

Hosts and trophic specialization of bloodsucking biting midges (Diptera: Ceratopogonidae, Leptoconopidae) in southeastern Kazakhstan

Круг прокормителей и пищевая специализация кровососущих мокрецов (Diptera: Ceratopogonidae, Leptoconopidae) Юго-Востока Казахстана

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КЛЮЧЕВЫЕ СЛОВА: *Culicoides*, *Leptoconops*, Юго-Восток Казахстана, кровососы, автогенность, прокормители, рептилии, рукокрылые.

ABSTRACT. Original data, both published and unpublished, are briefly reviewed on hosts and trophic specialization of bloodsucking biting midges (Ceratopogonidae: *Culicoides*; Leptoconopidae: *Leptoconops*) in southeastern Kazakhstan. Direct observations and field experiments proved feeding of biting midges (*Leptoconops* spp.) on lizards and bats in Kazakhstan. The published records of biting midges feeding on reptiles are briefly reviewed. Bats are recorded for the first time as hosts of bloodsucking biting midges. Autogeny was experimentally studied in four *Culicoides* species; 100% autogeny of *C. riethi* females was confirmed. Host ranges and trophic specialization of biting midges are discussed in light of the epidemiological role of blood-suckers.

РЕЗЮМЕ. Кратко суммированы данные автора (как ранее опубликованные, так и неопубликованные) о прокормителях и трофической специализации кровососущих мокрецов (Ceratopogonidae: *Culicoides*; Leptoconopidae: *Leptoconops*) Юго-Восточного Казахстана. Наблюдения и полевые эксперименты позволили установить, что различные виды рода *Leptoconops* являются кровососами ящериц и летучих мышей в Казахстане. Приведен краткий обзор опубликованных данных о питании мокрецов на рептилиях. Летучие мыши впервые отмечены как прокормители мокрецов. Возможность автогенного развития яиц экспериментально изучена для 4 видов рода *Culicoides*. Подтверждена 100%-ная автогенность самок *C. riethi*. Круг прокормителей и пищевая специализация мокрецов обсуждаются в связи с эпидемиологическим значением кровососов.

To date, the females of most species in the genus *Culicoides* Latreille, 1809 and of many species in the

genus *Leptoconops* Skuse, 1889 are known as obligate blood-suckers on birds and mammals. Some species of *Culicoides* feed on engorged mosquitoes, for example, *C. anophelis* Edwards, 1922 [Edwards, 1923; Das Gupta, 1964]. Many species of *Culicoides* and *Leptoconops* readily attack humans. Trophic specialization of blood-sucking dipterans and their trophic relations with vertebrates are important for studies on the transmission and natural nidality of diseases. Data on host feeding patterns are very important in order to incriminate vectors of these diseases [Lvov, 1982; Glukhova, 1989].

Dedicated research on biting midges of Kazakhstan started as late as in the middle of the 20th century. M.S. Shakirzyanova is the author of the first publications devoted to the bloodsucking biting midges of Kazakhstan. In total, she gave descriptions of 29 species and provided data on their distribution [Shakirzyanova, 1963]. Zh.S. Smatov conducted long-term studies of bloodsucking biting midges in the Ili River basin, in Kustanai, Shymkent, Semipalatinsk and East Kazakhstan provinces [Smatov, 1966, 1976, 1978; Smatov & Kravets, 1973, 1976; etc.]. Smatov provided information on distribution of biting midge species in these regions, and on mass attacks by blood-suckers on humans and farm animals, but without precise quantitative data; his collections were made by net and aspirator. In southeastern Kazakhstan, the fauna of bloodsucking biting midges and their trophic links with hosts were studied mainly by Auezova (Kravets) and published in several papers [Auezova, 1979, 1982a–c, 1985, 1987a, b, 2006; Smatov & Auezova, 1979; Auezova et al., 1985, 1990; Glukhova & Auezova, 2005, 2006]. Some of these data were considered in monographs by Gutsevich [1973] and Glukhova [1989].

Material and methods

This paper is based on material collected and field observations made by the author in Dzhungar Alatau and adjacent territories in 1973–1998. One of the goals of the author was to acquire field data on poorly known hosts of biting midges [Auezova, 1982a, c; Auezova et al., 1985, 1990; etc.].

Natural conditions of the study region

Southeastern Kazakhstan is situated between Altai and western Tien Shan, and incorporates peripheral parts of the Central Asian mountain ranges, reaching the environs of Lake Balkhash in the northwest. Bloodsucking midges were studied mainly in Dzhungar Alatau (42–45°N 67–82°E) [Auezova, 1987a, b; etc.]. This mountain system includes a wide range of elevations, and the ranges extend east to west and are separated by valleys. The massif is divided by the valleys of the Koxsu River flowing to Balkhash and to the Borotal River flowing in the opposite direction, to Ebi-Nuur Lake in China. Absolute heights reach 4464 m, and the landscapes include many plateau-like areas at different heights [Kaletskaia et al., 1945; Gvozdetskii & Nikolaev, 1971].

Climate is strongly continental. Annual precipitation is 500–800 mm per year. Vegetation cover is diverse, with vertical zonation from deserts to alpine meadows [Rubtsov, 1948]. River network is poorly developed; rivers mostly have glacial feeding, combined with lower atmospheric and subterranean inputs, and surface flows are mostly in deep canyons. Beds of numerous temporary streams are dry for most of the year. In the plains, there are many areas featuring sandy deserts and semi-deserts. In the level river valleys, sandy soil types include many wet and marshy habitats, as well as small spring-fed pools and lakes between dunes. They are habitats of large-scale development of biting midges. The localities and habitats used to study feeding of biting midges on reptiles and bats will be described below in more detail.

Methods

Adult midges were collected by standard methods [Gutsevich & Glukhova, 1970; Gutsevich, 1973] with minor additions. Midges were collected near humans, domestic and farm animals with a net and an aspirator. Faunal collections were made by net-sweeping trees, bushes and grassy vegetation, and also at light. Sticky traps were used to collect midges near birds' nests and holes of small mammals (mostly, rodents). Commonly, 20 × 20 cm tracing paper sheets covered with castor oil on one side were used. Sticky sheets were placed near and above the open nests, on the walls and eaves of buildings near the hidden nests, and at the entry to holes. Sheets were removed and examined on the next day. The midges were cleared in 96% ethanol and stored in 70% ethanol.

When possible, blood-suckers were collected directly from nestling birds and other animals with an aspirator. The technique of sampling from lizards and bats will be described below. The midges were collected from their hosts only while they were blood-feeding, to ensure validity of data.

Autogeny of biting midges was studied by rearing adults from field-collected larvae and pupae, according to the technique described by Glukhova [1989, 2002].

Bloodsucking biting midges on different hosts in southeastern Kazakhstan (a brief review of original data)

Bloodsucking females of *Culicoides* and *Leptoconops* in southeastern Kazakhstan have a wide range of hosts, including man, domestic and farm mammals and poultry, as well as numerous wild birds and mammals, including rodents and (as reported here) bats. Some *Leptoconops* also feed on reptiles.

The highest number of species (28) has been recorded to take blood from larger farm mammals, mainly from horses (*Equus caballus* Linnaeus, 1758) and cattle (*Bos taurus* Linnaeus, 1758). There are 21 species of *Culicoides* and 7 species of *Leptoconops* that attack these two hosts: *Culicoides chiopterus* (Meigen, 1830), *C. chitinosus* Gutsevich & Smatov, 1966, *C. desertorum* Gutsevich, 1959, *C. fascipennis* (Staeger, 1839), *C. festivipennis* Kieffer, 1914 (= *C. odibilis* Austen, 1921), *C. griseus* Edwards, 1939, *C. heliophilus* Edwards, 1921 (= *C. latifrontis* Shakirzjanova, 1962), *C. kibunensis* Tokunaga, 1937 (= *C. cubitalis* Edwards, 1939), *C. manchuriensis* Tokunaga, 1941, *C. maritimus* Kieffer, 1924, *C. minutissimus* (Zetterstedt, 1855), *C. mongolensis* Yao, 1964, *C. obsoletus* (Meigen, 1818), *C. odiatus* Austen, 1921, *C. pictipennis* (Staeger, 1839), *C. punctatus* (Meigen, 1804), *C. puncticollis* (Becker, 1903) (= *C. algecirensis* (Strobl, 1900)), *C. riethi* Kieffer, 1914, *C. subfascipennis* Kieffer, 1919, *C. tadjikistanicus* Zhogolev, 1969, *C. turanicus* Gutsevich & Smatov, 1971, *Leptoconops amplifemoralis* Chanthawich & Delfinado, 1967, *L. bidentatus* Gutsevich, 1960, *L. borealis* Gutsevich, 1945, *L. lucidus* Gutsevich, 1964, *L. laurae* (Weiss, 1912) (= *L. mediterraneus* Kieffer, 1921), *L. montanus* Konurbaev, 1965, and *L. turkmenicus* Molotova, 1967.

A relatively large number of species (25) attack man (*Homo sapiens* Linnaeus, 1758). Among these, there are 18 species of *Culicoides* and 7 species of *Leptoconops*: *Culicoides asiaticus* Gutsevich & Smatov, 1966, *C. chiopterus*, *C. chitinosus*, *C. desertorum*, *C. iliensis* Gutsevich & Smatov, 1966, *C. heliophilus*, *C. kibunensis*, *C. manchuriensis*, *C. minutissimus*, *C. mongolensis*, *C. obsoletus*, *C. odiatus*, *C. punctatus*, *C. puncticollis*, *C. riethi*, *C. subfascipennis*, *C. tadjikistanicus*, *C. turanicus*, *Leptoconops amplifemoralis*, *L. bidentatus*, *L. borealis*, *L. lucidus*, *L. laurae*, *L. montanus*, and *L. turkmenicus*.

The number of species collected from smaller vertebrates is much lower, possibly because of limited sampling effort. Eleven species have been recorded as blood-feeders on poultry and wild birds: *Culicoides circumscriptus* Kieffer, 1918, *C. festivipennis*, *C. heliophilus*, *C. kibunensis*, *C. minutissimus*, *C. mongolensis*, *C. punctatus*, *C. simulator* Edwards, 1939, *C. turanicus*, *Leptoconops lucidus*, and *L. bidentatus*. Six species were

recorded as blood-feeders on dogs (*Canis familiaris* Linnaeus, 1758): *C. chiopterus*, *C. minutissimus*, *C. subfascipennis*, *C. turanicus*, *L. lucidus*, and *L. laurae*. Four species were recorded as visitors of inhabited burrows and probably therefore are blood-feeders on the Libyan jird (*Meriones libycus* Lichtenstein, 1823) and other small rodents in sands of the Sary-Eshik-Otyrau Desert south of Lake Balkhash (46°N 75–76°E). These species are *Culicoides desertorum*, *C. odiatus*, *Leptoconops lucidus* and *L. bidentatus*. In addition, one species, *L. bezzi* (Noè, 1905), was recorded as blood-sucker of bats (see below), and two species of the same genus, *L. minutus* Gutsevich, 1973 and *L. sp.*, as blood-suckers of lizards (see below and also Auezova [2008, in this volume]).

In floodplain forest habitats *C. punctatus* was predominant in the collections from larger farm mammals, and *C. griseus* was the subdominant species. In contrast, humans were attacked in floodplain habitats mainly by *C. minutissimus* (usually 20–40%), and in some samples this species accounted for 100% of total numbers of biting midges attacking people. In steppe habitats, *C. subfascipennis* was predominant in the collections from larger farm mammals (50–99% of the total numbers); *C. punctatus* and *C. puncticollis* were abundant as well. In steppe habitats *C. subfascipennis* predominated also in the collections from humans (up to 79%). In the desert habitats, *C. puncticollis* and *Leptoconops* spp. predominated as blood-suckers of larger farm mammals. On the other hand, humans were attacked by *L. lucidus* (dominant) and *L. turkmenicus* (subdominant).

Collections of biting midges from birds are of particular interest. Some species of *Culicoides* were recorded in different regions of the former USSR as predominantly (*C. reconditus* Campbell & Pelham-Clinton, 1960) or exclusively ornithophilic (*C. salinarius* Kieffer, 1914, *C. circumscriptus*, *C. sajanicus* Mirzaeva, 1971, *C. sphagnumensis* Williams, 1955) [Butenko, 1967; Chunikhin & Gutsevich, 1968; Glukhova, 1989]. In the region under study *C. minutissimus* was the most abundant blood-sucker of poultry—hen (*Gallus gallus* Linnaeus, 1758) and duck (*Anas platyrhynchos domestica* Linnaeus, 1758). The percentage of *C. minutissimus* in the collections was from 86 to 99% [Auezova, 1982b]; *C. kibunensis* and *C. heliophilus* each contributed up to 10% in some collections. All other species of *Culicoides*: *C. circumscriptus*, *C. festivipennis*, *C. salinarius*, *C. simulator* and *C. turanicus*, were common but not abundant. Ducks were attacked also by *Leptoconops lucidus*. Several species of bloodsucking midges were collected from nestlings and trapped with sticky paper sheets at nests of wild birds: the little owl (*Athene noctua* (Scopoli, 1769)), rock pigeon (*Columba livia* Gmelin, 1789), lesser spotted woodpecker (*Dendrocopos minor* (Linnaeus, 1758)) common swallow (*Hirundo rustica* Linnaeus, 1758), house sparrow (*Passer domesticus* (Linnaeus, 1758)), tree sparrow (*Passer montanus* (Linnaeus, 1758)), and magpie (*Pica pica* (Linnaeus, 1758)). Seven species have been collected from those hosts: *Culicoides circumscriptus*, *C. festivipennis*, *C. minutissimus*, *C. simulator*, *C. salinarius*, *C. turanicus*, and *Leptoconops lucidus*.

Biting midges as blood-suckers of reptiles

Reptiles as possible hosts of bloodsucking biting midges deserve special investigation. Reptiles can be very important for transmission of infections and for maintenance of focal or perhaps zoonotic infections, because the abundance of these animals in arid regions is usually higher than that of birds and mammals. In this case, it is sometimes difficult to assess which group is more important as hosts of bloodsucking dipterans.

At the same time, reptiles are very poorly studied as hosts of bloodsucking insects. Among reptile blood-suckers, ticks of medical importance are the best-studied group [e.g., Paraskiv, 1956; Bogdanov, 1965]. Among the Diptera, Phlebotominae and Culicidae were recorded feeding on reptiles in Uzbekistan [Bogdanov, 1965]. The first observations of biting midges feeding on lizards were made and published by Auezova, Brushko and Kubykin [Auezova et al., 1985, 1990; Auezova, 1987]. No other published data were found about parasitism of biting midges on reptiles in Kazakhstan and Middle Asia.

There are only a few other publications about reptiles as hosts of biting midges in the World. Among them are records only from lizards and turtles. *Leptoconops californiensis* Wirth & Atchley, 1973 and *L. sp.* near *knowltoni* Clastrier & Wirth, 1978 fed on five species of lizards in California and Mexico [Mullens et al., 1997], and *Forcipomyia (Lasiohelea) sp.* fed on iguanas in Costa Rica [Borkent, 1996]. *Culicoides testudinalis* Wirth & Hubert, 1962 was found to take blood from freshwater turtles in eastern USA [Wirth & Hubert, 1962], *C. phlebotomus* (Williston, 1896) was observed feeding on a sea leatherback turtle (*Dermochelys coriacea* Linnaeus, 1766) in Costa Rica [Borkent, 1996]; finally, *Leptoconops bezzii* (Noè, 1905) and *L. irritans* (Noè, 1905) were recorded biting on the terrestrial tortoise *Testudo graeca* Linnaeus, 1758 in Syria and Lebanon [Moravec & Országh, 1998; Široký et al., 2007]. Apparently it is very difficult to observe blood-feeding in the nature on most of smaller motile terrestrial reptiles, such as lizards or snakes.

The material reported here was collected in two adjacent localities in southeastern Kazakhstan (Taldykogran Province, Dzhapalakkum Sands in Ili Valley north of the Ili River, ca. 44°N 79°E; and Almaty Province, Ul'kunkum sands near Charyn River and Charyn village, Ili Valley on the opposite bank of the Ili River, ca. 43°50'N 79°15'E) since early June till mid-July 1979. The habitats included sites of partly stabilized coarse sand with gravel and stones, and small patches of solonetz and takyrs. The predominant tree was *Populus pruinosa* Schrenck; other common plants were *Haloxylon aphyllum* (Minkw.) Ilin., *Ferula iliensis* Krasn. (Apiaceae), *Berberis iliensis* M. Pop. (Berberidaceae) and *Calligonum triste* Litw. (Polygonaceae). In the study localities, a total of ten lizard species and four snake species were recorded [see Auezova et al., 1985 for details].

During the study of fauna, abundance and diel activity of biting midges in these localities, high levels of biting activity of midges attacking humans were observed from 5-00 until 22-00, with *Culicoides* active mostly early in the morning and late in the evening, and *Leptoconops* active from 10-00 until 19-00. Numbers of biting midges collected from man in ten minutes ranged from 63 to 527 individuals, depending on the time of day (on the average, 376 ind.). Most abundant species were *Leptoconops lucidus*, *L. bidentatus*, *L. turkmenicus* and *Culicoides minutissimus*.

At the same time, observations on the activity of lizards during the day revealed that resting and hunting lizards were often attacked by small biting midges, later identified as *Leptoconops* [Auezova et al., 1985, 1990]. Biting midges were recorded on three lizard species: *Phrynocephalus versicolor* (Strauch, 1876) (Agamidae), *Eremias velox* (Pallas, 1771) and *E. intermedia* (Strauch, 1876) (Lacertidae). Midges took blood from young and adult *Eremias* spp. of both sexes, and from adult and subadult *P. versicolor* of both sexes.

From June 17 till July 11, eight instances of blood-sucking by *Leptoconops* on *P. versicolor* were recorded. The attacks by midges were observed from 9-00 until 19-00 at air temperature of 29–35°C. In three of these cases, midges fed on *P. versicolor* when the weather was cloudy, wet or rainy. A single midge was observed on six individuals of *Eremias*, and two and six midges, respectively, on two more individuals. Maximum numbers of midges were recorded on moulting lizards. The midges preferred to bite the sides of the body, neck, head (e.g. near eyes), and legs of lizards. Apparently, the attacks were annoying for the lizards, as they tried to remove the blood-suckers.

To collect midges from lizards in the field, the following technique was used. Small wooden boards were prepared, with small nails driven in their lateral sides. Each lizard caught was temporarily and carefully tied to a board by the legs with soft strips of cloth. The strips were attached to the nails. The board with the lizard was placed for several hours in the shade of a bush in the same place where the lizard was collected. The experiment was conducted in three replicates with each species.

Midges attacked the same body parts as described above. Blood-sucking lasted 2.5–3 minutes. Each midge took the full portion of blood (the abdomen became swollen and red in colour). After that, the midge fell away from the lizard and did not move for 20–30 seconds. Then, if not collected, it crawled a short distance and flew away. At the time of observations, air temperature near the soil surface in the shade was 44.0–48.5°C, at 1–1.5 m from the soil surface, ca. 34°C.

The midges collected in the field experiments were determined as *Leptoconops minutus* and *L. sp.* Some data on their morphology are given in Auezova [2008, in this volume].

In the study area, all reptiles except the tartar sand boa (*Eryx tataricus* (Lichtenstein, 1823)) and two species of Gekkonidae are active by day. They are active

during 8 months of the year, from March until October. In the hottest period of the year, in June–July, their activity is lower, but no summer dormancy is recorded [Auezova et al., 1985]. Thus, it is quite possible that reptiles play an important role as natural hosts of biting midges, and the range of reptiles as hosts for midges is much wider than is currently appreciated.

Biting midges as blood-suckers of bats

Several groups of arthropods are known as parasites of bats in Kazakhstan. Among them are ticks (*Argas vespertilionis* (Latreille, 1802), *Spinturnix* sp., etc.), fleas (*Ischnopsyllus elongatus* (Curtis, 1832)) and hippoboscids flies (*Stenopteryx hirus* (Linnaeus, 1758)) [Gvozdev & Strautman, 1985]. However, there are no data on bloodsucking biting midges feeding on bats in Kazakhstan. Furthermore, no published records of Ceratopogonidae or Leptoconopidae from Chiroptera are found in the world literature.

The material was collected on 27 June 1983 and on 15 July 1991, in two caves in the mountains of northern Tien Shan. They are situated in Boroldai Massif near the junction of Talas Range and Karatau Range (ca. 42°50'N 70°E, 760–1100 m above sea level; Shymkent Province in extreme south of Kazakhstan) and in Daubaba Massif of Talas Alatau Range near the village of Talas and the same-named river (ca. 42°30'N 72°30'E, 1500–1700 m; NW Kirghizstan near the border with Kazakhstan). The caves preferred by bats in the region are confined to uneven terrain in the foothills, with rocks and well-developed karstic formations [Shaimardanov, 1982].

The first colony of bats included 150–200 individuals, which were hanging from the ceiling and in a niche about 65 cm in diameter. The cave consisted of a corridor about 25 m long, 7–8 m wide and 4–5 m high, with a temperature of 13–15°C. The second colony included about 300 bats and was situated in a smaller karstic cave (10 × 7 m, 5 m high). Both colonies consisted mainly of greater horseshoe-nose bat (*Rhinolophus ferrumequinum* (Schreber, 1775)) and lesser mouse-eared bat (*Myotis blythi* Tomes, 1857).

Biting midges were sampled using sticky paper sheets (20 × 20 cm), which were attached to walls along the perimeter of the cave (the technique similar to that used near birds' nests). Several tens of sheets were placed at 0.5 m intervals, up to a height of 3 m in 30–40 cm from the aggregations of bats and then were exposed for 24 hours. Along with this technique, three bats were caught to observe blood-feeding by midges at the cave. The bats were fixed as described above for lizards.

Biting midges were found on the sheets of sticky paper in both the caves on the following day. Commonly, sheets contained from 3 to 12 individual midges. All specimens belonged to the same species, *Leptoconops bezzii*. As a rule, the abdomen of the females was engorged with fresh blood. Midges were collected from all the sheets, testifying to the ability of *L. bezzii* to attack hosts in the darkness of caves. However, the

highest numbers of midges were trapped on sheets exposed near the exits from the caves.

In the field experiment, midges attacked the three bats and the collector. Blood-sucking on bats lasted 2–5 minutes. Judging from the appearance of midges, each of them took the full portion of blood (the abdomen was swollen and red). *L. bezzii* was known to feed on humans, domestic and wild mammals and birds [Gutsevich, 1973]; recently it also was recorded as a blood-sucker of tortoises [Šíroký et al., 2007].

Data on autogeny of biting midges in southeastern Kazakhstan

Some species of biting midges are autogenous, i.e. they are able to produce the first egg batch without blood-sucking, using only reserves accumulated during the larval stage [Glukhova, 2002]. However, after the first autogenous oviposition the females of autogenous species have to feed on blood in order to deposit eggs again. Apparently, a portion of autogenous females die after laying the first egg batch, and, consequently, autogenous species should be less dangerous epidemiologically, because they may have a lower percentage of females which take blood repeatedly. At present, five autogenous species are known in Kazakhstan — *Culicoides desertorum*, *C. manchuriensis*, *C. riethi* and *C. salinarius*; one more species, *C. filicinus* Gornostayeva & Gachegova, 1972, is known from neighbouring territories [Glukhova, 1989, 2002].

Autogeny of biting midges was studied in 1974–1981 in the Ili River valley (Almaty Province, the localities from the Ili mouth zone at Lake Balkhash, to villages Khorgos and Baskunchi close to the border with China; 44–46°N 74–80.5°E) [Auezova, 1982c, 1985]. Several hundred larvae and pupae of *Culicoides* from floodplain bodies of water were reared to adult females. All newly-emerged females of *Culicoides riethi* reared from larvae and pupae proved to be autogenous. After copulation, almost all females deposited autogenous eggs. The number of eggs in autogenous egg batches of *C. riethi* ranged from 89 to 147. These eggs yielded viable larvae, which emerged on days 7–9. In contrast to this, all the females of *C. circumscriptus*, *C. festivipennis* and *C. puncticollis* were anautogenous in all localities studied. These results are in agreement with the data obtained by other researchers in other regions of the former USSR [reviewed by Glukhova, 2002].

Conclusion

The data presented show that bloodsucking biting midges in southeastern Kazakhstan have a broad range of hosts. However, in order to understand the role of different groups and species of vertebrates for blood-sucking Ceratopogonidae and Leptoconopidae, it is necessary to study a broader range of hosts under natural conditions.

Polyphagous species of biting midges should be most important epidemiologically. These are species collected from many host groups, including man, different mammals, birds and reptiles. The following 12 species belong to this group: *Culicoides chiopterus*, *C. festivipennis*, *C. heliophilus*, *C. kibunensis*, *C. minutissimus*, *C. punctatus*, *C. subfascipennis*, *C. turanicus*, *Leptoconops lucidus*, *L. bidentatus*, *L. laurae*, and *L. bezzii*.

Newly revealed trophic links of biting midges with bats and reptiles can be very important, because these animals, especially bats, are widely known as natural carriers and vectors of dangerous diseases.

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