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The Ecology and Control of Blood-sucking Ceratopogonids*

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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. bequaerti* 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. bequaerti* 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. barbosai* and *L. becquaerti* [58]) have been shown to be autogenous. The percentage autogeny was high in two populations of *C. barbosai* 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 auto-gogenous, 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 becquaerti* (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. becquaerti* varies with the size of the female. At a constant size *L. becquaerti* 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. becquaerti* 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 auto-generously 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. becquaerti* (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 cals/cm²/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^{32} 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_2 . 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. becquaerti* 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. becquaerti* 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. becquaerti*. 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 1 $\frac{1}{4}$ 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. becquaerti* 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).

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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 sanguins 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.