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# The Ecology and Control of Blood-sucking Ceratopogonids\*

D. S. KETTLE

This account of recent developments in the ecology and control of bloodsucking ceratopogonids takes as its starting point an earlier review which appeared in 1962 (47). Since then the main advances have been the first detailed biological study on a species of *Lasiohelea* (31), increasing fieldwork on the genus *Leptoconops* and the colonisation of *Culicoides* in the laboratory. These are the only three genera of ceratopogonids which feed on vertebrates.

## Ecology of Adults

(a) *Feeding*. As with other biting nematocera only the female feeds on blood and takes a surprisingly large amount. Both *Leptoconops kerteszi* and *L. becquaerti* imbibe more than their own body weight (24, 62). It is difficult to find engorged females in the field to identify the natural host range. Some success has been had with *L. kerteszi*, which feeds during the day and burrows into loose surface sand at night. It can be dislodged and collected (25). In the laboratory *L. becquaerti* behaves in a similar manner, the engorged females burrowing into sand (59), but this has not been observed in the field.

Some measure of host preference can be obtained by collecting females attracted to particular hosts. Thus MESSERSMITH operated light traps in poultry houses to identify potential vectors of avian infectious synovitis (72) and Japanese workers used the same method, supplemented by the precipitin test, to investigate the transmission of *Leucocytozoon caulleryi* among poultry (53, 79). The combination of light trap and host yielded a large proportion (83–97%) of engorged female *C. arakawae* (34) but only a few engorged *C. obsoletus* (72). In North America *C. downesi*, a vector of *Haemoproteus*, feeds extensively on ducks (19).

GARNHAM et al. (27) collected wild *C. adersi*, which had engorged on captive infected monkeys, to follow the life cycle of *Hepatocystis kochi* in East Africa. *C. variipennis*, which can trans-

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mit blue tongue virus to sheep experimentally (21, 70), has been found biting sheep in large numbers during an outbreak of the disease in Colorado (44). Australian workers, stimulated by an outbreak of ephemeral fever, have investigated the feeding habits of some 50 species of ceratopogonids (56, 82).

Species differ in the part of the body they attack and knowledge of this assists in collection of specimens and protection of the host. *L. kerteszi*'s preference for the head and shoulders of man has been exploited by fixing the metal funnel of a portable petrol driven suction trap above the head of the operator (26). In contrast *L. becquaerti* shows a marked preference for the lower limbs, being four times as abundant on the leg as the arm in a sitting individual (48). *C. paraensis* also selects the leg and its bites cause a dermatitis requiring medical attention (90, 91).

LAVOPIERRE (54) classifies bloodsucking insects into pool or vessel feeders. His list includes one ceratopogonid, *L. torrens*, which is classified as a pool feeder. An interesting attempt has been made by JAMNBACK (38) to relate structure of mouthparts and antennae to feeding habits. Ornithophilic species have more olfactory sensilla on their antennae than species which feed on mammals.

(b) *Autogeny*. A blood meal is normally required for maturation of the oocytes and before 1961 autogeny had only been reported for a small number of species, whose feeding habits were unknown (47). By 1968 thirteen species of *Culicoides* and one of *Leptoconops* had been recorded as autogenous, including some economically important species (18, 57, 58, 69, 75). For example the three main man-biting species in Jamaica (*C. furens*, *C. barbosa* and *L. becquaerti* [58]) have been shown to be autogenous. The percentage autogeny was high in two populations of *C. barbosa* and three of *C. furens* but zero in two other populations of *C. furens*. Autogeny may therefore be under genetic control as in the *Culex pipiens* complex (95).

The situation in *L. becquaerti* is more involved. Autogeny is closely correlated with wing length (65), the autogenous form having shorter wings than the anautogenous. Both forms occur in the same breeding sites and within any one site are clearly separable on wing length. However, the ranges of the two forms overlap when the results from several breeding sites are pooled. Both forms appear to breed true, the female progeny of an autogenous parent being also autogenous and vice versa. The autogenous form mates on the surface of the soil while the anautogenous form swarms above it. The nuisance caused by this species is considered to be largely, if not entirely, due to the anautogenous form. In many ways these

two forms behave like different species but the crucial cross mating experiment has yet to be carried out.

A similar situation has been reported for *C. austeni*, another important man-biting species, in which MURPHY recognises three biological forms (75). One (form a) is anautogenous, breeds in banana and the males swarm. The other two (b and c) are autogenous, mate in a confined space and breed in mangrove swamps. They differ in their choice of mangrove zone for oviposition and in the degree of pigmentation.

(c) *Ovarian Cycle*. The potential increase of a species depends in part on the frequency of oviposition and the number of eggs laid per batch. Detailed studies of the gonotrophic cycle have been carried out on *Leptoconops bequaerti* (59), *Lasiohelea sibirica* (31), *C. furens* and *C. barbosai* (63). All four showed gonotrophic harmony but the number of eggs laid depended on several factors – age and size of the female, temperature of maturation and availability of supplementary carbohydrate solution. The first batch of eggs in *L. sibirica* is 30 per cent larger than the second. The number of ovarioles in *L. bequaerti* varies with the size of the female. At a constant size *L. bequaerti* matures the maximum number of eggs at 25°C, being 40 per cent more than at 33°C. Sugar solution increased egg yield in *L. sibirica* and *L. bequaerti* but not in the two *Culicoides* species. One unexpected observation was made on the pest species *C. barbosai*. It produced its first batch of eggs autogenously and then, when fed, took very little blood and matured only a few eggs (10–20), much less than in the first batch. This could indicate either that man is an unsuitable host for this species or that it is evolving towards independence of blood feeding.

It is useful to be able to determine the age structure of a population. In mosquitoes relict bodies in the ovarioles indicate the number of gonotrophic cycles completed (16). Similar bodies have been reported in *Culicoides* (55) and in *L. bequaerti* (61). Only single bodies were observed in wild caught *C. furens* and *C. barbosai* (61), which would indicate that they both normally mature only two egg batches. If this is generally true for *C. furens* in nature then it will militate against this species being the vector of *Mansonella ozzardi*. The parasite requires seven to eight days to complete its development in the vector while the time between two blood meals is less than four days (4, 63).

(d) *Daily Cycle and Meteorological Conditions*. The activity of ceratopogonids varies throughout the 24 hours, being controlled in all probability by an endogenous rhythm, modified by external

conditions. *L. becquaerti* is diurnal with maximum biting activity between 08.00 and 09.00 hours and a lesser peak at 15.40 to 17.15 hours (sunset 17.55 hours). This is positively correlated with temperature and illumination, negatively with wind speed and independent of saturation deficit (49). Although no biting was recorded at wind speeds above 12 mph adults were taken in wind traps at speeds up to 20 mph (10). *C. variipennis* reaches maximum activity in the late afternoon but is inhibited by temperatures over 32°C (40). *L. sibirica* behaves rather similarly, reaching maximum activity at 25°C (31). *C. sinanoensis* is nocturnal, reaching peak activity two hours after sunset (78).

Most *Culicoides* species are crepuscular with morning and evening peaks. These include *C. pallidicornis* (73), *C. obsoletus*, *C. paraensis* (92), *C. grisescens*, *C. stigma* (31), *C. sanguisuga* (39). Such species are often active during the day in suitably shaded and sheltered spots (38, 89) showing a negative correlation between activity and evaporation rate (39). The effect of meteorological conditions has been investigated further in *C. impunctatus* where flying activity was positively correlated with humidity, negatively with wind speed and was independent of temperature (81). Radiation, including visible light, as measured on a black metal strip, operated on an all or none basis, with activity being inhibited above 22.7 cal/cm<sup>2</sup>/h. This would effectively prevent the exposure of *C. impunctatus* to high temperatures and might account for the lack of correlation between air temperature and its flight activity.

The landing rates of *C. sanguisuga* and *C. impunctatus* were low at first and required 10–15 minutes to reach maximum activity (39, 89). This was particularly apparent in the daytime and suggested that the adults were inactive until stimulated by the presence of a host, a phenomenon described earlier by GLUCHOVA (29) for other species of *Culicoides*. No similar delay was discernible with the diurnal *L. becquaerti* (49).

(e) *Seasonal Cycle and Flight Range*. The correct timing and extent of control measures depends on a knowledge of the seasonal cycle and the species flight range. The season may be short and intense as with *L. torrens* (100) or sustained throughout the year with the monthly maximum being only four times the minimum as in *L. becquaerti* (49). In the temperate regions the season depends on temperature and species may have one or more periods of abundance throughout the warmer months. *C. odibilis*, *C. arakawae* (53), *C. sanguisuga* (39) have single peaks in May, August and July respectively, while *C. sinanoensis* (78) and *C. impunctatus* (81) and *C. hollensis* (50) have two. The effect of temperature is



shown by the fact that in the subtropics *C. hollensis* occurs in small numbers even in the 'winter'. In the tropics seasonal peaks may be related to tides, rainfall or cool season. Thus the emergence of *C. furens* (8), *C. subimmaculatus*, *C. ornatus* (83) from tidal swamps was at a maximum during neap tides and *C. austeni* at spring tides (75). The density of *L. becquaerti* in wind traps was linearly related to rainfall two weeks earlier when both variables were expressed logarithmically (10). In Salvador *C. paraensis* was most troublesome during the cooler months of the year (92).

There have been few recent studies on dispersal. *C. furens* has been found to fly four miles and cross hills 1200 feet high (103). *L. becquaerti* flies half a mile in density after which numbers decrease rapidly to about a mile and a few gravid females have been found three miles away (8, 10). The latter may be important in colonising new breeding sites. A single *C. barbosai* labelled with P<sup>32</sup> was recovered one mile from its source (9, 10).

Sampling of flying insects by operating traps at different heights gave maximum numbers of *C. impunctatus* (81) and *L. becquaerti* (10) at 3 ft., but under humid conditions the largest catch of *C. impunctatus* shifted to 6 ft. For *L. becquaerti* there was an inverse linear relationship between log. density and height with such a rapid fall in numbers so that only one percent of the catch was above 10 ft. Studies of the resting places of *C. barbosai* in mangrove gave maximum numbers at 2 ft. with males extending up to 8 ft. and females to 5 ft. Gravid females were most abundant among the ground litter where presumably they oviposit (6, 7).

(f) *Longevity*. The supplementation of blood feeding with sugar solution increased the longevity of *C. obsoletus* from 10 to 51 days (36). Increased survival as a result of carbohydrate feeding has also been recorded for *C. furens*, *C. barbosai* (63), *L. becquaerti* (62) and *L. sibirica* (31). Nectar feeding in nature has been confirmed for *L. becquaerti* (62). *L. kerteszi* does not survive after laying one batch of eggs (93) and there is doubt whether the autogenous form of *L. becquaerti* lives to lay a second batch. Equally the failure to find more than one relict body in *C. furens* and *C. barbosai* may indicate very low survival after the second oviposition.

Methods of sampling adult populations have been improved by the use of UV light and CO<sub>2</sub>. UV traps sometimes give embarrassingly large catches and are excellent for nocturnal species of which they collect both sexes (51, 88, 107). Carbon dioxide baited traps not only attracted nocturnal species (15, 96) but also diurnal species such as *C. variipennis* (76), *L. kerteszi* and *L. torrens* (76, 86, 101). As expected only females of the *Leptoconops* species were

attracted but both sexes of *C. variipennis*. This may indicate that mating of *C. variipennis* may occur in the vicinity of the host as previously recorded for the closely related *C. nubeculosus* (80).

(g) *Colonisation*. Many field problems await detailed analysis in the laboratory but require the establishment of self maintaining colonies. This has now been achieved for *C. variipennis* (42, 43, 46), *C. furens* (68) and *C. guttipennis* (32), permitting experimental studies of larval biology (69), disease transmission by adults (21) and susceptibility of all stages to insecticides (33) and radiation (45). In other species eggs can be obtained from wild caught females (60, 74) and the resulting larvae reared on various media (1, 30, 43, 93), but the greatest difficulty in establishing a colony is the achievement of successful mating between laboratory reared adults.

### Ecology of the Early Stages

*Breeding Sites*. Field observations on the early stages are concerned first with identifying the type of habitat (87), e.g. mangrove swamp (103), rice fields (52, 53, 97), acid bogs (77, 102), cow dung (5) or rotting vegetable matter (104, 105). These can be studied by emergence traps (11, 22) or pupal collections (41). Secondly, there is the need to define quantitatively the relative production of the different zones of the habitat and the conditions found there (94). Both *C. furens* and *C. barbosai* breed in mangrove swamps where *C. barbosai* is associated with *Rhizophora* and *C. furens* with *Avicennia* (8, 13). A similar habitat separation was observed between two biological 'races' of *C. austeni* (75). *C. furens* larvae occur in mud without surface water (2). They follow a retreating water line both horizontally (64, 103) and vertically (103). The latter habit gives rise to adult emergence within a week of reflooding an apparently dry area (103). *C. furens* larvae are carnivorous and although they spend long periods partially emerged from their burrows they feed in the soil, not on the surface (64). Successful pupation only occurred when the larva was in contact with air and took place 6–18 in. above the water line. This is important as pupae do not survive prolonged submersion, i.e. 36 hours, and successful eclosion requires solid support. Three patterns of behaviour have been described for Australian pupae – some float, others burrow into the substrate and a few alternately rise and descend from the water surface (17).

*L. torrens* breeds in cracked clay soils with preference for areas where the cracks are less than one inch across (100). *L. kerteszi*

and *L. bequaerti* inhabit sandy areas where the subsoil water is within 18 in. of the surface so that capillary action keeps the sand damp (66, 84). The sites of *L. bequaerti* are sheltered from tidal or wave action and characterised by a subsurface algal growth on which presumably they feed (67). Movement of sand in the breeding sites by wave action or heavy rain catastrophically reduced numbers.

Quantitative observations require standardised techniques (14) and considerable care. Emergence traps can be misleading when they retain wandering, negatively phototactic larvae, and give enhanced estimates of the larval population size (11). This feature can be an advantage when assessing low residual populations resulting from control measures.

### Control

Measures against adults include the use of repellants such as deet (Diethyl toluamide), DMP (Dimethyl phthalate) and TMPD (Trimethyl pentanediol) (12, 20, 28, 106) with deet being the most effective against *L. bequaerti*. Mosquito screens painted with Malathion effectively kept out *C. sanguisuga* for the length of the season, i.e. 4–6 weeks (35, 37). The application of DA-14-7 to poultry houses and birds produced only a temporary reduction in the percentage of *C. arakawae* engorging (34). Weekly fogging with Malathion in Jamaica is psychologically very reassuring to the human population but its value in reducing the 'sandfly' population has not been critically determined (12). In the USSR BHC smokes freed pastures from biting flies, including *Culicoides* but only for 2 days (106).

As a larvicide Dieldrin gave 90 per cent control of *L. torrens* at 4 lb/acre (100), satisfactory control of *C. furens* at 1¼ lb/acre (3) and good control of *C. melleus* at less than 1 lb/acre (98, 99). *C. melleus* larvae live in the intertidal zone and spraying was undertaken at low tide. *C. barbosai* occupies a similar habitat but the tidal range in the Caribbean is too small to make this a practical proposition in Jamaica (12). *C. furens* which lives above the water line can be controlled by application of Malathion at 10-day intervals (12). In the laboratory heptachlor was the most toxic of 15 insecticides tested against *C. variipennis* (33).

Greater promise is given by environmental control. Impounding of water to keep areas flooded continuously has been successful against *C. furens* in Jamaica (12) and Florida (71, 85). Felling of mangrove trees reduces the number of *C. barbosai* but takes a year to reach maximum effect. It has no effect on *C. furens* (12). *C. fu-*



*rens* can be eliminated by felling the trees and filling the swamp with sand but unless done properly this may merely create breeding sites for *L. bequaerti* and make the situation worse than before, as happened in Jamaica in 1960. To prevent this the fill must raise the level of the swamp so that the subsoil water is 30 in. below the surface, the surface must be covered with a layer of marl and vegetative growth encouraged (12). *L. kerteszi* can be controlled by ditching to reduce the moisture content of the surface soil (23) and *L. torrens* by increasing the moisture content to prevent cracking (100).

Use of the sterile male technique is a long way off but a start has been made by studying the effect of different dosages of gamma radiation on larvae, pupae and adult *C. variipennis* (45).

#### References

1. BIDLINGMAYER, W. L. (1957). Studies on *Culicoides furens* at Vero Beach. — Mosquito News 17, 292-294
2. BREELAND, S. G. (1960). Observations on the breeding habitats of some *Culicoides* and other Heleidae in the Panama Canal Zone. — Mosquito News 20, 161-167
3. BREELAND, S. G. & SMITH, J. P. (1962). Observations on the importance of flight range in the control of *Culicoides* in the Panama Canal Zone. — Mosquito News 22, 147-154
4. BUCKLEY, J. J. C. (1934). On the development in *Culicoides furens* Poey of *Filaria (Mansonella) ozzardi* Manson 1897. — J. Helminth. 12, 99-118
5. CANNON, L. R. G. & REYE, E. J. (1966). A larval habitat of the biting midge *Culicoides brevitarsis* Kieffer (Diptera: Ceratopogonidae). — J. ent. Soc. Queensland 5, 7-9
6. CASTLE, T. A. (1965). A study of the resting habits of *Culicoides barbosai* in a selected area of the Bogue Swamp. — Report to the Ministry of Health, Jamaica
7. CASTLE, T. A. (1965). An assessment of catches made by sticky cylindrical traps of four different colours compared with sticky panels, in an attempt to determine the resting sites of *Culicoides barbosai* in a mangrove swamp. — Report to the Ministry of Health, Jamaica
8. DAVIES, J. B. (1964). Research and the sandfly problem in Jamaica. — Inf. Bull. sci. Res. Coun. Jamaica 5, 33-39
9. DAVIES, J. B. (1965). Three techniques for labelling *Culicoides* (Diptera: Heleidae) with radioactive tracers both in the laboratory and in the field. — Mosquito News 25, 419-422
10. DAVIES, J. B. (1965). Studies on the dispersal of *Leptoconops bequaerti* Kieffer (Diptera: Ceratopogonidae) by means of wind traps. — XII Int. Congr. Ent. Lond. 1964, 754-755
11. DAVIES, J. B. (1966). An evaluation of the emergence or box trap for estimating sandfly (*Culicoides* spp.: Heleidae) populations. — Mosquito News 26, 69-72
12. DAVIES, J. B. (1967). A review of the research into the biology and control of the biting sandflies of Jamaica with recommendations for future control measures. — Mosquito-Sandfly Res. Unit, Ministry of Health, Jamaica
13. DAVIES, J. B. (1967). The distribution of sandflies (*Culicoides* spp.) breeding

- in a tidal mangrove swamp in Jamaica and the effect of tides on the emergence of *C. furens* (Poey) and *C. barbosai* Wirth & Blanton. — W. Indian med. J. 41, 39-50
14. DAVIES, J. B. & LINLEY, J. R. (1966). A standardised flotation method for separating *Leptoconops* (Diptera: Ceratopogonidae) and other larvae from sand samples. — Mosquito News 26, 440
  15. DE FOLIART, G. R. & MORRIS, C. D. (1967). A dry ice-baited trap for the collection and field storage of haematophagous Diptera. — J. med. Ent. 4, 360-362
  16. DETINOVA, T. S. (1962). Age-grouping methods in Diptera of medical importance with special reference to some vectors of malaria. — Geneva: Monogr. Ser. Wrld Hlth Org. Nr. 47, 216 pp.
  17. DYCE, A. L. & MURRAY, M. D. (1966). Notes on the pupal behaviour and collection of larvae and pupae of some Australian *Culicoides* (Diptera: Ceratopogonidae). — J. ent. Soc. Queensland 5, 37-39
  18. DYCE, A. L. & MURRAY, M. D. (1967). Autogeny in *Culicoides waringi* Lee and Reye and *Culicoides mackerrasi* Lee and Reye (Diptera: Ceratopogonidae) from Australia with notes on breeding places and behaviour. — J. Aust. ent. Soc. 6, 119-126
  19. FALLIS, A. M. (1965). A review of observations on the feeding, longevity and flight range of Simuliids and Ceratopogonids. — XII Int. Congr. Ent. London 1964, p. 754
  20. FEDDER, M. L., TSETLIN, V. M. & GRIKITYS, E. YA. (1964). Experiments in the use of diethyltoluamide in aerosol cylinders. — Med. Parazit. 33, 61-63
  21. FOSTER, N. M., JONES, R. H. & MCCRORY, B. R. (1963). Preliminary investigations on insect transmission of bluetongue virus in sheep. — Amer. J. vet. Res. 24, 1195-1200
  22. FOULK, J. D. (1966). A flower pot emergence trap for *Leptoconops kerteszi*. — J. econ. Ent. 59, 225-226
  23. FOULK, J. D. (1966). Drainage of a desert spring creek for control of *Leptoconops kerteszi* (Diptera: Ceratopogonidae). — Mosquito News 26, 230-235
  24. FOULK, J. D. (1967). Bloodmeal size of *Leptoconops kerteszi* (Diptera: Ceratopogonidae). — Mosquito News 27, 424
  25. FOULK, J. D. (1968). The resting behaviour of the desert ceratopogonid *Leptoconops kerteszi*. — J. med. Ent. 5, 223-229
  26. FOULK, J. D. & SJOREN, R. D. (1967). A collection device for *Leptoconops kerteszi* (Diptera: Ceratopogonidae) biting gnats. — J. med. Ent. 4, 281-283
  27. GARNHAM, P. C. C., HEISCH, R. B., MINTER, D. M., PHIPPS, J. D. & IKATA, M. (1961). *Culicoides adersi* Ingram & Macfie 1923, a presumed vector of *Hepaticystis* (= *Plasmodium*) *kochi* (Laveran 1899). — Nature 190, 739-741
  28. GERBERG, E. (1966). Field and laboratory repellency tests with 2,2,4-trimethyl-1-3-pentanediol (TMPD). — J. econ. Ent. 59, 872-875
  29. GLUCHOVA, V. M. (1958). Types of attack in *Culicoides* Latr. (Diptera: Heleidae). — Entomol. Obozrenie 37, 330-335
  30. GLUCHOVA, V. M. (1967). On the technique of collecting and cultivation of larvae of bloodsucking midges (Diptera: Ceratopogonidae). — Parasitologia 1, 171-175
  31. GORNOSTAEVA, R. M. (1965). The gonotrophic cycle of the biting midge *Lasiohelea sibirica* Bujan (Diptera: Heleidae). — Ent. Obozrenie 44, 770-784
  32. HAIR, A. J. & TURNER, E. C. (1966). Laboratory colonisation and mass production procedures for *Culicoides guttipennis*. — Mosquito News 26, 429-433

33. HARRIS, R. L. & JONES, R. H. (1962). Larvicide tests with colony reared *Culicoides variipennis*. — J. econ. Ent. 55, 575-576
34. HORI, S., TORIUMI, T. & TANABE, A. (1964). Studies on the prevention of *Leucocytozoon* infection of the chicken. I. The behaviour of *Culicoides arakawae* to an insecticide DA-14-7. — Sci. Rep. Fac. Agric. Okayama University 24, 47-54
35. JAMNBACK, H. (1961). The effectiveness of chemically treated screens in killing annoying punkies *Culicoides obsoletus*. — J. econ. Ent. 54, 578-580
36. JAMNBACK, H. (1961). Observations on *Culicoides obsoletus* (Meigen) in the laboratory (Diptera: Ceratopogonidae). — Mosquito News 21, 48-53
37. JAMNBACK, H. (1963). Further observations on the effectiveness of chemically treated screens in killing biting midges *Culicoides sanguisuga* (Diptera: Ceratopogonidae). — J. econ. Ent. 56, 719-720
38. JAMNBACK, H. (1965). The *Culicoides* of New York State (Diptera: Ceratopogonidae). — Bulletin Number 399, New York State Museum and Science Service. 153 pp.
39. JAMNBACK, H. & WATTHEWS, T. (1963). Studies of populations of adult and immature *Culicoides sanguisuga* (Diptera: Ceratopogonidae). — Ann. ent. Soc. Amer. 56, 728-732
40. JONES, R. H. (1961). Some observations on biting flies attacking sheep. — Mosquito News 21, 113-115
41. JONES, R. H. (1961). Observations on the larval habitats of some North American species of *Culicoides* (Diptera: Ceratopogonidae). — Ann. ent. Soc. Amer. 54, 702-710
42. JONES, R. H. (1961). Equipment for blood feeding and holding large numbers of *Culicoides* in experiments with sheep. — J. econ. Ent. 54, 816-818
43. JONES, R. H. (1964). Mass production methods in rearing *Culicoides variipennis* (Coquillett). — Bull. Wld Hlth Org. 31, 571-572
44. JONES, R. H. (1965). Epidemiological notes: incidence of *Culicoides variipennis* in an outbreak of bluetongue disease. — Mosquito News 25, 217-218
45. JONES, R. H. (1967). Some irradiation studies and related biological data for *Culicoides variipennis* (Diptera: Ceratopogonidae). — Ann. ent. Soc. Amer. 60, 836-846
46. JONES, R. H. (1967). *Culicoides* — biting midges. In: Insect colonisation and mass production. Edited by Smith, C. N. — New York (etc.): Academic Press
47. KETTLE, D. S. (1962). The bionomics and control of *Culicoides* and *Leptoconops* (Diptera: Ceratopogonidae = Heleidae). — Ann. Rev. Ent. 7, 401-418
48. KETTLE, D. S. & LINLEY, J. R. (1967). The biting habits of *Leptoconops bequaerti*. I. Methods, standardisation of technique; preferences for individuals, limbs and positions. — J. appl. Ecol. 4, 379-395
49. KETTLE, D. S. & LINLEY, J. R. (1967). The biting habits of *Leptoconops bequaerti*. II. Effect of meteorological conditions on biting activity; 24 hour and seasonal cycles. — J. appl. Ecol. 4, 397-420
50. KHALAF, K. T. (1966). The seasonal incidence of *Culicoides* in Southern Louisiana (Diptera: Ceratopogonidae). — Ann. ent. Soc. Amer. 59, 881-883
51. KITAOKA, S. & ITO, K. (1964). Attractiveness of black light to biting midges and mosquitoes. — Jap. J. sanit. Zool. 15, 208-209
52. KITAOKA, S. & MORII, T. (1963). Observations on the breeding habitats of some biting midges and seasonal population dynamics in the life cycle of *Culicoides arakawae* in Tokyo and its vicinity. — Nat. Inst. Anim. Hlth Quart. 3, 198-208

53. KITAOKA, S. & MORII, T. (1964). Chicken biting Ceratopogonid midges in Japan with special reference to *Culicoides odibilis* Austen. — Nat. Inst. Anim. Hlth Quart. 4, 167-175
54. LAVOPIERRE, M. M. J. (1965). Feeding mechanisms of bloodsucking arthropods. — Nature 208, 302-303
55. LEBIED, B. (1959). Détermination de l'âge physiologique des diptères. Nouvelle méthode basée sur la recherche des vestiges du processus de l'ovulation. — Riv. Parassit. 20, 91-106
56. LEE, D. J., REYE, E. J. & DYCE, A. L. (1962). "Sandflies" as possible vectors of disease in domesticated animals in Australia. — Proc. Linn. Soc. N.S.W. 87, 364-376
57. LEE, V. H. (1968). Parthenogenesis and autogeny in *Culicoides bambusicola* Lutz (Diptera: Ceratopogonidae). — J. med. Ent. 5, 91-93
58. LINLEY, J. R. (1965). Autogeny in Jamaican "sandflies" (Ceratopogonidae). — XII Int. Congr. Ent. Lond. 1964, 800-801
59. LINLEY, J. R. (1965). The ovarian cycle and egg stage in *Leptoconops bequaerti* (Kieff.) (Diptera: Ceratopogonidae). — Bull. ent. Res. 56, 37-56
60. LINLEY, J. R. (1965). Technique for obtaining viable eggs of *Leptoconops bequaerti* Kieffer, *Culicoides furens* Poey and *Culicoides barbosai* Wirth & Blanton (Diptera: Ceratopogonidae). — Mosquito News 25, 452-456
61. LINLEY, J. R. (1965). Changes in the ovaries of certain biting midges (Diptera: Ceratopogonidae) following completion of the gonotrophic cycle. — Mosquito News 25, 306-310
62. LINLEY, J. R. (1966). Effects of supplementary carbohydrate feeding on fecundity and life length in *Leptoconops bequaerti* (Kieff.). — Bull. ent. Res. 57, 19-22
63. LINLEY, J. R. (1966). The ovarian cycle in *Culicoides barbosai* Wirth & Blanton and *C. furens* (Poey) (Diptera: Ceratopogonidae). — Bull. ent. Res. 57, 1-17
64. LINLEY, J. R. (1966). Field and laboratory observations on the behaviour of the immature stages of *Culicoides furens* (Poey) (Diptera: Ceratopogonidae). — J. med. Ent. 2, 385-391
65. LINLEY, J. R. (1968). Autogeny and polymorphism for wing length in *Leptoconops bequaerti* (Kieff.) (Diptera: Ceratopogonidae). — J. med. Ent. 5, 53-66
66. LINLEY, J. R. (in press). Seasonal changes in larval populations of *Leptoconops bequaerti* (Kieff.)
67. LINLEY J. R. (1968). Studies on the larval biology of *Leptoconops bequaerti* (Kieff.) (Diptera: Ceratopogonidae). — Bull. ent. Res. 58, 1-24
68. LINLEY, J. R. (1968). Colonisation of *Culicoides furens* (Poey) (Diptera: Ceratopogonidae). — Ann. ent. Soc. Amer. 61, 1486-1490
69. LINLEY, J. R. (in press). Studies on larval development in *Culicoides furens* (Poey) (Diptera: Ceratopogonidae). I. Establishment of a standard rearing technique; some effects of diet and crowding. — Ann. ent. Soc. Amer.
70. LUEDKE, A. J., JONES, R. H. & JOCHIM, M. M. (1967). Transmission of blue-tongue between sheep and cattle by *Culicoides variipennis*. — Amer. J. vet. Res. 28, 457-460
71. MACLAREN, J. P., HAWKINS, J. L., MURDOCH, W. P. & BUSH, R. G. (1967). *Culicoides* control in the Canal Zone by water management. — Mosquito News 27, 513-519
72. MESSERSMITH, D. H. (1965). *Culicoides* (Diptera: Ceratopogonidae) associated with poultry in Virginia. — Mosquito News 25, 321-324
73. MINÁŘ, J. (1962). Pozorování vlivu meteorologických činitelů na aktivitu



- něketerých parazitických dipter (Ceratopogonidae, Simuliidae, Tabanidae). — Čsl. Parasit. 6, 331-342
74. MOLEV, E. V. (1958). The rearing of Ceratopogonids of the genus *Culicoides* in laboratory conditions. — Zool. Zh. 37, 1563-1568
75. MURPHY, D. H. (1961). Biological species confused under the name *Culicoides austeni* (C.I.M.). — Nature 192, 186-187
76. NELSON, R. L. (1965). Carbon dioxide as an attractant for *Culicoides*. — J. med. Ent. 2, 56-57
77. NIELSEN, B. O. (1963). The biting midges of Lyngby Aamose *Culicoides* (Ceratopogonidae). — Nat. Jutland 10, 46 pp.
78. NISHIJIMA, Y. & ONO, H. (1963). On the seasonal prevalence of Heleid biting midges at Nukabira in Hokkaido. — Res. Bull. Obihiro zootech. Univ. 3, 505-511
79. NISHIJIMA, Y. & ONO, H. (1964). Identification of blood meals of Heleid biting midges by the precipitin test (Diptera). — Jap. J. sanit. Zool. 15, 131-135
80. POMERANTZEV, B. I. (1932). Beiträge zur Morphologie und Anatomie der Genitalien von *Culicoides* (Diptera: Nematocera). (In Russian with German summary.) — Mag. Parasitol. 3, 183-214
81. REUBEN, R. (1963). A comparison of trap catches of *Culicoides impunctatus* Goetghebuer (Diptera: Ceratopogonidae) with meteorological data. — Proc. roy. ent. Soc. Lond. A. 38, 181-193
82. REYE, E. J. & LEE, D. J. (1961). An investigation of the possible role of biting midges (Diptera: Ceratopogonidae) in the transmission of arthropod-borne virus diseases at Townsville. — Proc. Linn. Soc. N.S.W. 86, 230-236
83. REYE, E. J. & LEE, D. J. (1962). The influence of the tide cycle on certain species of *Culicoides* (Diptera: Ceratopogonidae). — Proc. Linn. Soc. N.S.W. 87, 377-387
84. RIOUX, J. A. & DESCOUS, S. (1965). Détection du biotype larvaire de *Leptoconops* (*Holoconops*) *kerteszi* Kieffer, 1908 (Diptera: Ceratopogonidae) dans le « Midi » méditerranéen. — Ann. Parasit. hum. comp. 40, 219-229
85. ROGERS, A. J. (1962). Effects of impounding and filling on the production of sand flies (*Culicoides*) in Florida salt marshes. — J. econ. Ent. 55, 521-527
86. ROGERS, C. J.; SCHOEPPNER, R. F. & WHITSEL, R. H. (1967). A wind oriented attractant trap for gnats. — J. econ. Ent. 60, 1190-1191
87. ROWLEY, W. A. (1967). Observations on larval habitats and the winter bionomics of some common species of *Culicoides* (Diptera: Ceratopogonidae) in the central Columbian Basin. — Mosquito News 27, 499-505
88. ROWLEY, W. A. & JORGENSEN, N. M. (1967). Relative effectiveness of three types of light traps in collecting adult *Culicoides*. — J. econ. Ent. 60, 1478-1479
89. SERVICE, M. W. (in press). Studies on the biting habits of *Culicoides impunctatus* Goetghebuer, *C. obsoletus* (Meigen) and *C. punctatus* (Meigen) (Diptera: Ceratopogonidae) in southern England. — Proc. roy. ent. Soc. Lond. (A)
90. SHERLOCK, I. A. (1963). O problema do *Culicoides* em Salvador Bahia. — Rev. bras. Malariol. 15, 567-591
91. SHERLOCK I. A. (1964). Dermatozoonosis by *Culicoides* bite (Diptera: Ceratopogonidae) in Salvador, State of Bahia, Brazil. I. Entomological survey. — Mem. Inst. Oswaldo Cruz 62, 53-62
92. SHERLOCK, I. A. (1964). Dermatozoonosis by *Culicoides* bite (Diptera: Ceratopogonidae) in Salvador, State of Bahia, Brazil. II. The bionomics of the *Culicoides*. — Mem. Inst. Osw. Cruz 62, 145-159



93. SJOGREN, R. D. & FOULK, J. D. (1967). Colonisation studies of *Leptoconops kerteszi* biting gnats. — Mosquito News 27, 394-397
94. SMITH, W. W. & VARNELL, J. H. Jr. (1967). Hydrogen ion concentration (pH) as related to the occurrence and abundance of tree hole dwelling *Culicoides* spp. (Diptera: Ceratopogonidae) in northern Florida. — Mosquito News 27, 519-521
95. TATE, P. & VINCENT, M. (1936). The biology of autogenous and anautogenous races of *Culex pipiens* L. (Diptera: Culicidae). — Parasitology 28, 115-145
96. THOMPSON, P. H. (1967). Sampling haematophagous diptera with a conical trap and carbon dioxide with special reference to *Culex salinarius*. — Ann. ent. Soc. Amer. 60, 1260-1263
97. TOKUNAGA, M., TAKIYAMA, K., TANAKA, M. & YOSHIKAWA, H. (1961). Early stages and breeding place of *Culicoides arakawae* (Diptera: Ceratopogonidae). — Rep. Kyoto Univ. Agric. 13, 53-59
98. WALL, W. J. (1960). Control of *Culicoides* (Diptera: Heleidae) in small plots in Cape Cod, Massachusetts. — Mosquito News 20, 371-375
99. WALL, W. J. & DOANE, O. W. (1965). Control of *Culicoides melleus* (Coq.) (Diptera: Heleidae) with granular insecticide and the effect on other fauna. — Mosquito News 25, 191-196
100. WHITSEL, R. H., LAURENT, T. H., VICKERY, C. A. & MUNSTERMAN, H. E. (1961). Studies on the biology and control of *Leptoconops torrens* Townsend. — Proc. 29th Conf. Calif. Mosquito Control Ass. 1961, 32-38
101. WHITSEL, R. H. & SCHOEPPNER, R. F. (1965). The attractiveness of carbon dioxide to female *Leptoconops torrens* Tns. and *L. kerteszi* Kieff. — Mosquito News 25, 403-410
102. WILLIAMS, R. W. (1960). Quantitative studies on populations of biting midge larvae in saturated soil from two types of Michigan bogs. — J. Parasit. 46, 565-566
103. WILLIAMS, R. W. (1962). Observations on the bionomics of *Culicoides furens* (Poey) on St. John, U.S. Virgin Islands (Diptera: Ceratopogonidae). — Mosquito News 22, 155-157
104. WILLIAMS, R. W. (1964). Observations on habitats of *Culicoides* larvae in Trinidad, W.I. (Diptera: Ceratopogonidae). — Ann. ent. Soc. Amer. 57, 462-466
105. WILLIAMS, R. W. (1966). *Culicoides* (Diptera: Ceratopogonidae) in the vicinity of Ibadan, Nigeria, with special reference to cocoa pods as a breeding habitat. — Ann. ent. Soc. Amer. 59, 862
106. YANOVICH, G. I. (1961). A study of the bloodsucking Diptera of the Taiga regions of Western Siberia and experience in their control. — Med. Parazit. 30, 323-324
107. ZHOGOLEV, D. T. (1959). Light traps as a method for collecting and studying insect vectors of disease organisms. — Rev. Ent. URSS 38, 766-773

### Zusammenfassung

Dieser Artikel gibt eine Synopse der wissenschaftlichen Arbeit über Ökologie und Kontrolle der blutsaugenden Ceratopogoniden seit 1961. Die Übersicht umfaßt drei Arten, und zwar eine Unterart von *Lasioheles (sibirica)*, drei von *Leptoconops (becquaerti, kerteszi und torrens)* und viele von *Culicoides*. Eine besondere Aufmerksamkeit wurde der Arbeit der Sandfly Research Unit in Jamaika geschenkt, welche während der letzten Jahre wahrscheinlich das aktivste Zentrum war.

*Résumé*

Le présent article passe en revue les travaux sur l'écologie et le contrôle des cératopogonides sangsues depuis 1961. Cette revue s'étend sur trois genres dont une espèce de *Lasioheles (sibirica)*, trois espèces de *Leptoconops (becquaerti, kerteszi* et *torrens)* et un grand nombre d'espèces de *Culicoides*. Une appréciation plus minutieuse est faite des travaux de recherche du Sandfly Research Unit en Jamaïque, qui probablement fut le centre de recherche le plus actif pendant la période envisagée.