abdominal segments contract, the abdomen is raised at an approximate 30° degree angle. The head and prothorax wave from side to side each time the abdomen contracts and is elevated. When the contractions cease, the abdomen drops and the prothorax and reflexed head are raised to an angle of ca. 50°, partially caving in the mesothorax. The prothorax then drops and the process is repeated. This process apparently serves to loosen the thin pupal cuticle which encases the adult. This behavior is identical to that reported by Smith (1922) for the Chrysopidae. The expanding meso- and metanota eventually rupture the cuticle. The split proceeds anteriorly and the exuvium begins to part laterally from the prothorax. Simultaneous contractions of the abdominal and meso- and metathoracic segments separate the pupal exuvium from the adult. Finally, the adult works its way forward until the head, tucked under the prothorax and encased in the pupal cuticle, is free.

After emergence the snakefly adult directs the wings downward and obliquely as they inflate and begin to harden. Initially, the wings appear as opaque, gray flaps and are positioned in a swept-backed fashion extended outwardly from the body. The wings clear and expand to their full size in ca. 10 minutes, after which time the typical roof-like position over the abdomen is assumed. Further changes involve darkening of the wing veins, hardening of the mouthparts and antennae, and expansion of the prothoracic margins to cover the underside of the prothorax. Adults (Fig. 4) would generally not attempt flight for at least 24 hours after emergence. Longevity of adults in the laboratory 74 ± 11.99 days (n=7). The complete life cycle in the laboratory was 411.71 ± 19.87 days (n=7).

LARVAL AND ADULT BEHAVIOR

Larva. Field observations: Six larvae of R. bicolor were collected under bark of Juniperus ashei, 21 April 1986, at Inks Lake State Park, Burnet Co., TX. These larvae were small and active and difficult to collect. Subsequent examination in the laboratory indicated that these represented one 3rd, three 4th, and two 5th instar larvae. The arthropod fauna under the bark of this tree was surprisingly abundant and diverse. Potential prey for

![Figures 5-8: SEM Micrographs of early instar larvae of Raphidia bicolor. Fig. 5. First instar. Fig. 6. Second instar. Fig. 7. Third instar. Fig. 8. Sixth instar.](image-url)
snakefly larvae included clerid larvae, psocopterans, pseudoscorpions, collembolans and mites.

**General Behavior**: First instar larvae of *R. bicolor* were observed to be gregarious in the laboratory and usually clustered in groups of four or more individuals. These and subsequent instars appear to be negatively phototrophic and positively thigmotactic. First instar larvae drink water and feed on pollen/water mixture, but neither appears to be necessary for development. Second instar larvae are also gregarious and unaggressive but they are more mobile than 1st instar larvae. Water and food are also accepted but are not required for molting. Third instar larvae continue to cluster but they are more mobile than preceding instars. Whereas 1st and 2nd instar larvae appear to be restricted to forward movement, 3rd instar larvae are capable of moving backwards rapidly, using the terminal segment of the abdomen which has become modified for grasping the substrate. Reverse locomotion is improved in subsequent instar larvae by further lengthening and tapering of the terminal abdominal segment combined with the development of fleshy lobes surrounding the anus. The first signs of aggression are demonstrated by 3rd instar larvae. Fourth instar larvae are solitary and may become cannibalistic in confined quarters. This behavior continues in subsequent larval stages.

**Feeding**: When feeding on the eggs of *Sitotroga cerealella* or other prey, the larvae masticate and completely devour food items. Larvae freely drink water and respond quickly by elevating the head and prothorax from the substrate when a drop is placed nearby and, while swinging these portions of the body side to side, advance to the water source. Soon after reaching the 10th instar most larvae cease feeding and become relatively inactive, possibly indicating the beginning of diapause. They may continue to drink water. Wiegum and McGregor (1958, 1959) reported that they reared larvae of *Raphidia astuta* and *Raphidia bractea* on eggs and crawlers of black scale, *Saissetia oleae* (Olivier). Larvae of *R. bractea* were observed to eat scrambled eggs, ground beef, covers of dead scale insects, and the exuviae of their own species.

**Adult. Feeding**: During this study adults of *R. bicolor* were maintained almost exclusively on water and an artificial diet (Hagen and Tassen 1970) developed for chrysopid adults. Both were consumed readily. Several types of soft-bodied insects (lepidopterous larvae, aphids, psocopterans, and scale insect crawlers) were also offered and most were accepted as food. The latter insects occur on *Juniperus ashei* and may constitute the principal food for snakefly adults in nature. In the process of procuring live food, the snakefly raises its head and prothorax and with the mandibles open strikes downward on the prey. Small prey such as aphids and psocopterans are captured with the mandibles, masticated and rapidly ingested. Adults tend to remain stationary while feeding on small, soft bodied insects and use the mandibles to manipulate the prey. When small lepidopteran larvae were offered the snakefly initially used its mandibles to make an incision along the length of the caterpillar. The prey was then macerated and formed into a ball which was continually rotated while being consumed. Snakeflies often had considerable difficulty subduing large, active lepidopteran larvae. A snakefly may try to slit the integument of the intended prey and/or grasp it with the mandibles and shake it violently. During the ensuing struggle, the snakefly sometimes walks backward dragging the prey. The forelegs may be used to hold the prey against the surface while changing the grip of the mandibles. The voracious nature of snakefly feeding is indicated in a report by Tilden (1951) that an adult female of *Raphidia adnixa* Hagen confined with aphids ate the entire colony of 57 individuals in less than 9 minutes. Non-animal food is apparently sometimes eaten by snakeflies. Acker (1966) observed *R. bicolor* feeding from nectar glands of *Freemontia californica* Torrey, a flowering shrub.

**Grooming Behavior**: The grooming behavior of *R. bicolor* is similar to that of the Palaearctic species *Raphidia notata* Fabricius (Jander 1966). Adults of *R. bicolor* were observed to periodically groom the antennae with the forelegs, especially after feeding. This behavior requires that the head be drawn toward the center of the body so that the forelegs can reach the antennae. This is accomplished by a combination of both elevating the prothorax and lowering the head so that the head lies close to the front coxae. Typical grooming behavior begins by the snakefly passing the protibia and tarsi through the mouthparts. Both forelegs are then elevated and the tibiae are crossed, gathering the basal portions of the antennae together. Then in a quick motion the crossed forelegs are extended forward and downward while the prothorax and head are simultaneously elevated, drawing the antennae along the notch formed by the crossed forelegs. The other protibia and tarsus
are then passed through the mouthparts and the process is repeated. Variations of this
typical grooming behavior were frequently observed. Examples include continual rubbing
of a single antenna by an ipsilateral foreleg and prolonged ipsilateral movement of a foreleg
through the mouthparts. Grooming behavior is apparently confined to the forelegs and
antennae.

*Abdominal Stretching:* A distinctive behavioral trait of adults of *R. bicolor*
involves periodical movements of the abdomen. A similar habit, which he called abdominal
stretching, was observed by Acker (1966) in *Raphidia* sp.; he concluded this to be a part
of the courtship ritual. Although this behavior may play a part in courtship, it was observed
many times in non-courting snakeflies during the present study. Abdominal stretching is
common to both sexes. When engaged in this behavior, the insect seems to be secreting a
chemical substance to the undersides of the wings from the apex of the abdomen. The apex
of the abdomen, vibrating rapidly, usually traces an arc across the under surfaces of both
pairs of slightly elevated wings from stigma to stigma. Sometimes wings on only one side
of the body are involved. Adults stretch their abdomens at times other than during

**FIGS. 9-10. SEM Micrographs of larva and pupa of *Raphidia bicolor.* Fig. 9. Tenth instar
larva. FIG. 10. Pupa of female:**
encounters with the opposite sex, especially when exposed to new environmental conditions such as when fresh plant material is put in the cages or when caged adults are placed out-of-doors. Glands are not apparent on the abdomen and the source of the suspected secretion remains unknown. Microscopic examination of the wing stigmas of living individuals revealed that they are thickened and waxy. When a drop of water is applied to the stigmatic surface of a live snakefly it is gradually absorbed. This procedure was repeated with several individuals of both sexes with the same results. Wing stigmas of dead individuals do not absorb water. The absorbent stigma may serve for storage of an unknown secretory product, the function of which remains undetermined.

**Courtship and Mating:** Courtship in *R. bicolor* is a gradual, complex process. Interactions between the two sexes are initially violent but gradually decrease in intensity. The male generally initiates the courtship behaviors. Vigorous sustained vibrations of the abdomen are the most obvious aspect of the courtship ritual of this species. Prolonged vibrations by a courting male often elicit a similar response from the courting female. When a courting male stops signaling, the female often responds with short vigorous vibrations which may cause the male to resume calling. The antennae of both sexes vibrate at a high frequency when signaling. Henry (1979) states that vigorous abdominal vibrations (similar to those described above) are an integral part of the courtship of chrysopids. He points out that drumming is not involved as the abdomen does not strike the substrate. The abdominal vibrations are transferred to the substrate through the legs of the chrysopids. The acoustical signals of the courting male are transmitted a distance of several inches, and are detected through the sensory receptors in the legs. Several other behavioral aspects of chrysopid courtship reported by Henry (1979) have counterparts in the raphidiid ritual. These include touching of mouthparts, wing fluttering, vibration of antennae, and lunging, biting attacks.

Simultaneous abdominal arching and wing movement is a courtship behavior which is apparently unique to *R. bicolor* males. The male raises its abdomen between the wings (sometimes abdomen curls outside of wings on one side) and arches it over the metathorax while simultaneously vibrating the wings. The male often rubs the tip of the abdomen over the inner surface of the partially extended wings prior to extension of the abdomen. Although wing movements of males are generally restricted to a slow flutter, occasionally vibrations were rapid enough to produce an audible buzzing sound. A male engaged in this display usually walks a slight distance from the female and then returns to meet her face-to-face. The antennae of the male vibrate at high frequency during this behavior. A less frequent aspect of the same general behavior involves the male rubbing its abdomen and/or prothorax against the substrate. If a pheromone is secreted during this behavior, wing movement may serve to disperse it.

Abdominal stretching is a commonly observed behavior among courting snakeflies. Other behaviors noted in *R. bicolor* and also recorded by Acker (1966) for *Raphidia* sp. (as *Agulla* sp.) are antennal grooming (usually occurring during interludes between engagements), and antennation of the air and the substrate. Another courtship behavior observed is facial contact between the two sexes which is referred to as "kissing" by Acker (1966). This involves intertwining of the antennae, mouthpart contact, and grazing of the cheek. Males may also initiate lunging, driving attacks on females. Attacks are often violent with the male driving back the female for several centimeters. Females sometimes initiate the attacks.

When an unmated male is introduced into a cage with an unmated female both sexes usually begin abdominal stretching and the male may initiate abdominal vibrations. The male commonly explores the substrate with its mouthparts and antennae. This behavior also was observed in *Raphidia* sp. by Acker (1966). In the present study one newly introduced male was observed to cautiously approach a female with a vigorously vibrating abdomen. Upon reaching the female, facial contact was made followed by a lunging attack which drove the female backwards. At the end of this violent confrontation, the two individuals wandered off in different directions. A female is able to initiate courtship in a male by repeatedly stretching her abdomen followed by a period of abdominal jerking.

Acker (1966) stated that immediately prior to copulation, the male of *Raphidia* sp. lowers its head and crawls beneath the abdomen of the female. A receptive female responds by raising her abdomen allowing the male to curl its abdomen upward to grasp the female's genitalia. Similar behavior was observed in *R. bicolor* although none of the actions resulted in copulation.
White objects identified as spermatophores were reported by Acker (1966) adhering to the 7th and 8th sternites of females of Raphidia sp. after copulation. Although mating was not observed in R. bicolor, spermatophores were found protruding from the genital region of two females which were confined with males.

**Oviposition**: Oviposition by R. bicolor was not observed in the field and field-deposited eggs were not located. However, females probably deposit eggs on the rough bark of Juniperus ashei in Central Texas since the early instar larvae are found under the bark of this tree and adults in the laboratory deposit eggs in crevices of juniper bark. The following observations on ovipositional behavior were made on seven females in the laboratory. This information is incomplete because the females were collected in the field and their reproductive history prior to capture is unknown. The number of fertile and infertile eggs deposited and the clutch size are presented in Table 3. Several females began depositing eggs within a week of capture. The interval between deposition of clutches of eggs ranged from 2 to 8 days. During the 2 to 3 weeks following capture, all eggs deposited proved to be fertile; however, all eggs subsequently deposited were infertile. Oviposition is usually preceded by a period of increased activity of the female. When oviposition is imminent the female begins walking about, intermittently stopping to probe the surface with the ovipositor. She may continue to search for several hours before depositing eggs. Eggs are generally deposited in crevices or other concealed places. The minimum number of eggs deposited by a field-collected female was 35, and the maximum number was 610; clutch size ranged from 9-121. Although females generally deposited all of their eggs in one localized area, they occasionally oviposited in two or more areas in the container.

**Table 3. Egg Deposition by Field-Collected Raphidia bicolor**

<table>
<thead>
<tr>
<th>Female No.</th>
<th>Fertile</th>
<th>Eggs</th>
<th>Infertile</th>
<th>Eggs</th>
<th>Total eggs deposited</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. clutches</td>
<td>Total eggs</td>
<td>No. clutches</td>
<td>Total eggs</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>3</td>
<td>272a</td>
<td>8</td>
<td>337</td>
<td>610</td>
</tr>
<tr>
<td>2</td>
<td>4</td>
<td>336</td>
<td>4</td>
<td>151</td>
<td>487</td>
</tr>
<tr>
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<td>1</td>
<td>35</td>
<td>0</td>
<td>0</td>
<td>35</td>
</tr>
<tr>
<td>4</td>
<td>3</td>
<td>156</td>
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<td>5</td>
<td>345</td>
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<td>3</td>
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<td>5</td>
<td>251</td>
<td>435</td>
</tr>
<tr>
<td>7</td>
<td>2</td>
<td>188</td>
<td>0</td>
<td>0</td>
<td>188</td>
</tr>
</tbody>
</table>

*a one clutch partially infertile

The ovipositor is extremely flexible and can be tucked completely under the body while the female is probing for an ovipositional site. Sensory appendages at the apex of the ovipositor are used to probe the surface for any crevices into which the eggs may be placed. The wings are held slightly above the abdomen while the female is probing. When a suitable place is found, the ovipositor is introduced; the abdomen becomes still and taut, swelling slightly as an egg enters the ovipositor. After eggs are introduced into the proximal end of the ovipositor they move rapidly distad, the ovipositor visibly expanding during passage. Eggs are apparently covered with a substance which causes them to adhere to the substrate and to each other. Once the egg has cleared the ovipositor, the terminal portion of this structure is used to position the egg against others in the cluster. After each egg is deposited and positioned, the female probes the entire cavity with the tip of the ovipositor for 10-20 seconds. Eggs deposited in a tight crevice are usually arranged in a single row. If more space is available the eggs may be stacked several layers deep. It takes approximately 8 seconds for each egg to be deposited. The interval between deposition of eggs was usually 20-30 seconds but may be up to one minute. One female was observed to deposit 18 eggs in 10 minutes. In one case the entire ovipositional event lasted approximately one hour.
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**LITERATURE CITED**


