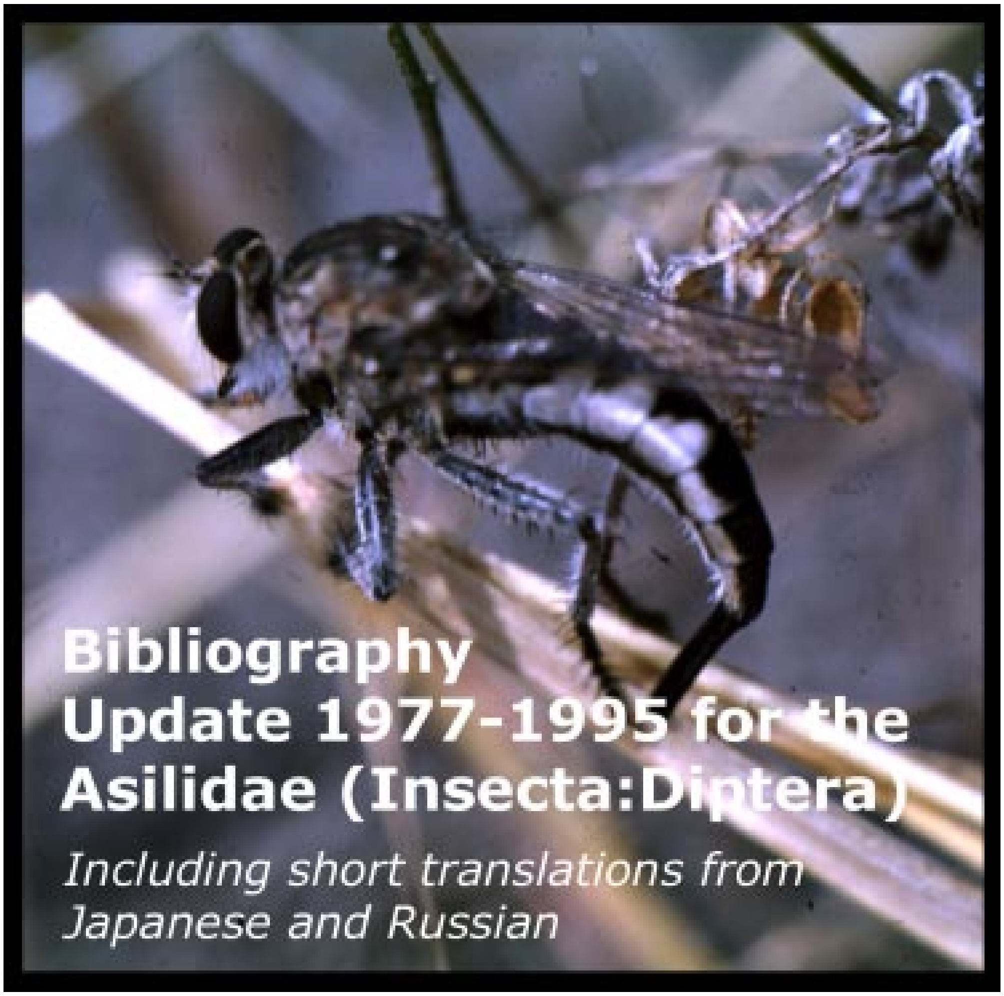

Bibliography Update 1977-1995 for the Asilidae (Insecta:Diptera)

Including short translations from Japanese and Russian

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Introduction

Twenty years ago, Lavigne et al. (1978) published the first update for robber fly (Diptera: Asilidae) literature (1956-1976). Their update included the first complete review of recent literature since that produced by Hull (1962) in the second volume of his work entitled *"Robber flies of the world."* In recent years, a significant number of papers relating to various aspects of asilid taxonomy and behavior have been published. Because of the number of papers published over 19 years and the increasing interest in robber flies, it was felt that it was again time to update the literature.

Advances in taxonomy have been striking with large numbers of new species described. Since Lavigne's last update, more than 200 papers were published on the subject, in addition to 14 catalogs. The female spermatheca as a taxonomic tool has been increasingly utilized by taxonomists, such as Theodor (1976), Bullington and Lavigne (1984a and b), Nagatomi and Nagatomi (1989), and Artigas and Papavero (1988-1995). The taxonomy of South American robber flies has been admirably addressed by Artigas and Papavero (1988-1995), while that of Africa has been admirably covered by Londt (1977-1995). Londt (1994d) has introduced the innovation (following a description of a genus) of using couplets in a key, plus male genitalic illustrations, to serve as the description of a species. Quite recently, Yeates (1994) has reclassified the position of the Asilidae in the taxonomic hierarchy in relation to Bombyliidae, Apioceridae, and Mydaidae, while Artigas and Papavero (1988-1995) have increased the number of subfamilies of the Asilidae from the generally recognized five to eight. Papers extending our knowledge of the distribution of robber flies, not counting the numerous taxonomic treatises, numbered 130.

Morphology has been covered in numerous taxonomic papers, while physiology has been addressed in six papers. Of particular importance, the ultrastructure of asilid venom glands was illustrated (Donadey and Musso, 1977), while the toxicity of the venom was covered in a later paper by Musso (1978). Immature stages have been discussed or referred to in at least 20 papers, the most important being Musso's (1981), which dealt with the development and morphology of immature stages of some asilid species, and Dennis and Knutson's (1988) describing the pupal cases of some South American robber flies. Investigations have begun on the chorionic microstructure of asilid eggs as evidenced by the papers of Lawson and Lavigne (1984) and Castillo et al. (1994).

In the area of asilid biology and behavior, numerous papers (N = 62) have appeared such as those by Lavigne and cohorts (1976-1994). Some innovative techniques have been utilized in recent years, particularly those of O'Neill and cohorts (1990-1992), Tricca and Trujillo-Cenoz (1980), Scarbrough (1981c), Shelly (1985b, 1986 a and b), and Hastings et al. (1994). Papers dealing strictly with predation numbered 61, although predatory activity also was covered in a number of ethological papers. Courtship of several additional species has been described: *Cerotainia albipilosa* Curran (Scarbrough 1978b), *Cyrtopogon montanus wilcoxi* James (Bullington and Lavigne 1992), *Glaphyropyga dryas* Fisher and Hespenheide (Fisher and Hespenheide 1982), *Heteropogon stonei* Wilcox (Alcock 1977), *Holopogon seniculus* Loew (Lavigne et al. 1993), *Mallophora ruficauda* Wiedemann (Tricca and Trujillo-Cenoz 1980), *M. minos* (Wiedemann) [as *schwarzi* Curran (Shelly and Weinberger 1981)], *M. schwarzi* Curran (Teschner 1989), *Nannocyrtopogon neoculatus* Wilcox and Martin (Hespenheide 1978), *Promachus albifacies* Williston (Hastings et al. 1994) and *P. interponens* Walker (Daniels 1976). As Fisher and Hespenheide (1992) noted, they have "accumulated extensive unpublished data on courtship behavior of other species, especially of smaller species in the genera *Atractia*, *Oidardis*, *Cerotainia,* and *Eumecosoma*." However, much work on reproductive behavior remains to be done.

Biodiversity, an emerging discipline, was discussed in a paper by Scarbrough and Kuhar (1992) as it related to robber flies. Bernon (1981) investigated asilid species diversity associated with the cow dung community in South Africa. Ecological comparisons were covered for a few species in Mexico by Dennis et al. (1986) and in Panama by Shelly (1985b). A potential ecological classification system for Afrotropical asilids was recently proposed by Londt (1994c), based in part on work by Lehr (1979d - in Russian) in which he amplified an ecological classification he had previously proposed (Lehr 1967, 1969 - in English).

Robber flies have their own set of enemies, which include tiger beetles, praying mantids, dragonflies, several kinds of wasps, and other asilids as noted by Lavigne et al. (1978). Wasp specialists have even named a sphecid wasp, *Gastrosericus asilivorus* Pulawski, based on its habit of stocking its burrow with two species of *Xenomyza* (Krombein and Pulawski, 1986).

The occurrence of robber flies in amber has been documented by Larsson (1978, Baltic amber), Schumann (1984, Saxon amber), and Scarbrough and Poinar (1992, Eocene).

As was the practice in the previous update, papers published before 1978 are included in this bibliography as they were published in earlier years, but were missed by both Hull (1962) and Lavigne et al. (1978). Unless otherwise noted, papers are written in English. In most cases, so as to expedite the understanding of content of papers, English translations of the titles, written in other languages, have been included. New species are noted in boldface at the end of a reference when only one or a few new species were described within the paper. In order to relieve readers of the necessity of searching through obscure papers for a particular genus or species, an attempt has been made, where copies of papers were available, to note the species covered in the cited article. For other obscure papers dealing with taxonomy and distribution (especially those written in Japanese), a listing of species may occur in boldface at the end of a citation.

Many readers will have ready access to the Internet. Consequently, they should be made aware that Fritz Geller-Grimm, of Frankfurt, Germany, is in the process of compiling a complete listing of the literature citations for the Asilidae. Readers may download the listing in its present form from his Web page: http://www.geller-grimm.de.

Because a number of papers are not readily available and have been published in languages for which translations are not currently offered, translations of a few obscure short articles from Japanese and Russian (which were of particular interest to the author and hopefully will be to the reader) have been included in this monograph. In the interest of space, the literature citations attached to those papers have not been included as they are in the native language and contain numerous misspellings. Readers are, therefore, referred to the original papers for those citations. Additionally, in the long Russian paper, tables and figures have not been included because of the complexity of the tables and the poor quality of the figures. Additional article translations from Russian, German and Spanish dealing with robber fly biology and/or portions of taxonomic works dealing with robber fly biology are in the process of being published on the Internet at: http://www.geller-grimm.de/data.htm.

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Zahradník, J. and J. Hobrlandtova. 1981. Náš hmyz [Our insects]. Albatros, Praha. 444 pp. (In Czech) [**Asilus crabroniformis**, **Dioctria atricapilla**, **Laphria flava**, **Laphria gibbosa**]

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Additionally, note needs to be made of the recent bibliographies updating Czechoslovakian Diptera citations provided to me by Mr. Bosák. There have been two previous bibliographies and these additional two volumes continue the excellent tradition. A directory of Czechoslovak dipterists, including their specialities, is appended to the 1998 volume.

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Vaňhara, J. and R. Rozkošný. 1997. Czech and slovak dipterological literature 1986-1995. Masaryk University, Brno, Czech Republic. 179 pp.

Translation from Japanese by Tetsuaki Nihashi* and Robert Lavigne

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Kuribayashi, Den. 1954. **[On the prey of *Promachus yesonicus* Bigot]**. New Entomologist. The Entomological Society of Shinshu **3**: 38-41. (In Japanese)

On the prey of *Promachus yesonicus* BIGOT

The majority of insects attacked by *Promachus yesonicus* BIGOT are insects injurious to agriculture. The author describes those species in this paper.

I Introduction

If the number of prey a predatory insect kills in its life is small, the predator cannot be a useful insect. Predatory robber flies prey upon both harmful and useful insects. Therefore, the investigation of feeding behavior is important to decide if a predator is useful or not. But this is not a matter that can be decided easily, because in such investigations much time is wasted looking for these harmful insects, and research on their period of activity is required. This is not a matter to be decided hastily either. The writer has been investigating the prey and predation patterns of three predatory flies which belong to the genera, *Promachus yesonicus* BIGOT, *Astochia virgalipes* COQUILLETT, and *Laphria isshirii* MATSUMURA.

Among these three, *Promachus yesonicus* is the most commonly distributed in every district, and the information collected on this species is greater than that for others. Herein, prey catching behavior and prey of these species will be presented.

II Investigative Method

This was carried out by setting the area of investigation as follows:

Area 1	Rice paddy and upland soil field
Area 2	Forest and grove, including fields of crops close to mountains
Area 3	Highlands, cultivated land, and grassland on the highland and tree nurseries

Area 1 and 2 are in Shokushina County in Nagano Prefecture. The highland is in the Sugadaira Highland and the Shikasawa district in Gunma Prefecture.

III Results of the Investigation

A. Species that were preyed upon in Area 1

1) *Halyomorpha picus* FABRICIUS

This species is often preyed upon. The remains of the prey lacked the head and were attacked on the back; most often the bite was made at the neck dorsally before the thorax.

2) *Nazara antennata* SCOTT

This species was preyed upon as often as the one mentioned above. Since the point of attack was very similar, it seems to be the same type of predator.

3) *Camponotus herculeanus japonicus* MAYR

This species was rarely preyed upon and was gathered only twice in this investigation. The point of attack is the same on both collected specimens; the head was missing and no point of attack was found in any other part of the body. Therefore, the predator must be the type that bites in the neck.

4) *Minera costata* HOPE

This species was often found to be preyed upon. The point of attack is most often dorsal in the thorax. The bite was made on the back. Injuries resulting from the bite were found on the side of the abdomen, but this type was less common than the former type of attack.

5) *Popillia japonica* NEWMAN

Fewer prey were collected than for the previous species. Injury was noted on the side of the abdomen.

6) *Eugnathus distinctus* ROELOFS

This species was preyed upon in soybean fields. The head was lost, so the predator must be the type that attacks the neck and the thorax.

7) Hamushi (leaf worms)

These insects were preyed upon quite often, but the head and thorax were both lost and the insect could not be identified exactly. Types of injury were varied.

8) Others

Small insects were preyed upon also. The bodies of these insects were broken and it was impossible to identify them exactly.

B. Species that were preyed upon in Area 2

1) *Tanna iaponesis* DISTANT

This prey was found on the road. Because *Promachus yesonicus* is not strong enough to carry this prey, the predator seemed to have attacked the prey in the air and dropped to the road where it bit the cicada. When this prey was collected, it was still alive. The point of attack was at the joint of the right wing. This proves that this predator preys upon insects larger than itself.

2) *Popillia japonica* NEWMAN

This species was most often collected in cultivated fields in the mountains. The site of injury is the same as that in Area 1.

3) *Phyllopertha orientalis* WATERHOUSE

This species is very commonly preyed upon. When collected, some had injuries at the intersegmental membrane dorsally, and others were injured along the segmental membrane and the back.

4) Hamushi (leaf worms) and others

Leaf worms and other small insects were found attacked just as described for those in Area 1. Identification was impossible. The number attacked was very large.

C. Species that were preyed upon in Area 3

1) *Eristalomyia tenax* LINNÉ

This species is very commonly preyed upon. The site of injuries is not consistent. *Astochia virgatipes* also preys upon this species quite frequently. *Laphria isshirii* often preys upon this, though collection of this kind was not as common at this time. The fact that these three predators prey upon this insect suggests that *Eristalomyia tenax* must be the main prey in the highlands.

2) *Phyllopertha orientalis* WATERHOUSE

Collection of this species was less than that in Area 2. Most often the species was found in the forest. The sites of attack were not so different from those of Area 2.

3) *Mimela costata* HOPE

Collection was less compared with that for Area 1. Injury sites were on the side of the abdomen and about the same as those for Area 1.

4) Others

Small insects were found to be preyed upon in large numbers, but bodies were broken and identification was impossible.

IV Summary of the Investigation

The insects preyed upon were as shown in Chart l.

Chart 1 Insects Preyed Upon

Area 1	*Halyomorpha picus, Nezara antennata, Camponotus herculeanus, Mimera costata, Popillia japanica, Eugnathus distinctus* Leaf worms, other unidentified insects
Area 2	*Tanna isponensis, Popillia japonica, Phyllopertha orientalis* Other unidentified insects
Area 3	*Eristalomyia tenax, Phyllopertha orientallis, Minera costata* Other unidentified insects

V Conclusions

This investigation focused on insects preyed upon but did not involve statistics for time of day of predator/prey, weekly activity, or length of the activity period. Based on the results of this investigation, the following conclusions can be made:

1) A great majority of the insects upon which *Promachus yesonicus* preyed are harmful to agriculture. Therefore this species is a very useful insect.

2) *Promachus yesonicus* does not seem to eat dead insects. It is worthy of notice that many of the prey are insects that do harm as adults.

3) It is very significant that this useful insect is widely distributed in every district in large numbers. The investigative area was limited and the collection was not large, but we will continue the investigation to provide better supplemental information. I hope this report will help to further investigations on this predatory insect.

Aoki, Akira. 1949. **[On some alpine Asilidae from Formosa and Japan]**. Kontyû **17**(6): 59-60. (In Japanese)

On some alpine Asilidae from Formosa and Japan

Up to this time, the alpine robber fly has not been given very much attention. These insects have escaped our attention because the number of species is small. I will report here on the four species I have found in Formosa and Japan. Asilinae are classified into the four Palaearctic subfamilies as follows:

Leptogastrinae

Asilinae.................*Neoitamus nokoensis* Aoki
Neoitamus n. sp.

Dasypogoninae............*Cyrtopogon* n. sp.

Lasiopogon cinctus Fab.
Laphriinae

Two species of *Neoitamus* inhabited a small area in the mountain across from the Karen Port when I accompanied Professor Isshiki of the University of Formosa in June 1943. They are smaller than those eight species living on the lowland plains, and they resemble *Neoitamus angusticornis* Loew, which lives in Japan proper. The body is black with yellow hair along the distal edges of abdominal segments. The legs are black. White hair-like bristles on the male's and female's 6th abdominal segment, followed on the female by a slim shiny ovipositor, are characteristic of this species.

Also collected with this species was *Neoitamus* n. sp. The distal edges of abdominal segments of the new species have black bristles. Male tibia of front-mid legs have patches of white hair growing outward like a comb, and the abdomen has a beautiful silver blue color. These characters are found only in the male. The female has not been discovered yet.

A Japanese indigenous species was found on rocks near the top of the Mesu-Akan Peak in the Akan National Park in Hokkaido in June this year. It is *Crytopogon* n. sp. and resembles *C. nikkoensis* Mats.; four species of the same genus are already-known, but this new species is much smaller in size, and there are no spots on the wings. It is identified by the yellow color of the third joint of antenna and of the tarsus.

The last species, *Lasiopogon cinctus* Fab, is indigenous to Europe. Dr. Matumura explains in the *Illustrated Book of Japanese Insects* that this species inhabits Hokkaido, the Japanese mainland and Europe. It is said to be common in the Nikko district, but we haven't seen any in those districts in Japan yet.

Kimura, Teruo. 1958. **[Miscellaneous notes on Asilidae of Japan (Diptera) (I)]**. Akitu **7**: 55-56. (In Japanese)

Miscellaneous notes on Asilidae of Japan (Diptera) (I)

1. *Eutolmus rufibarbis* (Meigen)

   1820 *Asilus rufibarbis* Meigen, Syst.

   Beachreib.II, 311.6. Kami-Kuroda (1F, 31/VIII, 1939), Sobuya (1M 1F, 18/VIII, 1940). Hanase Pass (3M, 23/VI, 1940; 2M 1F, 24/VII, 1949), Kanigahata (2F, 29/VII, 1940), Ashio (1M 2F, 26/VII, 1940; 1M,5/IX, 1940). All in Kyoto-fu, collected by Teruo Kimura.

Of the *Eutolmus* genus, only one species, *E. brevistylus* Coquillett (1898) has been known previously. With the addition of *E. rufibarbis* Meigen, we now have two species in Japan. This is not a rare species in the Kitayama mountain district in Kyoto, as shown in the above note. This species was first reported in Europe, but Engel (1933) recorded the same species gathered by Svan Hedin's expedition in the northeastern Sisen District and the eastern Kanshuku District in China. The male has a remarkable projection in the center of the terminal abdominal segment, which is very common with other *Machimus* species. The European species has yellow and black hair mixed on the projection, and the Chinese one has only black hair (Engel). The species collected in Japan has the same yellow and black hair mix as that of the European species. Also, in Japan there is another species that can be distinguished by antennal differences. I will report on this latter species some other time.

2. *Epholkiolaphria gilva* (Linné)

   1758 *Laphria gilva* Linné, Syst. Natur. Ed. X, 605, 6.

   Teizankei (1M 2F, 15/IX, 1945, collected by Katsuji Tsuneki)

This species is distributed widely in Europe, Siberia, North America, and other needle-leaf tree belts in the Northern Hemisphere. It is natural to find this in Japan. *Laphria sapporensis* Matsumura might be a synonym of this species, and in Matsumura's description a very characteristic form of the male copulatory organ is illustrated. Compared with the European species, the Japanese one has only a little pale golden hair on the abdomen.

3. *E. dispar* (Coquillett)

   1808 *Laphria dispar* Coquillett, Proc. U.S. Nat. Mus. 316.

   Kaga Hakusan, Sugitani (1M, 1/VIII, 1956 collected by Katsuji Tsuncki)

This species was recorded by Coquillett with *Laphria mitsukurii* and others from Japan. Since then, there has been no other record from Japan. In August of this year, two males and one female were collected in the Northern Alps of Japan. They do not have the shiny abdomen described in Coquillett's paper, but do have a dark black color. According to the original description, this species has white hair dorsally on the thorax and abdomen. This is a singularity of Japanese species that is not found among other species in the genus. But the species Muramatsu describes as *L. dispar* Coquillett "Kuroishi Abu", with an illustration in the *Illustrated Books of Japanese Insects*, has "black hair on the shiny black abdomen." This is not true for *L. dispar*, but for a species close to *L. mitsukurii* or *mitsukurii* itself. I suspect the reason for this error is that both species were reported on the same page of Coquillett's report. I had been looking for the real *L. dispar* for many years and finally found it in the samples sent by Mr. Katsuji Tauneki. At that point we confirmed the identity of the real *L. dispar* and decided to change the original Japanese name into “Shirohoso-ishiabu.”

4. *E. amurensis* (Hermann) “Momobuto hoso ishiabu” (new name)

   1914 *Laphria amurensis* Hermann, Entom. Mitt. III Nr. 3, 92.

   Oofuse, Kyoto-Fu (1M, 19/VII 1937, gathered by Teruo Kimura)

This species was first recorded from the Amur and Ussuri River district in Japan. The upper half of the hair on the mystax is black; the lower half is white. Wings are light brown, except for the basal part. The abdominal segments expand one by one. Thick, golden short hair occurs dorsally on the abdomen.

5. *E. fulva* (Meigen) “Kinmou hoso ishiabu” (new name)

   1801 *Laphria fulva* Meigen, Klassif. I, 264, 9.

   Oodaigahara Mt., Nara (1F, 17/VIII, 1959, collected by Masaaki Takcuchi)

This species is well-known in Europe and also there was a record from Shisen, China. The body is covered with thick, short golden hair. This is the first record for Japan.

Each of the above five species inhabits flowering fields on high mountains, but no physical adaption for the high mountain habitat has been noted. Generally, their flight is slow. The length of each species is less than 10mm.

Two species of robber flies from Korea

Among the robber fly specimens that Tsuneki Katsuji collected and presented to me two years ago, I found two Korean species. I appreciate that Tsuneki Katsuji gave these important specimens to me.

1. *Epholkiolaphria ogumae* (Matsumura) (1911) redlegged robber fly

   Ham north White rock, South snow range (1 male,19/VIII,1943)

   Whitehead mountain, Three pond river pool (1 male, 4/VIII,1943)

This species has been reported from Saghalien Island. Dorsally, the abdomen has short hair with irregular spots. This character distinguishes it from other species.

2. *Cyrtopogon* (s.str.) *centralis* Loew (1851)

   Shoyoran (1 male, 29/IV,1942, 3 males,14/V,1942)

This species has been previously known from Siberia. Five brown spots occur in the center of the wing. This is a very pretty species.

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Lehr, P.A. 1958. Biologiya ktyrya pitayushtshegosya saranchovymi **[The biology of a robber fly feeding on acridids]**. Doklady Kazakhstan Akademii selskokhoz. Nauk (Alma-Ata) 3: 16-23. (In Russian)

The biology of a robber fly feeding on acridids

The robber fly, *Stenopogon porcus* Loew (Diptera, Asilidae), is a specialized predator. The larvae of harmful locusts makes up more than 75% of its food. Data on the biology of the adult robber fly was accumulated in 1958 in the Keless district of southern Kazakhstan on state lands where there was a large number of Morrocan locusts (*Dociostaurus moroccanus* Thunb.) and turanian locusts (*Calliptamus turanicus* Tarb).

The color of *S. porcus* Loew is light red with grayish overtones that blends well with the yellow-gray background of the ephemeral desert, its usual place of habitation. This species is distinguished from other robber flies by short wings, which cover only 4-4.5 abdominal tergites. These robber flies vary in length from 18 to 25 mm.

The species is known only in the Soviet Union and western China (Pamir, Chardara, Turkmenia and Kuldzha, Engel, 1930). In Kazakhstan, the species was found in the districts of Alma-Ata and Taldy-Kurgan (Lehr, 1958), in the district of Dzhambul (the collections of M.P. Maklovsky and I.D. Mityaev), and in southern Kazakhstan, where the major observations were conducted.

Aside from the typical ephemeral desert (with sedges and meadow grass), *S. porcus* Loew lives in deep ravines among saline growth, on slopes and in gorges of small desert mountains, in meadow grasses among swampy vegetation, in irrigation ditches, in oases, and in fields, but is rarely found in hard-packed sand. On April 6, 1962, in the ephemeral desert of the Alma-Ata district where there is an abundance of meadow grass, the population density was 0.053 individuals/m^2. The average density in the research grounds of Zhana-Kuduk (Southern Kazakhstan) where there were small gatherings of locusts was about 0.025 individuals/m^2 in 1958. The robber fly population in places abundant with locust larvae is shown in Table 2.

In the ephemeral desert of southern Kazakhstan, this species flies in May and June. The spring of 1957 was exceptionally dry, and the vegetation burned out early in the season. Under these conditions, the first individuals were observed on May 8 and the last on May 16 (in wheat fields the last individuals were found on June 20). In 1958, when the spring was exceptionally wet and the vegetation thick and tall, the first individuals were observed May 18 and the last on June 20. The maximum flight of the species occurs during the first part of June. In southeastern Kazakhstan, this asilid flies in June and July.

The adult individuals emerge from their pupae between 10 and 11 A.M. when the temperature of the soil at a depth of 4 cm is a little higher than 20°C. A small condensation of the soil does not present any obstacle to the emergence of the imago; hence on May 17, 1957, we observed at 10:00 A.M. a robber fly emerging on hard-packed ground in front of the entrance to our tent.

After the chitin has hardened, *S. porcus* Loew begins to hunt.

During the flight, each individual stays on a small territory (within the limits of a hectare) on which are found the hunting grounds, measuring 1-1.5 m^2 (Lehr, 1958a). Robber flies hunt sitting on the upper parts of plants and even on racimes of grain plants blowing in the breeze. During the maturation of meadow grass bulbs the top part of the stalk often bends and the panicle hangs down. Such panicles are the favorite places of *S. porcus* Loew for hunting and devouring prey. At this time the robber fly disguises himself. At a quick glance, the impression is created that the panicle is simply more abundant with seeds. Robber flies are rarely seen seeking their prey on the bare ground. *S. porcus* Loew is especially active during the heat of the afternoon when its flight is swift and the grayish-yellow color blends well with the color of the dry desert vegetation. With bright sunlight it quickly disappears from view. During these hours, it is difficult to catch this robber fly or to conduct any observations. *S. porcus* Loew is peculiar in that it hunts insects over short distances (5-35 cm), usually those insects crawling upon a plant and rarely those flying past. This method of hunting applies more fully to locust larvae, and only by this hunting peculiarity is it possible to explain the appearance of immobile beetle larvae and hunting spiders among the prey of the robber fly. The predator and its prey often fall to the earth together. At this moment, the robber fly usually seems to be crushed by its victim, but until the prey ceases to move, the robber fly does not attempt to free itself. Only after 1-2 minutes does the robber fly extricate itself from underneath the victim, and climbing with it back onto the plant, begin to suck. The amount of time for sucking a prey is varied. The locust larva of the third instar is devoured within 30-35 minutes and that of the fifth instar within 1 hour and 20 minutes. The robber fly begins to suck the prey through the head (the eye), after which it turns the prey and sucks through the abdomen near the thorax. If the victim is small and the day hot, the prey serves not only as a source of food but also of liquid; the robber fly sucks it quickly, and then, before it discards the victim, it alternates between sucking through the head and through the thorax several times. Thus, on May 28, 1958, the robber fly sucked a victim for 43 minutes, alternating from the head to the abdomen and vice-versa seven times, successively changing position at 8, 5, 8, 6, 2, 8, and 6 minute intervals.

The number of prey eaten by a robber fly during the first and second parts of the species flight period depends greatly on the temperature and humidity of the air. During the first half of the flight period, the prey is hunted probably for food alone, and the robber fly needs only two or three specimens a day. At this time, the predator discards its prey at the slightest sign of danger. Later, at the end of May, when it is hot and the need for liquid increases, the predator finds it difficult to leave its victim, and during June it becomes easy to capture robber flies with their prey with forceps. An observation on June 7, 1958, is especially curious. At approximately 2 P.M., two female *S. porcus* Loew simultaneously sucked a female winged Morrocan locust: one in the head and the other in the abdomen. When the locust was seized with pincers, the robber flies flew away, but one female quickly returned and pierced the eye of the victim. Probably, the need for liquid was so great that the instinct for self-protection was momentarily suppressed. During hot days, the robber fly sucks the female morrocan locust, which exceeds it in size, until the locust's abdomen is transparent and all extra food is discarded by the robber fly in the form of moisture drops through the anus. During the heat we were able to observe how locust larvae devoured another locust larva that was in the process of being eaten by a robber fly through the head. First the legs were chewed off, next the abdomen, and finally the lower half of the thorax.

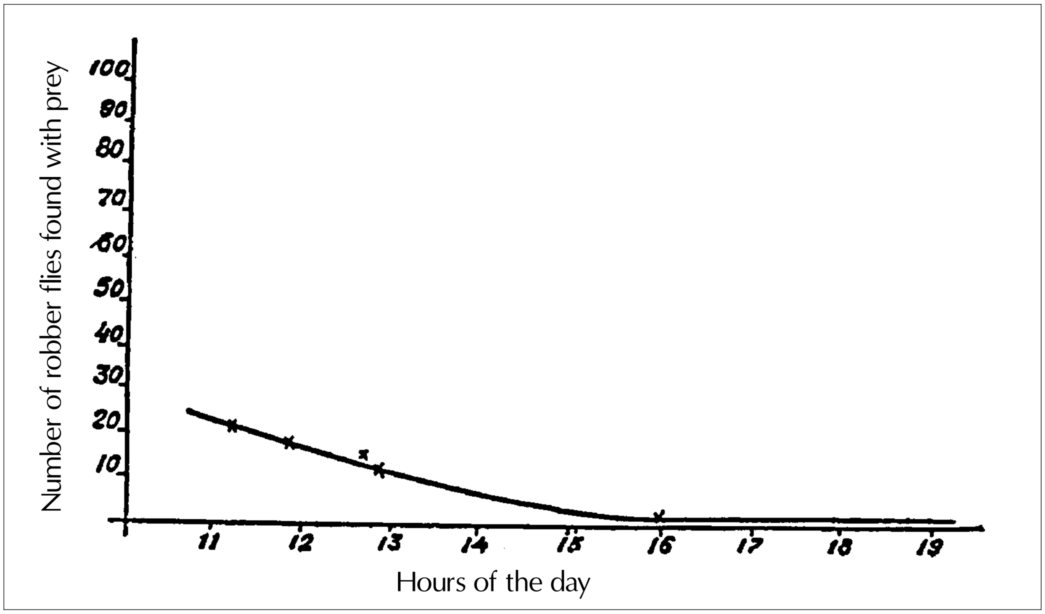

Figure 1. Intensity of hunting prey during a single day, June 7, 1958, when robber fly density was 7.7 individuals per 100 mm^2.

The robber fly hunts most of its prey during the morning (Fig. 1). The hunt for prey begins around 8 A.M. and ceases around 9 P.M. before sunset. Feeding intensity falls sharply during cloudy, cool, and windy weather. Despite the fact that during the beginning of the robber fly flight the size of prey is small (locust larvae of the third and fourth age) and at the end of the flight period the size is quite large (larvae of locusts of the fifth age and adult locusts), the number of insects eaten during a single day continually increases. It is possible that the main reason for this is the need for liquid. On average, a female robber fly eats not less than two to three prey specimens per day. If we calculate that *S. porcus* Loew flies from May 15 to June 20 (i.e., 36 days) and that the intensive flight period lasts about 26 days, and if the average density of robber flies on a 100 m^2 area is 9.4 individuals (Table 2), and the robber fly eats two prey per day (which is less than the average), then we can figure that during the flight period the robber fly destroys 488 insects. This number is calculated, of course, not for just 9.4 individuals but for a larger number since a gradual replacement of robber flies occurs. Some individuals die and others emerge (the last female laying eggs was observed on June 7, 1958).

The composition of prey for *S. porcus* Loew is not very colorful in comparison with other species of robber flies. Locust larvae make up 75.9% and other insects, mainly moths and hover flies, are seldom found during the mass flight period (Table 1). Prey were collected in various places, including deep ravines with saltwort growth where there were few locusts. Hence, the actual number of locusts in the diet of the robber fly is greater than the number shown in the chart.

Figure 2 illustrates the gradual increase of locusts in the diet of the robber flies and conforms with the following: as the vegetation dries out, fewer and fewer flies appear, and moths and locusts become the basic element of the entomofauna. On June 5 and 6, the places where the basic supply of prey for the robber fly occurred were treated with poison to exterminate the locusts. On the second and third day after this treatment, the number of locusts decreased sharply, and on the fifth and sixth days,

Table 1. Prey of *Stenopogon porcus* collected in 1957 - 1958 in southern Kazakhstan.

Group	Prey	Number	Percent
	CLASS ARACHNOIDEA	2	2.53
1	Order Araneae	2	2.53
	CLASS INSECTA	77	97.59
2	Order Orthoptera	60	75.9
	Included		
	Calliptamus turanicus Tarb	26	32.91
	of these III instar	3	3.79
	IV instar	13	16.45
	V instar	10	12.66
	Dociostaurus maroccanus (Thumb.)	12	15.19
	of these III instar	1	1.26
	IV instar	1	1.26
	V instar	4	5.06
	Subtotal	6	7.59
	Dociostaurus tartarus Uv.	16	20.25
	of these III instar	3	3.79
	IV instar	7	8.86
	V instar	4	5.06
	Notostaurus albicornis (Ev.)	4	5.06
	of these III instar	1	1.26
	IV instar	2	2.53
	V instar	1	1.26
	Oedipoda miniata (Pall.)	1	1.26
3	Order Hemiptera	4	5.06
4	Order Diptera	10	12.66
	Included		
	Family Asilidae	5	6.33
	Stenopogon porcus Loew 3	4	1.26
	Saropogon dasynotus Loew	1	1.26
	Family Syrphidae	4	1.26
	Family Larvivoridae	1	1.26
	Order Lepidoptera	3	3.79
	TOTAL	79	

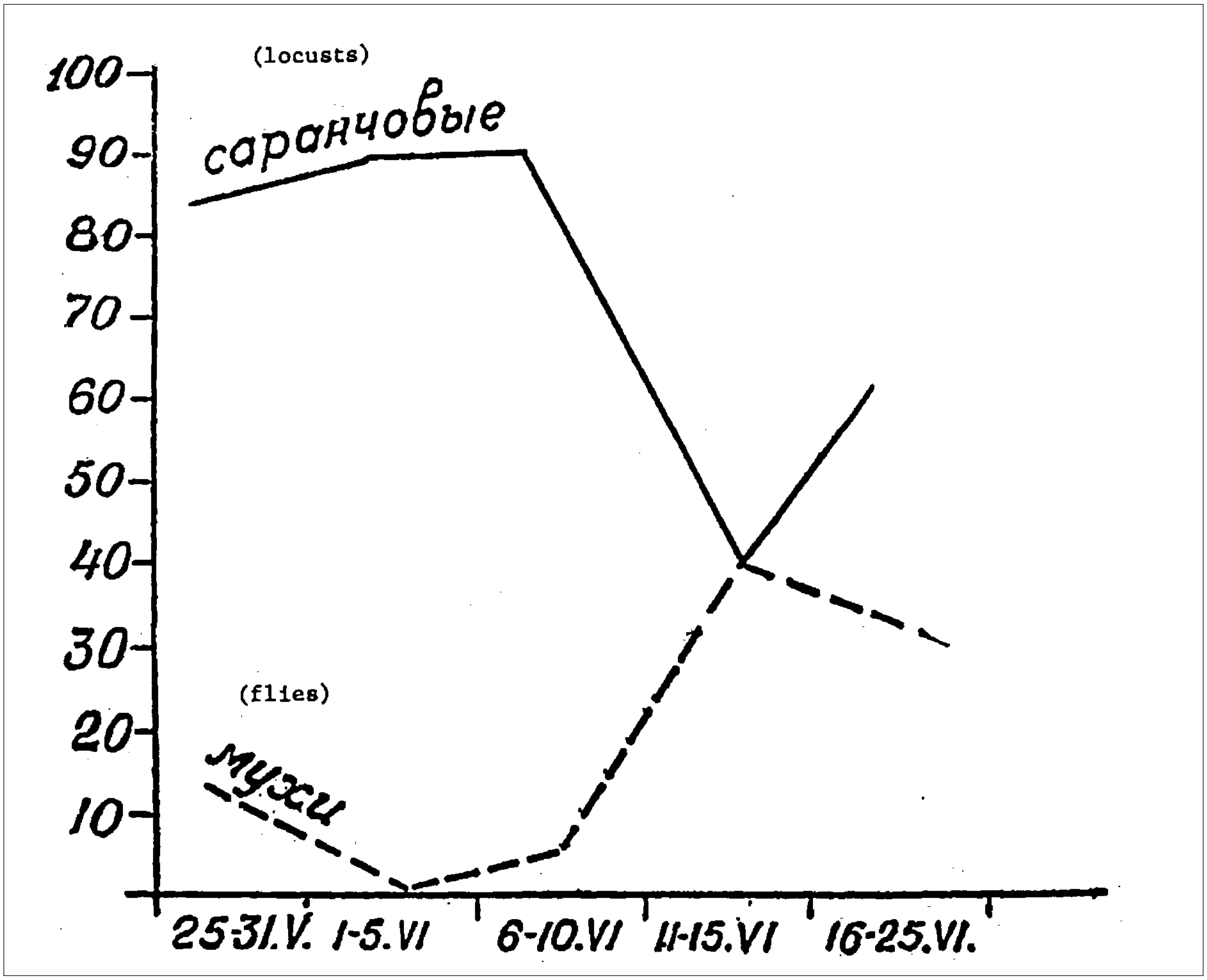

Figure 2. Change in prey composition of *Stenopogon porcus* Loew during the flight period.

there remained only a few individuals. The robber flies, as a result, were under conditions of great hunger stress, but hover flies and individuals of the same robber fly species soon appeared as prey items (shown in Fig. 2 by the fall of the curve). The further increase of locusts in the robber fly diet, shown in Fig. 2, is a direct result of the prey gathering in a new, untreated place.

Females feed more often than males. Of 62 feeding individuals collected in southern Kazakhstan, 48 (77.4%) were females. In the collections of *S. porcus* Loew from southeastern Kazkhstan, females composed 69% of the total number of individuals. Hence, it becomes necessary to consider the possiblity of unequal activity patterns between sexes by a comparison of the feeding activity of males and females.

Copulation begins several days after the imago has emerged (in 1958 the first copulation was noted on May 20). The daily behavior of *S. porcus* Loew is made up of the following interrelated three biological elements: 1) egg-laying, 2) feeding, and 3) copulation.

The morning is dedicated to feeding (Fig. 1). In the afternoon, individuals, having received enough food for the day, gradually begin to mate so that towards sunset up to 80% of the individuals are mating (Table 2). Copulation of 100% of individuals in the population is not possible due to the unequal number of each sex.

It is possible to show graphically the increase of mating individuals during a day, the curve of which contrasts with that of feeding (Fig. 1).

From Table 2 it is clear that each female mates, if not daily, then many times. However, during cloudy and windy days (June 8 and 10), because of less intensive feeding and other unfavorable conditions, fewer mating pairs are found. Based on these observations it is possible to confirm the fact that the fertility of the robber flies depends directly on the amount of available food and the weather.

We did not observe any courtship of the female by the male before mating, but the male does fly in search of the female. Mating individuals are arranged in chain-like rows (Lehr, 1958a). Copulation can begin in the morning and continue all night (11-16 hours). However, it is very rare to find mating pairs during the morning and at lunch time. In cases where they are observed, copulation continues for a shorter length of time.

Eggs are laid in the soil near the mat of grain-growing plants (meadow grass). At this time, several segments of the female's abdomen are buried in the earth, the pollen is brushed off, the abdomen takes on a reddish-brown hue, and the secondary difference of the sexes appears in the color.

Predator spiders and large robber flies are among the enemies of *S. porcus*.

The typical ephemeral desert, covered with meadow grass and sedge, is the favorite place of habitation for *S. porcus* Loew and the Turanian locust. Locusts found here are the desert locust (*Dociostaurus tartarus* Uv.), the morrocan locust, the skewbald locust (*Notostaurus albicornis* Ev.), and the red-winged locust (*Oedipoda miniata* Pali.).

All of these, when encountered by the robber fly, become food. In the research camp of Zhana-Kuduk, where our work took place in 1958, the average density of locusts varied between 2.5 to 4 individuals per 1 m^2, but on the southern slopes near the mountain crests it was from 10 to 15 individuals. The density of locust species, other than these four, was considerably less.

Based on the density of the robber fly population in an observed area of 300 m^2 (Table 2)

Table 2. Number of matings of *Stenopogon porcus* Loew on an area of 300 m^2.

Date	Time of count	Total	Number of robber flies No./ 100 m^2	No. not mating	No. mating	Percent mating	Notes
7.VI	18 hr 45 min	22	7.3	4	18	81.8	cloudless, weak wind, intensive hunting
8.VI	18 hr 45 min	23	7.7	11	12	52.3	massive cloud formations, temp. @ 1400 hr reached 35o, little hunting, males searching for females at these times
9.VI	20 hr 15 min	40	13.3	10	30	70.5	cloudless, weak wind
10.VI	1900 hr	28	9.3	16	12	43.2	during the afternoon thunderclouds appeared, strong wind
Average figures		28.2	9.4	10.2	18	61.9	

and accepting the locust population density as being 250-400 individuals per 100 m^2, it is possible to conclude that *S. porcus* Loew destroys from 40-60% of locusts during its flight (Table 3).

In 1958 two research sites, Zhana-Kuduk and Saugabai-Sai (covering an area of 8,000 ha), were treated with a mixture of calcium arsenate and nitrogen arsenate (the director of the area was A. F. Isinger and the chief technical advisor was O. Kekelbakov). Due to a thorough treatment, the mortality of locusts was very high. In the entire area (especially on those sites treated with calcium) not only locusts and other insects were destroyed, but also all animals living there, including birds, snakes, turtles, lizards, etc.

The robber flies on those sites treated with calcium died of poison and those on the other treated area died of hunger. As a result of the near extinction of predators and parasites, the offspring of the single remaining locusts in these areas are living under exceptionally favorable conditions. And if the weather is favorable, then in two to three years there should occur a rapid increase in the number of locusts in these localities.

Table 3. Approximate number of arthropods destroyed by *Stenopogon porcus* Loew, on an area of 100 m^2 during the 1958 flight period.

Group	Kinds of prey	Number of specimens destroyed
1	spiders	12
2	insects	476
	including:	
	locusts	370
	of these:	
	Turanian locust	161
	Moroccan locust	74
	desert locust	99
	skewbald locust	25
	red-winged locust	6
3	beetles	25
4	flies	62
5	moths	18
	TOTAL	488

Lehr, P.A. 1962b. [**Some aspects of the evolution of robber flies**]. Trudy nauchno-issled. Inst. Zasch. Rast., KazASKhN, Alma-Ata 7: 347-382.

**** Note that because of the complexity of most of the Figures and Tables in the original paper, these Figures and Tables are not included in the present translation. The reader is referred to the original paper for these and the list of citations.**

Some aspects of the evolution of robber flies

It is hardly possible that a group of animals exists which has not been more or less thoroughly studied and, concerning which, research has not noted facts of even small changes during variations in climate, habitat, or during a migration from one area to another. Darwin provided a great number of examples on this very subject (1951). With insects, adaptation can be most easily seen in the example of pigmentation. It is widely accepted that a darkening of color occurs in those animals that live in areas of high temperatures and of high humidity. Similarly, a lightening of color takes place under low temperatures and low humidity (Schowen, 1953). A fuller and more precise statement of the interdependence of color and climate is found in Gloher's rule: "Among mammals and feathered creatures, races which populate warm and humid areas have a pigmentation richer with melanin than those races living in colder and dryer places; arid regions are characterized by an intensification of yellow and reddish-brown pigmentation with a predominance of phaeomelin" (Kune, 1958, p. 30). From the physiological point of view, dull color contributes to heat absorption while red and yellow colors "aid as antithermal isolators" (Kuznetzoff, 1953). Shvanvich (1949) mentioned Ruikker's experiments that show that shiny and lustreless colors have almost no difference in their ability to reflect visible spectrum rays. In agreement with the statement of this author, small scales covering the body have a maximum reflexive faculty. Hence, taking as a basis deviations in pigmentation of individuals from different habitats, we can always assume that "the influence of all factors of natural environment and artificial experiment on pigmentation, in essence, is an influence on all body change which is, obviously, seen in pigmentation" (Kuznetzoff, 1953, p. 302-303).

The influence of habitat and flight season on coloration

A more precise illustration of the change in color in connection with a difference in temperature and humidity of a habitat is seen in the genus *Stenopoqon*. The species of this robber fly group are well-known in many regions throughout the world. In the Soviet Union they are absent only north of 56° latitude. We had the opportunity to examine 38 species in all (33 of which are mentioned in this article) from the USSR, Mongolia, China, Iran, Turkey, and Western Europe. They exist in grassy regions and are found in the glades of Siberian forests, in the steppes and deserts (aside from sand deserts), and on alpine and subalpine meadows. We do not know of a more ecologically flexible genus of robber flies.

We shall consider the connection between habitat, the flight season, and peculiarities of abdominal color in five genetically related groups of the above mentioned genus (Table 1). We are better acquainted with the biology of the group Macilentus. In July toAugust, *S. flavibarbis* Enderlein flies on the alpine and subalpine meadows of Tyan-Shan and Pamiro-Altai. The abdomen of this robber fly is shiny black.

Simultaneously, *S. macilentus* Loew was found on the southern slopes of lower mountains, in the dry steppes, and semi-deserts. Its abdomen is a shiny dark reddish color; only a faint black stripe passes from the top of the sides of the tergites. The area of distribution of this species reaches 50° latitude. But in the plains of Kazakhstan, it is found on the southern slopes of small hills and ravine slopes. At the beginning of the summer (May through the beginning of June), *S. albociliatus* Herm. is found in the deserts near Zail iiski Ala-tau and on plateaus. Its abdomen is shiny or slightly dull from pollen, but a black-brown color is characteristic for the tergites. *S. callosus* Pallas, which flies during the summertime on the steppes of northern Kazakhstan, has the same abdominal color. *S. maricovskii* Lehr lives in the mountain valleys covered with prairie vegetation, in the prairielands of river flood areas, and in ravines, and the abdomen of this species is always covered with a thick pollen. Hence, five of the mentioned species have four types of coloration (Fig. 1).

In order to understand the significance of color in the lives of the aforementioned species of robber flies, it is best to begin with an explanation of the behavioral characteristics of these insects. Since robber flies are predators, the possibility for laying large numbers of eggs depends on successful hunting. On the one hand, this is determined by the abundance of prey, and on the other, by the mobility of the predator. In places where *S. flavibarbis* exists (alpine meadows), prey is rarely as numerous as, for example, in the foothills or even in the desert during the spring and beginning of summer (locusts). In order to catch enough insects, the robber fly must possess great speed and mobility. However, high in the mountains this is not always possible because of the changing weather (i.e.,clouds gather quickly, rain or snow falls, and within l-2 hours the sun comes out and heat returns. This can continue over an entire season). The ability to rapidly change from a torpid to an active state is a quality demanded from the insects of high-mountain regions, especially from such mobile insects as robber flies. And the black color of the insects helps in this case. “Orthoptera, flies, and some moths are not able to raise their body temperature by means of their own organism, but their temperature is raised by the reaction of ecological factors, i.e., by sun radiation” (Strelnikov, 1940, p. 403). It is known (Melin, 1923; Lehr, 1958) that during cool weather many robber flies “warm themselves” by turning one side toward the sun. The possibility of raising the body temperature by direct use of the warmth of sun’s rays helps the robber flies to survive in such a severe climate. However, the black color also has a negative sense. It is possible to find these robber flies on paths, bare plots of land, and on rocks, but rarely on plants. Due to their color they are more noticeable to their enemies. But it is possible that in this case protective color is reduced to second place.

The habitat of *S. macilentus* is characterized by steady hot and dry weather (steppe and semi-prairie mountain slopes). There are no such sharp transitions from hot to cold. It is possible to assume that the shiny-black body color of the insects in these surroundings would be harmful; they would quickly become “over-heated” in the sun. And in actuality, the abdominal color of *S. macilentus* is antithermal—of reddish-brown tones—although in the morning this robber fly often turns the black side of its body to the sun. Evidently such color harmonizes better with the surroundings. At least it is a good camouflage among the drying or dry plants.

The inhabitants of the desert, especially those flying in June and July, occupy a particular place. In these conditions, additional heat is completely unnecessary; on the contrary, a reduction of heat is necessary. Independent of the color of the sclerites, the bodies of the insects are thickly covered with pollen. And it is generally known that light-colored pollen is the best reflector of sun rays. But the pollen has another and no less important function—camouflage. Here protective coloration is seen in a complete picture. For example, the color of the female *S. avus* Loew, especially of the thorax, blends with the soil color of her habitat (Lehr, 1961). This is a necessity. When the female lays her eggs and sits motionless, burying her abdomen in the ground, she is completely defenseless. In such a position she can be noticed only when her landing place has been observed. The male of this species is colored in natural reddish tones. He blends more with the burnt vegetation of the desert.

The habitat of *S. albociliatus* and *S. callosus* is characterized by steadier weather in comparison with the alpine meadows. There is not an intense heat that is normal for the desert. These insects usually fly in the south during the spring or in the northern steppes in the summer. Their abdomens are black with a brown or red tone or, if possible, with antithermal tones. However, black is the basic color of the inhabitants of cool places.

Is the interdependence between the various robber fly colors and their habitats really so strictly observed? It seems that it is observed and very strictly, as can be seen in a detailed analysis of the variations presented by the already mentioned species. The area of distribution of *S. macilentus* stretches from the steppes of northern Kazakhstan to the semi-desert slopes of Tyan-Shan. Within the boundaries of this large area, the species has similar visible markings. But on the edges of this distribution area, in the north as well as in the southern mountains, there are many individuals of various colors. These variously colored insects are often not distinguishable by color from the representatives of indigenous species (with immutable genitalia). In 1956, L. G. Serkova collected in the Sara-Ark steppe 16 robber flies that had color patterns more typical of *S. macilentus* than of *S. callosus*. The problem would seem difficult if these species could not have been distinguished by their hypandrium. To confuse them is impossible. In addition, individuals of *S. macilentus* are much larger in size. In other respects, it is difficult to find markings that would help to distinguish these species. The fact (Table 2) that males rather than females present extreme color variations deserves special attention. Out of 13 individuals similar to *S. callosus,* only one female had red spots remaining from a red abdominal stripe (14/VII/1951, Kamyshin area, MGU museum, collection of Panfilov). To repeat, on the northern edge of the distribution area, *S. macilentus* has color variations not distinguishable from *S. callosus,* which lives in the same or neighboring places. We must note that *S. macilentus,* having acquired characteristics of a representative of another topography, still retains the same genitalic structure. An analogy to this can be seen on the southern edge of the distribution area of this species. In the collections of ZIN, there are four males from the alpine meadows that have shiny-black abdomens characteristic of the inhabitants of these places. In the series of specimens of *S. marikovskii* from the marshes of the Syr-Darya river, there were two females whose abdomens were not so thickly covered with pollen and a red stripe was visible along the top of the abdomen (a color typical for the inhabitants of the semi-deserts—*S. macilentus*). In this case, the hypandrium helped to avoid a mistake in identification, as the difference in them was too apparent. There are more such analogies. Table 2 contains material on this order pertaining to five species.

The problem of *S. albociliatus* is slightly more difficult (not included in Table 2). This species has all types of colors, ranging from the usual color (mentioned earlier) to that characteristic of *S. macilentus*. But the pattern is still more interesting. If the region to the southwest of Lake Balkhash is considered as the central point of distribution, then the farther we go to the periphery of this distribution area the lower the percentage of individuals bearing a color characteristic for *S. macilentus*. But in Siberia where this species is common, there are almost no such variations. Hence, depending on the peculiarities of habitat, *S. albociliatus* analogous to *S. macilentus* has an abdominal color typical of a group of robber flies for one or another topography. The hypandrial structure and the large number of varied individuals preclude the possibility of applying the aforementioned variations to other species.

Is there an analyzed diagram for other species of the genus? This can be seen from the data in Table l. It seems that all 33 species have a definite place in it. When we were working on the study of this genus, we divided the robber flies into five groups according to their genitalic structure. Some groups are divided into subgroups. These same 33 species also have been arranged into climatic-topographical groupings by their abdominal coloration. This can be seen from the data in Table l. We found that the majority of groups and subgroups have their own representatives in all the belts (and zones) of mountains and plains. The regularity of this appeared general. It is therefore not astonishing that earlier Engel (Engel, 1930, 1933, 1940) distributed individuals among several species according to the color of a certain species. At that time, the distributional areas of various species were considered the distribution area of one species, when in reality these were different species with the same habitat, which was reflected in their coloration.

Hence, this double grouping of species on the basis of genitalia and abdominal color (body) was most natural. On the alpine meadows of the Himalayas, Tyan-Shan, Pamiro-Altai, the Caucasus, Tavor, and the European mountains, we find one and the same type of body color among robber flies. We are able to say the same thing about other representatives of other topographical groups (Fig. 2). This regularity came about due to the great ecological plasticity of the genus that spread its representatives into the most varied climate zones and is unheard of for any other family group.

How much does our diagram of the dependence of color of the genus *Stenopogon* on environmental conditions agree with Gloher's rule? For *S. macilentus*, this can be stated in the following manner. Robber flies populating cool and wet regions have a pigmentation richer in melanin than races of the same species living in warmer and dryer places. For inhabitants of drought areas, yellow and reddish-brown pigmentation is more characteristic. Therefore, the first part of our statement does not agree with Gloher's rule. We are speaking of cold-blooded animals and Gloher of warm-blooded animals. The body temperature of robber flies rises from the warmth of the sun, while with vertebrates it is constant. But the second part of the statement concerning *S. macilentus* does not contradict the rule since the temperature of the air and the robber fly's body in the desert during the summer are close at flight time, and pigmentation is not the factor promoting heat absorption. The pigmentation of both groups of animals fulfills a similar antithermal function. However, in our opinion, it is possible to assume that the dependence of color on climatic peculiarities of habitat holds true for the majority of animals also. The above statements applied to one species of the genus *Stenopogon* (we are familiar with its ecological variations) are true not only for intraspecies changes, but, as is seen in Table l, also for interspecific peculiarities of pigmentation. As it will be shown later, those conclusions more or less abruptly expressed here are characteristic of all species of robber flies, the ecology of which is known to us.

Let's turn to an examination of other groups of robber flies. Species of the genus *Promachus* are less flexible than those of *Stenopogon*. They do not go as far north and do not go above an altitude of 2,000 m in the mountains, even on the southern slopes. Aside from this, their flight in the desert is in May to June. In the USSR, there are six species of *Promachus* if we accept Engel's (1930) and Paramonov's (1931) concepts of species independence. The first species is *P. leoninus*, which lives in Asia Minor and enters the Soviet Union in the Crimea and near the Caucausus. The second, *P*. *yesonicus* Bigot, is found only in the Far East. The remaining four species are known in Central Asia. A schematic distribution of these species according to zones can be seen. *P. canus* Loew keeps mostly to wet places, namely marshes, deserts, and plateaus. This corresponds to a strip between 34°-35°and 50°52° latitude. The distribution area of *P. leontochlaenus* Loew is limited to dry clay prairies, foothills, and dry steppe plots of mountain slopes. *P*. *albopilosus* Macq. is found in the marshlands along the banks of the Syr-Darya river (possibly, in the wet mountain valleys). *P*. *pallipennis* Macq. usually lives on the very dry slopes of Tyan-Shan and Zailiiski Ala-Tau. In the example of this genus, we are dealing with inhabitants of dry steppes and deserts, and from the above statements it becomes clear that pigmentation in these topographies is not as distinct as, for example, with *Stenopogon* of the high mountains. Here external conditions are seen only in second-degree signs, in the color of hairs and setae on separate parts of the body. *P. albopilosus*, a dweller of warm and wet places, has all white body hairs, but the setae of its antennae, part of its face and head setae are black; the number of black setae on its legs is greater. *P. canus*, which lives in dryer places, has a slightly yellowish hair color and never has black hairs or setae on its head. And both are rarely found on its legs. The hairs and setae of the entire body of *P. pallipennis*, which lives on dry mountian slopes, have a light to bright yellowish-red color.

Because the distribution area of the three mentioned species partly or completely enters upon the distribution area of *P. canus*, we can probably assume that transitional individuals are found there. We already know that during a single day in the marshes of the Syr-Darya river for a distance of four kilometers, individuals were caught that ranged in color variations from *P*. *canus* to *P. pallipennis* (Lehr, 1961).

One of the basic differences distinguishing *P. leontochlaenus* from *P. canus* is the presence of black stripes on the upper part of the fore and hind tibia (Loew, 1871). In 1960, on the slopes of the Nuratau mountains (Uzbekistan) we gathered a series of specimens with various markings. Those whose stripes were evident were from the lower part of the slope. Those in the form of separate spots or unclear stripes and darkenings were from the central part of the slope and those whose marks were completely lacking were from the upper part of the mountains. In 1961, the members of the Kazakh Institute of plant protection, headed by M. P. Malkovskii, collected 35 individuals of *P. canus* s. str. on the Mangyshlak penninsula of which 18 in the conception state had the indicated stripes. There were no examples of a single typical *P. leontochlaenus*.

All four species have a similar genitalic structure. They differ from related species by the presence of an appendage on the hypandrium. *P. albopilosus* and *P. pallipennis* were described in eastern China. It is possible to assume that if the first “Mongolian” *Stenopogon* penetrated into eastern Europe no earlier than the beginning of the pliocene age, then *Promachus* (type *canus*), at the present time reaching as far as the Volga, probably spread from Central Asia at a later period during one of the last drought periods of the interglacial age. Forms close to *P. albopilosus* and *P. canus* were the first pioneers. When the climate changed, becoming dryer and warmer, possibly already in the holocene age, the dry-steppe form close to *P. canus*, at this time occupying the plains of Central Asia, appeared to be most dominant. During a later adaptation to climatic conditions, *P. canus* moved northward into Middle Asia and to the present time has remained on mountain slopes higher than l,000 - 1,500 m above sea-level, in the deserts (Kzyl-Kumy and Muyun-Kumy) and in the marshes, where the mesophilous form of *P. albopilosus* has been preserved near the river banks. At the same time, a new form appeared creating *P. leontochlaenus,* which was able to adapt to the most xerophilous conditions of our time.

On the dry slopes of the foothills of Central Asia where the brightly colored species *P. pallipennis* was isolated and under conditions similar to those of Middle Asia, there appeared the similarly colored individuals of *P. leontochlaenus*. Therefore, we can assume the exact division of the four species of robber flies took place in the not-so-distant past approximately 8-9,000 years ago and their distinctive characteristics are due solely to climate and a change of habitat.

I want to pause for one interesting observation. While sucking prey, the liquid content and saliva stick the setae of the robber fly's facial beard (mystax) together. The robber fly smooths apart the setae of the mystax with tarsal setae and the upper part of the tibia, thus cleaning off the food particles. The particles which cling to the leg setae are removed by the head setae (Lehr, 1958 for *Stenopogon octonotatus* Loew). In the desert where humidity is low, the liquid food particles quickly dry and fall from the setae in the form of a small case, therefore the presence of head setae is not at all necessary. On the contrary, in the damp air near the river, liquid food particles cling for a longer time, and are harder to remove; therefore, the head setae are used to hasten the process. It is remarkable that head setae are well developed only on *P. albopilosus* where they are black and stronger. *P. canus*, that lives in dryer places, rarely has them. *P. leontochlaenus* and *P. pallipennis* completely lack them. In an example of the division of individuals of *P. canus* that was gathered in 1957 in the marshes of the Syr-Darya river, we can trace the entire sequence of change from the black strong setae of individuals living on the river banks to the weaker white setae of inhabitants at a distance from the river to a complete absence of the setae among specimens collected in an area near the desert. There is a direct connection between structure and function. Here again, we see how a distinctive marking, produced by climatic conditions, has an important functional significance. This example is similar to the one of *Stenopogon,* a desert dweller. The pollen covering, on the one hand, protects the body from sunburn and, on the other, serves as a camouflage.

Therefore, the four analyzed species of *Promachus* cannot be considered equal. On the edges where their different habitats meet, there exist transitory forms; and futhermore, the appearance of structural modifications on one or another species depends greatly on the characteristics of its habitat. The question arises, should we consider these as species, subspecies, or forms of a lower taxonomic rank? We are inclined to consider them subspecies on the following basis.

For five years we studied the behavior of the Turanian and desert locusts (*Calliptamus turanicus* Tarb and *C. barbarus* Costa.) in Southern Kazakhstan. There is an astonishing similarity between the ecology and distribution of these locust species and the ecology and distribution of the robber flies, *P. leontochlaenus* and *P. canus*. It is only fair to take into consideration that locusts are more mobile than robber flies; therefore, their zones of distribution are always somewhat larger. The individuals of a certain locust population rarely remain in one place for more than a year. According to our observations, the main mass of locusts annually moves 7-15 k from their emergence site. Sometimes an insignificant number of the population will remain in the old place but not always. During its "migratory flight", the locust probably moves up to 30 k and farther. Under favorable circumstances, robber flies usually remain on an area of several hectares, and only hunger can force them to move more than short distances.

The tribe Calliptamini is widely represented in Africa (Mischenko, 1952). It is possible that *C. italicus*, a more mesophilous locust species than our fauna, was the first to win Europe and Western Asia. In the marshes of the Syr-Darya river it is found in the same places as *P. albopilosus*. In the Pliocene age, the original form of *C. barbarus* appeared most probably in Iran as a possible center of the formation of desert fauna. This species gradually penetrated into the Central Asian deserts and occupied areas near to those of *P. canus*. In the Holocene age we find the locust in the sandy deserts and higher mountain belts (Naratau), after it had moved from the plains to the river marshes as a result of later adaptation to dry climatic conditions. A new endemic form, *C. turanicus*, ecologically similar to *P. leontochlaenus*, remained in the clay deserts of Central Asia. It is interesting that according to the general habitus of the discussed insect species, the Turanian locust, compared to other related species, is distinguished by its massive body. This is also characteristic of *P. leontochlaenus*. I want to add that the distributional area of the related but well isolated *P. zeoninus* is almost completely the same as that of *C. tenuicercis* Tarb. (Mischenko, 1952).

Since evolution of two of the analyzed species of locusts and robber flies took place under similar climatic changes and led to the formation of distinctly marked locust species, we consider the Central Asian *Promachus* we have seen, that change in color, are directly and most regularly dependent on the conditions of a habitat. However, these peculiarities of color, characteristic of the great majority of individuals in the population, are impossible to confuse with abnormal color digressions of separate parts of the body under the influence of weather changes during the year. *Eutolmus implacidus* Loew serves as an illustration of this (Lehr, 1962). In 1871, Loew described two species of the genus *Eutolmus* from Przhevalsk and the Zeravshan river valley. Aside from other color patterns, these species are distinguished by the color of their tibia. Dividing our collections of *Eutolmus* from Southern Kazakhstan according to this characteristic, we discovered that in humid years *E. implacidus* Loew was predominant. Only *E. implacidus* is found in the dry foothills of the Nuratau mountains. Finding no difference in the genitalic structure, we were convinced that we were dealing with only one species. It is interesting to note the fact that, as occurred in the above case, color can be a very accurate indicator of the weather in the habitat of the species. This confirms the hypothesis that color of the individual is determined in the pupal phase before the exit of the imago.

Therefore, in a single family of flies we have, within species, the most varied reactions to weather changes. If it were not for the differences in hypopygium, we could consider *Leptogaster cylindrica tesquorum* Lehr merely a diminutive form of *L. cylindrica* s. str. because of the complete absence of a difference in color (Lehr, 1961). *Promachus leontochlaenus* is the same throughout its wide distributional area; even deep in the desert of Kzyl-Kumy (habitat of *P. canus*) 4-5 k along clay and sand valleys, there are no transitional forms. This illustrates the actual solidity of distinguishing color markings. But at the same time, on the slopes of the Naratau mountains and on the Mangyshlak peninsula, we find actual transitional forms between the desert and steppe representatives. Individuals of *Eutolmus implacidus* possess a contradictory characteristic that allows them to change color depending on the weather conditions of a particular season. An even more complete picture of the influence of climatic factors on color is seen in the genus *Stenopogon*.

However, other hypotheses regarding changes in color are possible, i.e., atavism. These causes do not exclude but rather supplement one another. Judging by the abundance of species of the genus *Stenopogon*, living in the dry steppes and deserts and also by their behavior and daily regime (Lehr, 1961), we can assume that the dry steppe lands were the original site of their formation. In connection with this, it is possible to assume the high mountain forms, *S. flavibarbis*, *S. flavibarbis occidentalis* Lehr, and *S. hradski* Lehr, derived from the analogous form *S. macilentus* (Table 1). In actuality, if the first of the mentioned species has a large number of transitional forms similar in color to *S. macilentus*, then for the latter there are few cases where color similar to that of the first three species is acquired (Table 2). Here there is room for analogy with *Vanessa urticae* L. and *V. ichnusa* Bon. (Fischer, 1916). *S. macilentus* in its turn arose from steppe forms with a habitat and flight period similar to *S. callosus*. However, *S. macilentus* has digressions in color identical to the mentioned species, while *S. callosus* has no such analogous changes. In other words, at the present time in Central Asia there are probably no ancestral forms of *S. flavibarbis*, *S. macilentus*, or related species. They either died out, disappeared, or live in as yet uninvestigated areas. It is possible that the first species remained in Central Asia and the second in Mongolia, the supposed centers of their origin. At the same time, *S. laevigatus* Loew and *S. sabaudus* Fabr. are very close to one another and have all the transitional forms according to color and genitalic structure (Table 2). Here we find that both forms exist in the present time and in places close to one or the other's origin.

The above facts make it possible to assume that a species gradually acquires a new color following a climatic change. For example, at the beginning of a new ice age it is completely possible to expect that color must darken, and at the end of it, individuals of a species once again assume their original color. In other words, if a contemporary typical form of *S. macilentus*, which lives in the steppes and on the slopes of the Zailiiski Ala-Tau foothills, would survive a new mountain glacier destroying the fauna in the plains, it would have the color of *S. callosus*, that is, the color that its mesophilous form acquired in the Sara-Akinskii steppe. In this form it would survive the cold. After the melting of the glaciers and following the rise in temperature, this form would partly return to the mountains and partly remain on the plains. This explains the contemporary insular distribution of the mentioned species. *S. macilentus* would have gradually acquired the dark reddish color that distinguishes it today. In time, this color would become dominant. If this hypothesis is accurate, it would be easy to explain the modern distribution. Thus it is possible to assume that during the advance of the mountain glaciers of the Reiss-Wurmian interglacial period, the original form, very close to the modern *S. macilentus*, descended onto the plains where at the present time it has an insular distribution on small hills. When the glacier disappeared, this species returned to its former habitat on the slopes of Tyan-Shan. The Sara-Akinskii individuals are similar in form to those that survived the glacial epoch. Based on this point of view, if the distribution of this species were clarified, it would be simple to explain the distribution of other robber fly species living in similar areas (for example, *Neomochtherus maricovskii* Lehr). But this is only an hypothesis, which must still be confirmed by additional observations.

Color or a change of color serves as an indicator of the habitat of a species and of the species formation process. Therefore, a number of analogical facts will assert that a subspecies, even a well-isolated species in nearby distributional areas or those replacing one another during flight periods, have a color variation that is seen in the color changes of the cited types. *Leptogaster cylindrica* is very close to *Promachus canus* in distributional area and in the peculiarities of pigmentation. The difference between the black form of *L. cylindrica hispanica* Mg. and *L. cylindrica* proper is seen most of all in the color of the head setae; that is, there is an analogy here to the descriptions of *P. canus* and *P. albopilosus*. But here there is a difference in the genitalic structure, so it is easy to recognize the large number of subspecific individuals on this basis. Although their distributions adjoin, they are sharply delineated. Just as the dominant species of *P. canus* is able to possess a well-known form of *P. leontochlaenus* in the desert, *Leptogaster cylindrica* has *L. c. tesquorum,* which is almost identical in pigmentation. A similar example of the difference in leg color, but on a higher taxonomic level than with *Eutolmus implacidus*, is seen among the species of *Machimus rusticus* Meig. and *M. alatavicus* sp. n. (in lit.). *M. rusticus* has red coloration only on the base of the tibia, while *M. alatavicus* has red coloration on a significant part of the tibia and over onto the femurs. The red coloration of *M. alatavicus*, depending on the dryness of its flight period, appears in a pattern of red (antithermal) tones. These separate species have great differences in their hypopygium. *M. rusticus* flies during May and June, a more humid season, while *M. alatavicus* flies in the same places, but during July and August. Paly (1960), in his observations on flea beetles, made an even more astonishing analogy concerning the dependence of beetle body color on flight season and habitat.

In the analysis of color and pollination for the species of the genus *Stenopogon,* we indicated that pigmentation, the result of the reaction of determined climatic components, only remains unchanged when color plays a large role in survival as camouflage and vice-versa. This is reaffirmed in the example of the desert genus *Ctenota* of the tribe Laphriinae. We have added a fourth species, not yet described, to the well-known three species. In the summer of 1961, we became acquainted with habitats of these robber flies. It seemed they kept solely to the same sites. *C. molitrix* Loew is an inhabitant of shifting sandhills, and its color blends well with the color of the sand. The three other species are inhabitants of saltmarshes. *Ctenota* sp. is an inhabitant of salt-ridden lands, which remain damp the entire summer. *C. armeniaca* Paramonov is found in places containing similar soil. The color of the bodies of both species corresponds to the color of the salty soil. We found *C. ruficornis* v.d. Wulp entirely on thickets of *Gamanthus*. During the flight period of this species, the plants are usually rose colored. And the body of this robber fly has a rose color identical with the color of the named plants, under which it awaits its prey. Most probably genus *Ctenota* is ancient, dating back at least to the Neocene period. The habitats of its species are sharply delineated despite certain associations crossing into others. Moreover, there are actual morphological variations in venation, position of hairs and setae, even in form, not to mention genitalia. We did not note any change in color of these insects from year to year. Consequently, protective coloration is the primary factor here and changes of pigmentation do not occur under the influence of the air in the damp saltmarshes and in the hot sandhills. Selection neutralized this indicator of the peculiarities of climatic conditions. The majority of the other genera of the named tribe acquired their color by imitation. Representatives of the genus *Laphria,* and those related, present astonishing examples of mimicry of stinging Diptera and Hymenoptera. Porchinskii (1876-1877) has reported a small number of similar examples.

We shall spend some time on the natural development of the seemingly insignificant influence of climate on the appearance of robber flies, evident over large territories. *Leptogaster fumipennis* Loew and *L. turcmenica* Paramonov differ first of all in the intensity of wing color. In addition, they have variations in the structure of their genitalia. The first species is an inhabitant of the coastal areas of southern Europe and the Pacific Ocean. The second species combines the distributional areas of the first into the more continental conditions of Middle and Central Asia, inhabiting marshlands and damp mountain valleys (Lehr, 1961). We observed the very same thing with *Selidopogon octonotatus* and *S. diadema* Fabr. but in the size of the hairs of the mesodorsum (the primary distinctive mark of the species). The hairs of *S. diadema* are long and thick while those of *S. octonotatus* are short and thin. The distributional boundaries of these species passes near 45°to 55° longitude. In the collections of L.V. Zimina from outer Caucasia (collection of the museum MGU), there are typical individuals of the two species as well as transitional forms based on discriminatory markings. It is also possible to determine by the characteristic of the hairs whether individuals are from a dry or humid habitat. The same was observed in the collection of these robber flies from the area located between the rivers Volga and Ural. But in the center of the distribution of *S. octonotatus*, even in the ravines of the Nuratau and Ortau mountains, we do not find variations of markings similar to *S. diadema*. With the majority of species of the genus *Stenopogon* from the Mediterranean area (*S. junceus* Wied, *S. brevipennis* Wied, *S. schisticolor* Gerst., *S. caracinus* Loew, and others), usually the males and more rarely the females have milk-white colored anal lobes and wings. Often this is accompanied by the presence of crooked stripes on the hind parts of the tergites from the presence of silvery pollen. These same markings occur on Middle-Asian species when they appear in the Mediterranean (for example, *S. flavibarbis occidentalis*). In addition, *S. laevigatus* and *S. sabaudus* in the north-eastern part of their distribution do not have a light color. Probably, individuals moving from humid zones to drought zones are subject to rather sharp changes in external markings.

Hence, the settling into a new habitat with a different climate is seen externally in the change in the robber fly’s coloration. These changes are natural for all groups of animals, but they can be hidden, suppressed, or transformed, especially if it would be harmful to the existence of a species.

Peculiarities of habitat and the down of robber flies

As was already noted, a change in color is not the only factor that reflects the habitat of a species. A less definite but rather steadfast sign is the characteristics of down: length, thickness, and abundance of setae and body hairs. The outstanding majority of adult robber flies fly during the beginning of the hot season, the end of May to August. However, as always, there are exceptions. For example, *Hystrichopogon hirticeps* Herm. flies in April on the foothills of Tyan-Shan and during years with an early spring, in the latter part of March. At this time, cold spells and snowfall may occur and the temperature drops to 5°to 8°C. These gray insects have a shiny black spot with metallic blue or violet on the upper part of the tergites. We have already spoken about the significance of such coloration. The body of the insect, especially the thorax, is covered with thick and long hairs (Fig. 4). Representatives of a late autumn species (*Illudium hebernum* V. Ricter) are also thickly covered with hair. This species even has a thick mane of long hairs down its mesodorsum. If we examine the representatives of our genera in detail, from this point of view, we obtain a very interesting picture. The species of a single or related genera, one that flies in the south in the spring and fall or is a typical northern inhabitant, has longer and more developed hairs and setae. The structure of the ovipositor in the genus *Dysmachus* is close to that of *Eutolmus*, which is linked to the ability to lay eggs (Lehr, 1962). The genera are differentiated by the following rule: if the dorsocentral setae of the mesodorsum reach its anterior border, it is *Dysmachus*; if they do not, it is *Eutolmus*. It seems that all the known species of *Dysmachus* living in the southern steppes fly only in the spring. Even in the foothills they fly not later than the middle of May. We do not know of a single species of *Eutolmus* that flies here (in the southern steppes) so early, and if a species should appear at the end of April, then it occurs farther south, in the deserts of Middle Asia.

Analogous subdivisions can be found in the genus *Machimus*. In the development of body setae, these robber flies are close to *Eutolmus*, but there are species which fly early in the spring in humid areas of the south, that have mesodorsal setae and hairs similar to *Dysmachus*. This served as the basis on which they were distinguished as a subspecies, *Conosiphon* (Becker, 1923).

Hence, the varying degree of development of body down of robber flies, which in a number of instances allows the systematic grouping of species into genera, is often merely a necessary and reciprocal reaction of an organism to humid and cool habitats and vice-versa.

The dependence of the development of the setae of the facial beard on the peculiarities of habitat is less general and clear. For example, the majority of species of *Habropogon* fly in the desert at the end of April to May. Their facial beard setae extend beyond the middle of the distance between the edge of the mouth opening and the base of the antennae. *H. verticalis* Beck, which lives during the latter part of May to June on the hot sandhills, has a narrow row of hairs above the mouth edge. All the southern species of *Leptogaster* have facial beard setae that are short, few in number, and arranged in a single row; while those of the inhabitants of the most humid places, *L. cylindrica* and *L. hispanica*, are arranged in more than one row, are numerous, and thick. Similar examples are found with *Satanas gigas* Eversm. and *S. minir* Prtsch., *Polysarca gussakovskiji* Paramonov and *P. violacea* Schin., *Philodicus spectabilis* Loew, and *P. ponticus* Bigot, although their ecology is not always known to us. It is possible that the facial beard setae play a sensory role in determining suitability of prey and to better determine odor, and that under humid conditions the facial beard setae must be farther from the edge of the mouth.

Characteristics of body structure, behavior of robber flies, and radiation from the sun

Cyrtopogon daimyo Speis flies in the foothills of Tyan-Shan during October. This interesting hairy robber fly is quite similar to a small bumblebee, and the similarity is completed by the “bee hum” it emits during flight. During the flight period of this robber fly, the weather is characteristically very unpredictable with quick rising and lowering of the temperature. The upper abdominal portion of this insect is shiny black, sometimes shot with a metallic color. The part of the tergites not covered by the wings (the sides) has thick red hairs. This robber fly regulates the penetration of the sun’s heat by opening and closing its wings over the black parts of the tergites. There can hardly be a more illustrative example of exploitation of sun energy (Fig. 5). These same bare black parts in the upper region of the abdomen are found in other species and among genera that are more developed among those representatives of cool and humid places. For example, among *Promachus* they are best developed in the case of *P. canus* and *P. albopilosus* and are almost absent in other species. Similar spots are found on the spring species, *Hystrichopogon hirticeps* (April), and on individuals of *Illudium hibernum,* which fly in the foothills of Middle Asia during the autumn. It is possible there are even more analogies. This proves once again that sun energy plays an important role in the active behavior of these insects. At the same time, “usually the temperature of different segments of the body, especially of large insects, varies within very large limits. The highest temperature is always in the thorax as in this part of the body are found the flight muscles which play a large part in the output of heat. The temperature of the abdomen is a great deal lower,” (Showen, 1953, 427). This is in direct reference to the robber flies, which are the most mobile predators, usually seizing their prey in flight and carrying it several meters. The thorax of the majority of these flies is covered with pollen.

Hence the part of the body that has the highest temperature due to muscular activity is carefully isolated from unnecessary heat by the most perfect means—squamellas of pollen (Fig. 6). There does exist a large group of genera, the individuals of which are entirely covered with thick pollen on all parts of the body. We classify them as northern forms by origin. They are inhabitants of the forests and meadows in the temperate climate belt of Europe and Siberia. In Middle Asia they are found in the humid mountain belts or on the plains in the spring or fall. These are the common *Machimus, Eutolmus, Dysmachus,* and others. During the evolutionary process, they developed completely different needs for heat and have acclimated in a most astonishing manner. We shall concentrate on the “southern” forms. Although these live in the desert during the hottest months, they can also adapt well to the conditions on the northern plains and cool mountain chains. These “southern” forms are distinguished by a color variation which indicates weather conditions, and *Stenopogon* serves as an excellent example.

The possibility of ecological classification on the basis of color and down

It is possible to arrange the majority of robber flies known to us into four topographical groups, according to the color characteristics of the abdomen (Table 1). This has already been done for the genus *Stenopoqon,* and for a small number of other genera and species in Table 3. Since a detailed account would require too much time, we shall deal with only a few species from the first topographical group. The black color of the abdomen (and body) of *Stenopogon*, inhabitants of alpine and subalpine meadows, is necessary for a quick rise in body temperature from the effect of the sun’s rays. From this viewpoint, how is it possible to justify the black body color of the species of the genera *Polysarca* and *Polysarcodes*? Both of the mentioned genera have a form of venation similar to that in the genera *Promachus* and *Satanas*. The genitalic structure of *Polysarca* is similar to that of *Promachus* and that of *Polysarcodes* to *Satanas*. Therefore it can be assumed that the causes for the variations of the above pairs of genera in the past are the same as for the genus *Stenopogon*, for example, the group Macylentus. The same, possibly, can be true for a second pair of genera. Of *Polysarca,* we were able to become familar only with *P. neptis* Loew. These robber flies stay mainly on the sandy soil of the Priliiskii deserts and fly at the beginning of May when the weather is still cool. Hence, no contradiction between color and flight period can exist.

The southern species of *Loewinella*, like the majority of *Dioctria*, live in thick grasses, usually under bushes and trees. But aside from the fact that they seek the shade of plants in intensive heat, the same situation holds true for them as for *Holopogon*.

Representatives of the genus *Holopogon* are found in the steppes, deserts, plains, and mountains. In Southern Kazakhstan, their flight takes place in April or, more rarely, in May. We have already covered the behavior of *H. claripennis* Loew. These small robber flies seek their prey, sitting on the tops of dry stalks of dead plants such as sagebrush, reeds, harmel, and others. This is usually at a height of 30-50 cm or more from the ground (2.5 m in the Priliiskii desert). The daily regime is as follows. They hunt in the morning from 8 to11 A.M. prior to the advancing heat, during the mass flight of small insects (plant lice, small beetles, gall midges, and others). During the afternoon, they mate, lay eggs, and sometimes hunt prey. At this time, the majority of insects stay in thick bushes. In the evening, when small insects are most active, they hunt once again. In the evenings and on April mornings when it is still cool, a constant flow of heat is necessary for the mobility of these small predators. They receive heat energy from the sun due to their black color. As Strelnikov indicated, the slightest wind (up to 1 m per sec) significantly lowers the body temperature of these insects. So, during windy weather, these small robber flies gather on the sides of plants protected from the wind. In this respect, *H. priscus* Meig., the only species of the genus in the steppes of Kazakhstan that has moved as far north as 57° latitude, is very interesting. During its flight (July to August) cold winds often blow. And this is the only species whose body, especially the mesodorsum, is thickly covered with long heavy hairs—snow-white on the males and brownish on the females. "Obviously, the highly developed hairy cover of certain arctic insects (particularily, the more mobile male of the flies (Cordyluridae)) has some significance in the preservation of the insects' body heat. This downy cover creates a zone of weak heat-conductibility around the insect" (Shtakelberg, 1940, p. 262). This supposition is completely acceptable for the non-arctic *Holopogon*. The black body of *Holopogon* corresponds directly to the situations in which we find *Stenopogon*. Let's try to picture how a species of the genus *Holopogon* would be if it adapted to a desert habitat in the heat of summer, but retained its former behavior patterns. First, it would have to have a light color (fourth topographical group, Table l) or else it would quickly be burned by the sun while sitting on the ends of bare branches. But during the summer in the deserts of Middle Asia, strong winds blow steadily. Hence, this robber fly waiting for prey high above the ground must be covered with thick hairs. *Jotopogon leucomallus* Loew (Fig. 7) answers all the above requirements.

It is possible to frequently see these snow-white robber flies in places with sandy soil, sitting on the tops of dry stalks of sagebrush, etc. They are very similar to a piece of fluff. It is remarkable that in all the places where they are found there exist objects similar to them. For example, the white galls on gray sagebrush are the same size; the dried fruit of the Accurai are similar in shape and color. But most often, these robber flies can be confused with balled up spider webs that cling to the end of a branch.

This species is particularly changeable. The variations in the thickness and arrangement of abdominal hairs is very great. Individuals, which are found on sandhills where dry plant stalks reach a height of two or more meters (and consequently the robber flies sit high above the earth), have abdomens covered thickly and evenly with hairs. In places where robber flies have to seek prey on sagebrush at a height of 30 to 50 cm above the ground, the abdomen (and the entire body) is covered with thinner hairs, and there are more spots of silvery pollen on the tergites.

Consequently, in places where robber flies are forced to hunt prey near to the ground and there is less movement of the air, pollen serves as an "isolator." Where there are heavy winds high above the ground, they are covered with thick hairs.

All of these examples reaffirm the connection between habitat (climate), season, way of life, and the down of the robber flies, and they correspond with the situations found for *Stenopogon*. In the example of the genus *Holopogon,* we see once more that it is concentrated in one or rarely two topographical areas, while *Stenopogon* is found in four. Therefore, it is difficult to separate the dependence of external physical characteristics from conditions of environment.

Possible exceptions

In the preceding part of this article, examples were given showing that similarities in the coloration of different robber fly species (their bodies and down) correspond to the characteristics of their habitats. I will deal concisely with the exceptions among males. *Selidopogon octonotatus* flies in the desert during May to June. The body of the male is black and the abdomen is not covered with pollen, which, according to our classification, agrees with a habitat in the northern plains and high mountains (topographical groups I and II, Table l). At the same time, the female has a red abdomen, characteristic of the species of the third landscape group of the type *S. macilentus*.

Living in the desert, the females possess an "antithermal" color on the abdomen. Why then is the male's abdomen black? It was noted that during the flight period of *S. octonotatus* the large *Sphex* flies in the same places. There is a direct correlation of male and female color among these species. Earlier (Lehr, 1958) we considered that these Hymenoptera serve as a model for our robber flies. The question then arises, what color variations are there between the sexes of the digger wasps? The difference in male and female robber fly behavior might shed some light on this question. The males of *S. octonotatus* appear earlier than the females, and their flight ends later. Their daily regime consists of exhausting searches for the females. This male robber fly flies several meters, looking into every small corner, stopping to rest only for a few seconds. When he finally finds the female he enters upon a lengthy and complicated courtship.

The major portion of the day for the female is spent hunting prey. Even during the male's courtship she does not cease capturing insects. Waiting for prey, the female sits on the short grass "of the meadows", near tall plants of the Compositae family, most often sagebrush, briars, etc. She sits where there is no wind and it is hot and where there are many Dipterous and Hymenopterous plant pollinators, which compose 63% of her food. In other words, the greater part of the female's day passes in a hot, quiet atmosphere, close to the ground.

The male, however, for the greater part of his day flies above the plants, where there is more wind and the air temperature is lower. His life passes in the "*Holopogon* zone."

Possibly, this behavioral difference is the basic reason for a color variation between the male and female. Shtakelberg's proposition (1940) that in the arctic the more mobile males lose heat easily and therefore have more developed body down can be accepted as an explanation of the pigmentation difference of the robber fly sexes. Does a similar explanation fit the digger wasps? In search of prey (food for the larvae), the females of these insects run on the ground and dig holes in the earth. They spend a greater part of the time in hot air close to the soil. But the male, as a rule, keeps to flowers, i.e., in the "*Holopogon* zone." From this we can assume that difference in behavior clarifies the color variations of the sexes. A great part of the lives of the different sexes from these species is passed in environments with different microclimates.

S. octonotatus is not the only exception, at least in sexual color variation, but rather the rule for an entire group of desert species. A complete analogy is observed with *Saropogon dasynotus*. The female *Saropogon pittoproctus*, which flies in July to August in sandy deserts, is of a yellow color, but some males have black color patterns on the abdomen.

The males and females of the majority of species have the same body coloration. But the development of individuals under conditions noticeably distinguished from the optimum (boundaries of distribution areas, sharp digressions from the average weather for the season) is accompanied by two possibly interdependent causes: the male population is more active than the female, and the color of the male differs from the general type approaching that of *Selidopogon* (Table 2). Thus, the females of *Stenopogon macilentus mongolicus* Lehr are almost indistinquishable from *S. macilentus*, while at the same time the males' abdomens are almost completely black. Enderlein (1933) described two species of *Stenopogon* from Pamir where the female had white body hairs and the male black. In fact, they belonged to the same species. At any rate, since then there have been some 20 individuals of this species collected from Pamir (by Gorodkov and Lopatin), but not a single male had white hairs and vice-versa. We could cite additional similar examples. Incidentally, the red abdominal color of the forms *S. hradskji* often appears on the females and very rarely on the males (Table 2).

Mimicry

In the preceding chapter, we discussed the causes of color similarity among individuals of opposite sexes of the robber fly *Selidopogon octonotatus* and of digger wasps. On the basis of these examples, can we consider that, under the influence of lengthy selection, a form of robber fly developed that had such differently colored representatives of the sexes only because the identically colored stinging digger wasps flew at the same time?

The numerous *Dioctria* are found in the northern areas of Kazakhstan, among the thickets of the southern mountains and in tall, thick grasses during the first summer months. In the foothills of Zailiiskii Ala-Tau, these robber flies are often seen during the first part of their flight (end of May) sitting on top of plants. Later, when it is hotter and drier, they disappear under bushes in thick fruit orchards or in tall grass. The body of these flies is narrow, easing their flight in thick underbrush. As inhabitants of dark places, they naturally have a black color.

Wasps of the Ichneumon family, similar to *Dioctria* in external features, flight, and color, can also be found in these same places. Even after a lengthy study of both types, it is often difficult to establish whether a specimen is a representative of *Dioctria* or Ichneumonidae. According to the widely accepted literature on mimicry, it is possible to assume the robber flies are imitating the ichneumon flies. But knowing their way of life and the influence of environment on color, it would be more correct to consider habitat as the cause of their similarity.

On the other hand, among robber flies we do have examples of indutible imitation of Diptera, Hymenoptera. The larvae of *Hyperechia* feed on the larvae of *Xylocopa* (Poulton, 1924) in their nests. Externally the adult predator and the victim are quite similar, and they even hunt and gather food in the same places. *Saropogon alternatus* Loew is found on the mountain slopes of Middle Asia, and this insect is similar in body shape and red color to the plicate winged wasp (Vespidae). The wasp builds its nest where the robber fly flies. Many *Laphria* imitate bumble bees in all aspects. It would be difficult to negate mimicry in these cases.

We are able to present the following picture of the formation of robber flies that are externally similar to the stinging Hymenoptera. The possession of a new habitat by insects, as a rule, is accompanied by changes in color and sometimes in body shape. In the course of time, the similarity of pairs of such species of phylogenetically remote groups can, under the influence of an identical environment, obtain such closeness that their general and possible enemies (birds, lizards) often mistake them. From this moment, natural selection, which serves to perfect the primary similarity, acquires a greater significance.

Factors that compel species to move to new habitats

We shall consider the factors that cause the relocation of individuals of a species from a large territory to other habitats or the changing of the flight period to another season. For this we will again return to the genus *Stenopogon. S. avus* is possibly more universal in this matter. A special article (Lehr, 1961) has been devoted to its biology in which it is referred to as *S. heteroneurus* Macq. In that article, the population of this species was divided into two parts: the first occurs at the time of the flight of the Morrocan locust (*Dociostaurus maroccanum* Thunb.) and the second at the flight of the Turanian locust. Males of *Calliptamus barbarus* compose the basic food of this species. As subsequent observations indicated (1960-1961), this difference occurs even in places where there are no Morrocan locusts, and the entire population of this species appears when the Turanian locusts becomed winged. In our opinion, this division of population according to flight time is the beginning of a split of one species into two, a parallel adaptation to hunting prey with other characteristics also taking place. The change of a flight period by a species is equal to a change in habitat with different climatic factors. It is possible to illustrate this with many examples, especially among related species of robber flies that live in the same places but differ in genitalic structure and flight period. These are *Eremisca vernalis* Zinov. and *E. autumnalis* Zinov., *Apoclea helvipes* Loew and *A. trivialis* Loew. These have already been mentioned, as have *Machimus rusticus* and *M. alatavicus*. Their flight periods partially overlap one another, and for the species of *Apoclea* we possess an actual hybrid (a female). The move to a habitat in saltmarshes can serve as another example. *S. avus* is found exclusively on the prairie, ventures into the desert only on the boundaries of Kzyl-Kumy following the loess areas, but never is found in marshes or saltmarshes. Differences among this group are in the lengthening of the top of the basistylus of the hypopygium and in smaller overall measurements.

Aside from this, females are distinguished by the length and thickness of the hairs on the mesodorsum. The small external differences and the complete lack of color variation cause us to think that this subspecies was isolated only recently. The course of the process can be presented in the following manner. During certain years, the prairie vegetation burns out early and even the locusts become rare, flying to new places with richer growth. At this time, despite the weather, saltwort blooms in the saltmarshes. These thick and succulent plants attract numerous types of insects, such as locusts, flies, and bees—pollinators of the saltwort. Several species of robber flies fly at this same time. The saltmarshes are surrounded by prairie, which is usually populated by many *S. avus*. During drought years, the prairie is poor in prey, and it is completely natural that robber flies would move to places where prey is abundant. It is completely possible that part of the population gradually adopted a permanent habitat among saltwort. It is interesting that another species, *S. markovskii*, is found in the saltmarshes. This species is very similar in size and color to *S. avus solsolacearum*. Both sexes of these two species have the two final abdominal segments almost always colored red, which distinguishes them from other related species of the genus. But in the structure of the hypopygium this species is close to *S. macilentus*, i.e., to another group of robber flies. Analogous examples also can be found for species of other genera.

Therefore, the migration of some individuals of the population of a species to new places can be forced by the need to seek areas abundant with prey. In the new conditions, changes occur, first of all in color, but sometimes in size. Often the appropriate pigmentation cannot become apparent, however, as it is suppressed by adaptative factors (*Ctenota* and the saltmarshes in the prairie). But almost always in such situations the genitalic structure changes, although insignificantly. The stimulus of these changes is still unclear, so it is best to proceed from correlative causes. Habitat plays the most important role. Each part of the male's hypopygium fulfills its function of supporting the female during mating. The migration to new areas creates other positions for the mating individuals, depending on characteristics of the landscape, vegetation, wind, etc. And this can serve as the basic cause of the lengthening or shortening of certain parts or of the formation of new growths. It is possible that some small changes in the ovipositor, in connection with new egg-laying sites, are reflected in the structure of separate parts of the male's hypo-pygium. We often can speak seriously of a new species when variations in the hypopygium occur. In related forms, the latter changes after a long existence under conditions differing from the original environment. In other words, we can assume that migration into new habitats or a change in flight period is usually compulsory and occurs from lack of food. For predatory flies the ability to propagate depends upon this primary stimulus.

The question arises, is the change in diet one of the positive factors that determines the “split” of a species? In our opinion, this is hardly credible for robber flies. A great majority of these predators feed on the most diversified groups of insects. On the left bank of the SyrDarya river in 1957, 37.8% of *Promachus leontochlaenus* prey was composed of beetles of which 15.2% were *Cyriopertha glabra* Gebl. and 13.4% were a *Gymnopleurus* dung beetle. In 1959, in the Golodny steppe, another population of this same species had a diet composed of 29.3% beetles, of which only one specimen was of the species abundant in the feeding for 1957, and 67.3% Diptera, of which 32.7% were house flies. We did not notice any difference among the individuals of these populations; although judging by the vegetation, their prey composition must be approximately the same every year for each of the mentioned sites (Lehr, 1961). The prey of *Eutolmus implacidus* was composed of 42% (in separate years up to 60%) of *Blitopertha variabilis* Ball (Lehr, 1962). The individuals of the population in south-eastern Kazakhstan, however, are unable to have it in their ration since this beetle is not found there. However, among individuals of these separated populations there do not appear to be any differences. Strictly speaking, we know of only one robber fly that displays narrow specialization. This is *Neolaparus mesasiaticus* Lehr, which feeds exclusively on the ant, *Cataglyphus pallidus* Mayr. It is true that during the hunt for different types of prey robber flies develop a conditional reflex (Lehr, 1961). *Promachus leontochlaenus* is only able to capture the rapid flying *Gymnopleurus* when it “trains” itself to hunt the slower flying beetles that are similar in size and color. Conversely, it was observed in 1959, when the Diptera and Hymenoptera disappeared the entire population died off as its members were unable to adapt themselves to hunting the numerous *Gymnopleurus*. It may be entirely possible that such a difference in acquiring a hunting habit by individual insect groups could serve as the basis for a digression in their detailed structure, a structure that provides them with the opportunity to capture a certain species of prey. However, in such a case, the cause of change would not be in the food composition but in the behavioral characteristics of prey in particular. In the above case, the cause of change is the speed of flight. And it is in this category that we must make note of a structure that distinguishes the tribe Acanthocneminae: the presence of a thorn-like spur on the front tibia.

All the robber flies known to us and systematically classified into groups feed on Diptera and Hymenoptera. This is the single group of any species whose hunting objective is divided by narrow constriction between thorax and abdomen. In order to completely suck the prey dry, it is necessary to turn it over so that first the abdomen and then the thorax is emptied. The above mentioned growth is to ease the quick turning of the prey. The special need for hunting a particular prey caused the development of such a growth. It then became the mark of an entire generic group. In Koshanchikov’s opinion (1959), the lone case, “which cannot be repeated in ecological experiment ,” where the forming of a species is due to feeding specialization, is seen in the example of the willow beetle. However, in his opinion, much time is needed for such cases. Morphological variations of filial species are practically lacking.

Peculiarities of robber fly evolution

In a comparison of our 38 species of *Stenopogon*, we noticed an astonishing consistency in body shape, size, number and arrangement of setae and hairs, and an amazing similarity of the color of definite topographical robber fly groups. Therefore, in composing a descriptive table of a genus it is very difficult to find exact markings that would help to distinguish related species. Together with this “absolute” similarity, inhabitants of close or the same environmental conditions have a distinctive difference in their hypopygium, which shows the long isolation of some of these homologous forms. At the same time, the presence of species similar in body form but related in genitalic structure to different groups convinces us that these species arrived in the same place by different routes. These conditions alone are the cause of their complete external similarity. However, exceptions do exist, created by specific robber fly behavior. *S. porcus* Loew (Lehr, 1958) can serve as one of the examples of an exception among known species of *Stenopogon*. Although the main prey of species of the genus is composed of flying insects, the prey of *S. porcus* is composed of 75% locust nymphs, bugs, and spiders. All (other) robber flies throw themselves at insects flying past. It is a characteristic of *S. porcus* to notice any insect seated on a plant (attracted by the movement of legs or antennae) and at once capture it. The robber fly attacks its prey from a short distance. After the prey has been paralyzed, the majority of robber flies carry it onto a plant. *S. porcus* crawls onto the ground to devour its prey. In addition to hunting peculiarities, this robber fly species has a certain atypical form. Its body is narrower and wings are shorter (they cover only 3 to 3.5 segments of the abdomen) than for the other species (Fig. 8 and 9). Aside from this, it has numerous well-developed dorsocentral setae in the prescutal part of the mesodorsum. An acquaintance with the behavior of other representatives of the genus makes it possible to picture how this species was formed. *S. avus*, which flies later than *S. porcus* but in the same places and hunts flying locusts, has a method of hunting prey similar to *S. porcus*. This is especially noticeable in hot and dry years or under unfavorable conditions. Usually the measurements and type of insects that serve as food for *S. avus* are uniform (Lehr, 1961). Primarily, food sources are locusts, but before the locust masses receive wings, they can be any of a number of insects. But in 1959, we took from a robber fly a female *Sphingonotus satrapes* Sauss., which significantly surpasses the robber fly and its usual prey in size. She was captured after several days of hunger because of strong winds. There was an even more astonishing case in 1961, a year of very high temperatures and dry air. The robber flies were obviously hungry and, in addition, they were forced to compensate for the dryness by sucking on a large number of insects. Under such conditions the robber fly prey consisted of 8 (5.3%) praying mantis nymphs and even one adult *Empusa* (Mantidae). For the past 10 years we had not come across any of these immobile insects. We can say the same for crickets and female locusts. In normal years, they are seldom found among robber fly prey. Hence, hunger and thirst compelled this robber fly to hunt prey rarely found in its diet (nymphs of immobile praying mantids). Under similar conditions during the drought of 1955 in the Priliiskii desert, we were able to observe how *S. avus* seized a cricket (*Mitrioptera*) that had already seated itself on the ground when the predator attacked.

Under extreme desert conditions, sometimes more severe than the present, one of the species of *Stenopogon* (of the group laevigatus) gradually began to feed on locust nymphs, causing a series of changes in the form of this species and distinguishing it from other representatives of the genus. In our opinion, the formation of *S. porcus* is not completely finished since only 25% of flying insects are found in its diet. But, simultaneously, this species has become very specialized, which can be seen by the presence of not only spiders but of other largely immobile nymphs of *Cadophila varia* F. (pentatomids) in its feeding. These bugs are very numerous in the desert. Having acquired the habit of hunting these bugs, the robber fly can still widen its feeding circle. But at the same time, the shortening of the wings could hardly allow this robber fly, or any other similar species, to hunt flying insects. In most cases, winged individuals were captured while sitting on plants. In general, the ability to capture sitting insects was observed at times among other species of the genus (*S. albociliatus, S. avus*). This eases the transfer process of hunting larvae (nymphs), almost immobile, or sitting insects considerably. *S. porcus* is more flexible than *S. avus* and many other species of the genus. It is found in saltmarshes and marshes. We did not observe any change in its external form in these places.

In the example of *S. porcus* we can see the cause of a sharp morphological variation from original forms. This is seen first of all in its peculiar behavior. It is the exact similarity in behavior, manifested most of all by a conformity in hunting prey, that makes all the remaining 30 species of the genus externally indistinguishable. Their old methods of hunting provided these insects with enough food in the most varied climatic conditions. And if it were not for color and the hypopygium, we would not be able to find variations, despite the great difference in habitat conditions. Due to the fact that various topographical areas caused color digressions, we can say that we are dealing with different species. Since their separation from the original forms, these species have adapted to a great number of habitats, while others, possibly, have gradually returned to the original forms.

Continuing a discussion on the conformity of structure and of behavior of *S. porcus*, we can assume that due to its peculiarities, the indicated species could develop into an original form of a specialized group of robber flies. Because it has acquired the ability to hunt immobile or seated insects (for example, bug nymphs), this species could cease hunting locust nymphs and begin to feed on insects of different groups that are similar in behavior. Then it would be in the position to assimilate even greater varied biocoenoses and, not finding any competitors in other topographical areas, to acquire another color and corresponding digression in genitalic structure. This group of similar species could then be separated into a larger taxonomic class. Based on an analogy of the structure of species that feed on immobile insects (Leptogastrinae), it can be expected that if the future *S. porcus* moves among thick plant undergrowth as the present form does, there will be a greater narrowing of the body; i.e., it will change to become more similar to *Leptogaster*. Hence, *S. porcus* of the future (with a further specialization of feeding on immobile, seated insects) could acquire a distinctive form close to that of *Leptogaster*. However, it is necessary to take into consideration the difference in original forms.

Therefore, it is possible to assume that the formation of new species takes place with the migration of a significant part of the population, usually on the edges of distributional areas, to a habitat in places with a different climate and a different environment. Such a migration is connected to the possibility of obtaining enough prey in new conditions (*S. avus solsolacearum*). This is helped by a tangible competition in biocoenosis. In the example of *S. porcus*, this is seen in the abundance of locust nymphs and in the absence of serious predatory competitors. Most probably, the lengthy existence of a particular numerous species or of a group of species related in behavior patterns always attracts a number of specialized predators that live at their expense. If these large species, after producing distinctive predatory forms, become rare, then the special features acquired by the predator lose their meaning. And these species either die out or become “original material” for the formation of new forms that will adapt to living upon other large groups of insects. It is possible that a species or a separate population within the limits of a distributional area can be forced to adapt to new conditions because of climatic changes, which we have seen in the example of *Leptogaster cylindrica tesquorurn*. If the prey that is abundant in new places demands different methods of hunting, then the external form of the species gradually undergoes a series of changes. These are found in more or less sharp morphological digressions (*S. porcus*).

Summarizing all the previous examples and discussion, we shall endeavor to present a general picture of the evolution of some robber fly species based on the conviction that species-formation begins with the migration to places with different climates (a different environmental habitat). This migration is accompanied by biochemical changes in the organism and is secured by behavioral characteristics. In our article, we have often stressed the fact that a species moved into new conditions or that a similarity speaks of the recent isolation of a species. But at the same time, we always assume this process is not sudden but very long and slow, and that qualitative variations, especially morphological ones, reach a "finished form" only after many generations.

The formation of robber fly species from the end of the Tertiary period to modern times

It is generally known that in places where the habitat has long remained unchanged there still survive ancient species who appeared millions of years ago. On the contrary, the land surfaces, subject to frequent and sharp climatic changes and mountain formation processes, are characterized by the dying out of some groups and the appearance and flourishing of others. "If the periods of warmth and rapid vegetation growth during the middle of the Mesozoic age, continuing for hundreds of millions of years, had remained until modern times, it is almost certain that we would not be writing these articles on climate" (Shepley, 1958, p. 9).

The stimulus to a change of the flora and fauna on the territory of Europe and Asia was a long climatic fluctuation, preceded by powerful mountain formation processes and by the drying up of the Tethys Sea. Later, this was helped by the beginning of the glacial age at the start of the Quaternary period, i.e., about six-hundred thousand million years ago.

From this period, we will try to systematically present the evolution of the species of several groups of robber flies. It is useless to follow these climatic fluctuations, recessions, and advances of glaciers. This problem still remains unclear, although it is precisely these sharp and frequent climatic fluctuations over small territories that are one of the causes of the appearance of such a variety of related or convergent species of *Stenopogon* at the beginning of the Holocene age.

In the Neocene, age the steppes and deserts probably covered a much larger area in Central and Middle Asia than at the present time (Krishtofovich, 1957). Due to the absence of significant mountain ranges on these areas, the Asian species were free to reach the Caspian Basin. In the spacious steppes at the end of the Tertiary period, we should find the original forms for our four to five distinctive groups of *Stenopogon*, each of which could have been at that time represented by one, or at least two, steppe species. The advance and recession of mountain glaciers in Middle Asia compelled the original species to move many times from the mountain slopes into the valleys and then to settle again in the mountains, constantly seeking the best environmental conditions. Such instability of habitat conditions enabled changes to take place in these species. Among them occurred an intensification of seasonal changes as shown in the example of *Eutolmus implacidus*. Most of all, among the original forms, close to the third topographical group (Table 1), there occurred digressions that, on the one hand, brought them closer to the northern forms, and, on the other, to the contemporary high-mountainous species. The more often such digressions occurred, the more sharply, at least, two new topographical forms were separated from the one original species. This process of division can take place (almost in parallel) in the most varied places of Eurasia (Fig. 2) under the influence of related climatic changes. The similarity of fluctuations in the weather on such a large area, accompanied by a similar process of shifts in the mountain belts of Europe, Middle and Central Asia, and Asia Minor, could determine the astonishing convergence among different groups of species. And it is possible that only for this reason we find the shiny black *Stenopogon,* with all the markings suitable for inhabitants of the high mountains, in the most divergent places of the continent. Of course, during this span of time, the species in the formation process did not limit themselves to migrations within the boundaries of their original territory, but took over much larger areas. For at least one half-million years, the species from Central Asia penetrated to the Mediterranean Sea where in mountain conditions it met with *S. caracinus* Loew, of another remotely related group. On the steppes of Central Kazakhstan, *S. callosus* and *S. albopilosus* in the same places were indistinguishable from one another. But despite the fact that within a short historical time these species passed through sharp climatic fluctuations, despite the great migrations, descents into the plains, and returns to mountain habitats, their habits of hunting and means of feeding remained as of old. All these varieties of species, extremely close in external form but differing in color, reflect within themselves the topographical-climatic characteristics of their habitats. And only in the severe conditions of the desert, when the drought climate was at times more xerothermic than at the present, did two to three species show sharp digressions from the general type due to new hunting habits (*S. porcus*) .

We shall discuss in more detail the species of the group Macilentus (Table 1). The distribution of this group is more typical for representatives of Anagrskii fauna, and the abundance of species in Middle and Central Asia confirms this. Variations in the structure of the hypandrium affirm the presence of smaller subdivisions within the group, i.e., subgroups whose dispersion took place in three migration waves from Central Asia. The first pioneers were *Pronigriventris*, whose relatives at the present time occupy Southern Europe and Asia Minor after having assimilated all topographical-climatic zones (Table 1). During the glacial periods, representatives of these subgroups were isolated from their original habitats, and this, possibly, can explain the great split in distribution between them and the Central Asian forms. Only in Outer Baikal do we find a variation of *S. macilentus* that is close in genitalic structure to *S. callosus*. The period of migration came, probably, at the end of the Tertiary period, during one of the first interglacial periods. Significantly later, possibly during one of the last xerothermic periods, a second migration occurred. On the one hand, *S. macilentus* penetrated into the European plains. But somewhat earlier, probably following the recession of the glaciers from Asia Minor, representatives of the group *sabaudus* moved there. Thus, in the form of a convergent species (*S. sabaudus*), a dweller of the same biocoenosis as *S. macilentus*, the latter met a serious competitor. This assumption can explain the rarity of *S. macilentus* in Europe and the absence of close representatives in other topographical-climatic groupings. At the same time, in Middle Asia during this time span *S. macilentus* possessed typical variations of both an inhabitant of alpine meadows and of the plains (Table 1). Aside from this, in the collections from the European part of the Soviet Union there are a total of six specimens of *S.*

macilentus that composes 3 percent of the collections of this species from other parts of the distributional area. At the same time, *S. sabaudus* was collected from the same places for a total of 224 individuals.

At approximately the same time, there probably occurred a resettlement of *S. flavibarbis* from Kuen-Lun to the sub-alpine and alpine meadows of TyanShan and Pamiro-Altai. The low position of the glaciers in the mountains of Middle Asia contributed to this species overcoming the low mountain ranges covered at the present by deserts and semi-deserts and to its reaching Tavor. Due to a rather long geographical isolation, the original form gave rise to a rather distinctive subspecies, *S. flavibarbis occidentalis*. Just as *S. macilentus* found a competitor in the form of *S. sabaudus* in the European territory, *S. flavibarbis* found *S. caracinus* in Asia Minor. At this time all the topographical zones were already occupied by forms, related to the last named species (Table 1), and this probably explains the absence at the present time of forms related to *S. flavibarbis* in other topographies. This species did not penetrate into the Outer Caucasus. This “corner” was already occupied by convergent forms of several groups that had succeeded in aptly adapting to the new environment. Finally, the third resettlement took place from the beginning of the Holocene period up to present time. Following a warm period, two convergent forms entered into the steppes of Kazakhstan: *S. callosus* from the west and *S. albociliatus* from the east. The former of these is more mesophilous, and this explains the occurrence of these species in one another’s distributional area. Hence, the migrations of species to larger areas during historically long periods contributed to their geographical isolation, i.e., to a geographical formation of a species.

But we are convinced that populations can diverge because of “their ecological preferences and can attain the state of a subspecies and even a species by sympathetic means” (Mayr, 1947, p. 303). Somewhat earlier Mayr wrote, “All geographical races represent at least to some degree, ecological races...” (p. 288).

The examples mentioned earlier showing how a species acquired a distinctive color and body down under the influence of a particular environment (climate) testify to the reality of ecological (sympathetic) species formation. In addition, the desert species of each robber fly group are always easily distinguishable by their genitalic structure from the original representatives of the third topographical group [*S. marikovskii*, *S. avus*, and others (Table 1)]. At the same time, the inhabitants of the first topographical group are easily distinguished by color from those considered original forms and are almost never discernable by their genitalic structure (*S. flavibarbis* and *S. macilentus*, *S. laevigatus*, and *S. sabaudus*). The degree of variation can be compared to the amount of time a certain topographical area has existed (their habitat). Alpine meadows of any of the aforementioned mountain ranges are probably much younger than the steppes or deserts. On this basis, the majority of groups and subgroups shown in Table 1 can be considered polytypical species, while their topographical variations are subspecies. And within this polytypical species, there will be forms on different levels of species evolution—from those very isolated, *S. avus* and *S. marikovskii*, to those practically indistinguishable, *S. laevigatus* and *S. sabaudus*. Here, possibly, it is better to consider not only the geographical but also the ecological isolation because contact between the mentioned “species” occurs constantly. Simultaneously, in spite of our small amount of material, we are convinced that the variations of several close forms from Asia Minor are more important than those of the same species found in the European part of the USSR. In the first case, these are actual species, but in the second they are merely subspecies. *S. harpax*, a typical specimen from Asia Minor, obviously differs from *S. sabaudus* and fits among the inhabitants of the fourth topographical group, while at the same time all six individuals from the Ukrainian steppes, which are close to *S. harpax*, can be only considered as transitional forms. We can say the same about *S. laevigatus* and *S. sabaudus*. The glacial epoch is, possibly, an explanation of this. When the Asia Minor forms were ecologically isolated for a relatively long time, the Europeans were still in the beginning stages of this process. Here we can clearly see the influence of two factors: environment (ecology) and time.

We can create an analogy to this for other robber fly genera, whose ecology is more or less known to us. We have already discussed *Promachus*, although with it this process is less definite than with *Stenopoqon*. There are no variations in genitalic structure that can be explained by their later start in division of forms (the beginning of the Holocene period). They did not move beyond the edges of the steppes or deserts and did not leave any representatives in the high mountain belts or on the cool northern plains. But a species formation similar to *Stenopogon* can be found in the example of *Leptogaster*. On the basis of distribution, characteristics of habitat, and pigmentation, we can compare the species formation process, on the one hand, of *Leptogaster cylindrica hispanica* with *S. flavibarbis* and, on the other, of *Leptogaster stackelbergi* and *S. macilentus*. Although we do not know very much about the ecology of *L. stackelbergi*, *L. cylindrica tesquorum*, compared to an original species, is the same as *S. marikovskii* in relation to *S. macilentus*. However, the sharp morphological differences of *L. cylindrica* s. str. from *L. stackelbergi* allow us to assume their division began before the advance of the glacial epoch. At the same time, *L. c. tesquorum* is a phylogenetically young form, whose evolution from an original form in the dry steppes began, evidently, before the end of the glacial period, and whose habitat in comparison with its original form is close to that of *P. leontochlaenus*. A subfamily of Leptogastrinae has typical relicts. This is *L. helvola* Loew, which has no close species, and probably has remained unchanged from the end of the Tertiary period or even more remote times. *Euscelidia conopsoides* Pallas is in the same position. However, if the former of these is an inhabitant of the ancient Central Asian steppes, then the latter is a dweller of the Mediterranean steppes. It is possible, of course, that *L. cylindrica* is also an almost unchanged "relict" of the Tertiary period, but all the same, under the influence of the sharp climatic fluctuations of the glacial age, it divided into two subspecies. An example of a relict genus with several species is *Ctenota*, which has remained unchanged at least from the beginning of the Neocene period when it reached its height of development on a huge area of saltmarshes of estuary basins—the remains of the ancient Tethys Sea.

Conclusion

We have attempted to present a picture of the process of species formation under the influence of climate, feeding, changes of insect behavior, and on a knowledgeable basis of the many sides of a robber fly's life.

In search of abundant or at least enough food, predatory robber flies, usually on the edges of a distributional area, gradually move from one zone or belt into another over a great span of time in sections of their populations. The final settlement of new areas probably incurred a "change in the albuminous conditions of the tissue" (Ushakov, 1958), which can be seen in the steady changes of pigmentation. An entrance into new biocoenoses created the necessity to develop new habits, another behavior pattern that contributed to changes in the genitalia. But differences in the characteristics of habitat were not so important as to change the basic form of these species. Despite their abundance and great variety, they have remained monotypes as their behavior and hunting methods have also remained monotypical. And only the severe conditions of the desert allowed a sharp morphological isolation of some groups, i.e., an intensified development of a particular habit—to hunt seated and non-moving prey. Locust nymphs, the prey that was able to support the existence of *S. porcus*, was one of the most numerous insects of certain deserts and steppes. Peculiarities of behavior as an evolutionary factor were the cause of new forms, more concrete and sharp than all the climatic changes of habitats during a great span of time and geographical isolation. But even this process was not at all sudden. In difficult conditions there developed and became secure one feature that appeared in separate years among many close species: the hunt for almost inaccessible, crawling, and non-flying insects.

In this article we have not tried to illuminate all the many actual and possible causes of robber fly species formation. The general assumptions about the influence of climate on an organism are widely known (Mayr, 1947; Shapov, 1955; and others). Many examples can be taken from the field of agriculture. Despite the seeming contradictions of these ideas, the cause is the same—a change in habitat and climate, the basic components of this environment. The turnip moth serves as a good example (Kozhanchikov, 1959).