CERATOPOGONIDAE AS INTERMEDIATE HOSTS FOR *HAEMOPROTEUS* AND OTHER PARASITES [1]

A. M. FALLIS AND G. F. BENNETT
Department of Parasitology, Ontario Research Foundation

INTRODUCTION. Species of ceratopogonids are known hosts for a virus, protozoa and six filarioid nematodes belonging in four genera. In addition they are suspected vectors of other parasites and may be responsible for other diseases. This paper lists (Table 1) ceratopogonids known to transmit various parasites, summarizes work on the transmission of several of these, especially that on *Haemoproteus,* and reports observations relating to the feeding behaviour of some flies.

The adverse effects of bites of midges on man and the severe reaction to the bites of some species, such as *C. furens* (4), are well known. Damage to livestock is also reported (56). The status of some species of biting midges in causing disease or transmitting parasites is still somewhat uncertain (Table 1). There are reports of allergic dermatitis of horses caused by *C. robertsi* (51) in Australia. Arnaud (5) reports eczema in man in Japan caused by *C. erairai* and sores that are caused by the bites of *C. obsoletus* and that take 3–4 months to heal. *C. pifanoi, C. filariferus* and *Leptoconops mediterraneus* may be hosts for certain nematodes (28, 31, 42). However, microfilariae can be found in any blood-sucking ceratopogonid that feeds on a host carrying them in its blood. It does not follow that the microfilariae will complete their development and that the species of insect is a suitable host for the worms. Likewise, first stage larvae of filarioid nematodes may develop in insects that are not necessarily suitable hosts for them. However, as indicated below, several species of these helminths complete their development in ceratopogonids.

HOSTS FOR VIRUSES AND NEMATODES. DuToit's discovery (23) in South Africa of the transmission of the virus of blue-tongue disease by *Culicoides* opened a new field of investigation. The disease was found in sheep in Texas in 1948 (18). Price and Hardy (50) transmitted the virus to sheep by injecting them with a broth suspension of infected *Culicoides variipennis.* However, the epizootiology is still incompletely known, and, as Cox (18) points out, blue-tongue disease still presents a serious challenge to the livestock industry of the United States. Van Saceghen (55) and DuToit (23) believed the virus of African horse sickness is transmitted also by *Culicoides,* and Lewis (40) reported that the seasonal incidence of midges in the Sudan and the occurrence of the disease support this hypothesis. *Culicoides* possibly transmit other viruses also as Karstad *et al.* (36) isolated the virus of Eastern encephalitis from species collected in Georgia and refer to an isolation of Venezuelan equine encephalitis from similar insects.

Search for midges that are hosts of parasitic nematodes (Table 1) was stimulated by the discovery of Sharp (53) that *C. austeni* is a host and vector of *Dipetalonema perstans.* This filarioid of man occurs in Africa but has been reported also from British Guiana (27). Later Chardome and Peel (17) showed that a second species, *D. streptocerca,* would complete its development in *C. grahami,* which species they considered a less suitable host for *D. perstans.* Subsequently, differences of opinion arose concerning the relative importance of different species of *Culicoides* as vectors of these two nematodes. Henrard and Peel (30) said that *streptocerca* but

[1] Adapted from a paper given in the symposium on "Systematics, Biology and Economic Importance of Ceratopogonidae" at the Joint Meeting of The American and Canadian Entomological Societies held Dec. 2, 1959 at Detroit, Michigan.

TABLE 1.—Ceratopogonidae as Hosts for Parasites

Species*	Parasite or disease	Distribution	Host	References
C. palpidipennis	Blue tongue virus	*S. Africa	sheep	23
C. variipennis	Blue tongue virus	*Texas	sheep	50
C. nubeculosus	*Onchocerca cervicalis*	*England, Europe, Australia	horse	8, 24, 43, 54
C. pungens, *C. oxystoma*, *C. shortii*, *C. orientalis*	*O. gibsoni*	*Malaya, Australia, India, Africa	cattle, buffalo, zebu	7, 16, 32, 33
C. austeni, *C. grahami*, *C. inornatipennis*	*Dipetalonema perstans*	*Africa, S. America	man	21, 22, 27, 32, 44, 45, 46, 53
C. grahami	*D. streptocerca*	*Africa	man, chimpanzee, gorilla	17, 30, 49
C. furens	*Mansonella ozzardi*	*S. America	man	14, 16, 27, 41
Culicoides nr. *piliferus*	*Haemoproteus nettionis*	*Canada	duck	26
C. sphagnumensis	*Haemoproteus canachites*	*Canada	spruce grouse	25
Forcipomyia velox	*Icosiella neglecta*	*France	frog	19
		More Uncertain Status		
C. mikurai	Fever	*Japan	man	37
C. erairai	Eczema	*Japan	man	5
C. robertsi	Allergic dermatitis	*Australia	horse	51
Culicoides sp.	Fowl pox	Asia	chicken	13
C. pifanoi	Microfilaria	*Venezuela	?	42
Leptoconops mediterraneus	Microfilaria	North Africa	mule	28
C. filariferus	1st stage larva (species unknown)	*Mexico	?	31
C. obsoletus	Cutaneous sores ?	*Japan	man	5
C. arakawae	*Leucocytozoon caulleryi*	*Japan	chicken	2
C. crepuscularis	*Haemoproteus sp.*	*Canada	crow ?	25
C. stilobezzioides	*Haemoproteus sp.*	*Canada	crow ?	25
C. stilobezzioides	*Haemoproteus sp.*	*Canada	purple finch	25
Culicoides spp.	Eastern encephalitis	*U. S. A.	?	36

* Distribution of some is limited and they are known hosts for parasites in certain countries only that are marked with an asterisk.

not *perstans* developed in *C. grahami* and they questioned whether Sharp had been working with *perstans.* However, Hopkins and Nicholas (32) confirmed Sharp's results but stated that *C. grahami* may be a less suitable vector than *C. austeni* except in places where *grahami* is the more abundant species. Nicholas and Kershaw (45) concluded that the occurrence of fewer larvae of *D. perstans* in *C. grahami* than in *C. austeni* indicated that fewer survived rather than that fewer were ingested. Duke (22) claimed that few larvae of *perstans* reach the infective stage in *grahami* but many do so in *C. inornatipennis.* He also confirmed (21) the work of Chardome and Peel. He thought the failure of others to observe development of *streptocerca* in *grahami* might have resulted from the examination of flies that had fed on *streptocerca*-free areas of the skin. Possibly these worms are transmitted also by other species of *Culicoides* as several are known to feed on man in localities where the worms occur (44, 46, 47).

In 1933 Steward (54) showed that *Onchocerca cervicalis* is transmitted to horses in England by *C. nubeculosus.* This worm occurs also in Australia, Europe and Asia (8, 24, 43, 51) but the vectors in some localities are unknown. Molev (43) reports 14 species of *Culicoides* in parts of Russia where the worm is present. Buckley (16) showed that another species, *O. gibsoni* in cattle, developed in four species of *Culicoides* in Malaya. The parasite is reported from several other places as well (7, 34, 52) but the vectors in these countries are unknown. The possibility of *Culicoides* being a host for a third species, *O. volvulus,* was investigated by Gibson and Ascoli (29). They found one of 47 specimens of *C. guttatus* infected with *O. volvulus* in Guatemala but as the species was rare they considered it unimportant in the spread of the parasite.

Culicoides furens was shown by Buckley (14, 15) to be a vector of another nematode, *Mansonella ozzardi,* that occurs in South America (27, 41). Perhaps other *Culicoides* transmit this worm also as it is reported from British Guiana from places where *C. furens* is rare but where *C. paraensis* is common.

In addition to these five species of nematodes that develop in *Culicoides* a sixth, *Icosiella neglecta* of frogs, is transmitted by *Forcipomyia velox* (19). Scores of other filarioid nematodes occur in various hosts throughout the world yet the mode of transmission is known for a few only. Most probably species of ceratopogonids will prove to be vectors of some of them.*

HOSTS FOR PROTOZOA. Recently, species of *Culicoides* showing ornithophilic behaviour have been shown to be hosts for *Haemoproteus* (25, 26). This has raised interesting questions concerning transmission of these parasitic protozoa and the feeding behaviour and other characteristics of *Culicoides* that are known hosts. Consequently, most of the remainder of this paper will summarize work which has shown that a species of *Culicoides* near *piliferus* and *C. sphagnumensis* are hosts for the species of *Haemoproteus* occurring in ducks (*Anas boschas*) and spruce grouse (*Canachites canadensis*) respectively.

Reports by Adie (1), O'Roke (48) and Baker (6) led us to suspect that species of Hippoboscidae were feeding on ducks and serving as hosts for *Haemoproteus nettionis* that was commonly found in them. While working on blood protozoa in ducks in Algonquin Park it was noted that most of our ducks placed outdoors on the lakeshore during June and July became infected with *H. nettionis.* Anderson, therefore, in 1955 (3) examined many of these ducks daily for several weeks during the summer. Hippoboscids were not recovered from them. This was not unexpected as Bequaert (9), following extensive work, stated that ducks are unsuitable hosts for these insects. The common insects feeding on the ducks during this time were simuliids and biting midges.

A series of observations and experiments were designed, therefore, to determine whether *Culicoides* and/or simuliids serve as intermediate hosts for *H. nettionis* of ducks. Four ducks were placed out of doors from 9.00 p.m. to 3.00 a.m. E.S.T. for seven days and from 9.00 p.m. to 12.00 midnight for an additional three weeks. (There is no evidence that blackflies are flying during these hours of the night.) All four ducks became infected with *Haemoproteus* indicating that transmission occurred at night; none became infected with *Leucocytozoon,* which is transmitted by blackflies. Two ducks left out of doors continuously during the same period became infected with *Leucocytozoon* and *Haemoproteus.*

During this same period specimens of *Culicoides* that fed on infected ducks were held in captivity, later macerated in saline and injected into 12 ducks. Infections were produced in nine which received suspensions of these flies, proving that *Culicoides* is a suitable host for *H. nettionis* of ducks (26). The cycle of development within *Culicoides* was investigated by collecting them following their engorgement on infected ducks, maintaining these midges in captivity, dissecting and sectioning them at intervals thereafter and examining the

* Mr. C. Hibbler, Colorado State University reported recently to the Midwest Fish and Wildlife Conference that species of *Culicoides* are intermediate hosts for species of *Splendidofilaria* in *Pica hudsonia.*

preparations for stages of development of the parasite. Thus various stages in the sexual cycle were demonstrated and the final stage—the sporozoite—was found in the salivary glands of specimens of *Culicoides*.

Using similar methods it was shown (25), during the summer of 1959, that *C. sphagnumensis* is a suitable host for a species of *Haemoproteus* occurring in the spruce grouse.

Sporozoites of *Haemoproteus* were seen also in the salivary glands of specimens of *C. crepuscularis* and *C. sphagnumensis* that were dissected 8 or more days after they had fed on crows (*Corvus brachyrynchos*) infected with this parasite. Sporozoites were found also in glands of *C. stilobezzioides* that had fed on an infected purple finch (*Carpodacus purpureus*) and in *C. crepuscularis* and *C. sphagnumensis* that had fed on infected white-throated sparrows (*Zonotrichia albicollis*). Although this does not establish that these midges are vectors of these particular parasites they are obviously suitable hosts for some species. The pattern of sexual development observed for two species of *Haemoproteus* in *Culicoides* is illustrated in Fig. 1.

Further indication that *Culicoides* rather than species of Hippoboscidae are responsible for the transmission of other species of *Haemoproteus* was obtained from comparisons of the infections in miscellaneous birds with the number of blood-sucking insects feeding on them. A measure of the abundance of *Culicoides* was obtained by collecting engorged specimens of them at different times during the summer, from selected birds which included ducks (Anatidae), grouse (Tetraonidae), robins (Turdidae), purple finches (Fringillidae), woodpeckers (Picidae), and white-throated sparrows (Fringillidae). Presumably the number of *Culicoides* recovered from these birds indicates the trend in the number of ornithophilic midges present throughout the season. The estimate of the abundance of hippoboscids was obtained from the actual number of these insects obtained from the birds examined.

The results (12) clearly indicated a high incidence with *Haemoproteus* in many birds and the presence of many with high parasitaemias before hippoboscids were recovered, and at the time *Culicoides* were abundant. Consequently, from the results of these various observations and experiments it is concluded that species of *Culicoides* will be shown to be vectors of all species of *Haemoproteus* occurring in Algonquin Park.

Dr. Jörg (35), who is working on the transmission of *Haemoproteus* in Argentina, notes the abundance of *Culicoides* in parts of that country. He found that parasite-free young magpies did not become infected with *Haemoproteus* if taken outside the area where *Culicoides* occurred, although these birds were exposed to other blood-sucking insects.

The situation may differ elsewhere. In New Zealand, for example, ceratopogonids are present but there is no record of *Culicoides,* and *Haemoproteus* is known to occur (38). However, Mr. Downes (20) has pointed out to us that *Leptoconops,* a related genus, is present. Further work on ceratopogonids in New Zealand, using collecting techniques similar to those employed here (10), may reveal *Culicoides* and other related genera. Dr. Lee in a personal communication (39) states ". . . the ecological niche into which *C. austropalpis* fits (in Australia) may well have its counterpart in New Zealand."

Brief reference should be made to another avian protozoan parasite—a trypanosome—that is common in many birds. Developing stages of trypanosomes have been observed in specimens of *Culicoides* that fed on birds infected with these parasites. Bennett (11) has transmitted one of these trypanosomes by injecting a bird with a suspension of specimens of *Culicoides* carrying the developing stages of the parasite. Other evidence (11) suggests, however, that *Culicoides* is not the important vector in this locality although elsewhere this possibility should be kept in mind.

Biting midges may be hosts for other parasitic protozoa also, as Akiba (2) re-

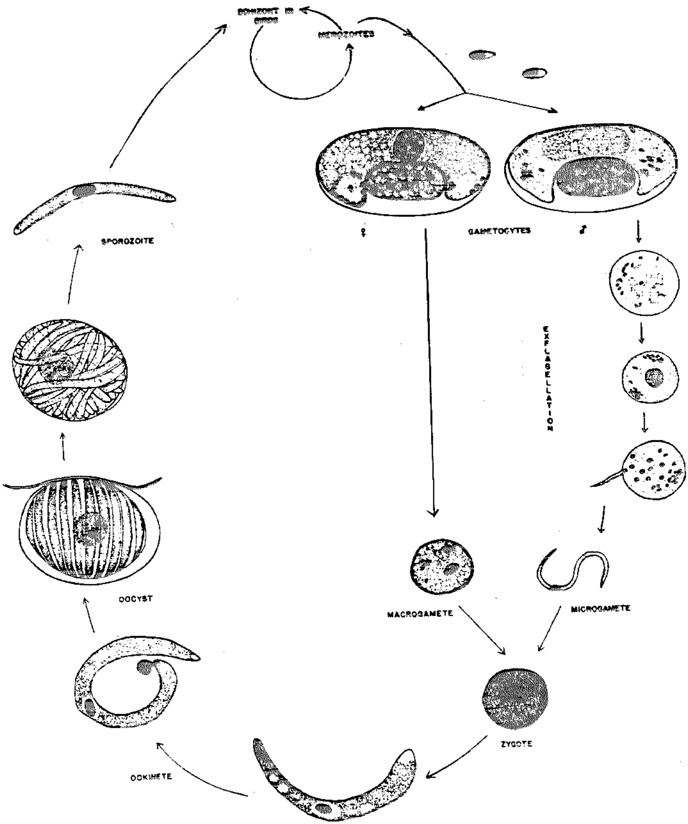

FIG. 1.—Composite diagram illustrating the sporogonic cycle of *Haemoproteus* in *Culicoides*.

ported recently sporogony of *Leucocytozoon caulleryi* in *Culicoides arakawae*.

COMMENTS ON FEEDING BEHAVIOUR. Limited comparisons of the number and kinds of *Culicoides* feeding on different birds in two habitats are available from data reported elsewhere (10). These data (Tables 2, 3) were compiled from collections of *Culicoides* made from ducks, grouse, crows, an owl and flickers, that were exposed by the lake-shore, on the ground at the edge of second growth boreal forest, and suspended 5–15 feet in the air at the edge of these woods.

The collections showed that *C. sphagnumensis, stilobezzioides, crepuscularis, haematopotus*, a species near *piliferus*, and *obsoletus* fed on some or all of the birds. Relatively few *obsoletus* were taken on birds, although at times, it was extremely abundant, fed commonly on man, and thousands could be swept in a net. On the other hand thousands of the species near *piliferus* were taken from ducks and large

TABLE 2.—Number and species of *Culicoides* collected after feeding on different birds at different times

	5–7 p.m.	7–9 p.m	9–11 p.m. E.S.T.	Grouse	Crow	Duck	Owl	Flicker
No. collections	168	111	20	66	60	122	13	7
C. sphagnumensis	28	688	383	38	878	0	10	92
C. stilobezzioides	11	64	39	22	43	0	6	14
C. crepuscularis	0	23	14	10	43	0	2	1
C. obsoletus	1	27	5	0	0	0	0	0
C. haematopotus	0	2	3	0	9	0	0	0
C. nr. *piliferus*	15	hundreds	hundreds	0	0	hundreds	0	0
Undetermined	160	580	0	0	0	0	0	0

TABLE 3.—Number and species of *Culicoides* collected from crow exposed in boreal forest and from miscellaneous birds exposed in the forest and at a lakeshore

	Collections from crow				Collections from miscellaneous birds		
	Boreal forest					Boreal forest	
Habitat	Ground	5′ in air	10′	15′	Lake shore ground	Ground	5′–25′ in air
No. collections	4	4	4	4	119	46	150
C sphagnumensis	24	280	360	160	0	26	1160
C. stilobezzioides	1	16	21	18	0	2	124
C. crepuscularis	5	5	6	7	0	5	61
C. obsoletus	0	0	4	5	22	0	11
C. haematopotus	1	1	0	3	0	1	8
C. nr. *piliferus*	0	0	0	0	hundreds	6	7

numbers of other species from other birds, but none of these were taken from man. *C. stilobezzioides, sphagnumensis, crepuscularis* and the species near *piliferus* are clearly ornithophilic. It is not surprising, therefore, that some are involved in the transmission of *Haemoproteus*. The species of *Culicoides* near *piliferus* was taken most frequently from ducks and by the lakeshore.

C. sphagnumensis, stilobezzioides and *crepuscularis* were taken more commonly from woodland types of birds and at elevations of 5′ to 15′ from the ground in the forest rather than at the forest floor. Large numbers of these ornithophilic species were obtained only by exposing birds in the tree tops and collecting the flies feeding on them. *C. sphagnumensis* seemed to feed more commonly on grouse and crows than on the passerine birds and *stilobezzioides* and *crepuscularis* were often on the latter. *C. obsoletus,* under certain conditions, fed during the day as well as at night. *C. crepuscularis, sphagnumensis* and *stilobezzioides* fed at dusk although on several occasions they were collected one or two hours later. The species near *piliferus* began to feed about the same time but many individuals have been collected throughout the night. *Forcipomyia velox* on the other hand is reported by Desportes (19) to feed on frogs during the day rather than at night. It was noticed also that ornithophilic species continue to feed when the air temperature drops to 50–55° F.

These limited observations on collections of *Culicoides* from different birds in different habitats indicate that the feeding behaviour of these insects may affect noticeably the incidence of infection with particular parasites in different animals.

ACKNOWLEDGMENTS

We are especially grateful to Mr. J. A. Downes, Entomology Research Institute, Department of Agriculture, Canada for generous assistance in identifying material, and to the Province of Ontario for financial aid through the Department of Planning and Development.

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