

Asilid Literature Update



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INTRODUCTION

Robber flies (Asilidae) are a widely distributed group of predatory flies that largely inhabit semi-arid and arid regions of the world. Over the past quarter century, there has been a tremendous surge of interest in these flies, both on a taxonomic and biological level. Much of the recent work has been carried out by scientists in Europe, Russia, and North and South America. The research by these asilidologists has appeared in publications scattered across the globe, and it is the purpose of this bibliography to gather together the more recent literature citations into a single source while providing a brief review of the "state of the art."

The first major attempt at compiling asilid references was that of Hull (1962), whose bibliography at the end of volume two of "Robber Flies of the World," included approximately 1,344 references. While the majority of the bibliographic citations ended with the year 1954, a few references for 1955 to 1960 were included. Castellani (1947) had previously listed the publications dealing with robber flies of Italy, while Oldroyd (1963) provided a comprehensive bibliography for the robber flies of Africa. Rudolf Rozkosny (1971), in his "Bibliography of Diptera of Czechoslovakia 1758-1965," provides references to the Asilidae of his country (Universita J. E. Purkyne, BRNO). Holotype citations for the Asilidae of the Oriental region were recently prepared by Delfinado and Hardy (1975).

In the present work, a serious attempt has been made to update Hull's bibliography. While major emphasis has been placed on the years 1956 to 1976, we have included many obscure references missed by Hull, as well as the important works of P.A. Lehr

and V.A. Rikter in the USSR. Publications, such as general entomology textbooks, that mention robber flies in general terms, have been largely excluded.

Citations were obtained by several means: (1) Some were obtained by use of biological abstracts and entomology abstracts; however, a great number of the citations did not lend themselves to being abstracted; (2) Lloyd Knutson kindly opened his literature file for our perusal; (3) A great many of the more obscure citations were the result of many years of general literature reviews by the authors; (4) The bibliographies at the end of various papers provided an additional source; (5) A few authors provided additional references. In this regard, special thanks is tendered to Gregory Daniels, who is currently preparing a bibliography, by asilid species, for the Australo-Papuan region.

The authors have taken certain liberties in the preparation of this bibliography. Because of the typographical difficulty in correctly rendering certain titles in the original language, these titles appear in their English translation. In these instances, a notation appears in parenthesis following the citation, indicating the original language. Occasionally, where the original paper contained a title and summary in another language, that other language has been used. In publications other than in English, translated English titles appear in parenthesis following the original title. The senior author should be chastised for any errors of translation. Where there are less than three asilid species mentioned in an individual article, the scientific names of these flies appear in parenthesis following the citation. If the title does not refer directly to the Asilidae, then the pages

upon which the particular reference occurs, are noted following the citation.

It is highly probable that despite diligent search, the authors have missed a few important papers that have appeared in languages other than English. To these scientists, the authors express regrets and ask that these citations be subsequently forwarded to the authors.

REVIEW

Systematics

From 1961 to 1975, numerous investigators contributed to the systematics of robber flies in all standard world regions. These investigators and their regions are as follows: Nearctic: Adisoemarto, Cole, Hull, Martin, Pritchard and Wilcox; Neotropical: Artigas, Bernardi, Carrera, Farr, and Papavero; Palearctic: Abbasion, Lintzen, Adamovic, Castellani, Ionescu, Lehr, Rikhter, Tsacas and Weinberg; Ethiopian: Janssens, Oldroyd, Tsacas and Weinberg; Oriental: Oldroyd; and Australian: Daniels and Paramonov.

As a result of the work of the aforementioned investigators, the systematics of this family are becoming more stabilized, however there are still a variety of opinions with respect to the higher classification of robber flies. Various investigators have classified the approximately 400 genera and subgenera into two (Dasypogoninae, Asilinae), three (the previously mentioned subfamilies plus the Laphriinae), four (three previously mentioned subfamilies plus the Leptogastrinae), five (four previously mentioned subfamilies plus the Megopodinae), or eight (Apocleinae, Asilinae, Dasypogoninae, Laphriinae, Laphystinae, Ommatinae, Stenopogoninae, and Trigonimiminae) subfamilies. Martin

(1968) proposed to elevate the subfamily Leptogastrinae to family status based on certain morphological and behavioral characteristics. Oldroyd (1969) believed the Leptogastrinae should remain a subfamily of Asilidae. Recently Papavero (1973) supported Martin's classification by not including the Leptogastrinae as one of his eight subfamilies. Although the importance of this controversy is recognized, for practical reasons the Leptogastrinae is treated as belonging to the family Asilidae in the present bibliography.

Morphology

The external morphology of adult robber flies has been further elucidated by the systematic studies of the various subfamilies, genera, and species. In addition, Karl (1959) has discussed in detail the morphology of male genitalia of several species.

As is true with most families of Diptera, there is little information concerning the internal morphology of adult robber flies. Recent studies have been concerned primarily with either the reproductive (Artigas 1971; Artigas and Reyes 1975) or digestive systems (Musso 1968, 1969).

Immature Stages

As Knutson (1972) pointed out in his excellent review of publications dealing with the morphology of immatures, "only about 2% of the approximately 5,000 world species are known in any immature stage." Since Knutson's paper, certain obscure publications that contain descriptions of immature stages of additional species have come to light. Most of these descriptions lack figures or are otherwise limited in their potential usage, however. These references are as follows and include a few that were published after 1972:

- Alcock, J. 1974. Observations on the behavior of *Mallophora fautrix* Osten Sacken (Diptera: Asilidae). Pan-Pacific Entomol. 50: 68-72. (Description of egg)
- Cuthbertson, A. 1934. Biological notes on some Diptera in Southern Rhodesia. Proc. & Trans. Rhodesia Sci. Assoc. 33: 32-50. (Description of egg of *Alcimus rubiginosus* Gerst.)
- Cuthbertson, A. 1936. Biological notes on some Diptera of Southern Rhodesia. Occ. pap. Nat. Mus. Southern Rhodesia 5: 46-63. (Description of egg of *Alcimus setifemoratus* Hobby)
- Copello, A. 1922. Biologia de "*Mallophora ruficauda*" (Wied.). Physis 6: 30-42. (Description of egg, larva, pupa, 2 pl.)
- Dekhtiarev, N. S. 1926. Materials on the biology of Asilidae of the Ukraine. Protection of plants in Ukraine, 1926, p. 70-72. (Description of egg and larva of *Satanas gigas* Eversm.) (In Russian)
- Dekhtiarev, N. S. 1929. Notes on the scarabaeid beetles attacking vines in Ukraine. Bull. Entomol. Res. 20: 95-98. (Pupa of *Satanas gigas* illustrated in Fig. 2, Pl. V)
- Dennis, D. S. and R. J. Lavigne. 1976. Ethology of *Efferia varipes* with comments on species coexistence (Diptera: Asilidae). J. Kansas Entomol. Soc. 49: 48-62. (Description of egg, Fig. 4)
- Dennis, D. S. and R. J. Lavigne. 1976. Ethology of *Leptogaster parvoclava* in Wyoming (Diptera: Asilidae). Proc. Entomol. Soc. Washington 78: 208-222. (Description of egg, Fig. 3)
- Dennis, D. S. and R. J. Lavigne. 1976. Oviposition of *Cyrtopogon inversus* (Diptera: Asilidae). Pan-Pacific Entomol. 52: 288-290. (Description of egg, Fig. 2)
- Dennis, D. S. and R. J. Lavigne. 1976. Descriptions and notes on the pupae and pupal cases of ten species of Wyoming robber flies (Diptera: Asilidae). Proc. Entomol. Soc. Washington 78: 277-303. (*Comantella fallai* Back, *Heteropogon wilcoxi* James, *Stenopogon inquinatus* Loew, *Efferia benedicti* (Bromley), *E. frewingi* Wilcox, *E. helenae* (Bromley), *Machimus callidus* (Williston), *Mallophorina guildiana* (Williston), *Proctacanthella cacopiloga* (Hine) and *Proctacanthus micans* Schiner, Fig. 3-43)
- Felt, E. P. 1915. White grubs and June beetles, p. 25-26 In: 29th Rept. of the State of New York entomologist on injurious and other insects of the state of New York. Univ., State of New York Bull. 175. 257 pp. (Description of larva of *Promachus fitchii* Osten Sacken, p. 26)
- Hine, J. S. 1922. Some robber flies in the University of Michigan Museum of Zoology, and the description of a new species. Occ. Pap. Mus. Zool. No. 121. 7 pp. (Description of pupa of *Proctacanthus rufus* Williston)
- Hudson, G. V. 1892. An elementary manual of New Zealand Entomology. London. 128 pp. (Description and illustration of larva and pupa of *Saropogon viduus*, Fig. 4a & B)

- Knutson, L. V. 1976. Key to subfamilies of robber flies based on pupal cases with a description of the pupal case of *Doryclus distendens* (Asilidae: Megapodinae). Proc. Biol. Soc. Washington **88**: 509-514.
- Krivoshenia, N. P. 1973. Larvae and pupae of robber flies from the genus *Laphystia* Lw. (Diptera, Asilidae). Zool. Zhur. **52**(3): 457-459. (Description of larva and pupa of *Laphystia carnea* Herm, Fig. 1-7) (In Russian)
- Krivoshenia, N. P. 1974. Larvae of robber flies (Asilidae, Ctenotini) - root inhabitants of desert plants. Biol. Nauki **17**(4): 16-21. (Description of larvae and pupae of *Ctenota molitrix* Loew, Pl. 3; those of *Ctenota ruficornis* van der Wulp, Pl. 4) (In Russian)
- Krivoshenia, N. P. and B. M. Mamev. 1975. Revision of materials on morphology and ecology of xylophyllic larvae of assassin flies of the Laphriini tribe (Diptera, Asilidae). Vestn. Zool., Kiev, **2**: 66-72. (Key to and descriptions of larvae of species of the genus *Choerades*: *amurensis* Hermann, *fimbriatus* Meigen, *fluvus* Meigen, *igneus* Meigen, *gilvus* L., Pl. 1-3) (In Russian)
- Krivoshenia, N. P. and B. M. Mamev. 1975. Revision of materials on morphology and ecology of xylophilic assassin fly larvae of the tribe Laphriini (Diptera, Asilidae). Communication II. Genus *Laphria* Mg. Vestn. Zool., Kiev, **6**: 46-50. (Key to larvae of 7 species of the genus *Laphria*: *ephippium* Fabricius, *flava* L., *gibbosa* L., *rufa* Rd., *varia* Loew, *vulpina* Meigen, unknown sp. with description, Pl. 1) (In Russian)
- Lavigne, R. J. and D. S. Dennis. 1975. Ethology of *Efferia frewingi* (Diptera: Asilidae). Ann. Entomol. Soc. Amer. **68**: 992-996. (Description of egg, Fig. 3)
- Lehr, P. A. 1966. Biology and taxonomy of robber flies (Diptera, Asilidae) of the genera *Cyrtopogon* Loew and *Grypoptonus* Speiser of Kazakhstan and Central Asia. Collection of Sci. Articles by Grad. Stud. & Res., Kazakh State Univ., Alma-Ata, p. 95-101. (Brief description of egg of *Grypoptonus daimyo*) (In Russian, see translation in Dennis and Lavigne 1976)
- Miller, D., 1924. The "turnip-fly" and its associates. New Zealand J. Agr. **28**: 239-247. (Illustration of larva and pupa of *Saropogon antipodus*, Fig. 7 & 8, p. 244)
- Petch, C. E. and G. H. Hammond. 1925. Parasites of white grubs in southern Quebec. A progress report. Proc. Entomol. Soc. Ontario **1925**: 85-91. (Description of pupa of *Asilus snowi* Hine)
- Riley, C. V. 1870. The Missouri bee-killer - *Asilus missouriensis*, n. sp., p. 121-124 In: Second Annual Report on the noxious, beneficial and other insects of the state of Missouri. (Description of the larva and pupa of *Erax bastardi*)
- Riley, C. V. 1878. Asilid larvae, p. 303-304 In: First Annual Report, U. S. Entomological Commission for the year 1877, relating to the Rocky Mountain locust. Dept. Interior, U. S. Geol. Surv., 477 pp. (Description of larva and pupa of *Erax bastardii*, Fig. 35b & c)

- Scarborough, A. G. and G. Sipes. 1973. The biology of *Leptogaster flavipes* Loew in Maryland (Diptera: Asilidae). Proc. Entomol. Soc. Washington 75: 441-448. (Description of egg, Fig. 2)
- Sweetman, H. 1958. The principles of biological control. Wm. C. Brown Co., Dubuque, Iowa. 560 pp. (Illustration of larva and pupa of *Erax lateralis* Macquart, Fig. 225b & c, p. 259)
- Walker, F. 1840-1842. (Description of pupa of *Laphria nigra*). The entomologist, No. X, Art. XXXV - Varieties by various contributors, No. 41, *Laphria nigra*.
- Wichmann, H. E. 1956. Untersuchungen über *Ips typographus* L. und seine Umwelt-Asilidae, Raubfliegen. Zeit. Angewandte Entomol. 39: 58-62. (Description of egg of *Laphria gilva* L.)
- Wilcox, J. 1935. Description of the male of *Willistonina bilineata* (Williston) together with a new form (Diptera-Asilidae). Pan-Pacific Entomol. 11: 31-34. (Description of pupal case of *Willistonina bilineata nigrofemorata* Wilcox)

Larval Food and Feeding

During the course of the literature search, a few additional observations on the feeding habits of larval asilids, not included in Melin's 1923 or Knutson's 1972 reviews, were encountered. Those observations support the conclusion reached by Knutson that many asilid larvae are predacious on the immature stages of other insects within their habitat. This conclusion is also strongly supported by Musso's radio-isotope experiments (1974), which showed that the asilid larvae he kept in cages were carnivorous.

Knutson (1972) did fail to mention the observations of Wichmann (1956). Wichmann reared larvae of *Laphria gilva* L., which fed as predators on larvae and pupae of *Hylobius abictis* L., on larvae of *Tetropium castaneum* L., and those of *T. fuscum* Fabricius as well as on cocoons of their parasites, *Xorides irrigator* Nees (Ichneumonidae) and *Atanycolus initiator* Nees (Braconidae) in pine stumps. Copello (1922) noted that larvae of *Mallophora*

ruficauda (Wied.) fed on larvae of "melolontoides (white grubs), especially those of *Phyleurus vervex*," while Dekhtiarev (1929) indicated that larvae of *Satanas gigas* feed on larvae of *Polyphylla fullo* L. as well as those of other Scarabaeid species.

Under laboratory conditions, Felt (1915, 29th Rept.) noted that specimens of *Promachus fitchii* Osten Sacken, reared by him, fed as larvae on white grubs. "The most interesting development was the discovery of numerous large Dipterous maggots in 1912. These preyed upon the white grubs and were carried through the season of 1913, and adults were secured in the spring of 1914, showing the species to have, like its host (*Lachnosterna fusca*), a three year life cycle." (Felt 1915, 30th Rept.).

In Peru, Wille (1952) noted that larval asilids attack "gusanos aradores" (white grubs) in the soil, the most common grub being *Ligyryus maimon* Erichs. Howard (1904) recorded that A. A. Eaton of

Seabrook, N. H. "has found the larvae of a robber fly feeding upon white grubs (larvae of *Lachnosterna*)." Larvae of *Promachus vertebratus* Say were reared by Davis (1916) from larvae feeding on white grubs in Wisconsin. Petch and Hammond (1925) noted that asilid larvae they collected fed on white grubs in rearing tins. These were reared and later identified as *Asilus snowi* Hine (Petch and Hammond 1926). In New Zealand, Miller (1924) recorded that the larvae of both *Itamus* (= *Neoitamus*) *varius* Walker and *Saropogon antipodus* Schiner prey upon the larvae of the grass-grub *Odontia zealandica* White (Scarabaeidae).

Myers (1929) recorded "Marlatt as indicating that asilid larvae feed on eggs of the cicada *Magicada septendecim*." This is a questionable record in these authors' opinion. In a later paper (1935), he recorded the larvae of an asilid *Mallophora calidis* (Fabricius) attacking white grubs.

In addition to white grubs, Shurovenkov (1962) recorded robber fly larvae as being "active predators, destroying the larvae of click beetles (*Agriotes sputator* L., *A. gugistanus* Fald., *Selatosomus latus* F.), darkling beetles (*Pedinus femoralis* L., *Blaps halophila* Fisch.) and grain beetles (*Anisopila austriaca* Hrbst., *A. agricola* L.)." The larvae of jewel beetles of the genus *Sphenoptera* (Buprestidae) are fed upon by larvae of *Ctenota molitrix* Loew and *C. ruficornis* van der Wulp in their mutual habitat, the roots of annual saltwort (Krivosheina 1974). The larvae of *Andrenosoma atra* L., *Pogonosoma lugens* Loew, *P. macrocanus* Fabricius and *P. minus* Loew are recorded by Krivosheina and Manaev (1973) as feeding on the larvae of wood wasps and wood borers.

Larval Habitat

It is probable that the larval and pupal stages of most species of robber flies are passed in the soil, but from what is presently known, members of the subfamily Laphriinae, develop in plant roots and decaying stumps and logs, usually within the galleries of wood boring insects.

Larvae of *Laphria gilva* L. develop as predators in pine stumps (Lundbeck 1908, Perris 1870, Wichmann 1956) and specifically in stumps of *Pinus sylvestris* along with those of cerambycids (Quentin 1948). Those of *L. astur* Osten Sacken live in stumps of alder in association with larvae of *Elator cordatus* (Grober 1935). Larvae of *L. marginata* L. develop in borings of lignicolous beetles in rotten oak branches (Skidmore 1966), in pine stumps (Melin 1923), and in spruce stumps together with larvae of *Leptura rubra* L. (Melin 1923, Moucha and Hradsky 1955). The larval stage of *L. thoracica* Fabricius is spent in dead tulip stumps (Greene 1917), as well as in those of apple, *Liriodendron tulipifera*, *Pinus* sp. (Bromley 1934) and chestnut (Rohwer 1912). Melin (1923) recovered the larvae of *L. gibbosa* L. from stumps of pine, those of *L. ephippium* Fabricius from beech stumps, and those of *L. flava* L., from stumps of pine, spruce, birch, and "possibly oak," while Sharp and Lamb (Verrall 1909) reported larvae of the latter species "in the burrows of large wood-feeding longicorn Coleopterous larvae in Scotch Firs (*Pinus sylvestris*)." More recently, Krivosheina and Mamaev (1975b) have recorded the larvae of several species of *Laphria* from the passages of arbovorous insects in various species of trees (*L. ephippium* in *Fagus silvatica*, *Ulmus laevis* and *Pinus silvestris*; *L. gibbosa* L. in *Fraxinus*

mandshurica; *L. rufa* Rd. in *Chosenia macrolepis*; *L. varia* Loew in *Populus tremula*, *P. maximowiczii* and *Alnus* sp.; *L. vulpina* Meigen in *Diceca alni*).

Oldroyd (1939) described the pupa of *Andrenosoma albopilosum* Villeneuve from pupal cases extruding from an old log on a beach. The larvae of *A. bayardi* Seguy and those of *A. atra* L. develop in stumps of *Pinus abattus* (Musso 1967). Champlain and Knull (1923) reared *A. fulvicauda* (Say) from pupal cells of *Chrysobothris femorata* Oliver taken from an oak log.

The larvae of *Andrenosoma atra*, *Pogonosoma lugens*, *P. macroccanum*, and *P. minus* live under bark or in wood populated with the larvae of wasps and borers on which they feed (Krivosheina and Mamaev 1973). The larvae of *Pogonosoma macroccanum* were found by Seguy (1927) in mines of *Dicerca pisama* (Buprestidae) in felled *Cytisus spinosus* and *Pistacia lentiscus*, as well as in the core of oak trunks inhabited by larvae of *Eurythrea austriaca* (Buprestidae). Mulsant and Reveliere (1859) had previously indicated that the larvae of this species lived in tree stumps along with those of *Dicerca pisama*, which served as prey.

It was well established by Poulton (1924) that the larvae of the genus *Hyperechia* "tunnel in wood containing cells of Xylocopid bees" (*H. nigripennis* Wied., *H. consimilis* J. G. Wood, *H. bifasciata* Grunb. and *H. imitator* (Grunb.)). In 1926, Poulton announced that Kunhi Kannan had recovered larvae of *H. xylocopiformis* Walker from tunnels of *Xylocopa tenuiscapa* Westwood in wood, while Tsacas et al. (1970) record the larvae of *H. bomboides* Loew living in the galleries of *Xylocopa*

pubescens (Spin.) and *X. olivacea* F. as ectoparasites.

It has been demonstrated by Krivosheina and Mamaev (1975a) that the larvae of species of *Choerades* develop in the galleries of arborvorous insects in beech (*Fagus* sp.), elm (*Ulmus* sp.), and oak (*Quercus* sp.). The description of the pupa of *Proagonistes austeni* Bromley was based on a pupal case "projecting out of a narrow hole in a tree" (Engel 1932). Champlain and Knull (1923) recorded the rearing of *Nusa fluvicauda* Say from larvae and pupae found in the pupal cells of *Chrysobothris femorata* Oliver in oak (*Quercus* sp.).

Hudson (1892) recorded that in New Zealand the larva of *Saropogon viduus* "inhabits rotten wood feeding on moist powdery portions." Since this genus falls in the subfamily Dasypogoninae, from which no wood-inhabiting species have been recorded, it is probable that the larval identification was erroneous.

Ecology and Behavior

Biological and behavioral studies have been conducted recently by several investigators, including Adamovic (1949-1974), Alcock (1974, 1977), Dennis and Lavigne (1975-1976), Johnson (1976), Lavigne (1963-1975), Lavigne and Dennis (1975), Lavigne and Holland (1969), Lavigne et al. (1976), Lehr (1958-1975), Linsley (1960), Musso (1970-1975), Powell and Stage (1962), Rogers and Lavigne (1972), Scarbrough (1974), and Scarbrough and Sipes (1973). The only comparative behavioral studies have been done by Dennis and Lavigne (1975) and Lavigne and Holland (1969). From these the following comments on robber fly ecology and behavior can be made.

Prey Selection

Adult robber flies are noted primarily for their predacious feeding habits. The majority of robber flies prey upon insects, although some capture spiders and various larvae.

The nature of the prey taken appears to depend on many factors, but the most important may be the composition of the local insect fauna. Lehr (1959, 1964) has shown that changes in the seasonal feeding habits of robber flies often correspond to changes in the composition of the insect fauna. Additionally, according to Adamovic (1963), the abundance of prey varies from year to year, and this may result in variation in the robber fly diet.

As far as specific characteristics of the prey that elicit attack, probably movement and size are the two most important characteristics. Other important characteristics include shape, color, density, flight characteristics other than movement, hardness of prey's exoskeleton, and general behavior of the prey. Dennis et al. (1975) showed that for *Efferia frewingi* Wilcox, different characteristics (i.e., size, shape, color) of models elicited different responses from male and female robber flies.

Each species of robber fly has attributes that, in addition to specific characteristics of the prey, determine the types of prey it can successfully capture. These characteristics include the robber fly's size, level of hunger, speed and manner of flight, powers of vision, structure of mouthparts (in particular the strength of the hypopharynx), place and time of hunting, and skill in capturing prey.

Estimates on the number of prey consumed by asilids have been given by Lavigne and

Pfadt (1966), Dennis and Lavigne (1975, 1976), Lavigne and Dennis (1975), and Lehr (1964, 1972). These estimates have been derived from data that deals with the major period of foraging activity, average feeding and interfeeding times, and the number of robber flies feeding in a given area. Thus, Lehr (1972) hypothesizes that asilids in Russia consume between 9 and 18 prey per day. Dennis and Lavigne (1975) estimated the theoretical maximum number of prey Wyoming robber flies could devour would be between 6 and 35, depending on size of predator and prey.

Foraging Behavior and Prey Capture

Robber flies initiate foraging behavior from either the ground or vegetation or both. In those species that forage from both ground and vegetation, foraging location depends upon the temperature of the soil surface and the species in question. Robber flies typically forage from the ground early in the morning or late in the afternoon when it is cool and from the vegetation when the soil surface is hot.

Robber flies frequently fly up to investigate potential prey without actually making contact. Such behavior is probably necessary because some species can only identify suitable prey at very close range.

Four types of prey capture have been identified for foraging robber flies. These are: (1) attacking and immobilizing prey in the air, (2) attacking prey in the air and immobilizing it at the feeding site or on the ground, (3) attacking and immobilizing prey on the ground or vegetation, and (4) attacking prey on the ground or vegetation and immobilizing it in flight, frequently while hovering.

Subduing and Extra-Intestinal Digestion of Prey

Once prey are captured and the robber fly has inserted its hypopharynx, the prey is subdued almost instantly. Kahan (1964) demonstrated the presence of a venom in asilid salivary glands that was toxic to mice, locusts, and *Paramecia* in varying amounts. Kahan's results also indicated that proteolytic activity is present in the secretion of the salivary glands and stomach juices, but not in the secretion of the labial glands. Musso (1968) also found that labial gland secretions are not involved in digestion of the prey's tissues. Digestion occurs when stomach digestive fluids and enzymes secreted by the salivary glands are injected into the body of the prey. The digested material is then pumped back into the stomach of the predator.

Lavigne and Holland (1969) dissected several prey after the asilids had completed feeding. They found that the muscles within the head and those holding the internal organs in place were completely dissolved or in a state of partial disintegration. The muscles of the femur were partially disintegrated, but those within the tibia were usually intact. The nervous system (including the brain), fat bodies, ovaries and testes, were usually missing, but the digestive system was always intact.

Prey Manipulation

During feeding, the prey may be manipulated one or more times, presumably, in order to more thoroughly digest the tissues. The method(s) and number(s) of times the prey are manipulated depends upon the prey size and shape. Large prey are frequently manipulated while the asilid lies on the ground and uses all six tarsi or just the

fore tarsi. Smaller prey are often manipulated with all six tarsi, while the asilid is hovering above the ground or vegetation. Hovering and manipulation of prey is particularly common in the subfamily Asilinae. If the hypopharynx is initially inserted into the prey's head, the asilid may manipulate the prey and reinsert its hypopharynx into the prey's thorax, and then into its abdomen, depending on the shape of the prey. Prey, such as Hymenoptera have narrow waists, are usually manipulated more often than prey, such as Orthoptera, which are tubular in shape. The amount of manipulation apparently is related to the ease with which the asilid's digestive fluids move through the body of the prey. Tubular bodies allow these fluids to pass easily between major body regions.

The sequence of manipulating prey may be divided into three phases: (1) subduing and positioning the prey so it can be immobilized, (2) moving the prey so its internal tissues can be more fully utilized, and (3) discarding the prey at the conclusion of feeding.

At the conclusion of feeding, the prey is discarded by either dropping it in flight or by pushing it off of the hypopharynx with the tarsi or through action of the mouthparts at the feeding site (Dennis and Lavigne 1975, Lavigne and Holland 1969, Rogers and Lavigne 1972).

Courtship

Prior to mating, some species of asilids exhibit courtship behavior. Patterns of courtship behavior, not including male searching flights for females, have evolved in at least nine genera of North American asilids: *Diogmites*, *Stichopogon* (Lavigne and Holland 1969); *Promachus* (Hull 1942,

Lavigne and Holland 1969); *Cryptopogon* (Hull 1962, Lavallo 1970, Lavigne 1970, Lavigne and Holland 1969, Powell 1969, Wilcox and Martin 1936); *Heteropogon* (Alcock 1977, Hull 1962, Lavigne 1970, Lavigne and Holland 1969); *Ablautus* (Lavigne 1972); *Holcocephala* (Johnson 1976), *Proctacanthella* and *Holopogon* (Dennis and Lavigne 1975). According to Lehr (1961, 1962, 1964, 1972) at least five genera in Russia, *Grypoctonus*, *Holopogon*, *Rhadinus*, *Saropogon*, and *Selidopogon*, exhibit this behavior. Additionally, *Dioctria* have been observed exhibiting courtship behavior in Sweden (Melin 1923) and Russia (Lehr 1965), *Pycnopogon* in Germany (Muhlenberg 1974), and *Promachus* in Australia (Daniels 1976).

Robber flies exhibit courtship behavior both on the surface of the ground and in the air. Types of courtship vary from that of *Proctacanthella cacopiloga* (Hine) where males walk along the ground and wave their fore tarsi (Dennis and Lavigne 1975) to more complex types such as the aerial oscillations and waving of the fore tarsi exhibited by males of *Heteropogon wilcoxi* James (Lavigne and Holland 1969). Lavigne (In Press) is currently reviewing courtship behavior in the Asilidae.

Mating

Robber flies usually assume one of two different positions while mating. The male and female are either facing in the same direction with the male remaining on top of the female (i.e., the male over female position), or they face opposite directions with their abdomens forming a more or less straight line (i.e., the tail-to-tail position). The latter position is modified in the case of *Heteropogon wilcoxi* and *H. maculinervis*

so that the male is at a 30 degree angle to the female (Lavigne and Holland 1969; Lavigne 1970). Among the *Leptogaster*, the female grasps the vegetation in her ordinary resting position, vertical to the ground, while the male either hangs below in the air or else supports himself below the female with his dorsum facing the same direction as the female's venter (Dennis and Lavigne 1976; Scarbrough and Sipes 1973). Most species of asilids mate during the daylight hours. According to Lehr (1959, 1964) and Newkirk (1963), some species, in particular those in the desert, mate during the night.

In field experiments using marked *Promachus leontochlaenus* Loew males and females, Lehr (1958) was able to establish that multiple mating by both sexes occurs. Males of *Promachus dimidiatus* (Curran) mate with more than one female (Lavigne and Holland 1969), while multiple matings for both sexes have been recorded for *Efferia frewingi* Wilcox (Lavigne and Dennis 1975).

Oviposition and Eggs

Robber flies begin to oviposit about 10 to 11 days after the adults emerge from the pupal case. There is considerable diversity in the methods and specific sites of oviposition, but no matter where oviposition occurs, the ovipositors, except in *Leptogaster*, are modified for positioning the eggs in some type of substrate and covering or protecting them (Melin 1923). Those species, such as *Diogmites* and *Stenopogon* sp., that oviposit in the ground usually have ovipositors equipped with spines. These spines aid the robber flies in digging the ovipositor into the ground and in sweeping soil over the eggs upon completion of oviposition (Lavigne and Holland 1969,

Dennis and Lavigne 1975). Species such as *Promachus*, *Machimus*, and many species of *Efferia*, which oviposit on or in vegetation, have long laterally flattened ovipositors that are used to penetrate crevices in the vegetation. Among the *Leptogaster*, the ovipositor is unmodified and females drop their eggs while resting on vegetation or while in flight (Melin 1923, Dennis and Lavigne 1976, Scarbrough and Sipes 1973).

The females of some species, such as *Mallophora fautrix bromleyi* Curran (Alcock 1974), *Mallophorina pulchra* Pritchard, *M. frustra* Pritchard (Linsley 1960), and *M. guildinana* (Williston) (Dennis and Lavigne 1975) lay large numbers of eggs in clusters covered with a soft chalky-white material and deposited on vertical dead stems of plants.

The eggs of robber flies are quite variable in size and shape. Their size is partly governed by the number laid. In general, the more eggs that are laid, the smaller they are. In *Leptogaster* (Dennis and Lavigne 1976, Lavigne 1963, Skidmore 1966), *Dioctria*, *Laphria*, and *Lasiopogon* (Melin 1923), the eggs are round or broadly oval. The eggs of most other asilid species are elongate.

The number of eggs deposited per oviposition varies considerably from species to species. In some species, only one or a few eggs are deposited in any one site, but females may oviposit several times.

Mimicry

Numerous investigators have observed robber flies mimicking bees in all parts of the world. According to Hull (1962), robber flies that exhibit mimicry are more common in hot, humid latitudes and may be absent in many temperate areas.

In the past, many investigators believed that robber flies exhibited aggressive mimicry, but Rettenmeyer (1970) states that no indisputable cases of aggressive mimicry among arthropods are known and concludes that robber flies exhibit Batesian rather than aggressive mimicry. This conclusion also was reached by Evans and Eberhard (1970).

According to advocates of Batesian mimicry, insects that lack protective devices, such as robber flies, have adapted by evolving color patterns that mimic those of stinging Hymenoptera. Potential robber fly predators, such as toads, quickly learn to associate these warning color patterns with stinging hymenopteran models after one error of judgment (Brower et al. 1960). Waldbauer and Sheldon (1971) maintain that for *Laphria flavicollis* Say and *L. thoracica* Fab., insectivorous birds are the main selective agents that determine the morphology and behavior of the mimics.

Predators, Parasites, and Associates of Asilidae

Asilids are attacked by other insects, such as tiger beetles, biting midges (Colyer and Hammond 1951), wasps (e.g. *Vespa* sp.) (Bromley 1914, 1931); praying mantids (Harshbarger 1894, Hull 1962); some Hemiptera and Mecoptera (Newkirk 1963); dragonflies (Adamovic 1963); and other asilids (Adamovic 1963, Bromley 1914, 1937, Brues 1946, Cockerell 1894, Goslin 1954, Hull 1962, Lavigne 1964, Lavigne and Holland 1969, Rogers and Lavigne 1972).

Adult female wasps of several genera sting and paralyze adult asilids for food for their wasp larvae (*Metacrabro*: Hamm and Richards 1926; *Bembix*: Evans 1957, 1960,

1966, 1970, 1976, Evans and Matthews 1973; *Glenostictia*: Evans 1966; *Steniolia*: Evans and Gillaspay 1964; *Rubrica*: Brethes 1902; *Zyzyx*: Janvier 1925, 1928).

Asilids also may be subject to attack by entomophagous fungi and mites (Colyer and Hammond, 1951); spiders (Adamovic 1963, Cole 1958, Colyer and Hammond 1951, Dennis and Lavigne 1975, Lavigne 1972, Lehr 1958, Newkirk 1963, Schmid 1969); birds (Adamovic 1963, Colyer, and Hammond 1951, McAtee 1932, Reid 1955, Wichmann 1956, Willis 1967), and lizards (Adamovic 1963, Hull 1962, Knowlton 1934-1953).

In addition to the above, robber flies are frequently cannibalistic (Alex, 1947; Bromley, 1914; Goslin 1954; Hobby 1931, 1935; Hull 1962; Iwata and Hagatomi 1962; Dennis and Lavigne 1975-1976; Lavigne 1964; Lavigne and Holland 1969; Lehr 1961; Rogers and Lavigne 1972). Lehr (1961) believes that cannibalism enables asilids to survive shortages of food, particularly after long periods of inclement weather.

Only four examples of parasitism have been noted. Wichmann (1956) records dissecting mermithids from adult specimens of both *Laphria flava* and *L. gilva*. *Anomalon reticulatum* (Cresson) (Ichneumonidae) was reared from an unknown species of asilid larva recovered from short grass rangeland soil (Lavigne and Pfadt 1965). An encyrtid parasitoid, *Oobius striatus* Annecke, was reared by R. H. Watmough from the eggs of *Hyperechia marshalli* (Austen), which were heavily parasitized (Annecke 1967, Watmough 1974). A second egg parasite, *Phanurus* sp., has been reared by Kinoshita (1940) in Japan who reported a 9.5% parasitism rate on eggs of *Promachus yesonicus* Bigot.

Some asilids may be accompanied by small flies of the genus *Desmometopa* (Diptera: Milichiidae), which attach themselves to the asilids' thorax and feed upon the prey (Colyer and Hammond, 1951; Oldroyd, 1964).

Lavigne and Holland (1969) observed *Olcella parva* (Ad.) (Chloropidae) and *Milichia* sp. (Milichiidae) feeding on the contents of a pentatomid oozing around the beak of *Promachus dimidiatus* (Curran) that was engaged in feeding.

Daily Rhythm of Activity

Robber flies tend to exhibit a daily or diurnal rhythm of activity. According to Dennis and Lavigne (1975, 1976), Musso (1970, 1972), Lehr (1961, 1971, 1973), in each population of robber flies, particular activities occur at certain times or time periods of the day. Additionally as the frequency of occurrence of one activity increases, another decreases.

During the main period of activity, numerous environmental variables affect a robber fly's behavior, but temperature appears to be one of the most important. In general, extreme conditions, such as high winds and cloudy weather, decrease the activities (i.e., foraging and feeding, mating, oviposition) in which robber flies engage.

Robber flies have developed various morphological and behavioral adaptations by which they continually adjust to environmental conditions (Lehr 1962, 1964, 1969) such as pressuring their bodies against warm substrates and the apparent use of super cooling by species belonging to the genera *Eucyrtopogon* and *Comantella*, which overwinter as adults.

Grooming

Robber fly grooming behavior has been described by Dennis and Lavigne (1975, 1976). Grooming behavior appears to be quite similar in all subfamilies of the Asilidae found in temperate North America. With all species studied by these investigators, the legs are used to groom a specific area of a robber fly's body in response to specific stimulation or in association with other sequences of behavior, such as feeding, mating, and oviposition (Scarborough and Sipes 1973).

Economic Status of Robber Flies

There is considerable disagreement with respect to the economic status of robber flies. The larvae are generally considered to be beneficial because of the growing body of evidence that they feed on the immature forms of economic pests (Shurovenkov 1962; see also previous discussion on larval food and feeding). Adults have been considered beneficial because of their predation of injurious insects (beet webworm - Shurovenkov 1962; click beetles - Shurovenkov 1959; Colorado potato beetle - Riley 1872; scarabaeids - Pratt 1943; house fly - Shurovenkov 1962; range caterpillar - Ainslie 1910; harmful forest insects - Moucha 1952, Schmid 1969, Schweiger 1950, Wichmann 1956; and

grasshoppers - Greathead 1963, 1966, Leonide & Leonide 1969).

On the other hand, adults have been considered to be detrimental to man's activities by preying on honey bees (Adamovic 1949, 1950, 1963a, 1972; Benton 1895; Brugger 1935; Cook 1894; Copello 1927, 1942; Insinger 1940; Johnson 1954; Lehr 1960; Liston 1875; Ma 1949; Parker 1878; Riley 1869; Rinaldi et al. 1971; Roff & Brimblecomb 1953; Smith 1896; Sonne 1875; Stuart & Bessey 1875; and Toumanoff 1939) and other useful insects, such as parasitic Hymenoptera (Adamovic 1963b, Poulton 1906). Additionally nonswarming of bees has been attributed to robber fly activity (Hull 1962), although this type of effect is highly unlikely.

According to Lehr (1964), there is the possibility that asilids could be used eventually as biological control agents in an integrated pest control program.

Phylogeny

A tentative phylogeny for the Asilidae was proposed by Hardy (1934). A more recent and more logical phylogeny was constructed by Lehr (1969) based on an ecological and morphological analysis of robber fly data collected mostly in the USSR.

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