BLACKFLIES (DIPTERA: *SIMULIIDAE*): A PROBLEM REVIEW AND EVALUATION

by

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ABSTRACT

An extensive review herein of world literature on blackflies (Diptera: *Simuliidae* Latreille) with references extending over nearly two centuries, and addressed to diverse interest groups, has highlighted the importance of these flies, their biological and resource-use impacts, the advances in knowledge concerning them, the gaps in the information, the obstacles to progress, the hazards of applying ill-considered heroic measures to cope with them, and the directions which research might profitably pursue.

Needs remain for clearer understanding of the components of blackfly behaviour in general, and at a species level, with due regard to determinant factors in attractance and repellence as these decide proneness to attack.

Needs remain for a clearer understanding of the factors of differential and changing physiological reaction of the host to the toxin injected by the flies.

Other needs remain for more thorough documentation of resource impacts caused by these insects.

A great need remains for more complete understanding of the population ecology of blackflies, as well as their role among primary consumers, and as food organisms themselves, in food chains in benthic ecosystems.

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* NOT MICROFILMED IN OTTAWA

THE BLACKFLY SONG

by

Wade Hemsworth

Twas early in the spring
when I decide to go
For to work up in the woods
in North Ontar-i-o,
And the unemployment office
said they'd send me thru
To the Little Abitibi with
the survey crew.

__CHORUS:__

And the blackflies - the
little blackflies,
Always the blackfly no
matter where you go,
I'll die with my blackfly
a-pickin' my bones
In north Ontar-i-o -i-o
In north Ontar-i-o -i-o

The man Black Tobey was the
captain of the crew
And he said I'm gonna tell you
boys, what we're gonna do.
They want to build a power dam
and we must find a way
For to make the Little Ab flow
around the other way.

(Chorus)

So we survey to the east and
we survey to the west
And we couldn't make our minds
up how to do it best.
Little Ab, Little Ab what shall
I do
For I'm all but goin' crazy
with the survey crew.

(Chorus)

Twas blackfly, blackfly everywhere
A-crawlin' in your whiskers,
a-crawlin' in your hair,
A-swimmin' in the soup and
a-swimmin' in the tea,
Oh the devil take the blackfly
and let me be.

(Chorus)

Black Tobey fell to swearin'
cause the work went slow,
And the state of our morals was
gettin' pretty low,
And the flies swarmed heavy -
it was hard to catch a breath
As you staggered up and down
the trail a-talkin' to yourself.

(Chorus)

Now the bull cook's name was
Blind River Joe;
If it hadn't been for him we'd've
never pulled through
For he bound up our bruises and
he kidded us for fun,
And he lathered us with bacon
grease and balsam gum.

(Chorus)

At last the job was over; Black
Tobey said - We're through
with the Little Abitibi and the
survey crew.
Twas a wonderful experience and
this I know
I'll never go again to North
Ontar-i-o.

(Chorus)

INTRODUCTION

There might hardly exist any family of organisms which encompasses a greater spectrum of biological, environmental, ecological, medical, economic, and sociological interests and problems on a world-wide scale than the blood-sucking flies of the Dipterous family *Simuliidae*. These flies are known in the English language as blackflies, buffalo gnats, sandflies, or turkey gnats, and in the literature of other languages they are found under such names as Kriebelmücken (German), Moscas de cafe (Mexican), Mouches de coloumbatz (Roumanian), and Mouches noires (French). They are not to be confused with a group of phytophagous aphids which also are known as blackflies.

Those who are familiar with these insects recognise them as small black or reddish-brown humped-back flies, whose general form is reminiscent of the North American "buffalo" or bison. From this similarity they have been awarded the scientific name "*Simulium*" from the Latin word *simulare*, to simulate.

Blackflies are significant primarily for the complications associated with the blood-sucking activities of the adult females on humans, and on various wild and domestic birds and mammals. A few species are entirely anthophilic, nectar-seeking, and thus entirely innocuous, but the nectar-seeking habit is shared also by haematophagous species. In their pursuit of blood, blackflies harass their hosts, disrupt the grazing activities of ungulates and their herd organization, hinder suckling by calves, and delay the reproductive process in cattle. The consequent late births may render the young animals poorly prepared for the rigors of winter. The blood-feeding causes blood deficiencies and blood-cell abnormalities in humans. Various dermal, pulmonary and systemic reactions result from envenomization by salivary toxins of the flies. In severe cases death accrues from anaphylactic shock.

The importance of these insects as a cause of human discomfort is testified by their being featured in a popular song "The blackfly song" (see preface).

Blackflies are significant also for their transmission of viruses, protozoa, and microfilarial nematodes to human, mammalian and avian hosts. These agents variously cause illness, blindness, dermal lesions and death.

In their injurious activites blackflies present problems of worldwide occurrence and importance for their effect on human health, recruitment and efficiency of the forest industries labour force, recreational use of forest areas, effectiveness of range-management for cattle, game, waterfowl and domestic fowl production. In some regions of the world where blackflies transmit disease to humans, valuable agricultural land along river valleys has been abandoned because of the afflictions conveyed to people by these insects.

The adults in flight are fed upon by various predaceous insects such as dragonflies, certain species of predaceous Diptera, and by birds, notably swallows. Hence they constitute an important item in the food chain of other organisms.

In the larval stage blackflies are an important form of aquatic life attached to stones and vegetation in rivers and fast flowing streams, as well as to the spillways of dams. In these habitats they feed upon micro-organisms and are in turn fed upon by aquatic larvae of other insect groups, and also constitute an important item in the food resources of fish in streams.

It is evident that control of blackfly populations cannot be undertaken without due regard to other consequences.

A special interest in blackflies derives from the suitability of their chromosomes for the study of genetics.

The concern over and interest in blackflies has generated a great amount of research on many aspects of the subject. Studies deal with the various biomedical problems associated with these flies. A few studies record rather sketchily the impact of the flies on resource use and development. Investigations aimed at alleviating the problem have sought to do so by population reduction through aquatic habitat control, chemical treatment of streams and rivers, and by evading attacks by provision of shelters, application of repellents and deterrents, and therapeutic treatment of bites and infections.

The literature is widely scattered in scientific publications in various languages, addressed to such different audiences as entomologists, physicians, parasitologists, and fisheries biologists, that no coherent and comprehensive account is available as a basis for evaluating the present state of knowledge, the gaps in knowledge, or the directions needed for research. Serious problems exist through the confusion in taxonomy, such that proper filing and retrieval of meaningful information is seriously hindered. Other problems reside in the lack of careful documentation of resource impacts caused by these insects.

Many of the earlier works are of refined caliber, but many are now inadequate in the light of present knowledge. With some notable exceptions, progress has been hampered by a fatalistic attitude toward the acceptance of misery, following the assumption that little can be done about it. Along with this attitude is the fact that firm documentation is lacking on the question of various impacts of these insects. Thus a vicious circle is set into motion: why solve a problem whose dimensions are unknown, and why measure the dimensions when there is no clear promise of a solution to the problem?

The present paucity of information and of understanding, not only impedes progress; it also carries the grave risk that, with increasing pressures on the development of the hinterlands, environmentally injurious actions may be made at any time by groups who decide to apply heroic tactics with ill-conceived measures which lack an overall strategic perspective.

It is evident that a need exists for clearer assessment of blackflies as a problem in human welfare, work efficiency, and resource uses. A need exists also for collation and evaluation of the specific problems and of the literature concerning the specific facts, alleged facts, and speculations pertaining to the biology and ecology of these insects. Thereby their possible inadequacies may be pinpointed and delineated for productive research objectives. Without such critical evaluation being made, the major needs may remain obscure, the more productive lines may remain neglected or subject to the caprice of human whims, and combative methods will remain empirical, inferior, and possibly environmentally detrimental.

Accordingly the purpose and scope of this thesis are set within the broad framework of blackflies as a group of worldwide occurrence and importance. The diverse biological, ecological, resource impact and combative phenomena are assessed. Directions for significant research are highlighted.

1. THE INDIVIDUAL ORGANISM

1.1 MORPHOLOGY

It seems worthwhile to place the subject of morphology of blackflies in the perspective of its purpose, for herein reside some of the problems of understanding them and of seeking means of coping with them.

A knowledge of general structure of all metamorphic stages of the group as a whole, and particulars of the different species within the group, merits attention for the purpose of establishing a firm foundation for all other work. It provides a definition of the basic plan to which all members of the group can be related, assigned a family group identify, and differentiated from other groups. Within the group, a description of the different morphs as the insect evolves ontogenetically forms an essential part of a definition of a group identity. Variations on details within the basic plan provide the basis for distinguishing successively lower taxonomic ranks to genus and species. Details of the external anatomy provide a map for the exploration of functional details such as the kind and distribution of sense organs, which may then be interpreted and explored experimentally. Details of the internal anatomy are important in respect to the investigation of salivary glands, their chromosomes, secretions, and possible immunological research. Other internal structures may be relevant to the study of food requirements. Such studies may involve examination of the alimentary tract of adults and/or larvae, or examination of thecondition of ovaries, testes, or state of insemination, as any of these may affect the blood-sucking habit.

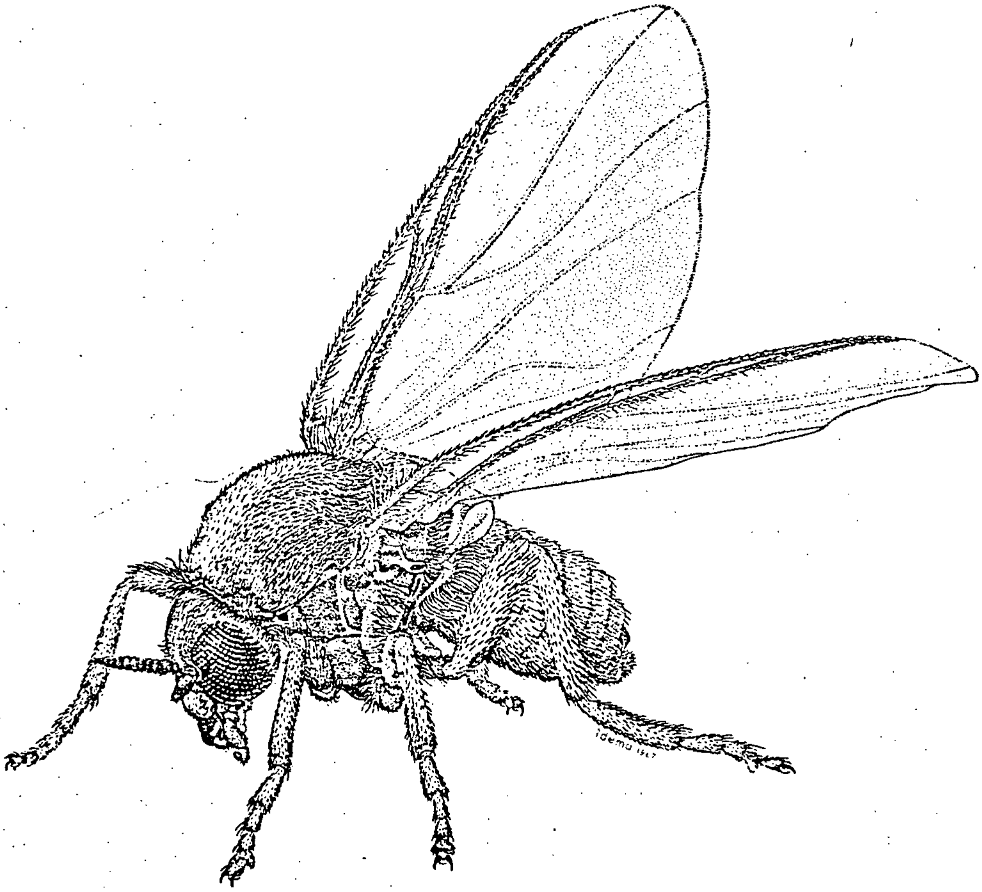
The relative consistency of morphological details of adults and larvae of such a ubiquitous group as the simuliids is remarkable. It is a cause of difficulties and disagreements among taxonomists who have different concepts for dividing the family into genera, and genera into species. With such difficulties in taxonomy, we find that other information which depends on correct and consistent identification, is confusing. From an evolutionary point of view, one might infer that the fluvial environment has imposed limitations on the scope for deviations from the common plan. It is conceivable, for example, that blackfly larvae have evolved an adaptation to a niche generally characterised by cold fast-flowing water, where attachment to substrata is within their means, appropriate supplies of food and oxygen are obtainable, where low water temperatures and fast-flowing water may reduce competition and predation. It is also conceivable that morphological adaptations which enable the adults to emerge from a flowing aquatic medium, and to dive into it for egg deposition, have imposed other limitations on morphological diversity.

1.1.1 Adult morphology

Blackflies constitute the family *Simuliidae* (Diptera: Nematocera). They are a very homogenous group and can be easily recognised in both adult and larval stages by their general form, as well as by certain unmistakable taxonomic characteristics. The different species are so similar in general appearance, and the distinguishing characteristics are so difficult to ascertain,

FIGURE 1.

ADULT BLACKFLY, *PROSIMULIUM MIXTUM* (X15)



FROM: Peterson, B.V. (1970).

that many species' descriptions in the literature might equally well serve for several species. This has led to obvious problems and confusion in taxonomy.

Adult flies are small, ranging in size from 1-6 mm., and most species are distinctly black-pigmented, though many appear silvery or yellow from their dense vestiture of short glistening hairs. Other species are brown, yellow or orange-pigmented. The thorax of the adult fly presents a strong development of the scutum and reduction of the prescutum, resulting in a prominent hump, which, together with the low-held head, has led these flies to be called "buffalo gnats" in the past.

Some species of blackfly are able to disperse great distances, and according to Lewis (1957), some can crawl underwater, indicating obvious strength of body construction.

The one pair of wings is broad and short with distinctly thickened longitudinal veins crowded toward the leading edge, other veins are indistinct.

Unlike otherNematocera, the antennae of blackflies are short and stout, usually no longer than the head itself. In both sexes the antennae are devoid of the long sensory whorls of hair characteristic of mosquitoes (*Culicidae*) and biting midges *(Ceratopogonidae)*.

In the female blackfly the eyes are dichoptic, i.e. widely separated by the frons, while in the male the eyes are holoptic (contiguous), and the upper facets can be sharply differentiated from the lower ones. This difference in eye size between the sexes is an easy way of approximately sorting the sexes. Ocelli are absent.

Mouth parts differ quite markedly between the sexes as it is only the female that is ever adapted to take a blood meal. It should also be noted that in some species of blackflies the females are non-biting, and have maxillae and mandibles without serrated edges. Generally, the blood-feeding female possesses a short, stout blade-like labrum having a finely serrated tip reminiscent of the toothed tip of a grapefruit knife. It is so formed that it incises the skin, cuts through capillaries, and wedges the wound open while the mandibles and maxillae, also serrated, sink into the wound. The mandibles and maxillae are channelled in such a way that when working together they provide salivary and food canals. The mandibles resemble broad flat plates, with the left blade over the right allowing transverse cutting movements to aid penetration. The maxillary blades are the galeae, which are housed, together with the mandibles and the hypopharynx, in the wide soft labium.

Male blackflies are presumed to feed on nectar and no record exists of them sucking blood. Their mouth parts are similar to the females but are considerably weaker, lacking the strength to penetrate skin, also the maxillae and mandibles lack cutting teeth.

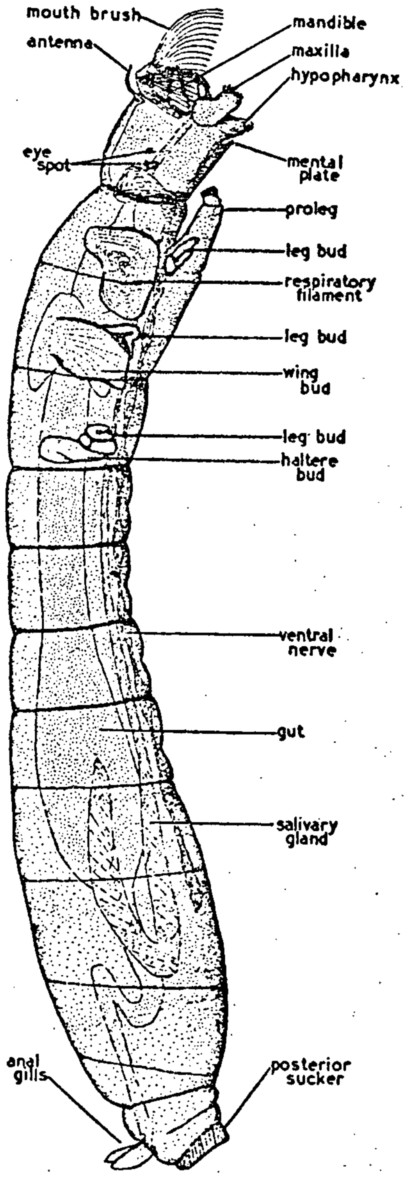
The actual function of each mouth part component, and the sequence of movements involved in penetration of the skin, lacks full description in the literature.

1.1.2 Larval and pupal morphology

Blackfly larvae have many distinguishing family characteristics, and can be fairly easily recognised in the field. All

FIGURE 2.

THE MATURE LARVA OF A BLACKFLY *ODAGMIA ORNATA*, LABELLED TO SHOW THE VARIOUS PARTS (X18)



FROM: Carlsson, G. (1962).

members of the family are aquatic, inhabiting fast-flowing streams and rivers throughout the world. Although certain diagnostic features will identify a blackfly larva *per se*, it is especially important, for correct filing and retrieval of information, to be able to recognise individual species when initiating a control program, or, for that matter, when undertaking any biological studies.

Unlike other Nematocera, which invariably have four larval instars, blackflies are stated to have six, seven, eight or nine such instars, depending on the source of reference and upon the species under discussion.

Mature larvae range in length from 4.5-12 mm. (Crosskey, 1973), and are characteristically rather swollen in the thoracic region and posteriorly in the abdomen. Individuals vary quite considerably in colour from grey to black, blackish-brown and off-white.

Although the typical blackfly larva is recognised as bearing a pair of large cephalic fans on the head, atypical species do occur in which the fans appear reduced (*Crozetia crozetense* and *Simulium oviceps*) and, furthermore, fanless species do occur, i.e. *Gymnopais* and *Twinnia* (Craig 1974). Very little literature is available on these atypical species, and most descriptive documents on blackflies ignore them altogether.

The cephalic fans are normally held extended by internal fluid pressure so as to act as food filtration organs in the current of the stream or river (Wood *et al.*1962). In their fine structure these cephalic fans may be of taxonomic value.

Antennae of the larvae can act as diagnostic features. Although all species appear to have four-segmented antennae, the ratios of the lengths of various segments and annuli to one another, and the number of annuli are of diagnostic value to species identification where such details are recorded.

Mouth parts consist of haired maxillae, each with a single-segmented maxillary palp, a pair of large toothed mandibles, a large anterior labrum, and a thickly haired hypopharynx. The best specific characters of this region are offered by the unsclerotized area on the ventral surface of the head, usually referred to as the post-genal cleft. The shape of this cleft varies from that of an inverted "V" to a more rounded shape, and is of great importance taxonomically (Wood *et al.* 1962).

Patterns of coloration on the head vary quite distinctly between species, and are of some taxonomic value.

Mature larvae can further be distinguished by having a mid-ventral proleg just behind the head, which is armed with a circlet of hooks and functions as a holdfast. Posteriorly, ventral to the anal opening, is a ring of many radiating rows of hooks, the anal ring. The number of hooks in each row of this ring varies between species. These two holdfasts, the proleg and anal-ring, are used by the larva in locomotion. Larvae can also release themselves on silk threads produced by the salivary glands, for attachment further downstream.

The larval rectum bears prominent, colourless rectal gills, believed to have an osmo-regulatory function (Crosskey 1973).

At maturity the larva possesses distinct gill-spots on the thorax, which are the future pupal gills. Also, the dorsal abdominal hooks of the future pupa show through the larval cuticle. Prior to pupation a cocoon is constructed from silk produced by the salivary glands. The shape of the cocoon varies between the different species. According to Crosskey (1973), some very rare forms have no cocoons at all. At this stage the arrangement of the abdominal hooks on the pupa, and the form of the pupal gills is of great taxonomic importance. The number of respiratory filaments in each gill is generally constant in each species, and may range between 4 to 60 in different species (Malloch 1914).

1.1.3 Egg morphology

Blackfly eggs are typically smooth, ovoid in shape, white when laid, becoming darker during embryogenesis. The long axis ranges from 0.1 to 0.4 mm. No special studies have been made on egg morphology but they are known to be relatively resistant to chemical insecticides.

1.2 REPRODUCTION, GROWTH AND MORPHOGENESIS

1.2.1 Reproduction

The mating process of adult blackflies is dealt with very briefly in the literature, and there is no clear understanding of how or when mating occurs. Presumably there is a certain time period, which has yet to be defined, in which the newly emerged flies undergo the necessary gonad development prior to mating.

It is recognised that most, if not all, of the blood-sucking species of blackflies need a blood meal before oviposition can occur. However, female flies do not usually suck blood until 24-48 hours after emergence as it takes this time for the salivary gland contents to accumulate.

Many reports have been made of swarms of blackflies flying great distances to their hosts, with no suggestion that the female returns to its river of origin for oviposition. Presumably, when such swarming occurs, the immigrant gravid females deposit their eggs in the nearest stream or river. One inference might be that while large numbers swarm, a certain percentage of an emerging adult population remains around the infested stream where they reproduce and perpetuate a resident population. However, this aspect, although vital for understanding the biology of the blackfly, has been almost completely by-passed to date.

Fredeen (1963) suggested that *Simulium arcticum* can emerge either as an autogenous or anautogenous population, dependent on the month of development. If early summer populations do not require a blood meal, as Fredeen suggests for *Simulium arcticum*, then these autogenous females could account for the reinfestation of the breeding site which so frequently occurs but is without suitable explanation.

Once mating has occurred the eggs are laid in a suitable aquatic habitat, which may be either a stream or river according to the species. Eggs are usually laid on trailing vegetation in the water or on submerged stones and rocks. Carlsson (1962), studying the egg-laying of *Simulium venustum*, *Odagmia ornata* and

Eusimulium aureum in Scandinavia, found all three species to display similar patterns of oviposition behaviour. The female flies laid eggs on objects at the water surface, and also climbed down underwater in search of suitable stones, sometimes to depths of 20 cm. Some blackfly species, such as *Simulium vulgare* and *Simulium arcticum*, are believed to deposit their eggs loosely and singly by flying low over the water surface (Carlsson 1962, Fredeen *et al.* 1951). Exactly what means the blackfly uses to attach newly laid eggs to a substratum is unclear. Information would be desirable, but presently does not exist, on the possible relationships between the mating and oviposition and such variables as light-intensity, relative humidity, temperature, and wind.

1.2.2 Morphogenesis and growth

The development period for blackfly eggs may vary from a few days to a few months depending on the species and the situation. Most workers agree, as might be expected, that the length of the egg stage depends upon temperature conditions of the stream or river. In the tropics eggs may develop in one or two days, whereas many temperate species have egg stages lasting for periods of up to several months. Some species are known to be able to develop from sub-arctic streams frozen over for the winter months. Egg diapause can also occur (Crosskey 1973).

The period of larval development involves eight or nine instars and varies greatly in overall duration. Crosskey suggests that larvae of northern climates, which over-winter and develop slowly, produce larger adults than are found in the tropics where larval development is rapid.

The true pupal stage also varies in length, but there appears to be some confusion over this. Crosskey (1973) suggests that as the pupal life is always short, its development is independent of temperature, but there seems to be no support in the literature for this assumption. In fact, Matheson (1950) reported the blackfly pupal stage as lasting from two to seven days, or longer, depending on the weather. Furthermore, Carlsson (1962) found that pupae of *Simulium vulgare*, *Simulium venustum*, *Simulium reptans*, *Wilhelmia equina* and *Odagmia ornata* emerge sooner in a warm stream than a cool one. Certainly it would seem that Crosskey's statement must be questioned.

Because the "timing" varies so greatly between species it is common to have different species emerging almost continuously, one species after the other, for the entire summer. The fact that the species are changing so frequently has led to great confusion in taxonomy and in clinical aspects of sensitivity and immunity.

1.3 FEEDING

An understanding of the feeding activities and specific food of blackflies, in both larval and adult stages, is necessary for interpretation of the ecology of the various species in their different and regional habitats. On this basis causal relationships, predictions, and environmental manipulations become possible.

1.3.1 Larval feeding

The diet of blackfly larvae is somewhat ill-defined in the literature, and this aspect very obviously needs closer study. Most workers refer to larvae feeding on "detritus", but few have defined this term. According to Jones (1949), "Detritus means amorphous vegetable matter mixed with fine grit and occasionally with a few empty algal cells".

Species that possess cephalic fans (most species) are able to strain "particulate matter" from the water by holding their fans out into the current of the water. The larvae are designated as filter feeders. The few species known to be without cephalic fans appear to feed by raking the substrate with the labrum (Craig 1974, Crosskey 1973). A detailed study on ingested food of the various species in their different habitats is needed.

1.3.2 Adult feeding

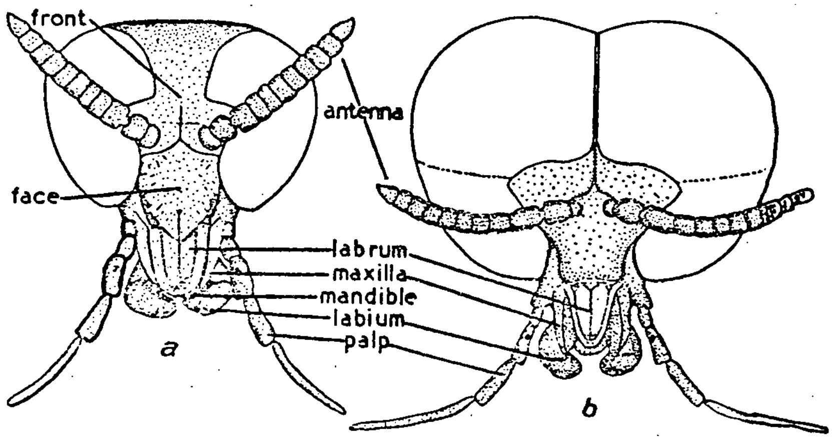
Knowledge of the feeding habits of adult blackflies, and the environmental conditions favourable to obtaining food, is surprisingly lacking for most species. The degree of dependency of blackflies on blood as a nutrient source is open to question. Certainly blackflies have been observed visiting flowers, and blood-sucking females have frequently been found with a colourless sugary fluid stored in the crop. It is not known how important blood is to the various species, or how much the females rely on nectar as a nutrient source. It is merely assumed that male blackflies feed on nectar, no proof appears to be available.

Blackflies feed on blood from a wide range of warm-blooded vertebrate hosts. Available field studies suggest that the majority of species show a distinct preference for feeding either on birds (ornithophilic) or on mammals (mammalophilic). No species is known to feed exclusively on humans. The degree of host specificity of blackflies is not fully understood, and many uncertainties exist in the observations reported so far. Problems arise when assumptions are made on the host preferences of certain species, when in fact such apparent "preferences" are an artifact of the circumstance that other hosts are lacking in the study area. Some blackfly species display much more specific feeding habits than others, preferences may also differ for the same species in different locations (Fallis 1964).

A detailed account of theimpact of blackflies on their hosts, the range of hosts and consequent host reactions is given in section 4.

Feeding mechanism: The female mouth parts, as previously described, are used to lacerate the skin of the host, and to provide an oozing reservoir of blood. During biting the skin is first stretched taut by the toothed labrum, which appears to make penetration by the mandibles possible. The saw-toothed mandibles are worked into the skin in a scissor-like manner, cutting across the capillaries in a way which causes subcutaneous bleeding. The mandible penetration is followed by the piercing maxillae and hypopharynx. This action does not cause immediate pain, as does the penetration of mosquito mouth parts. Once the mouth parts are firmly inserted, saliva is pumped down into the wound from the salivary glands, and blood is drawn up. The amount of blood taken at each meal is equivalent to rather more

FIGURE 3.



THE HEADS OF (A) A FEMALE AND (B) A MALE OF A SPECIES OF *SIMULIUM*, SHOWING THE MOUTH PARTS. (X30) FROM: Carlsson, G. (1962).

than the body weight of the individual fly (≃ 2 mgm.). Contrary to popular belief, the flies cannot bite repeatedly, in fact it may take two to four days for the salivary glands to become recharged with saliva after one blood meal, and during this time blood is excluded from the diet (Crosskey 1973, Davies and Peterson 1956). The saliva is generally believed to contain an anticoagulant, the nature of which is unknown, and an agglutinin. However, detailed studies of the saliva have been made for only a few species of blackflies (Yang and Davies 1974). The clinical details of biting, and the toxic reaction so induced, will be discussed in detail in section 4.

1.4 FLIGHT

The flight activities of blackflies are almost totally confined to the daylight hours, particularly 5 p.m. to 7 p.m. This is in contrast to mosquito behaviour, and furthermore, unlike mosquitoes, blackflies only rarely fly into buildings. This behaviour is taken advantage of in the practice of providing dark shelter for cattle. Because blackflies are on the wing out of doors during daylight working hours, very many outdoor activities are seriously affected. Forest activities are no exception; labour force efficiency is hit, group morale is lowered, and some work operations may even have to be suspended or abandoned.

The flight range of blackflies is greatly influenced by winds, and possibly by air-movements, although very little documentation exists. *Simulium arcticum* was reported flying in wind-borne swarms for 90 to 100 miles (144 - 166 Km) in the Saskatchewan Valley and *Simulium columbaschensis* is recorded to have "travelled" 124-280 miles (200 - 400 Km) with wind currents on the Danube (Herms 1969). Certainly, the flight range of blackflies seems to have great potential when any wind is involved.

A very important question, which so far has not been investigated, is whether flight is a necessary conditioner for feeding and/or oviposition, in conformity with the principle of successive induction, which has been shown to apply to other insects (Graham 1959, Kennedy and Booth 1963). If this does apply to other insects it might well explain one of the problems encountered with rearing blackflies in the laboratory. Only one group of workers has so far succeeded in rearing blackflies throughout a complete cycle in the laboratory (Wenk and Raybould 1972). Previously, researchers have found it impossible to get newly emerged adult flies (that have been reared from eggs) to feed on blood and to oviposit. No consideration has been given to adult flight requirements in any of these rearing experiments. This aspect warrants precise study before one might hope to rear blackflies successfully in the laboratory. Until laboratory rearing can be accomplished, progress will be hindered in experimental work which requires that the age in hours or days, or the biography of the individual insects be known. Fredeen (1963) has pointed out that *Simulium arcticum* does not appear to need any conditioning flight prior to oviposition in its early summer population, as these individuals are autogenous, and oviposition occurs within close proximity of the emergence area. However, it may still be that individuals require a certain period of short range flight around the river before they are "ready" to oviposit. This aspect has not been investigated.

1.5 BEHAVIOUR

A knowledge of the determinants of blackfly behaviour would provide a foundation for defining and predicting the circumstances under which attacks may be expected to occur. Also, such knowledge would provide an important key to techniques needed for rearing blackflies in the laboratory. Furthermore, a knowledge of the components and determinants of behaviour would provide the necessary basis for designing bioassay techniques for the development of chemical attractants for use in traps, or repellents for preventing attacks on individual hosts.

Behavioural studies to date have failed to consider the numerous determinants which must be considered before even the foundations of behaviour can be understood. The study of blackfly behaviour should involve a consideration of the following determinants: -

- The species under study must be known and classified without any doubt. Results obtained with one species cannot automatically be transferred to another.
- A knowledge of the sex of the individuals under study, or the sex ratio, is also of uttermost importance in any behaviour studies.
- Behaviour can alter radically with the age of the

individuals, therefore it is vital to know the physiological age of the population under study.

- Quite often flies used in either field or laboratory study have undergone some kind of "conditioning" possibly by heat, cold or flight. This possibility must be considered when reviewing the results of any behaviour studies.
- Whether or not a blackfly has had its first blood-meal will greatly affect the pattern of behaviour. Also, assuming the flies have already sampled blood, the time since the flies last fed should be known. Flies in different states of nutrition during a behaviour study cannot be freely compared.
- It may be that one response is inhibited by another, and that as Kennedy and Booth suggested for aphids (1963), one activity is influenced by the previous activity of the insect. If such a phenomenon occurs within blackfly populations it has as yet to be recognised, but the concept should not be ignored in any behaviour study.
- The ambient conditions under which behaviour is observed, either in the field or in the laboratory, are the behaviour determinants that have received most attention in the literature. Behaviour in relation to temperature, relative humidity, lighting, and air flow has been studied for some mosquitoes, but to a much lesser degree for any species of blackfly. Unfortunately many of the experiments have failed to take note of the behaviour

determinants mentioned previously.

- Further, there are the host factors to be taken into account in any study of insect behaviour, and this is the most extensively worked field. The physiological state of the host, the age, colour of the skin, and state of nutrition may all influence the behaviour of a blackfly. Too little is understood of the possible importance of spectral reflection and emission of the skin, or of the chemical products produced on the skin by sebaceous and sudoriparous glands.

The mechanisms involved in bringing an attacking blackfly into contact with its host are among the most significant of the factors in the survival strategy of the attacker, as well as in the consequences for the host. The most studied area of blackfly behaviour is that of host attraction and host selection by way of <u>host</u> factors, and these experiments will be reviewed here. However, it must be remembered that many of these behaviour experiments have ignored the other determinants of behaviour stated previously.

Although the host-finding procedure of blackflies is not fully understood, it is assumed that the blood-seeking females are attracted by both visual and air-borne stimuli.

1.5.1 Visual host factors of importance in attraction

Colour: Literature pertaining to the differential landing responses of the *Simuliidae* to colour is relatively scarce, (Davies 1951, 1961, 1972, relating to *Simulium venustum*; Fredeen 1961 relating to *Simulium venustum S. decorum, S. vittatum*;

Bradbury and Bennett 1974 a) relating to seven species of simuliids. The work of Peschken and Thorsteinson (1965) was concerned with the attraction of gravid female blackflies to oviposition sites, and such responses cannot be compared to the responses involved in landing to feed. Bradbury and Bennett's work (1974 a)) indicated that species emerging in the spring have colour preferences differing from those species emerging in the summer. It should be noted that background colours of the environment, offering either host contrast or host cover, change through the seasons, and a colour imposing an obvious contrasting spectral composition in the spring may blend with the background environment by the summer.

Davies (1951, 1961, 1972) found that landing frequency of blackflies varied inversely with the intensity of reflected light. Dark cloths, with the highest reflectance of ultra-violet and violet wave-lengths, had the highest "landing percentages". It is worth noting that Davies used two pieces of paper or cloth, side by side, for each of his experiments. It is highly possible that one colour could affect the attractancy of the other in such a situation. Also, he used 6" x 6" squares for all of his sample colours, so ignoring the possibility that size of target colour could influence the results.

The colours least frequented by blood-seeking simuliids are those that are found most attractive to ovipositing females (Peschken and Thorsteinson 1965). It is possible that the preference for yellow and green displayed during oviposition may occur around the host after the females have had their first blood meal.

Davies draws a comparison between his 1972 results for simuliid colour preference and the results of Brown (1956) for mosquito colour preference, as the same materials dyed to the same standard colours were used, together with the same spectro photometer. He notes that the order of attraction of colours for female *Aedes aegypti* differed from that for *Simulium venustum*, although, for both, the green, yellow and red were the least frequented, and dark purple and dark red the most. Not all such experiments can be so readily compared. It must be remembered that measurements of total intensity for one colour will differ if a photometer more sensitive to certain wave-lengths is used. In Davies' (1951) early work, reflectance was measured with an exposure meter carefully selected for its sensitivity similar to the human eye, and yet it was insect vision under test, not human.

Although red and blue are apparently more attractive than black for mammalophilic simuliids, Bennett *et al.* (1972) noted that *Simulium euryadminiculum* selected black "colours", but then this species of blackfly is attracted to only one host, as far as is known, and the host's natural colour is dark.

Although the most recent results on colour preferences (Bradbury and Bennett 1974 a)) conform with the general conclusions of the earlier workers, the need for detailed consideration of behaviour on a species level is strongly emphasized. The behavioural state and physiological age of the flies under study must always be borne in mind. The behaviour of a female blackfly may involve quite different colour responses before and after blood-feeding. It should be stressed that generalizations on the attractiveness of colours to simuliids, when regarded collectively, must be treated with caution. As yet there is no proof that blackflies can perceive "colours" at all.

If clothing colour is chosen and worn for its unattractiveness to blackflies, the exposed areas such as the face and hands, may, by reason of simultaneous contrast, become that much more attractive. While swarms of flies might be attracted to, and rest on, the back of a dark red jacket, a less attractive colour would leave the flies to find an alternative landing site such as the face or hands, which would also provide the desired feeding sites.

Shape, movement, and contour: The visual factors of shape, movement and contour have been shown to have some importance in the attractancy of certain blackfly and mosquito species to their hosts. Sippell and Brown (1953) demonstrated that attraction of *Aedes aegypti* to prairie deer mice (under laboratory conditions) was doubled if the mice were allowed to move freely, rather than being confined. Similar results were obtained for dull black canisters when compared in a stationary position or when moved along a straight line. It appeared from these experiments that, under laboratory conditions, visual were about equal to airborne factors in attractiveness for a still host, but for a mobile host visual was the more "powerful" attractant factor. For both inanimate and animate bodies, these experiments indicated a doubling of attractancy with movement. However, Wood and Wright (1968) could not agree that movement contributed any more than marginally to the attraction of *Aedes aegypti* in the laboratory.

The first work done on the attraction of blackflies to moving objects did not appear to agree with the above results (Peschken and Thorsteinson 1965). However, these blackfly behaviour experiments did not involve any natural hosts, the flies in the experiments being attracted to traps that were hung in a fixed position as well as some being hung freely to rotate in the air currents. The stationary cylinders attracted significantly more flies than the freely suspended ones. The need for further research on the involvement of host movement in attraction is evident.

Host shape in relation to attractancy of blackflies has been studied to a somewhat greater extent than has movement (Bennett *et al.* 1972, Fredeen 1961). Fredeen compared three trap shape designs for blackflies. The largest, a "cow" silhouette trap was 4 feet (122 cm) high, 5 feet (152.5 cm) long, and 2 feet (61 cm) wide, standing on four wooden legs and covered in the upper two-thirds with dark brown plywood. The "sheep" silhouette trap was constructed 18 inches (45.8 cm) high, 2 feet (61 cm) long and 1 foot (30.5 cm) wide. The third trap was a "pyramid" silhouette, 4 feet (122 cm) high and 3 feet (91.5 cm) square. No bait was used in the traps and it was found that *Simulium arcticum*, under field conditions, was not influenced in its landing responses by the shape of the traps. However, it appeared that the effectiveness of the traps was a direct function of surface area and size of opening on the underside of the trap, regardless of shape. These 3 types of trap were placed very closely together during the experiments, and this factor may well have influenced the results.

The attractancy of a host may be influenced by its contour. Sippell and Brown (1953) compared the landing rates of *Aedes aegypti* on an all black cube and on a series of black and white cubes. It was found that the attractiveness of the black and white cubes could be increased by as much as 60 percent by increasing the contour, i.e. by increasing the number of squares on the cubes while keeping the areas of black and white equal (Brown 1956).

Brown (1952) found that significantly more mosquitoes were attracted to a glossy black surface than to a dull black one. He attributed this to the mirroring surfaces presenting an attractive flicker effect to the insects' compound eyes.

Peschken and Thorsteinson (1965) compared the attractiveness of 2-and 3-dimensional targets to three blackfly species, but none of the species appeared able to distinguish between the different targets. However, *Simulium euryadminiculum*, the blackfly specific to the common loon, has shown a definite preference for black targets of 3-dimensional form rather than 2. It may be that this strong response to 3-dimensional black is a natural response of the flies to their hosts, remembering that *S. euryadminiculum* is an unusual species in its total restriction to one host, the common loon. Bennett *et al.* 1972 also found that this blackfly preferred the most pronounced portions of any silhouette shape offered.

It would seem virtually impossible to draw any conclusions on the importance of host shape to blackflies from the experimental work done so far. For one species (*S. euryadminiculum)* shape/dimension does appear to have some relevance, but this cannot be confirmed by workers who have tested *Simulium venustum*, *S. decorum* or *S. vittatum* (Peschken and Thorsteinson 1965).

1.5.2 Airborne host factors of importance in attraction.

Temperature and moisture: In 1910 Howlett conducted a series of very simple experiments on some Indian species of mosquitoes, and was able to demonstrate the importance of convective heat in the process of attraction. He did this by suspending a test-tube of warm water above and below a cage of mosquitoes. The flies were attracted only when the tube was held below them, so that they were in the convective currents emitted from it. These results were later confirmed by Peterson and Brown (1951), whose experiments involved the separation of radiation and convection currents by the interposition of an air-tight window of thallium bromiodide between a warm object and the test mosquitoes. Without this window, billiard balls warmed to 100 or 110^{o}F (39 or 43^{o}C) attracted twice as many flies as balls at 80^{o}-90^{o}F (27-32^{o}C). At temperatures of 120^{o}F (50^{o}C) this attractiveness was reversed. However, when the convective currents were shut out by the positioning of a thallium bromiodide window, this temperature response was eliminated, therefore suggesting that mosquitoes respond to convective and not radiant heat.

Similar temperature studies were conducted in the field using robots as the attractive bait (Brown 1951). The number of landings per minute on the robots clothing was taken as the criterion of attractiveness. The robots were simple water-filled tanks on legs, one of which was maintained at body temperature (37.5°C), while the other was filled with cold water 48-64°F (9-18°C). Only when the cooler robot was below 60°F (15.6°C) did the warmer attract significantly more flies. However, when the clothing of the warmer robot was moistened, and the temperature differential so increased, the robot became nearly twice as attractive as the cooler one. These experiments indicated that warmth was a significant factor in attractancy only when the air temperature was below 60°F (15.6°C). Above this temperature moisture appeared to be needed for the warmer body to show any greater attractancy. These results disagree with those obtained in the billiard ball experiments when the warmer ball was also more attractive, up to 110°F (43°C).

Brown's experiments continued with tests on the attraction of the human hand at different temperatures (Smart and Brown 1956). Only a very narrow temperature range was used, the subjects' hands not varying more than 4°C. A hand that was cooled to 22°C (71°F) attracted significantly fewer flies than a hand at normal body temperature. Although the warmer hand of each pair used in each test was always the more attractive, the results were not as highly positive as those obtained with the billiard ball experiments. It appears that the "best" results in temperature difference experiments are obtained when normal body-temperature attractancy is compared with that of a super-cooled body. Also, the heating of a hand above body temperature decreases its attractancy when compared with a normal hand.

It is not easy to draw conclusions from these experiments. Generally, it appears that temperature is of second place importance to moisture, and only when a dry body is cooled does attraction seem to alter at all. The combination of warmth plus moisture in a bait, which is in fact the most likely field situation, is significantly more attractive than a dry and warm bait.

The first work on blackfly attraction and the thermal question was that of Fallis *et al.* (1967). They noted that flies were taken in greatest numbers in fan traps during the 5 p.m. - 7 p.m. period. By adding heat to the fan traps they aimed to test the effects of heat on attractancy, but the results are unreliable as a constant amount of heat was not maintained. Together with the thermal stimulus, carbon dioxide (CO_2) was added to the traps, and the results suggested that more flies were attracted, but this did not hold for all the species tested. No generalizations are warranted until extensive work has been done on additional species.

From the experiments performed with air streams in the laboratory (Brown *et al.* 1951), and with wet and dry billiard balls in the laboratory (Peterson and Brown 1951), as well as with robots in the field (Brown 1951), it would appear that moisture is an important attractive factor to *Aedes aegypti*. Moisture, however, took second place to temperature when ambient air temperatures fell below 60°F (Brown 1951, 1952, 1966).

Researchers studying the human hand (Smart and Brown 1966) were surprised to find that hands with greater water output were less attractive than the normal. This was later confirmed with a large number of subjects (Brown 1966). No explanation was offered at the time for the apparent divergence in results. However, it is known that sudoriparous type sweat, such as that occurring on the hands, is significantly less attractive than the sebaceous type of under-arm sweat. It could have been a combination of water vapour and constituents of sweat that resulted in the repellency reported in Smart and Brown's work with the human hand, in fact they suggested factors other than, but related to, moisture output.

The results of moisture attractiveness experiments on a hand cannot be taken as any reading of the importance of moisture for the human body as a whole.

Sweat: The importance of sweat in attractancy has not yet been satisfactorily defined. Parker (1948) found arm-pit sweat to be more attractive to *Aedes aegypti* than moisture alone. Willis (1947) and Brown *et al.* (1951) agreed with this result. However, these initial experiments met with contradiction, as does the whole subject of sweat today. Earlier workers (Crumb 1922, Rudolfs 1922) using *Aedes solicitans* and Reuter (1936) working on *Anopheles atroparvus*, all agreed that sweat, either arm-pit sebum or forehead sudor, did not show any significant attractancy to mosquitoes.

Brown (1951) conducted a series of field experiments using robots as baits. He noticed that robots dressed in sweaty jerkins (arm-pit sweat) attracted more flies than robots in clean clothing of similar moisture content. Further laboratory experiments (Brown *et al.* 1951) indicated that human arm-pit sweat was repellent at high concentrations and attractive at low, when its vapour was passed through an olfactometer. However, it could be questioned whether they were observing repellence or arrestance.

It is known that arm-pit and forehead sweat differ in their chemical make-up, particularly in the sudor/sebum balance. Sudor is an aqueous solution of NaCl plus non-colloidal organic compounds present in the blood, and is produced all over the body surface, particularly in hairless regions such as the palms, soles and forehead. Sebum contains lower fatty acids, esters of higher alcohols, cholesterol, and albumin, and is produced mainly in the underarm and groin regions. Thompson and Brown (1955) decided to look into the differences in attractancy of sudoriparous and sebaceous sweat. After a series of olfactometer experiments, they concluded that although arm-pit sweat did appear attractive at certain concentrations, forehead sweat was not attractive at all. They were not able to increase the attractancy of moist clothing by the addition of arm-pit sweat, thereby contradicting the earlier results of Brown (1951) with the robots.

Observations made by various workers on the attractancy of sweat are so contradictory that it is obvious that the problem is a complex one needing deeper understanding. It appears that there is only a vague understanding of body surface excretions and secretions. For example, Brown and Carmichael (1961) suggest that "body odour" attractancy may be due to attractants such as amino acids, diffusing directly from the skin capillaries. This suggestion seems highly unlikely as amino-acids are not known to occur on the skin, apart from when they are excreted by sweat glands which occur all over the body surface. With regard to the individual amino-acids found in body sweat, it would appear that some attract while others repel (Hier *et al.* 1946). Interest has centered around lysine and alanine as attractive components (Brown 1956, Brown and Carmichael 1961, Lipsitz and Brown 1964, Skinner *et al.* 1965). Brown and Carmichael consider lysine to be more important than alanine.

The genetically determined basic body chemistry of an individual will determine individual body emanations and odour. Odour will differ between individuals, and this may well affect attractancy. It is also quite possible that body emanations of an individual will change with change in diet, and consequently attractancy may alter. The subject of diet affecting body emanations, and therefore attractancy, has not been given the consideration it warrants.

The whole question of body emanations and biting fly attractancy requires experimentation and understanding by persons competent in this field. It is not sufficient for entomologists to conduct small-scale experiments on the importance of sweat in attractancy when they do not have even the vaguest understanding of body emanations. Human phsyiologists, working together with insect behaviourists, are needed if this field is to be worked and understood. The work done by entomologists to date, if having done nothing else, has revealed the present confusion and lack of understanding, and has pointed the direction for future research.

Carbon dioxide: One of the most controversial materials in the study of attraction is carbon dioxide. Some workers have found it to attract mosquitoes (Brown 1951, 1956), while others have found it to repel (Brouwer 1960, Willis and Roth 1952). Various experiments with olfactometers have given quite contradictory results. Brown *et al.* 1951 showed dry air with 10 per cent CO_2 to be more attractive to *Aedes aegypti* than dry air alone, and yet moist air with 10 percent CO_2 was no more attractive. Willis and Roth (1952) used both large and small cage olfactometers, and in the former the addition of ten percent CO_2 had a repellent effect.

Many workers agree today that the role of CO_2 is that of a general activator, rather than an orientator (Fallis *et al.* 1967, Hocking 1971). The general trend of results suggest that although CO_2 may activate at low concentrations, it can also "repel" at higher ones. It should be noted that under the conditions of their olfactometers it is possible that the experimenters misinterpreted the effects, and failed to recognise that what they call "repellence" may in fact be a flight arrestant that leads to "landing".

Specific simuliid attraction to CO_2 has rarely been found. The results of Fallis *et al.* 1967 support the idea that CO_2 plus visual stimuli affects the movement of *Simulium venustum* toward test silhouettes. In collecting several species of blackflies, with the aid of different stimuli, Fallis *et al.* suggested an arrangement of the species into four groups. The first group includes flies that will move to an odour without added CO_2, but more are attracted if CO_2 is added. *S. euryadminiculum* is the only species known to respond in this way. The second grouping includes flies such as *S. rugglesi*, that come to CO_2, or CO_2 plus an odour alone (Fallis and Smith 1964). The third grouping involves those species that move to CO_2 alone, i.e. *S. venustum*. Finally, the fourth group includes those species that appear to react to visual stimuli, but not to CO_2. This group system is based on a minimum of evidence, and such extensive generalizations seem somewhat unwarranted. Further work needs to be done with other species taking full account of all prevalent conditions.

Golini and Davis (1971) performed upwind orientation behaviour experiments with *S. venustum* in the field. They found that *S. venustum* will fly upwind towards a source of CO_2, and will do so only when this gas is present. (This supports the laboratory results of Fallis *et al.* 1967).

Very recent work by Bradbury and Bennett (1974 b)) examines how vision and odour interact to affect the near range orientation and landing of simuliids. The experiments involved seven different blackfly species, although *S. venustum* was studied most closely. In summarizing the results they defined three hierarchical zones of orientation mechanisms, corresponding to the sensory inputs through which they are mediated. The first, long-range orientation, involves host specific odours, i.e. *S. euryadminiculum*. The second, middle-range orientation, occurs at the distance at which CO_2 initiates a more precise response for most simuliids. The third, close-range orientation, involves colour response, size of host, shape, movement, etc., CO_2 involvement being questionable. The final conclusion drawn from this work was that CO_2 does act as an activator of more precise orientation for most simuliids, but only at a distance termed "middle-range" (beyond 180 cm). More directed visual responses appear to occur at close range to the host. If these results are taken as a generalization of the role of CO_2 in biting fly orientation, it may help to explain, in part, the great discrepancies in past results when distance from the host to the flies under study was not given any great consideration.

Scanning electron microscope work (Mercer and McIver 1973 a) has revealed the presence of bulb organs in a sensory pit on segment three of the palps of four species of blackflies. The significance of these findings is that such sensilla have been found previously on other Nematocera, and are known to be sensitive to CO_2 (Bassler 1958, Kellogg 1970). It would seem credible that the bulb organs on blackfly palps would have a similar function. When the adult blackfly is in flight the palps are held in such a way as to expose the sensory pits to the oncoming air-stream, and the "CO_2 receptors" (the bulb organs) would appear to be in an ideal position for reception of odours. For the three species of blackfly examined, a pattern is clearly demonstrated with regard to the number of sensilla and the species' characteristic behaviour. The two species, *S. rugglesi* and *S. venustum*, both known to feed on blood, have significantly more bulb organs than *S. baffinense*, which does not take blood.

All of the male blackflies examined had considerably fewer sensilla than the females.

Although blackfly attraction cannot be reviewed fully without considering the extensive studies on mosquitoes, it must be emphasized that what appears true for any mosquito cannot be transferred into a generalization for blackflies.

Very many of the behaviour experiments to date have been conducted in the laboratory, under unnatural conditions and on unnatural hosts. For example, most of the experiments designed to test the importance of CO_2 in attractancy were based on CO_2 concentrations of 10 percent and greater, when, in fact, less than 3 percent CO_2 is expired in the human breath. Results achieved are taken to indicate the relative importance of various stimuli tested, but the value of such results is in doubt when so many factors are obviously ignored. Experiments involving different conditions of temperature or humidity may elicit totally different behaviour responses. Also, the physiological age of the flies under study must be known. Responses to various stimuli can be expected to change during the life of a blackfly as well as with different species emerging at different points in the season.

Simulium euryadminiculum has been used in many behaviour tests, but as this species is the only one known to feed specifically on one host, it would appear to be a poor choice.

It appears that both visual and airborne factors are involved, to varying degrees, in blackfly attraction. Bradbury and Bennett (1974 b)) made one of the most acceptable suggestions so far when they classified blackfly responses into hierarchical zones of orientation behaviour. Their work should be continued to greater depths, and with a wider variety of test species.

There is a need for experimentation to understand what pitfalls exist in the study of colour preferences. Further, an understanding is needed of the pitfalls that occur in interpreting flight arrestance, and distinguishing it from repellence in artificial olfactometer conditions. Finally, the ignorance of sudoriparous and sebaceous secretions must be recognised and research re-directed.

It can be concluded that the role of individual factors in attractancy (colour, shape, movement, moisture, CO_2, sweat, temperature etc.) will vary greatly with "other" conditions. Response thresholds are readily influenced by any change in environmental conditions of experimentation. Furthermore, extensive generalizations concerning the relative importance of various stimuli are unwarranted until further work has been done on additional blackfly species.

2. THE SPECIES CONCEPT

2.1 GEOGRAPHICAL DISTRIBUTION

Blackflies can be found almost anywhere in the world where suitable water courses exist for the development of the larval stage. Even small remote oceanic islands such as St. Helena and Crozet have been colonized by blackflies. On small islands where there may be no indigenous mammals, the blackfly species are invariably bird feeders of the genus *Eusimilium*. Mountainous areas, where fast-flowing streams are abundant, are frequently richer in species than the lowlands. Anthropophilous species, those which bite humans, have not been recorded above 5,000 feet (1,530 m), but other species have been found at 15,275 feet (4,700 m) in the Chilean Andes, and up to 14,700 feet (4,250 m) on Mt. Kenya (Crosskey 1973).

Carlsson suggested in 1962 that approximately 1,000 species of blackflies had been recognised throughout the world, and Crosskey (1973) has since reported over 1,000 species. This number is likely to continue to rise as previously unworked areas of the world are explored. The evident disagreements on taxonomic criteria for defining species has been, and continues to be, confusing to the species count.

Canada boasts over 100 species of blackfly (Fredeen 1974). Carlsson (1962) has reported 36 species and 3 varieties for Scandinavia. Rubzov (1959-1962) described 331 species and 64 varieties for the U.S.S.R. In England 35 species of blackfly are recorded, although only two are known as pests of man

(Crosskey 1974, pers. comm.).

Information on the range of individual species is incomplete, although some distribution maps exist for the disease vector *Simulium damnosum* (Crosskey 1973). However, it would be useful to know the exact range of other important blackfly species.

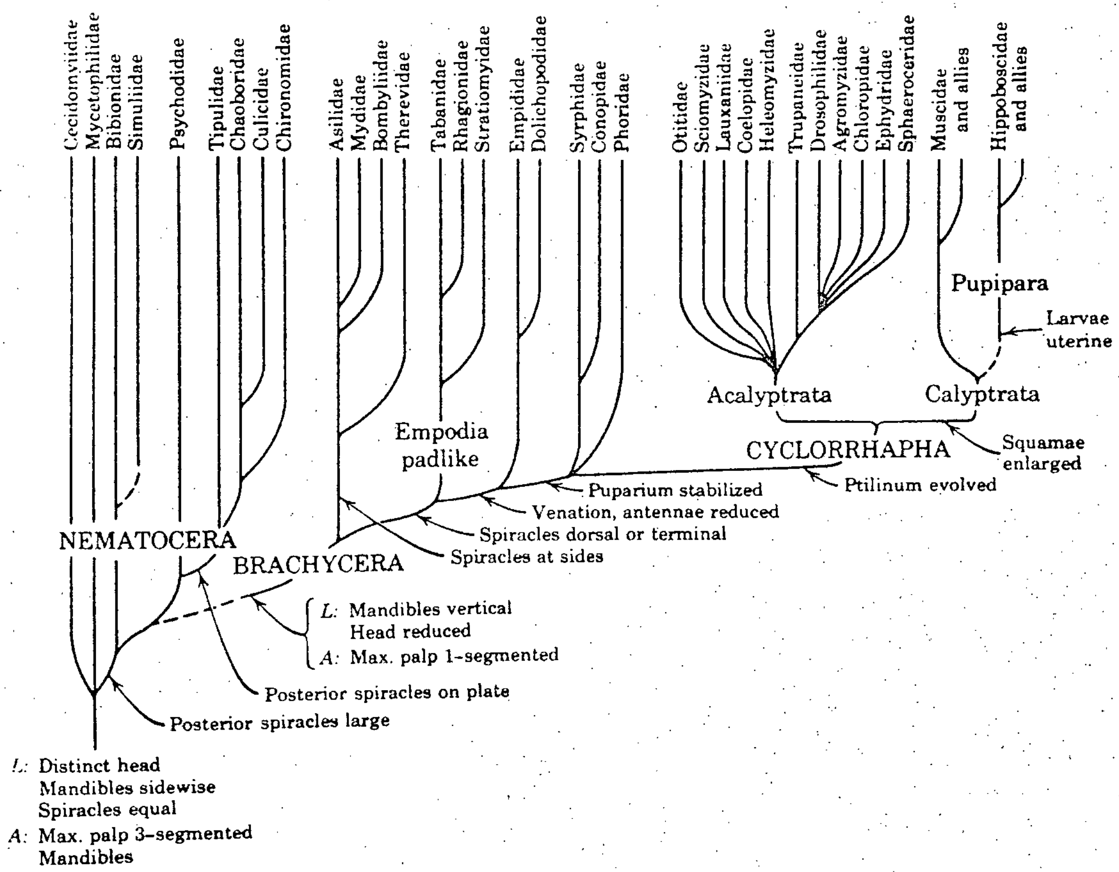
2.2 TAXONOMY

All aspects of blackfly research require a firm and correct identification of the species involved. Comparatively little work has been done on blackfly taxonomy, particularly in recent years, and most researchers today rely heavily on the criteria established at the turn of the twentieth century. However, there is no general agreement among researchers today as to which family divisions to follow for the *Simuliidae*. The possible extremes are presented by Enderlein (1922) who, on the one hand, recognised 7 sub-families and 50 genera, and Edwards (1915) who, on the other hand, suggested 2 genera and 5 sub-genera. Other authors differ still. Smart (1945) suggested 2 sub-families and 6 genera; Dyar and Shannon (1927) recognised 3 genera; and Rubzov (1959-1962) recognised 2 sub-families and 17 genera. As there has been no firm acceptance or rejection of any of these family divisions, more recent taxonomic work is based on one of the afore-mentioned authors' criteria, the choice being entirely that of the researcher. This has very obviously led to considerable confusion in the literature.

It would appear that even the generic criteria are still in dispute. For example, in 1914 Malloch described a certain

FIGURE 4.

A SIMPLIFIED FAMILY TREE OF THE ORDER DIPTERA



From: Ross, H.H. (1965).

blackfly species as *Prosimulium pecuarum*. Since that date this species has been placed in three different genera; Bradley (1935) described a species as *Eusimulium pecuarum*; Rempel and Arnason (1947) referred to *Simulium pecuarum*, and more recently Crosskey (1973) refers to *Cnephia pecuarum*. Either the generic criteria have never been satisfactorily defined, or possibly the species have been confused in the past. Certainly there are confusing similarities between the different species recognised to date, and very often taxonomy appears not to be based on well-defined and consistent criteria. Occasionally a species name suddenly appears in a piece of literature, when virtually no mention has been made of it before, and yet it is not described as a new species. For example, Fredeen (1973) refers to *Simulium defoliarti* as a species outbreaking in British Columbia, and yet there do not appear to be any other references to this species.

Even less work is done on blackfly larval taxonomy than on adult, and yet it is usually the larval stage involved in control programs where correct species identification is essential.

It is reasonable to expect that some clarification of taxonomic relationships may accrue incidentally from the current studies being made by cytogeneticists on the chromosomal morphology of the salivary glands in blackfly larvae (Basrur 1959, Basrur and Rothfels 1959, Dunbar 1959, Rothfels and Dunbar 1953).

Taxonomic confusion may arise with the different species that frequently follow one another, often overlapping, from a particular breeding area during the summer months.

In conclusion, it is obvious that blackfly taxonomy is in somewhat of a state of confusion. The taxonomic criteria suggested need much closer examination, and the whole system of classification should be agreed upon by the majority of present day workers. An essential part of any aspect of blackfly research is the correct identification of the species concerned, based on well established and accepted criteria such as are lacking to date.

3. THE ROLE OF BLACKFLIES IN ECOSYSTEMS

3.1 PREDATOR, PARASITE AND COMPETITOR RELATIONSHIPS

It is highly pertinent to know what organisms act as natural parasites or predators of blackflies inasmuch as such agents might be protected or enhanced so as to utilize their beneficial effect in control programs. Furthermore, the role of blackflies in natural ecosystems cannot be fully understood until all parasites, predators and competitors are recognised.

3.1.1 Predators

Natural predation by a wide range of organisms, Carlsson (1962) quotes more than fifty predator species, is known to occur in blackfly larval, pupal and adult stages. However, there is relatively little literature available on predation studies, and that which exists usually only refers to one blackfly species in a specific habitat. It is obviously difficult to assess the relative importance of various predators on a blackfly population. It appears to be generally agreed that the primary blackfly predators are other insects, which usually attack blackfly larvae. Peterson (1960) found Trichoptera (caddis fly) larvae to be the most important destroyers of blackfly larvae in Utah. Several other authors have recorded caddis-fly larvae as blackfly predators (Carlsson 1962, Peterson and Davies 1960, Twinn 1939).

In Carlsson's study of Scandinavian blackflies, the stomach and intestinal content of those animals living in the same habitat as the blackfly larvae was closely examined. Plecoptera, Trichoptera, Ephemerid and Chironomid larvae had all been feeding to some extent on blackfly larvae and pupae. Peterson (1960) also observed aquatic beetle (Coleoptera) larvae, Hymenoptera and Diptera species, preying on simuliids. The Hymenopterans involved were ants, and although published records of such predation are few, Peterson considered that predation by ants is more common than had been previously suspected. The Dipterans observed as predators in Utah were adult dance-flies (empidids) and adult long-legged flies (dolichopodids). The dance-flies were observed by Peterson to be feeding both on adult and larval simuliids. Long-legged flies have been recorded as predators on larval simuliids (Twinn 1939); however, Peterson observed only one dolichopodid to prey on an adult blackfly.

Dragonflies (Odonata) are known to capture and kill adult blackflies. Although there is very little documentation of this (Twinn 1939), the "protection" given from biting flies by the predaceous habits of dragonflies, is well known by many workers and travellers out of doors in the summer months. Twinn reported that "when dragonflies were introduced into infested tents in the woods, they would feed upon the mosquitoes and blackflies present until thoroughly gorged." Presumably dragonflies would have to be numerous before their feeding activities could make any impact on a blackfly population.

Fish are known to be important predators of blackfly larvae, yet there is no definitive work on the role of blackflies in fish food chains. Evidence that certain fish species feed on blackfly larvae is usually based on stomach content analyses, but very few such analyses have been performed. Cameron (1922) considered that the common sucker, *Catastomus commersonii*, is much more important as a natural control factor in Saskatchewan than any other predatory species. He stated that "the contents of the alimentary canal appeared to consist of nothing else but *S. simile* (= *S. arcticum*) larvae and pupae, of which the larvae were more abundant. The fish were simply gorged with them." Baranov (1937) (Cited Twinn 1939) indicated that in the Danube, the small sturgeon, *Acipenser ruthenis*, feeds almost exclusively on the larvae of *Simulium columbaczense* from March to June, and destroys large numbers of them, about 2,000 have been found in one small fish. Hocking and Pickering (1954), in studying the bionomics of northern *Simuliidae*, found blackfly larvae in the stomachs of whitefish, but only in the female fish. In Peterson's study of Utah blackflies (1960), small schools of rainbow trout, *Salmo gairdneri*, were observed feeding voraciously on simuliid larvae attached to loose rocks in shallow rapids of the study area. Carlsson's study of Scandinavian blackflies (1962) included stomach content analyses of *Salmo trutta* and *Thymallus thymallus*, both resident in blackfly infested streams. Both species are considered to feed, to a great extent, on blackfly larvae. Certainly, what few observations have been made, suggest that certain fish species are important predators of blackfly larvae. The question still unanswered is, what degree of dependence do the fish have on blackfly larvae as food?

Records of birds as predators of blackfly larvae are relatively few. Hocking and Pickering (1954) observed *Zonotrichia* *leucophrys*, the white-crowned sparrow, feeding on adult *Simulium venustum* at a rate of 54 flies per five minutes. Carlsson (1962) has recorded the importance of dippers feeding on blackfly larvae, and swallows feeding on the adults. A short study of shore and wading birds preying on blackfly larvae in Ontario has revealed some very interesting figures (James 1968). All of the birds collected (2 to 4 individuals of each bird species feeding) contained *Simulium*. One mallard, *Anas p. platyrhynchos*, was found to have eaten 6050 larvae and pupae, another, 2970. James concluded that birds may be more important regulating agents for blackflies than hitherto realized.

The insectivorous plant *Pinguicula vulgaris* is reported to feed on blackflies in Scandinavia (Carlsson 1962).

3.1.2 Parasites

The most frequently recorded parasites of blackflies are *Microsporidia*, Nematodes of the genus *Mermis*, and certain fungi. The parasites attack in the larval stage, invariably causing mortality.

Microsporidia: No up-to-date keys exist for the *Microsporidia* known to infect blackflies, but eighteen species have been recorded for North America (Jamnback 1973). Infected larvae are easily recognised by large, globular, opaque-white masses, visible beneath the cuticle of the abdomen. Strickland (1913) reported various species of *Microsporidia* as causing from one percent to 80 percent mortality in simuliid broods around Boston. Few other figures appear to be available with regard to the impact of this parasite. Twinn (1939) recorded 24 percent as the highest rate of larval infection around Ottawa, various species being affected. It is not clear in the literature whether or not all microsporidian infections are fatal.

Hocking and Pickering (1954) reported Protozoan infections in the pupae of *Simulium venustum*, but this infection might not have been initiated in the larval stage. I can find no reference to adult blackflies being parasitized by *Microsporidia*. More information is needed on this host/parasite relationship.

Mermithids: Mermithids are obligate nematode parasites, generally associated with larval blackflies. Although adult blackflies infected with nematodes of the genus *Mermis* have been collected, it is uncertain whether these represent infections acquired late in the larval stage of the blackfly, or different species of *Mermis* that do not inhibit pupation. Advanced infections can be detected readily in the larva, as the parasite can be seen lying coiled in the hemocoele of the semi-transparant blackfly abdomen. Pupation is either retarded or prevented by such infections (Jamnback 1973). In North America some blackfly populations are parasitized by various genera of mermithids with mortalities of up to 95 percent (Maser 1973). Mermithids are presently being considered as biological control agents for blackflies (Laird 1972). Field and laboratory studies by a team of researchers in Newfoundland are being directed towards detailed biological studies of the mermithids present in natural populations of Canadian blackflies. Certainly these natural parasites are being seriously considered for introduction on an enormous scale, with the hope of gaining some degree of control over blackfly populations.

Fungi: The fungus *Coelomycidium simulii* has been known as a parasite of blackfly larvae since 1913 (Strickland). It has been recorded from Africa, Europe, North and South America (Jamnback 1973). Infected larvae are not swollen or distorted, as with microsporidian or mermithid infections, but round cysts can be seen below the larval cuticle. Several species have been found infected in New York, but the total percentage recorded by Weiser, (1964) for that area, was only one percent. There do not appear to be any other indications of the importance of this fungus in the literature, except that it is usually, if not always, fatal to the host larva.

Beyond these three groups of parasites other organisms have received very little attention. Reference has been made to larvae of water mites (*Hydrachnoidea*) parasitizing blackfly pupae and adults (Peterson 1960, Twinn 1939), but these arthropods are not considered of any great importance.

3.1.3 Competitors

Although Carlsson (1962) reports more than 50 species of blackfly predator, and the same number of parasites, nowhere in any of the literature can I find reference to blackfly competitors. There is one brief reference to "competitors" in streams emerging and competing with male blackflies on the stream margins, but no identifications are given (Carlsson 1962).

It seems somewhat lacking that no ecological study of blackflies has taken note of competitors. In order to understand the full role of blackflies in ecosystems, potential competitors must be identified. It may be that different blackfly species compete within a certain habitat, a possibility which could be turned to use if non-biting species could be introduced to dominate and eliminate species that are serious biting pests. Research into blackfly competitors in both larval and adult stages is needed.

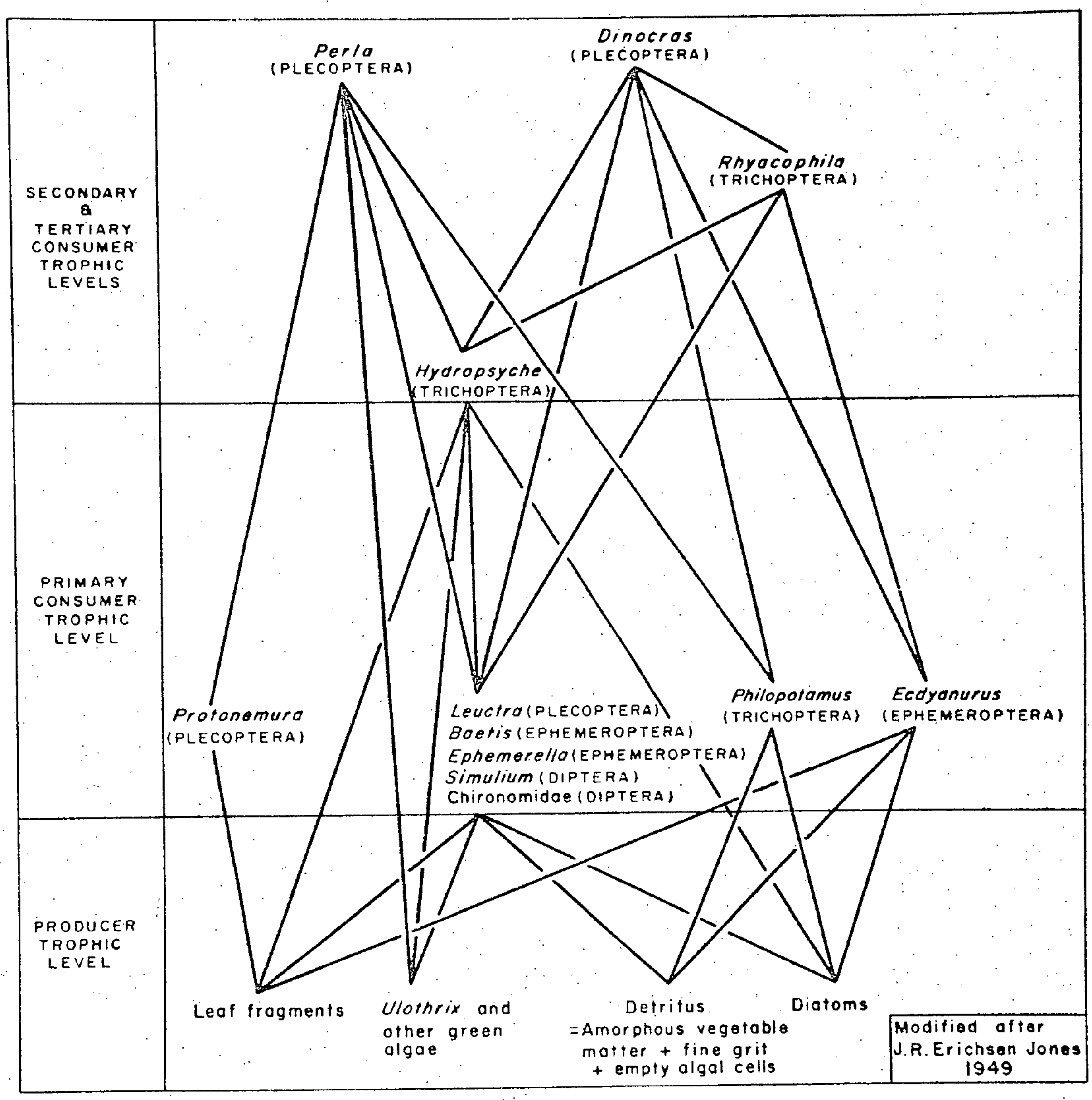
3.2 THE ROLE AND IMPORTANCE OF BLACKFLY LARVAE AND ADULTS IN FOOD CHAINS

Important reasons may be designated for a consideration of blackflies as consumers and consumed organisms. The larvae are consumers in streams, and in turn become food constituents in the dietary of fish, certain predaceous insects, and birds. To whatever extent they may be important harvesters of microbiota, and in turn, important prey for fish, either directly or indirectly, any programs of control of these insects in streams must be planned with caution. Otherwise, even such forms of combat which do not pollute fresh water systems could act to the detriment of fisheries. Furthermore, an evaluation of the role of various microbiota in the food, and of the predators and competitors, may provide clues to some of the causes of differences in blackfly populations at different times, places and water conditions. However slight the feasibility may appear at the moment, it is conceivable that some manipulations might be imposed on some of the foregoing factors, for the purpose of reducing blackfly populations without causing damage to other resources.

Conceptually, competitors for food and microhabitat would provide the best media for control, inasmuch as they would still

FIGURE 5.

TROPHIC LEVELS IN FOOD CHAINS INVOLVING BLACKFLIES



be available in the food chains.

Information on the ecological role of blackflies is scanty, scattered and difficult to trace. Some of the most informative literature has been produced by, and addressed to, fisheries biologists and ecologists of fresh-water systems. This important aspect of the subject has been largely ignored by entomologists. An example of the place of blackflies in food chains is shown diagrammatically by Jones (1949) in the accompanying diagram.

3.2.1 Fish food chains

Blackfly larvae are an important element in the food chain of many fish species. This is well documented by fish-gut-content studies performed on a variety of fish species in the past (Baranov 1937; Carlsson 1962; Edwards 1921; Hocking and Pickering 1954; Marlier 1952; Mundie 1968). It is important to know which fish species depend on a food supply of blackfly larvae, how great this dependence is, and whether or not the fish can survive without a blackfly population should a control program be selectively aimed at blackflies.

Blackfly larvae are usually found attached in areas of shallow turbulent water, where it would appear that there are few resident fish species. However, it is not so much the larvae attached to rocks that fall prey to fish, as the larvae that are drifting as part of a general invertebrate drift downstream. Blackfly larvae are recorded as "abundant in the drift" (Mundie 1968). In the small stream and river under Mundie's study, *Simulium* larvae were the most important item of food, in terms of biomass, for the resident coho fry. Usually "drifting" occurs at night when fish are not concerned with feeding, but *Simulium* larvae are known to drift by day as well as at night (Waters 1968). The effect of drifting is to carry invertebrates from an area of their production, such as turbulent shallows for blackflies, to an area suitable for fish consumption, and to a wider assemblage of fish species. There is considerable variation in the composition and utilization of drift by different fish species, but in one test area of the Stamp River on Vancouver Island British Columbia, Mundi (1968) found the drift to comprise 14 percent (by number) *Simulium* larvae. Over a 24-hour period the diet of cohoe fry, in the same test area, comprised 14 percent *Simulium* larvae.

Some fish species are known to feed on blackfly larvae by scraping individuals off the substrate. *Varicortinus tanganicae* Boullenger feeds primarily on *Simulium* larvae in Tanganyika, which it scrapes from stones with its sharp-edged mouth. All species of this genus are adapted for feeding in this way, and are also able to ascend very rapid streams. Marlier (1952) suggests the introduction of this fish in Africa where large simuliid populations are a problem.

Although there is no comprehensive study on the importance of blackflies in fish food chains, several authors, while dealing with more general aspects of biology, have made reference to fish feeding. Hocking and Pickering (1954) found blackfly larvae in the stomachs of female whitefish (*Coregonus clupeaformis* Mitchell) from the Saskatchewan River, and indicated that such fish may be useful predators. Cameron (1922) looked at three common species in the same river, the common sucker (*Catastomus* *commersonii*), the flat-headed chub (*Platybogio gracilis*) and the western goldeye (*Hyodon chrysopsis*). He found remains of blackfly larvae in all of the suckers examined, but not in either of the other two species. The "browsing" habit, common to suckers, may explain this apparent feeding difference. Baranov (1937) (Cited Twinn 1939) noted that the small sturgeon (*Acipenser ruthenis*) fed almost exclusively on blackfly larvae in the Danube; 2,000 larvae were found in one small ten-inch fish. Peterson (1960) reported a small school of rainbow trout (*Salmo gairdneri* Richardson) feeding voraciously on simuliid larvae attached to rocks in shallow rapids of a stream in Utah.

Carlsson (1962) suggested that the blackfly larvae are a valuable food to fish only when they are "drifting" in the organic drift, i.e. when streams are broken by many lakes. In his opinion drifting larvae in forest streams find suitable substrata readily, and are, therefore, not available for fish food, whereas small streams broken by lakes provide a lake habitat for fish, and blackflies that drift into such lakes become an available food source. This interpretation is disputable, inasmuch as there is considerable evidence that blackflies do drift in streams which are not interrupted by lakes, and that they are an important food to fish species during this drifting. Carlsson obviously took drifting to mean aimless floating from a river or stream into a lake, whereas blackfly larvae very often become part of the drift during their process of "dangling" on silken threads in the current. Also, there is a period when blackfly larvae feed by browsing. Craig suggests that 30 percent of larval life is spent on the move, browse feeding (pers. comm. 1974). During this feeding period, and during movements on silk threads, blackfly larvae in any stream could become part of the drift, and an important food to the resident fish.

At present there appears to be no definite answer to the questioned dependence of various fish species on blackfly larval populations. Results indicate great variation in the composition of invertebrate drift, and in the fish utilization of this food source. Blackfly larvae and pupae appear to play a highly significant role in the food chain of various fish species, but this role urgently needs further definition before more control attempts are made in ignorance.

3.2.2 Avian food chains

Both adult and larval blackflies are eaten by certain bird species, but the importance of this food in the diet of birds is uncertain. Observations on bird feeding suggest that individuals consume large numbers of blackflies at one feed. Hocking and Pickering (1954) observed white-crowned sparrows eating adult blackflies in northern Manitoba at a rate of approximately 54 flies in five minutes. Carlsson (1962) noted swallows in Scandinavia flying with open beaks through blackfly swarms. In fact there are probably very many bird species that feed on adult blackflies at some time in their lives, but as yet such documentation is lacking.

An interesting study on wading and shore birds (James 1968) around a blackfly infested stream in Ontario, revealed traces of blackfly larvae in all of the different bird species observed feeding in the area. In the mallard (*Anas p. platyrhynchos*) over 90 percent of the insect remains in the gizzard were *Simulium* larvae, and one individual was found to have 6050 larvae and pupae within its digestive system.

In order to understand the complete role of blackflies in the various ecosystems, a more definite knowledge of the role of adult and larval blackflies in avian food chains is urgently needed. Beyond the casual observations made so far, detailed analyses of the gut content of various bird species will be necessary.

4. THE IMPACT OF BLACKFLIES ON THEIR HOSTS

4.1 THE SPECIES INVOLVED

The majority of blackfly species that feed on blood show a distinct predilection for feeding either on birds (ornithophilic species), or on mammals (mammalophilic species). All of the species recorded as feeding on humans (anthropophilic species) feed on mammals or birds also, and no species is known that feeds exclusively on humans.

Because of these apparently "distinct" feeding preferences, many assumptions have been made regarding species identification based on host type. These assumptions have led to considerable confusion in species identification. Species known to bite humans, such as *Simulium damnosum* in Africa, or *Simulium decorum*, are not known to bite humans over their entire range. *Simulium aureum* was reportedly observed feeding on goslings in 1927 (Davies and Peterson 1956), but later Twinn (1939) re-identified this species as *Simulium venustum*. A later re-examination revealed the flies to be *Simulium rugglesi*. Because of the original mis-identification, other authors have referred to the feeding of *Simulium aureum* on ducks and geese, when in fact this host/blackfly relationship has not been demonstrated.

Such points of confusion are not uncommon in the study of blackfly species and host relations. It should be remembered that the stated associations between particular blackfly species and observed hosts, are often based on local observations, which therefore do not include all of the potential host species.

Extreme narrowness of hosts (stenophagy) is rare but is exemplified by *Simulium euryadminiculum* and its host the common loon.

4.2 HOST REACTIONS

The nature of mechanical wounding by the bites, the chemical identity of the toxic constituents of the fly saliva, the physiological action and the cytological response of tissues at the point of wounding, and the systemic effect which is relayed to other tissues of the body, such as the lungs, are significant for various reasons. They provide criteria for defining the kinds, intensities and duration of host response, and the ranges of variability of these in relation to definable insect species, age of the flies in days, nectar meals, and other variables in the flies, as well as in numerous factors which differ and change between and within individual hosts. There is need for a clearer understanding, for example, of the role of physiological age, physiological state, general nutrition, and specific nutrients or previous exposure of the host to bites. Clinically it is desirable to have definitions of the sequence of dermal and systemic changes which take place, so that either satisfactory progress may be noted or abnormal trends can be detected for special treatment. The clinical features of bites provide the immunologist with certain criteria by which immunologic reactions may be compared with controls. In the event that they are haptenic, non-proteinaceous, and non-antigenic in themselves, and in the further event that the host has no mechanisms for converting such haptenic substances into antigens, then hapten-protein complexes may be synthesised or extracted from the insect (Graham, K. 1975, pers. comm.).

4.2.1 Clinical details of host reactions

Human reactions to the bites of blackflies are both physiological and psychological, and although the physiological aspect has received most attention in the past, it must be emphasized that the psychological effects are equally serious.

Most work on biting flies and host reactions refers to mosquitoes, whereas relatively little work has been done on the host reactions to blackfly bites. However, the clinical aspects of the bite, and the secondary condition of infection following scratching, have been fairly well described in the literature (Fallis 1964, Georgevitch 1923, Gudgel and Graver 1954, Hocking 1952, Peterson and Wolfe 1958, Stokes 1914). What is apparently lacking is a clear understanding of the determinants of acuteness of the reaction, and of the nature of the toxins involved. It is not known why some people react more than others, or why susceptibility appears to change during a season when there is no evidence of any antigenic property to the blackfly toxin, or of an antibody response in the host.

When the blackfly bites it injects saliva into the wound it has made, before sucking up blood. The saliva is alleged to contain anticoagulants and agglutinins; the latter helps to form a semi-solid blood mass in the fly gut (Yang and Davies 1974). The injection of saliva into the host very often causes acute swelling and itching, which may persist for several weeks. Furthermore, the reactions may involve a condition known as "blackfly fever", which is manifest as a headache, swollen-glands, fever and nausea. Such reactions are not uncommon among children bitten by blackflies in eastern Canada, and even deaths have been reported (Hocking 1952).

When cattle are bitten by blackflies, deaths are frequently recorded. Within an hour of biting, under severe attack, the animal's respiration becomes deep and rapid. In a fatal case, rapid respiration is followed by shivering, the animal drops to the ground, gasps for breath and dies without a struggle. Deaths occur rapidly within 15 minutes to 2 hours after the first observable signs. If recovery is to occur it will be complete within 24-28 hours (Peterson and Wolfe 1958). The actual cause of death is not fully understood in cattle, but post-mortems suggest that the causal mechanism involves reaction to toxic factors in the blackfly saliva. The toxin apparently induces a process which might be termed pneumohydrorrhoea. Accordingly, one of the accompaniments to the process is the filling of the lungs with fluid, so that death results in part from drowning, and not by mechanical choking or inhalation of the flies as was at one time speculated.

It is clear that individual people differ markedly in reactivity to blackfly bites, furthermore their susceptibility changes during a season. It is unclear whether such change is attributable to physiological changes in a person in the field, and to acquisition of passive immunity, or to differences in the toxicity of the venom of different species of blackflies at different times during a season.

The chemical nature of the salivary toxins is unknown, but it does not appear to be necessarily antigenic. There is, in fact, no evidence that any form of antibody immunity develops in response to the blackfly toxin, either in humans or in livestock. Indeed, on *a priori* evolutionary considerations one might reason that advantages go to those blood-seeking organisms which do not contain antigenic constituents in the saliva. If the toxin is non-proteinaceous it may be regarded as a haptenic substance which exists either in precursor combination, or which might be susceptible to combination with a protein to become an antigen for a hapten. This is an area of investigation well worthy of examination, and one which has not, as yet, been considered.

Thus the chemical composition of the salivary toxins, and the causes of the different reactions to blackfly bites, as well as the causes of differences in incidence of attack, merit special investigation if host reactions are to be understood and manipulated for the needs of protection.

4.3 DISEASE TRANSMISSION

Blackflies are insects of particular medical and veterinary importance not only because they harass, toxify, debilitate and kill their hosts by their attack sequences, but also because certain species transmit various pathogenic organisms to humans, mice, rabbits, cattle and birds. The list of pathogens presently associated with simuliid vectors includes viruses afflicting turkeys, mice and rabbits, blood-inhabiting protozoan parasitizes of the genus *Leucocytozoon* Ziemann among birds, and skin inhabiting filarial nematodes of the genus *Onchocerca* Diesing in mammals, including humans.

4.3.1 Human onchocerciasis

Although blackflies are not known to transmit any human diseases in North America, certain species in tropical Africa and in parts of the tropical Americas transmit the nematode *Onchocerca volvulus* to humans, prolonged infection with which causes the blinding disease onchocerciasis ("river blindness"). The two chief vectors in Africa are *Simulium neavei* and *Simulium damnosum*. In the tropical Americas *Simulium ochraceum*, *Simulium metallicum* and *Simulium woodi*, as well as the two forementioned species are implicated.

As vectors of this agent of disease, blackflies rank amongst the most troublesome and pain-causing insect pests of humans and animals in many parts of the world. It is noteworthy that onchocerciasis is not recorded over the entire ranges of the vector blackfly species, either in tropical Africa or the tropical Americas. The reasons for the present pattern of disease distribution are uncertain and require further study.

"Onchocerciasis in man is characterised by intense itching, lichenification and fissuring of the skin, the occurrence of subcutaneous nodules where the tissues are thin over the bones, and, in the worst cases, of irreversible blindness" (Crosskey 1973).

Adult worms are to be found in the human host in small nodules immediately below the skin surface, each nodule containing one or several male and female worms. In this stage the male worms are 2-4 cm long and the female 35-70 cm. Each fertilized female worm produces thousands of tiny microfilariae that move slowly around the host under the skin, but apparently do not enter the blood stream. The precise route of these microfilariae is not clearly stated. It is known that dead parasites, particularly microfilariae can cause most of the damage to the skin and eyes, as a result of damage and reaction following absorption of their contained substances (W.H.O. 1966).

When an infected person is bitten by a potential vector blackfly, microfilariae are taken up during the blood meal. As many as 200 may be ingested at one feed, but often not more than one or two survive to develop in the intermediate host. The microfilariae migrate to the thorax of the blackfly, where development and maturity occur in about 7 days. Mature individuals enter the salivary glands, and so are injected, with the blackfly saliva, into a host during normal blood-feeding activities (Symes *et al.* 1962). Unlike malarial parasites, the microfilariae do not multiply in the insect host. In fact relatively few survive to enter the human body, and even those may not produce disease. The cycle is completed when injected microfilariae mature in the host and adult worms aggregate to nodules where reproduction occurs and disease signs appear.

The movement of microfilariae within the human host body is inadequately described in the literature, although apparently they do not enter the blood. This aspect warrants a fuller understanding particularly if certain forms of therapy are to be effective.

Over 30 million people in tropical Africa and the tropical Americas are known to be suffering the effects of onchocerciasis, and many individuals are partially or fully blinded as a result. As this is mainly a rural disease, the blinded victims, unable to work, become a heavy burden on their families, and the consequent economic hardships are severe. This has happened to such an extent that large fertile and potentially productive areas, including one tenth of the total area of the savanna regions of West Africa, now lie abandoned.

4.3.2 Bovine onchocerciasis

In certain temperate and tropical areas of the world cattle suffer the effects of infection with filarial worms of the genus *Onchocerca*. However, comparatively little documentation exists of either the outbreaks of this disease, or of the effects on the cattle hosts. *Onchocerca gutturosa* Neumann is known to be transmitted by the blackfly *Simulium ornatum* in England (Crosskey 1973). Eichler and Nelson (1971) report the occurrence of the parasite in Europe, Asia, North and South America, Autralia, and Africa. In Berkshire and Hertfordshire, England, more than 50 percent of the cattle examined in abattoirs, during 1964-1969, were infected with this parasite, although veterinarians and meat inspectors were totally unaware of the parasites' presence.

Steward (1937) suggested considerably more concern exists over the disease in Australia, as "worm nodules" due to *Onchocerca gibsoni* Cleland and Johnson, were estimated to be causing losses of £500,000 per annum to Queensland alone. The carrier in Australia is unknown.

In the U.S.S.R. Gnedina (1959) (Cited Eichler and Nelson 1971) has claimed that injuries to the skin, caused by infections of *Onchocerca gutturosa* in cattle, are responsible for a significant proportion of the losses to the leather industry.

In Japan, Nimmi and Kuono (1954) (Cited Eichler and Nelson 1971) found that 90 percent of the cattle infected with the microfilariae of *O. gutturosa* had signs of inflammatory lesions conceivably, other skin disorders might be attributable to this parasite.

It appears that *O. gutturosa* has not been implicated in human afflictions, either directly or through meat consumption, although it is closely related to the worm *Onchocerca volvulus* previously described.

Although infections with *Onchocerca gutturosa* do not appear to be implicated with the ill-health of cattle, it is obvious that no substantial study has ever been made of this host/parasite relationship.

4.3.3 Leucocytozooniasis of birds

Of the many blackfly species that are pests to birds, some are vectors of a fatal malaria-like disease known as "leucocytozooniasis". This disease is prevalent in a wide variety of avian hosts, particularly waterfowl, in the North American continent, as well as other parts of the world.

Several species of haematogenous protozoa of the genus *Leucocytozoon* are involved in this disease, although it is believed that each species of *Leucocytozoon* parasites only one family of birds (Crosskey 1973). The range of hosts includes robins, grouse, turkeys, and a wide variety of waterfowl; some species of simuliid have been implicated with more than one species of *Leucocytozoon*.

In North America *Leucocytozoon smithi*, transmitted by *Simulium meridionale* and *Simulium jenningsi*, is responsible for considerable losses to the turkey industry, and ranks as the most destructive *Leucocytozoon* of domestic birds.

In the later 1950's, leucocytozooniasis caused the failure of federal efforts to establish pilgrim geese in Ungava Bay. The geese were shipped from Montreal in an attempt to establish food reserves for native Eskimos. However, the non-immune goslings proved vulnerable to a *Leucocytozoon* infection, and all attempts at establishing the population failed.

The effects of *Leucocytozoon* infections upon birds in nature range from pathogenic to benign, and yet they remain inadequately understood. This condition of ignorance surely merits attention. To quote Laird (1972), "Leucocytozooniasis causes a great deal more sickness and death among birds than persistent synthetic pesticides have done, or are ever likely to do, however rashly the pesticides have been used in the past".

4.3.4 Other diseases

Although there appears to be no evidence at present to indicate that simuliids are involved in the transmission of viruses to man, experimental virus transmission to mice has recently been demonstrated (Austin 1967). *Austrosimulium ungulatum* was used as the experimental transmitting agent. Viruses have also been isolated from some ornithophilic blackflies, for example, eastern encephalitis (E.E.V.) has been isolated from *Simulium meridionale* exposed to brooder house turkeys (Anderson *et al.* 1961).

Simulium melatum is reputedly involved in the transmission of myxomatosis virus among rabbits in Australia (Mykytowycz 1957).

The list of pathogens transmitted by blackflies has yet to be completed. So far it includes 3 nematode genera, 3 protozoan genera and a few incompletely identified viruses. As blackfly research slowly advances around the world, and as transmission research progresses, it would seem likely that this list of pathogens will expand within and beyond the presently described genera.

5. THE IMPACT OF BLACKFLIES ON NATURAL RESOURCE USE AND MANAGEMENT

Blackflies impose their impact on many aspects of natural resource use and management, particularly forest resources. The mere presence of these flies has proved an obstacle to the effective development of many areas, particularly the northern regions, at a time when pressures are being exerted for greater access and development. Blackflies are implicated as having been a barrier to the exploration and economic development of the north since the earliest phases of European contact (Laird 1972).

A full evaluation of the diverse impacts of blackflies is urgently needed. As these flies are active out of doors by day, the greatest impact is felt within the forest industry, tourist industry, building, mining, and farming enterprises. Blackflies impair the use and value of forest recreational areas by harassment of people, as well as of horses used for packing or riding. They impair the productivity of forest wildlife and the waterfowl associated with lakes and rivers. They impair the health and efficiency of forest workers, and impede the process of willing labour forces. Blackflies also impair cattle productivity within the forested range and on many areas of open range.

The impact of blackflies on natural resources may involve further environmental problems when actions are taken, under public or industrial pressure, to alleviate the blackfly problem. The haphazard use of insecticides, especially when introduced directly and deliberately into rivers, introduces risks to associated resource and environmental values, such as, the domestic water supplies may become polluted, and fisheries and wildlife may suffer. Damage to higher organisms may accrue indirectly from destruction of blackfly larvae themselves and other aquatic forms which are involved directly or indirectly in food chains for fish and higher forms. Damage might result also from the direct injuries of pesticides to the higher forms of life, and if chemically-stable, fat-soluble pesticides are used, they may enter food chains and become progressively concentrated and increasingly dangerous in successive consumer organisms, and relayed from place to place.

5.1 THE EFFECT OF BLACKFLIES ON LABOUR FORCE EFFICIENCY AND GROUP MORALE

Attracting and maintaining a stable labour force for any outdoor work can be seriously impeded by the activities of blood-sucking flies. The mere knowledge that blackflies are present may be sufficient to discourage many workers. As blackflies are active by day, and as they can occur throughout the summer months, it is virtually impossible to be unaffected by their presence and activities.

Most people suffer more severely from blackfly bites than from mosquito bites, and the effects can be both physiological and psychological. Blackflies not only attack exposed areas of the body, but enter any openings there may be in clothing, such as sleeves, pant cuffs, shirt collars or other areas which are not tightly fitted against the body. The flies then work their way beneath the clothing, and bite in areas where the clothing comes into firm contact with the body. Clothing which is made to exclude blackflies becomes uncomfortably hot, and if kept to minimum weight, is in some cases penetrable by mosquitoes. Blackflies are avid feeders and are not readily dislodged once settled to feed. The constant manual removal, necessary in heavy blackfly attacks, is obviously extremely disturbing and enervating to the victim. After a short period of exposure to blackflies the mere presence of these flies, whether engaged in feeding or not, is sufficient to evoke an instinctive removal reaction, psychologically not inducive to an efficient work state.

Individual efficiency, and even more so group morale, is drastically lowered by the psychological and physiological effects of the presence and activities of blackflies. Hocking (1952) suggested that individuals may become ineffective far sooner from the psychological effects of blackflies than from direct physiological causes. The continually accelerated and increasingly ineffective removal reactions, can rapidly reduce a susceptible person to an inefficient emotional state.

The attractiveness and comfort of field working conditions are highly significant factors in forest labour recruitment, particularly with the general growth and development of our present day economy. Blackflies, and other haematophagous Diptera, are regarded as one of the major causal factors of the high labour turnover in pulpwood cutting camps during the summer months (West 1958). This problem is intensified by the trend towards greater summer activity in the woods during the months when the flies are active. West records that improved morale and greater efficiency result from a reduction of biting fly activity.

Long-term management plans are seriously upset when blackflies disturb the work force. It is not uncommon for work to stop altogether on particularly bad fly days. For example, in the spring of 1974 near Squamish, in south-western British Columbia, blackflies were sufficiently troublesome to cause the contracted forest tree planters to suspend work until they could be protected by head nets and veils, which impeded the planting operations (Wyeth, M. 1974 pers. comm.).

5.2 THE IMPACT OF BLACKFLIES ON RECREATIONAL ACTIVITIES

The rapidly increasing development of outdoor recreation as a service derivable from forest areas brings with it the need and demand for increased attention to public needs and comforts. As other amenities improve, the fly problem will become proportionately more critical for the less stoic individuals.

Blackflies are so abundant in many places during the summer months, and their activities so harassing, that a person may be bitten dozens of times within minutes of leaving the protection of a vehicle or other shelter. Even a very low biting and annoyance rate can discourage recreationers from visiting otherwise attractive areas. Individual reactions to blackfly bites vary quite considerably and it is not understood why this is so. Some people may suffer fever, nausea and headache, as well as pain and itching at the points of individual bites.

The scenic turbulent streams in forested areas, where mosquitoes as less likely to be serious, are most likely to suffer from blackflies which breed in such areas. Although very little documentation exists on the impact of blackflies on recreational activities, they are recognised as having a deleterious economic effect on the tourist industry (Crosskey 1973).

At Mont Apica, Quebec, blackflies were reportedly the most formidable nuisance for R.C.A.F. personnel in the late fifties, to the extent that all scheduled outdoor events had to be cancelled due to the nuisance caused by these flies (Snider 1958). It was utterly impossible to even sit out of doors during the fly season.

5.3 THE IMPACT OF BLACKFLIES ON FOREST RANGE MANAGEMENT

Various species of blackflies, breeding in large rivers and fast-running streams, are invariably associated with grassland/forest ecotones, and frequently emerge in great numbers at a time of year coinciding with the herding of cattle onto summer ranges. Mass attacks on cattle by blood-thirsty blackflies are a fairly regular event in many areas such as the Canadian prairies, where farmers experience considerable losses.

The most notorious species of blackfly attacking cattle is the Goloubatz fly *Simulium columbaschensis* of middle and southern Europe. In the summer of 1923, Romania suffered two immense attacks in which 16,474 domestic animals were killed (Ciurea and Dinuflescu 1924).

In Canada, the blackfly *Simulium arcticum* has been responsible for considerable livestock losses. Outbreaks of this fly were recorded during 1917, 1918 and 1922 (Cameron 1918, 1922).

Only poor records were kept over the next thirty years, until the devastating outbreaks of 1944 (Millar and Rempel 1944). A serious blackfly outbreak was recorded for 1946 in Saskatchewan. In this outbreak flies were borne for distances of 100 miles (170 Km) from their breeding site, and a very large local area was involved, with considerable cattle losses resulting.

Closely related to *Simulium arcticum* is the species *Simulium defoliarti*, which is found in certain intermontane valleys of British Columbia (Fredeen 1973). According to Fredeen, *S. defoliarti* rarely kills animals, but outbreaks can be prolonged sufficiently to cause a decline in productivity of both beef and dairy cattle. Curtis (1954) reported an outbreak of blackflies in the Cheryville district of British Columbia, but it is not clear whether the species involved was actually *S. arcticum* or a species similar to it. In this outbreak the area affected was only small, but the severity of losses in weight of cattle, attributable to this pest, were considerable. Some ranchers even doubted their ability to remain in business unless relief is to be obtained. A loss of $24,160 was calculated on beef cattle alone.

The cattle that suffer most in a blackfly outbreak are the mature individuals, the dense hairy covering of calves apparently offering some protection.

Biting is usually concentrated in areas where the hair is least dense, such as the udder of cows and scrotum of bulls. This leads to obvious problems when udders become inflamed and calves are unable to feed freely. Furthermore, severe inflammation of the penis sheath in bulls can cause temporary impotence, and consequent displacement of mating and calving to an unpropitious season for development and survival. Bulls are especially susceptible if they are newly released onto the range during an outbreak period. The alternative to releasing bulls in the field during the blackfly season is to provide stabling or other shelter. However, the obvious disadvantage to this is the expense and inconvenience to ranchers in providing the necessary food and attention.

The constant harassment of a blackfly swarm around cattle will seriously disrupt the grazing activities, and both milk and weight losses are frequently associated with outbreaks of these flies.

The reaction to blackfly bites is usually rapid, and within an hour of biting oedematous swellings may be noticeable (Fredeen 1973). Under a severe attack the animals respiration becomes rapid and deep, and in fatal cases, this condition is followed by shivering, the animal drops to the ground, gasps for breath, and dies without a struggle. Deaths occur rapidly - within fifteen minutes to two hours after the first observable signs. If recovery is to occur it is usually complete within 24-48 hours (Peterson and Wolfe 1958). The actual cause of death is not fully understood, but post-mortems suggest that the toxic action of the insect's saliva is the causal agent. In earlier days the idea of mechanical suffocation, occasioned through the inhalation of large numbers of flies, with a consequent obstruction of air-passages, was widely held by laymen. However, post-mortems have ruled out this assumption, and death appears to be caused by an increase in permeability of the capillaries, with a consequent great loss of fluid from the circulatory system into the tissues spaces and body cavities (Jamnback 1973). Internal organs, body cavities and tissue spaces show considerable imbibition of a clear serous fluid, and of internal haemorrhages.

As most cattle that die as a result of blackflies are mature individuals, the financial loss to ranchers can be great. Also, the interruption of grazing activities, and consequent weight losses, means reduced returns for the ranchers when ordinarily cattle might gain two pounds (1 kg) a day, in summer months, without fly harassment.

There remains a need for more precise monitoring of information on occurrences of mass attacks of blackflies. Rempel and Arnason (1947) note that blackflies attack particularly under the light shade of trees, i.e. in forest range situations. This interpretation appears to be somewhat inconsistent with the evidence that day-time shade-providing shelters provide protection from attacks. However, no study of biting habitat preference has been made for blackflies and cattle. The precise climatic conditions prior to and during infestations should be recorded if the development of damaging outbreaks is to be understood. In fact, all of the events associated with the development of outbreaks need documentation, so that eventually it should be possible to predict the time and severity of each impending attack. Such information would also serve to relieve the great element of suspense that ranchers face each year. Also, the information could be incorporated into the planning of livestock management and larviciding programs.

6. PRINCIPLES, PRACTICES AND PROBLEMS IN CONTROL OF BLACKFLIES

Amelioration of the blackfly problem may be sought through various means which are embraced within several broad categories. The theoretical as well as the tried approaches to be considered may be identified as follows:

Population reduction.

Direct killing of population numbers

- Application of larvicidal chemicals such as synthetics, plant alkaloids or insect growth regulators.
- Application of adulticidal chemicals.
- Trapping of adults by lures such as pheromones, or host attractants. (Theoretical possibility for limited use, unexplored).

Manipulation of agents of biotic control (not tried on an operational scale).

- Introduction, inundation with, or enhancement of, predacious or parasitic or competitive insects, nematodes, mites, or birds.
- Inundation of area with sterile males.
- Introduction of defective gene characters.

Manipulation of aquatic habitats by modifying flow characteristics through impoundments of stretches of water behind dams.

Refuges from attack comprise shaded shelters for cattle.

Individual protection to prevent attack.

Chemical repellents or deterrents applied to skin or clothing; special nutrient regimes to modify chemical factors in dermal secretions.

Protective clothing that minimizes attraction, and excludes flies; head nets.

Immunization to avert physiological effects of salivary toxins injected by flies. (This remains within the realm of theory).

Therapy for bite victims.

Topical applications on skin after bites occur.

Systemic administration of antihistamines or other medications (needs researching).

Hospitalization for severe cases of toxaemia or cases of secondary complications from infections following scratching.

Therapy of filarial and other conditions which are conveyed by blackflies.

6.1 DE-POPULATION

One of the traditional strategic approaches to alleviation of the blackfly problem is aimed at reducing their population numbers. Various tactical means are to be considered, some of which have been used on an operational scale, while others remain as theoretical possibilities, even if not yet apparently technically feasible, economically reasonable, or environmentally acceptable. In principle, population reduction may be sought through chemical agents, biological agents, and water management.

6.1.1 Chemically-induced de-population

A wide spectrum of natural and synthetic insecticidal substances provides possibilities for killing the immature aquatic stages and the winged adults of blackflies. The chemicals include a wide variety of synthetics such as chlorinated hydrocarbons, carbamates, and organophosphates. Insecticides of plant origin such as pyrethrins, for example, are not mentioned. A special category of chemicals which has been the object of testing for possible control of blackfly larvae included juvenile hormones (McKague and Wood 1974). Other insect growth regulators and their laboratory-produced analogues might be contemplated. Pheromones or other possible attractants for luring and trapping blackflies appear yet to be researched.

One theoretical appeal of chemical "control" of blackflies is the immediacy of alleviation resulting from extensive aerial application of adulticides to kill the adult populations, and from the introduction of larvicides into rivers to decimate the immature stages before they can emerge as flies which might spread over great distances and areas.

D.D.T. has been used in many parts of the world, including West Africa, Canada, the United States, Mexico and Japan, since about the beginning of the nineteen fifties. The first report of this chemical's use for blackfly control in Canada was 1948 (Hocking *et al.* 1949). Effective results were claimed with a dosage of 0.1 ppm for 15 minutes. Further tests made to compare various formulations of D.D.T., T.D.E., lindane, chlordane, toxaphene, heptachlor, dieldrin, endrin, isodrin, trichlorobenzene, pyrenone, parathion,malathion and schraden. Only heptachlor could compete with the efficiency of D.D.T. (Hocking 1950).

In those early days D.D.T. seemed the obvious choice of insecticide with its rapid effectiveness, relative cheapness, and its low oral mammalian toxicity. Great control successes were announced for D.D.T., yet no attention was paid to any possible side-effects during that first decade of its use. Initial test applications of D.D.T. in the Saskatchewan River during the summer of 1948 were of aerially applied 12 percent emulsifiable concentrate of D.D.T. in fuel oil. Rates of 0.13 and 0.07 ppm D.D.T. for 36 and 34 minutes respectively were used. As an example of the flow-rate of the South Saskatchewan River, into which the D.D.T. was introduced, one may cite the value given for May 25th, 1948 at 8 a.m. as 35,220 cubic feet/second (997 cubic meters/sec.), equivalent to 13.2 million gallons per minute (60.1 million liters/minute) (Arnason *et al.* 1949). The D.D.T. content of the river, in parts per million, at the point of application, was calculated from the number of pounds of D.D.T. applied, divided by the volume flow of the river at the point of application (lbs. per minute), multiplied by the time period of application in minutes. The treatment with 1.13 ppm D.D.T. for 36 minutes was effective in destroying blackfly larvae for 17 and possibly 90 miles downstream (27.4-145 Km).

D.D.T. stream treatments were subsequently adopted by many organizations concerned with blackfly infestations. However, individual stream treatments in many areas of Canada are quite unpractical as there may be literally thousands of small, blackfly infested, streams in any one area of concern. Also, such an approach in areas of rugged terrain, heavy forest cover, and often without roads, is quite obviously beyond economic or practical considerations.

Ground-based larviciding techniques are used more often than aerial spraying in smaller and more easily accessible areas. In as much as access is not always possible, aircraft have a recognised place for larvicide applications. Kissam *et al.* (1973) recommended helicopters in South Carolina, in order to permit slow flying along river courses, but slow flight is not always considered necessary, (Collins *et al.* 1952). With ground-based applications, enough larvicide must be put into the river at one or two points to give a sufficiently high initial concentration for the chemical to remain effective for a somewhat extended time.

After the effects of D.D.T. on fish and other aquatic life became well documented, alternative insecticides received serious consideration in the late 1960's. When a total ban was put on the use of D.D.T. in Canada, its analogue, methoxychlor, took its place, although, not surprisingly, recent work has revealed that Abate, Dursban and methoxychlor (all 3 have been used since the banning of D.D.T.) all adversely affect non-target invertebrate stream fauna such as Ephemeroptera, Trichoptera, Plecoptera and Chironomidae larvae (Wallace *et al.* 1973).

Chemical controls, in aiming at direct de-population, have limitations inherent in the widespread dispersal of any toxic material, and in the possibility of damage to beneficial or non-injurious forms of life.

Diverse problems are associated with, and derivative from, the larvicidal approach. One form of problem consists of technical and financial limitations for dealing with vast areas, which also are often difficult of access. Other major obstacles consist of contamination of water supplies, the direct and indirect impact of pesticides on non-target organisms, the possibility of a pesticide exerting a genetic selection pressure which becomes self-defeative, and the impermanence of treatment.

Aside from the simpler local application of larvicides for limited results, a great problem in logistics resides in the need to treat large areas of territory which are interlaced with streams. The physical problem is especially difficult in rugged mountainous terrain.

The effects of pesticides on non-target organisms may lead through various sequences. However, very few citations on this subject may be found in direct reference to blackfly control. On the other hand, considerable relevant literature derives from studies of the effects on aquatic life caused by forest spraying for control of forest defoliators. Hazards may comprise direct injuries to humans, birds and fish, or they may accrue from the destruction of various uni-cellular and multi-cellular plant and animal organisms at different trophic levels in the flow of energy through the food chains. An indication of the effect on phytoplankton of various pesticides, some of which have been, and are being used for control of blackfly larvae in rivers, is clearly noted in the tabulation given by Butler (1963) (see Appendix of this Thesis).

Inasmuch as blackfly larvae themselves constitute important primary consumers of uni-cellular organisms (Jones 1948), and at various times and places are important direct constituents of the dietary of fish, or, possibly of dipper birds (water ouzels), and inasmuch as blackfly larvae also sustain secondary and tertiary consumers, a drastic reduction in their numbers by pesticides could have unwanted effects on the higher trophic levels of consumers. These effects would conceivably be serious regardless of the persistence or transience of the chemical, and regardless of whether its origin be a conventional synthetic, a plant product, or an insect juvenile hormone or analogue of same. Where persistent insecticides might be used, the progressive concentrations along the food chains, or progressive gathering at various points along the food chain can become highly dangerous to the ultimate consumer organisms such as birds or humans (Ent. Soc. Canada, 1970).

Few papers deal with the impact of pesticides as used explicitly for blackfly control. Fredeen *et al.* (1971) assert that 20 years of almost unbroken annual and semi-annual application of D.D.T. into the Saskatchewan River, for blackfly control, with concentrations reaching 0.1 to 0.3 ppm, sustained for 15 minutes in the volume of water passing the application point, resulted in D.D.T. residues in the muscle tissues of fish in the range of 0.01 to 0.05 ppm. It was remarked that these concentrations were well below the actionable level of 5.0 ppm of D.D.T. residues in edible fish. This finding, however, does not provide for other dimensions of the impact which relate to food chains and biomass productivity of the river.

Notwithstanding opportunities afforded by some large-scale and perennial applications of larvicides to destory blackfly populations in rivers, very little carefully documented information has become available on the effects of these operations on food chains and the biological productivity of rivers. High rates of reduction have been reported to occur among mayflies (Ephemeroptera), caddis flies (Trichoptera), stone flies (Plecoptera), and certain species of aquatic beetles after larvicidal treatments against blackflies (Arnason *et al.* 1949; Hoffmann and Surber 1948; Hynes and Williams 1962; McMahon *et al.* 1958). From these reports, the ability of non-target organisms to repopulate an area soon after treatment remains uncertain.

The impact of larvicides on populations of aquatic organisms and on their rate of repopulation must depend upon the specific toxic substance, the form in which it is applied, the dosage, the extent of area de-populated and the frequency of application. Results on small areas may not provide a sound basis for extrapolating on large areas.

The data of Gjullin *et al.* (1949) demonstrate the differences in absolute and relative toxicities of a number of insecticides, and show the importance of formulation in creating a differential effect which is more lethal to blackflies than to other stream organisms. (See Appendix 3).

One of the possibly undesirable effects of the intensive and extensive application of non-selective insecticides for blackfly control is that a temporary destruction of competitors and predators may favour a more rapid recolonization by blackflies than by other organisms. Thus, the blackfly problem may become intensified temporarily, as suggested by Hynes (1960). Indeed, Davies (1950) had noted a striking resurgence of a blackfly population in a stream three years after its treatment with D.D.T. Although a possible cause-and-effect relationship is presumptive, such a possibility merits further study, with attention given to the kind of pesticide, its formulation, dosage, extent, time of year when applied, and physical and biological features of the hydrological systems.

The conceivable direct and indirect effects of pesticidal control of blackflies on bird life seems not to have been reported. The direct hazards of pesticides for bird-life resulting from blackfly control, might be inferred from the general literature.

There remains to be explored the possible self-defeativeness of repeated intensive applications of insecticides against blackflies, as a result of such treatments acting as a genetic selection pressure favoring insecticidal resistance. However, a vast literature exists on the general subject as it relates to other forms of insects, including such haematophagous forms as mosquitoes. Two examples of literature dealing with the genetics of insecticidal resistance in mosquitoes may suffice here to indicate the scope of the problem: Beard (1965); Pennell and Hoskins (1964).

6.1.2 Biological control

Although non-chemical methods of blackfly control are being given increasingly more attention, progress is hampered by problems with mass rearing techniques and by gaps in the knowledge of blackfly biology and behaviour. Consequently no real attempts at biological control of blackflies have been made to date. However, preliminary laboratory trials have been conducted on the irradiation of mature blackfly larvae (Gross and Baldwin 1972), but without much success. For the principle of sterile male release to be effective in mosquito control approximately one million sterile males per day must be released to every 50 wild males born daily (Laven 1974). With numbers as large as these it seems hardly likely that such methods can be called economic, for mosquito control, blackfly control, or any other such pest species.

Recently attention has been paid to the possibility of utilizing parasitic nematode worms of the genus *Mermis* as biological control agents for blackflies. The natural occurrence of this parasite has been reported as causing mortalities as high as 95 percent in simuliid broods in North America (Maser 1973). Before *Mermis* can be used on the scale necessary in any blackfly outbreak area, a practical mass rearing technique must be developed for these worms. Presently, investigations are being directed toward laboratory and field studies of mermithids in natural population of Canadian blackflies, and of relevant aspects of biology and ecology of these insects.

6.1.3 Habitat management

Various applications of water management have been attempted, on a small scale, as a form of blackfly control. Impoundment of streams or rivers with dams will effectively modify the hydrodynamics and water aeration of a potential or existing breeding area, making it less suitable for larvae, and therefore less productive of blackflies. However, although dam construction has been attempted as a control measure (Dampf 1931), it has reportedly not been very effective. The reason is that although dams act to pond-up and reduce the flow along the main course of a river, thereby creating generally adverse habitat conditions for blackflies, they also provide exceptionally favourable blackfly breeding sites in their spillways (Peterson and Wolfe 1958). It is conceivable also that the resultant substitution of quiet bodies of impounded water for the turbulent flowing water of streams could create favourable habitats for mosquitoes.

Manipulation which would alternately raise and lower the stream levels in order to create a "flushing-action", sufficient to wash the larvae downstream, has been done in conjunction with log-drives, which act to give an additional battering action (West 1958). However, the effects of flushing are short-lived, even if the stream does possess the facilities to control its flow.

6.2 PERSONAL PROTECTION

For the individual who may be subjected to plagues of blackflies, the easiest form of immediate relief is in the form of personal protection with repellents and suitable clothing. Protective clothing against blackflies is particularly popular in the north, where work must always be done out of doors during the blackfly season. Blackflies are notorious for crawling under clothing, particularly around the wrists, neck and front openings of shirts and trousers. Zippers rather than buttons can help slightly, as also can the choice of lighter coloured clothing. Orange, yellow and light green materials are less attractive to blackflies than dark blue, purple and red (Fredeen 1973). However, the particular spectral composition and wave-length balance in these colours remain undefined.

The texture of clothing fabrics is also important, as certain biting flies have been shown to be more attracted to shiny surfaces than to dull matt ones (Brown 1952). This "preference" also draws attention to the importance of awareness of the difference between specular reflectance and wide-angle diffused reflectance. Studies of blackfly behaviour which involve light, should provide for this phenomenon.

Protective clothing is necessarily bulky and uncomfortable. Often it is difficult to combine the required characteristics of clothing designed as protection against both mosquitoes and blackflies, where both may be a problem. The tight fitting, often uncomfortable, clothing necessary for any degree of relief from blackflies may hinder work progress due to wearer discomforts.

Repellents are often used in conjunction with protective clothing, either applied to the fabric or directly to the skin. Although several chemicals are labelled "repellents", they are really no better than deterrents to feeding in that they do not generally prevent flies from landing. The so-called repellents usually show no action at even short distances from the host and must be applied as a complete covering to afford any degree of protection. Chemical deterrents are also available to protect livestock, but as such chemicals usually need spraying or brushing on daily, effective control is neither easy nor cheap. Furthermore, blackflies tend to attack the undersurfaces of cattle, so that devices for effective self-administration of deterrents have not been designed.

The issue of personal protection would be much simplified, if instead of using the presently known gustatory deterrents, an olfactory repellent would be sought. Progress is hampered partly by the lack of a rigorous study of blackfly behaviour in general, and blackfly attack strategy specifically. It is hampered also by a lack of understanding of the specific nature of factors in individual hosts which render some free and others highly attractive. It seems pertinent to understand not only the operation of the organisms we are trying to deter, i.e. blackflies, but also what attractancies we are trying to obscure in the host.

The search for deterrents remains largely empirical, trial-and-error, with some chance findings, and these used as a starting base for seeking improvement by synthesis and testing of analogues.

SUMMARY

This critical review was undertaken in the context of the apparent need for a perspective view of information relating to blackflies as a multidimensional problem, so that judgements might be made as to needs for further study and action. The present work is based on an evaluation of 450 literature references in five different languages, and some personal interviews. The literature came from more than 200 journals, special reports, monographs and textbooks. It was examined for the purpose of establishing the dimensions of the problems relating to blackflies, in respect to their biological attributes, impacts on various forms of life, impacts on resource uses and development, roles in food chains, problems in achieving protection, and environmental considerations in seeking control. The literature was examined for factual content, gaps in information, difficulties in research, misunderstandings, reasons for such difficulties, and examined for conceivable avenues that research might profitably take.

CONCLUSIONS

An extensive and diversified literature attests to the importance and complexity of the subject which deals with blackflies.

Much of the work done during the past two centuries remains valid today, but certain pitfalls need to be understood. Investigations on blackflies have related to morphology, taxonomy, histology, morphogenesis, cytology, food, respiration, blood circulation, reproduction, dispersal, attack habits, various aspects of salivary toxins of the flies, transmission of pathogenic micro-organisms and filarial worms, species distributions, habitat requirements, predators, parasites, roles in food chains, impacts on resource uses and development, undertakings by population reduction, and individual protection by clothing and chemical repellents.

Knowledge on the subject has lost much of its potential impact, and progress hindered because that knowledge is partially obscured in the depths of time, awkwardly scattered through the literature in different languages, compartmentalized in publications addressed to audiences having diverse thrusts of interest, and sometimes confused and misleading through disagreements on taxonomic identities.

The identity of factors, and determinant mechanisms in attractance and repellence for blackflies constitute a major aspect of the problems which remain obscure, and the information misleading. For various reasons the components of blackfly behaviour are unclear because investigators have not understood the principles of successive and simultaneous induction in insect behaviour; they did not, and do not, understand the physiology and chemistry of eccrine, apocrine and sebaceous secretions of human skin; and they have not considered the conceivable role of spectral reflectance of the skin. Consequently, the reasons for host-individual differences in proneness to being attacked cannot yet be explained or manipulated, and progress in development of fly repellents or deterrents proceeds through empirical processes.

The mechanisms of differential reactivity to fly-bites between host individuals, and of changing susceptibility within individuals, are unclear. Sources of confusion reside in unresolved taxonomy, and in ignorance by some investigators regarding the nature of mechanisms and requirements in immunology.

Documentation of impacts of blackflies on resource uses and values, though incomplete, demonstrates that these insects create severe problems.

Blackflies occupy an important place as primary consumers and as consumed organisms in food chains, so that for these reasons intensive depopulation schemes, even if non-polluting, could be damaging to both commercial and sport fisheries management. Release of larvicides into river systems for control of blackflies could be hazardous to consumer organisms which depend on blackflies and other aquatic life.

Progress in knowledge, and development of methods for alleviating the problems have been impeded by a frequent attitude of apathy which derives from a fatalistic acceptance of misery, especially by those who do not suffer it, and by an ignorance of blackfly behaviour, ignorance of the chemical, physical, physiological, and genetic determinants of host resistance and susceptibility, a fragmented, tactical approach to the problems, the chanelling of funds and efforts into outmoded practices, or into research which merely seeks to modify details of old concepts, or pursuit of lines which seek only local benefits, and failure in attempts to rear blackflies under laboratory conditions to serve the needs of experimentation with stock of known history.

Much remains to be done, but the directions which might profitably be taken should become clearer by a study of points highlighted in the present thesis.

APPENDIX I

<u>Checklist of the blackfly species referred to in the text.</u>

Genus: *Simulium*		Latrielle 1802
Species:	*arcticum*	Malloch
	aureum	Fries
	ornatum	Meigen
	baffinense	Twinn
	columbaschense	Fabricius
	columbaczense	Schönbauer
	damnosum	Theobald
	decorum	Walker
	defoliarti	
	euryadminiculum	Davies
	jenningsi	Malloch
	melatum	Wharton
	meridionale	Riley
	metallicum	Bellardi
	oviceps	Edwards
	pecuarum	Riley (referred to by Rempel and Arnason 1947).
	reptans	Linné
	rugglesi	Nicholson and Mickel
	venustum	Say
	vittatum	Zetterstedt
	vulgare	Rubzov
	woodi	de Meillon
Eusimulium		Roubaud 1906
	aureum	Fries
	pecuarum	(Riley) (referred to by Bradley 1935)
Cnephia		Enderlein 1921
	crozetense	(Womersley)
	pecuarum	(Riley) (referred to by Crosskey 1973)
Prosimulium		Roubaud 1906
	pecuarum	Riley (referred to by Malloch 1914)
Austrosimulum		Tonnoir 1925
	ungulatum	Tonnoir
Wilhelmia		Enderlein 1922
	equina	Linné
Odagmia		Enderlein 1921
	ornata	Edwards

APPENDIX 2.

Percentage decrease in productivity of natural phytoplankton communities during a 4-hour exposure to a concentration of 1.0 ppm of the indicated insecticide.

Pesticide	Percent decrease	Pesticide	Percent decrease
Chlorinated hydrocarbons		Herbicides	
		2,4-D acid	0
Aldrin	84.6	2,4,5-T acid	0
Chlordane	94.0	2,4-D dimethylamine salt	0
DDT	77.2	Diuron	87.4
Dieldrin	84.8	Eptam	0
Endrin	46.0	Fenuron	40.9
Heptachlor	94.4	MCP amine weed killer (formulation)	0
Kepone	94.7	Monuron	94.1
Lindane	28.5	Neburon	89.9
Methoxychlor	80.6	Tillam	23.8
Mirex	41.6		
Thiodan	86.6	Fungicides	
Toxaphene	90.8	Chemagro 2635	85.3
		Dyrene	91.3
Organophosphorus insecticides		Ferbam	97.0
ASP-51	29.5	Phaltan	31.9
Bayer 29493 (Baytex)	7.2		
Bayer 25141	0	Chlorinated acaricides	
Diazinon	6.8	Sulphonone	12.2
Dibrom	55.6	Tedion	39.0
Di-Syston	55.2		
Dylox	0	Soil fumigants	
Ethion	69.0	Dexon	14.6
Guthion	0	Nemagon	5.0
Imidan	7.7		
Malathion	7.0		
Meta-Systox R	0		
Methyl trithion	85.9		
Systox	7.11		
Carbamates			
Bayer 37344	38.7		
Bayer 39007	0		
Bayer 44646	0		
Sevin	16.8		

From: Butler, P.A. 1963.

APPENDIX 3

Insecticide toxicity levels for aquatic insects and fish.

Toxicant and Formulation	Organism and Tolerance Level: Blackflies: Minimum effective dosage p.p.m.	Rainbow Trout: Maximum nonlethal p.p.m.	Caddisflies: Maximum nonlethal p.p.m.
DDT			
Emulsion	0.7	3.	5.
Acetone solution	0.3	30.	10.
Wettable powder	1.	10.	10.
Fuel-oil solution	0.4	10.	10.
Kerosene solution	0.3	0.3	0.3
Gamma BHC			
Emulsion	1.	1.	0.1
Acetone solution	0.5	10.	10.
Chlorinated Camphene			
Emulsion	4.	3.	5.
Acetone solution	0.5	5.	0.5
Fuel-oil solution	0.5	0.5	0.5
Alkylated naphthalene solution	1.5	1.5	1.5
Chlordane			
Emulsion	4.	3.	5.
Acetone solution	0.5	20.	10.
Fuel-oil solution	0.5	6.	0.5
Commercial solvent	1.5	10.	1.
Pyrethrum			
Acetone mixture	0.1	0.1	--
Kerosene solution	0.1	0.1	0.1

This table shows differences between insecticides in their toxicity to the different organisms; and differences between forms of preparation. The influence of solvent on the absolute and relative toxicity of insectide varies with the insecticide.

From: Gjullin *et al.* 1949.

GLOSSARY OF TERMS

ANAPHYLACTIC SHOCK - An antigen-antibody reaction. The condition of being hypersensitive to a serum or foreign protein, caused by a first or sensitising dose.

ANAUTOGENOUS - Inability to obtain reproductive maturity without a prior blood meal.

ANTHOPHILIC - attracted to, and feeding on, nectar and/or pollen.

ANTHROPOPHILIC - Attracted to, and feeding on, humans.

APOCRINE SECRETIONS - Secretions of viscous type sweat from sweat glands with a distinct type of secretory cell, the duct of which usually opens into an adjacent hair follicle.

ECCRINE SECRETIONS - Secretions of a more watery nature from sweat glands with a distinct kind of secretory cell not associated with hair follicles. Such sweat glands are particularly abundant in the hairless regions such as palms, soles, forehead, etc.

ENVENOMIZATION - The injection of toxic substances.

HAPTENIC SUBSTANCE - A substance which when combined with a protein has the power to confer specific antigenic properties on that protein.

MAMMALOPHILIC - Attracted to and feeding on mammals.

PASSIVE IMMUNITY - A condition of non-reactivity without the involvement of an antigen-antibody reaction.

PNEUMOHYDRORRHOEA - Drowning from fluids within the lungs.

SPECULAR REFLECTANCE - The reflection of light from polished surfaces in which the angle of reflected light is equal to the angle of incident light.

SUCCESSIVE INDUCTION - The inhibition of one response by another response i.e. one activity of the insect is influenced by the previous activity.

WIDE-ANGLE DIFFUSED REFLECTANCE - The reflection of light from dull surfaces in which the light is scattered uniformly in all directions.

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