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Ministry of Overseas Development

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COLLEGE HOUSE, WRIGHTS LANE, LONDON W8 5SJ, U.K.
1977

ISBN 0 85135 087 9

Price £3 net

Printed in England for Her Majesty's Stationery Office by
Hobbs the Printers of Southampton

(890) Dd151347 800 7/77 G3313

CONTENTS

INTRODUCTION

Various species of Simuliidae are vectors of the filarial parasite of man, *Onchocerca volvulus,* which causes onchocerciasis and which can be a serious debilitating disease in parts of Africa and to a lesser extent in Central and South America and southern Arabia. Within recent years increased interest has been focused on the disease and the biology of its vectors. A WHO–co-ordinated vector control programme which is to last about 20 years has recently been initiated in seven countries in the Volta River Basin area of West Africa with the aim of eradicating onchocerciasis from the area (United Nations Development Programme 1973). From preliminary entomological surveys in this area and from other studies in the Americas it has become increasingly obvious that there is urgent need for better sampling techniques for the vectors. The purpose of the present report is to critically review available methods for sampling adult blackflies.

Changes in population density of adult Simuliidae have for many years been assessed almost entirely by human bait catches. Some ten years ago the Expert Committee on Onchocerciasis (World Health Organization 1966) meeting in Geneva recognised the need for improving sampling techniques for vector *Simulium* species. It was urged that some of the methods used in Europe and North America, such as those employing mechanical traps, light traps, sticky traps, etc., should be evaluated in the tropics, and that further studies should be made on the value of visual and chemical attractants. It was also recommended that better samples were required of blood-engorged and gravid females, physiological categories not usually encountered in bait catches. However, remarkably little progress has been made during the past ten years on sampling adult blackflies. In marked contrast there have been several new and novel traps and catching methods recently developed for tsetse flies (Moloo 1973; Vale 1969, 1974a, b, and see Jordan 1974 for general review). Several new traps and sampling methods have also been devised for mosquitoes (Service 1976, for review).

In Africa by far the most important vectors of river blindness are certain species within *Simulium* (*Edwardsellum*) *damnosum,* formerly considered a single species but now known to consist of a complex of sibling species. Examination of the banding of the polytene chromosomes of the larval salivary glands has shown that 26 cytotypes of the complex occur in tropical Africa (H. Townson, pers. comm. from R. W. Dunbar 1976). Vajime & Dunbar (1975) recognise seven cytotypes from West Africa which they consider represent eight species, whereas Quillévéré (1975) only recognises four species groups, and considers the naming of eight species premature (Quillévéré, Sechan & Pendriez 1976). Unfortunately adults of the complex cannot be identified by their chromosomes, nor with any certainty by morphological characters, although recently Quillévéré, Sechan & Pendriez (1976) have been able to separate females of six of the West African cytotypes on antennal characters and the maxillary teeth.

It appears that different species within the complex may have different geographical distributions (Garms & Vajime 1975; Quillévéré & Pendriez 1975; Vajime & Dunbar 1975), although in many areas certain species are sympatric. The diversity of behaviour and differences between vector potential that have been recognised for some considerable time in different populations of *S. damnosum,* can most likely be attributed to differences between the biology of the different species within the complex. Unfortunately it cannot be known what species within the complex were caught by the sampling methods reviewed in this report, probably there are differences between the efficiency of the different sampling techniques for the different species within the complex. Throughout this report whenever *S. damnosum* is referred to it should be remembered that a species complex is involved.

HUMAN BAIT CATCHES

The most direct method of sampling anthropophilic haematophagous flies is by human bait catches. The various techniques, the factors influencing catch size and quality, and difficulties of interpretation and analysis of the results have been fully discussed in connection with mosquitoes (Service 1976). Although there will be differences between the behaviour of blackflies and mosquitoes to host stimuli, many of the problems associated with sampling mosquitoes by bait catches will also apply to blackflies. The lack of standardisation in the methods of catching blackflies attracted to man often makes it difficult to compare catches.

One of the simpler methods entails one or more persons, seated, or more rarely standing, and usually wearing shorts, collecting all blackflies landing on him or his companions. Catches may be brief, such as 1–3 h at specific times of the day, or a team of collectors working in relays, may catch for longer periods, such as from about sunrise to sunset. Alternatively, collections may be restricted to about 15–30 min in each hour for one or many hours. Sometimes only blackflies biting are caught, but more usually any that land on the collectors are caught, usually in small tubes or aspirators and preferably before they have probed. In El Salvador Collins, Wilton *et al.* (1976) collected blood-engorged *S. ochraceum* from baits in 12 x 75 mm polypropylene tubes having snap-on caps. One or two minute aeration holes are made in the cap and also a small (3 mm) hole is punched in the bottom of the tube which is plugged with a small piece of cotton wool. A 60-mm strip of blotting paper is placed down the inside of the tube to leave a gap of about 15 mm between its end and the small wick at the bottom of the tube. One fly is caught in each tube. These are placed in plastic boxes lined with wet towelling and kept in the shade. Immediately after collections are completed all the flies are fed by dipping the wick in 10% sucrose containing 200 units of penicillin, 200 μg streptomycin and 0.5 μg fungizone/ml, which prevent bacterial and fungal infections. Boxes of tubes of flies are kept in large insulated cool boxes lined with damp towelling, and when necessary ice bags are added to reduce temperatures. This procedure reduces fly mortality during and after transportation of blood-fed individuals to the laboratory. Duke (1968a) caught flies in a pooter having a reservoir which was emptied hourly. Sometimes small hand-nets are used to sweep the air around the collector's body to collect flies that have not yet settled.

Not all Simuliidae behave the same at bait. Some species such as *S. callidum* and *S. metallicum* are easily disturbed when either exploring the skin or sucking up blood. These 'nervous feeders' (Dalmat 1955) are thus more difficult to catch and may be underestimated in bait catches. Various types of descending nets or curtains (Berzina 1953; Blagoveshchenskiy, Bregetova & Monchadskiy 1943; Minář 1962; Monchadskiy & Radzivilovskaya 1948; Service 1976) can be used to enclose the bait and hopefully get a more accurate assessment of these 'shy' species. However, because of their reluctance to bite they may be of limited importance in disease transmission.

Collections are not always restricted to a single place. A common procedure is for collectors to walk along a defined route stopping at predetermined places to undertake short, frequently 15-min, catches. Such fly rounds may cover many miles. Very occasionally the procedure is not to catch any flies, but merely to record the time taken for the arrival of the first fly, but this is unlikely to be a reliable method for comparing fly densities.

A number of variables are encountered in human bait collections. Some individuals are more attractive to simuliids than others (Crosskey 1955), and dark-skinned people, such as Africans, are usually more attractive than light-skinned people (Bellec 1974; Crosskey 1955; Hocking & Hocking 1962; Hughes & Daly 1951; Raybould 1967). Bellec (1974) concluded that the colour of clothing was relatively unimportant in determining the number of *S. damnosum* caught, with the exception of black, which resulted in larger collections. If fly densities are to be compared it is important to catch simuliids at the same places and times of day, and if possible under the same climatic conditions. Most anthropophilic blackflies are day biters, but different species may exhibit diurnal fluctuations in host-seeking activities. For example, in Kenya *S. neavei* bit mainly from 0900–1130 h, and then again from 1400–1700 h (McMahon, Highton & Goiny 1958). In Guatemala it can be difficult to assess the relative importance of the three most important anthropophilic species by brief catches because each has a different biting profile. *S. metallicum* bites from about 0700 h more or less continuously until 1730 h, but with a small peak from 0800–1000 h, whereas *S. ochraceum* bites from 0700–1600 h but has a well-defined peak of biting between 0800–1000 h. Biting by *S. callidum* extends from about dawn until 0900 h and again from 1500 or 1600 h to twilight, but with little activity at other times (Dalmat 1955). A common procedure, especially in West Africa, is for a team of collectors to work in relays for 3–4 h to collect *S. damnosum* biting from 0600–1800 or 1900 h (Lewis, Lyons & Marr 1961; Le Berre 1966; Le Berre, Balay *et al.* 1964). The biting peaks of this vector in West Africa are mainly in the mornings and afternoons, but as Crosskey (1955) working in Nigeria has pointed out, the biting cycle may vary seasonally, and also from place to place. In other countries different biting cycles have been sometimes recorded. In Ivory Coast Giudicelli (1966) found that in savanna areas there was a morning and evening peak in biting densities, but some 300 yd (274 m) away amongst thicker riverine vegetation biting densities were remarkably constant during the day. Duke, Scheffel *et al.* (1967) showed that in Cameroon peak biting of forest forms of *S. damnosum* was between 1600–1700 h, coinciding with the greatest density of microfilariae in the skin of individuals infected with the forest strain of *O. volvulus*, whereas in the Sudan-savanna peak biting by the vector was 2 h earlier, also coinciding with peak microfilarial density of the Sudan-savanna strain of *O. volvulus*. Recently Anderson, Fazen & Buck (1975) working in Guatemala have presented for the first time evidence that *O. volvulus* in the Western Hemisphere also exhibits microfilarial periodicity, and that there is a close relationship between the peak biting activity at around 1000 h of *S. ochraceum,* believed to be the principal vector, and maximum availability of microfilariae in the skin.

Crisp (1956) emphasised that comparisons of fly densities between different places and between different times of the year should not be based on single catches, because in any one place there can be considerable daily fluctuations in biting activity and hence numbers caught. Fifteen-minute collections were regarded as unreliable, because they could coincide with periods of great activity or inactivity. He also thought that time was wasted in walking to different catch sites in fly rounds, preferring 1-h catches at a few selected points, but avoiding villages and bridges where there might be expected to be concentrations of flies that had already fed on people.

When fly densities are low catches are probably best made at times of the day when maximum numbers are biting, but when there are high biting densities then catches at other times may be sufficiently large for reliable comparisons. Crosskey (1955) thought that bait catches were best performed during times of maximum activity, but cautions that even for the same species peaks of host-seeking activity may vary according to location.

Only very occasionally have human bait catches for simuliids been performed at different heights in trees. In Venezuela, however, Dalmat (1955) found that in catches at the base of trees and up to 120 ft (36.5 m) *S. metallicum* and *S. callidum* bit almost indiscriminately at all heights, whereas only a few *S. ochraceum* bit above 60 ft (18 m). Adults of all three species were also caught resting on vegetation up to 112 ft (34 m).

Some investigations on the behaviour of simuliids attracted to hosts suggest that hungry females, unlike tsetse flies, do not follow hosts for any great distance, and that host odours are more important in locating hosts than vision. However, Austen (1902) stated that *S. damnosum* followed people for several miles (!) and Crosskey (1955) considered that, in certain situations at least, *S. damnosum* hunts by sight, and that females may follow hunters, especially if accompanied by dogs, for some distances. Crisp (1956) queried these observations, and wondered how individual flies could be observed to follow baits for any great distances. In Russia Monchadskiy (1956) considered that simuliids have a watching type of attack. Few bites may be received by people slowly walking through areas harbouring large numbers of simuliids (Hocking & Hocking 1962), because there is insufficient time for host odours to stimulate nearby resting adults and induce host-seeking flights. A high initial catch, such as frequently observed with mosquitoes (Service 1976), is sometimes encountered while catching simuliids. Consequently, a series of short catches at different sites, such as in a fly round, often yields more flies than a longer catch at a single site. According to Lewis (1957) *S. damnosum* does not usually exhibit a high initial catch in grassland areas, but this is probably because few hungry females are resting amongst the immediate vegetation. As with mosquitoes (Service 1976) there may be waves of attacks by *S. damnosum,* i.e., several adults arriving together, followed by an interval of several minutes with none biting (Lewis 1960a).

From a series of experiments in Cameroon Thompson (1976c) concluded that in forested areas *S. damnosum* relies mainly on body odours for locating human hosts, although visual stimuli may also be important, whereas in savanna areas sight seems to be the most important factor in host orientation, smell and exhaled breath being of less importance. These differences may have been due to the existence of different species within the *damnosum* complex in the two vegetation zones. In forest trials washing with soap and water at 15-min intervals had no effect on the number of flies attracted to human baits, but their numbers were drastically reduced if petroleum jelly was smeared over the body. In savanna areas neither method greatly affected the number of flies attracted. Thompson (1977) found that the odours which attract forest populations of flies to humans are contained in sweat, especially that coming from below the waist. The actual components, however, were not isolated or identified. In Canada Bradbury & Bennett (1974b) studied the factors attracting *S. venustum* to silhouettes and carbon dioxide and proposed that in this species at least upwind flight behaviour of host-seeking females involves three hierarchial zones of orientation mechanisms: long range attraction involving host-specific odours, middle range attraction involving more precise host orientation due to the host's emission of carbon dioxide and finally close range orientation behaviour in which in addition to these olfactory stimuli such factors as colour, size, shape and possibly movements are important in guiding hungry females to the host. Smith (1966) also considered that visual stimuli to be the final behavioural element in host-seeking flight.

Thompson (1976c) developed four different traps, termed slat traps, enclosure traps, fan traps and sticky traps, to evaluate the stimuli attracting *S. damnosum* to its hosts. The former consisted of a triangular cage (30 cm high with 44 cm sides) covered with sandfly netting which extended downwards for 120 cm on two sides. The third side was composed of dark coloured slats obtained from a venetian blind and set at an angle of about 30° to the vertical. A wind vane mounted to the top of the trap ensured that the slatted side faced downwind. The attractiveness of worn clothing, exhaled breath and carbon dioxide was tested by this trap. Flies attracted to these stimuli entered through the slats and eventually flew upwards to be collected in the cage at the top. The enclosure trap consisted of dark coloured venetian blinds descending on all four sides from a rectangular wooden frame (130 x 130 cm). When a man entered this trap he remained unseen by blackflies although host odours were emitted. The fan trap consisted of a CDC miniature light trap mounted on its side, with the light removed, behind the attractant under test. Flies were sucked into the trap. The sticky trap consisted of a rectangular frame inclined at 20° having black plastic sheeting (61 x 30 cm) covered with adhesive stuck to the lower surface and test clothing tacked to the upper opposite side. Flies attracted to the smell of the clothing tended eventually to land on the lower sticky surface of the trap.

Using these above types of trap in forest experiments Thompson (1976c) found that in the absence of visual stimuli human smell alone attracted about four times as many *S. damnosum* as unbaited slat traps, but combined with exhaled breath about 16 times as many. Emissions of carbon dioxide at a rate of 400 ml/min near a slat trap attracted about 17 times as many flies as were caught in unbaited traps, however, this still only represented about two-thirds of the numbers attracted to a human bait. A hidden stationary man always attracted fewer flies (53–64%) than an exposed moving man, irrespective of whether he was exhaling normally or his breath removed from the area (Thompson 1976c).

There seems to be an overdue need for both laboratory and field studies on the factors responsible for the attraction of adult blackflies to their hosts. A better understanding of their response to various stimuli might aid the search for better trapping methods. There may, however, be limitations in interpreting laboratory results in terms of field behaviour, for example the responses of *Glossina morsitans* to odours and moving targets differ considerably under laboratory and field conditions (Vale 1974b).

In the *Simulium* control scheme (1956–66) at Abuja, northern Nigeria, the decrease in *S. damnosum* resulting from larviciding streams with DDT was monitored by 43 catching stations distributed along five fly rounds which were patrolled weekly. Fifteen-minute catches were made at each station and the (monthly) biting rates expressed as the numbers of *S. damnosum*/man/h. The annual mean densities (June–September) of *S. damnosum* before larviciding commenced were about 8–9 flies/man/h, after control there was at least an 89% reduction in fly densities, except for 1957 when a mean of 1.49 *S. damnosum*/man/h was still being caught. In an appraisal of the efficiency of the scheme Davies (1968) discussed the validity of fly rounds in monitoring population changes. One of the difficulties at Abuja was that the numbers of baits varied from 2–9 people. Calculating biting rates, by dividing the numbers caught by the number of collectors implies that doubling the number of collectors doubles the catch, and this is most unlikely. During high densities increasing the number of collectors probably increases the catch, although not necessarily linearly, but at low densities this is an unreasonable assumption, because at these times there is a limited number of flies available for collecting. Thompson (1976b) also experienced difficulty in interpreting catches per man-hour when more than one person was collecting.

The parous rate of man-biting *S. damnosum* is often greater in savanna areas of West Africa than in the forests (Crosskey 1958a; Duke 1968b; Le Berre 1966; Le Berre, Balay *et al.* 1964). Although the species is highly anthropophilic over most of its range, in certain areas it feeds to a varying extent on other animals (see page 10). Dissections of *S. damnosum* in Sudan-savanna areas of Cameroon indicated that nulliparous flies dispersed mainly inland away from larval habitats, whereas parous flies especially the older ones tended to stay closer to riverine vegetation (Duke 1975). In Cameroon Disney (1972) found that in the middle of the day the parous rate of *S. damnosum* attracted to chickens was lower than in those biting man. He concluded that although Le Berre's view that the parous rate of man-biting *S. damnosum* is a function of longevity, and this tends to be greater in savanna than forest areas, it also may be due to differences between the degree of zoophily of different populations. In some species marked changes have been observed in the proportion of the population feeding on man and other hosts, during different seasons and also at different altitudes. For example, in Utah *S. arcticum* normally feeds on cattle, but above about 2135 m man is bitten, similarly, *S. canonicolum* feeds on birds, but above about 2662 m feeds on man. Another example is *S. tuberosum* which stops biting man below about 2135 m. Reasons for these changes in feeding pattern are not known (Peterson 1959). DeFoliart & Rao (1965) showed that in Canada there was a shift in host selection by *S. meridionale* away from birds to man in the cooler autumn months. In Northern Sudan El Bashir, Jack & El Hadi (1976) observed that towards the end of the day adults of *S. griseicolle* became particularly active, aggressive and readily bit man and other animals, whereas at other times they fed almost exclusively on birds. It may therefore prove difficult in a few instances to measure changes in seasonal density by using only one type of bait.

Some of the different methods that have been used in performing human bait catches and estimating biting rates are described below.

In Liberia, when *S. damnosum* was very abundant bait collectors noted the time for the capture of the first 50 flies, after which they ceased collecting, but from this data Lewis (1960b) was able to estimate man-biting rates. Loosely constructed palm leaf shelters afforded the collectors protection against rain. Similarly, in all-day human bait catches in Venezuela Lewis & de Aldecoa (1962) issued each collector with 20 tubes for each hour with instructions that one blackfly be placed in each. When the tubes were filled within less than an hour, no more were collected and the biting rate each hour estimated.

In Nigeria Crosskey (1958b) introduced routine fly round collections for monitoring relative changes in population size. A number of collectors, usually three, caught all blackflies landing on them or their colleagues for 15-min periods at a number of predetermined catching sites. Monthly collections at each catching site were expressed as the number of blackflies/man/15-min or 1 h. In Tanzania, Haüsermann (1969) had three people working together catching blackflies for 20-min periods at eight selected sites on fly rounds, and in addition he employed continuous bait catches lasting from 0645–1815 h. In West Africa Le Berre & Wenk (1966) used table fans to blow blackflies, mainly *S. damnosum*, that had been attracted to human bait into a long sleeve-like collecting cage. Fans were either positioned on the ground or at about the level of the head, to blow flies attracted to these two sites respectively into the cages. In Cameroon fans were also used to blow into collecting cages *S. damnosum* attracted to human baits, worn clothing and carbon dioxide (Thompson 1976c).

In Labrador Hocking & Richards (1952) used two main methods for catching simuliids: a landing rate, which was a count of the flies landing on the front of the collector's trousers between waist and knee during 1 min, and a sweep count, which was the number of blackflies caught in (usually) 30 sweeps made with a 12-in (30·5-cm) net held at arm's length around the body. As many as 150 flies/min were caught in landing catches, and 300 in 30 sweeps. Collectors also bared their forearms and recorded the time for the first bite. Davies (1951) showed that landing rates of simuliids on coloured cloths varied with reflectivity for sunlight and ultraviolet radiation, because of this the reflectivity etc. of the materials of the catcher's trousers in Labrador were measured and compared with a black fabric. An attack rate for blackflies was computed as follows:

$$\text{Attack rate} = f_t f_s \left(a + \frac{f_c b}{2} + 100 - \frac{x}{9}\right)$$

where f_t, f_s and f_c are correction factors for temperature, saturation deficiency and clothing colour, a = total sweep count, b = total landing rate and x = time for first bite, the divisors 2 and 9 were used to balance the weight attached to these sets of observations. When these corrections were taken into consideration there was much better agreement between catches by different observers and a more uniform trend by any one observer at a particular site.

In Canada Davies (1961) found it convenient to catch *S. mixtum* and *S. fuscum* by netting them as they arrived at bait, making use of the fact that these species hover about the head for short periods before they settle and attempt to bite.

Wolfe & Peterson (1960) had three people simultaneously collecting blackflies for 24 or 48 h by counting (1) the numbers of blackflies landing/min on an 18-in (46-cm) square of blue serge cloth, (2) the numbers biting on the forearm/min and (3) the numbers caught in ten figure-of-eight sweeps with a 12-in (30·5-cm) diameter net around the collector. At the start of each collection, weather conditions were first recorded, then the landing catch performed followed by the biting catch and finally the sweep-net count. This routine occupied about 20 min and was repeated at the beginning of every hour. Catches consisted mainly of *S. venustum*. The landing catch was usually slightly bigger than the sweep-net catch, but both methods showed similar diel activity rhythms, with peak activity in the morning and early evening. The times of peak activity nonetheless differed when catches were performed in different habitats. For example, in exposed sites peak activity occurred 1 h after sunrise but under a forest canopy peak activity might not be until 4–5 h after sunrise. Moreover, in the evening, biting activity continued for about 2 h after sunset in exposed sites, but for only 1 h in shaded sites. During the day more *S. venustum* bit dark- rather than fair-haired people, but in the early morning and evening very fair-haired people received slightly more bites.

To measure *S. damnosum* biting densities at the Kainji development site in northern Nigeria Mr H. H. Goiny developed a skirt trap, which has been evaluated by Walsh (1970). It consists of a crinoline-like skirt of thick black cloth supported by steel wire and is fastened around the waist of the collector, who wears only swimming trunks. On arrival at a catch site the collector holds up the hem of the skirt to expose his bare legs and feet, and after about a minute drops the skirt. Flies on and around his legs are enclosed within the skirt and are attracted to the light entering through two Kilner jars which have one-way funnels and are fitted into the skirt near the waist. Inside the skirt there are two twig brooms with their handles protruding, and these are brushed against the legs to dislodge any flies that are feeding. Walsh (1970) considered these skirt traps 'quite effective' and had a number of advantages over more conventional catching methods. He thought they gave a more realistic estimate of the biting densities than direct bait collections. On one day, for example, three people catching blackflies in tubes succeeded in recording 186 flies/man/h, whereas a catch of 3350 flies/man/h was estimated from catches of two men employing the skirt trap. Walsh (1970) considered that only exceptionally skilled collectors can catch more than 120/h, even though there may be more biting. Duke (1968a), however, felt that the saturation point during a 2-h shift was not reached until a biting density of about 500–1000 flies/man/h was reached, and Thompson (1976b) considered the critical level was usually about 1000 flies/man/h. Walsh (1970) thought that the skirt trap largely overcame differences between individual collectors' personal skill in catching flies. Consequently, any differences between catches on individuals under the same conditions were due to variations in their attractiveness to the flies. The trap, however, is cumbersome and is likely to become torn and damaged on walking through the bush, and therefore has limited appeal in fly rounds where catches are for short periods at several separate sites.

Fly rounds and stationary human bait catches can give useful measures of relative changes in fly densities, but I do not think they are reliable for estimating fly-man contact, although this has sometimes been attempted. For example, in Liberia Garms (1973) studied the biting rate and seasonal prevalence of *S. damnosum* by bait catches from 0600–1800 h. By extrapolating the biting rates he estimated that a person would receive between 12,000–150,000 bites a year by *S. damnosum,* if exposed to the species for 12 h a day. Reasons why this type of calculation is unrealistic and misleading are detailed elsewhere in a discussion of mosquito biting rates (Service 1977), but basically the objections concern the artificial nature of biting catches, and the extrapolation of such limited data to represent average fly-man contact. On the other hand information on infective rates of flies and numbers caught biting man in standardised catches can provide *relative* levels of theoretical transmission, termed 'transmission potential' (Duke 1968a; Duke, Anderson & Fuglsang 1975). These can be used to compare inoculation rates in different seasons and in different places. Duke (1968b) also introduced the concept of an 'infective biting potential', which was defined as the number of potentially infective parous flies per 1000 nulliparous ones. In Sudan-savanna villages in Cameroon because of the differential dispersal of nulliparous and parous *S. damnosum* (Duke 1975) transmission potentials were more closely related to the density of parous flies than to total populations (Duke, Anderson & Fuglsang 1975). Although some insight has been gained into the epidemiology of onchocerciasis transmission, Duke (1970) criticised Mills (1969) for trying to extrapolate published biting rates (De León & Duke 1966) to estimate annual biting rates of *S. damnosum,* and from there to build a population model of onchocerciasis transmission. Duke (1970) considered that it was premature to construct such epidemiological models in West Africa, or anywhere else, on the quality of data available.

It is noted that many of the questions asked by Davies (1968), such as (1) how accurate are fly rounds in estimating *S. damnosum* populations? (2) can *S. damnosum* originate from undetected pockets of breeding which may have escaped insecticidal treatment?, or (3) are there immigrant flies arriving from outside the control area? and (4) how long do adults live?, are the questions now being asked in connection with the Onchocerciasis Control Programme in the Volta River Basin in West Africa.

BAIT ANIMALS AND ANIMAL-BAITED TRAPS

Although *S. damnosum* is regarded as highly anthropophilic it has been reported in many areas feeding on such animals as goats, cows, donkeys, dogs and sheep (Crisp 1956; Crosskey 1955; Disney 1972; Lewis 1948), game (Hargreaves 1925; Le Roux 1929), birds, including chickens (Crisp 1956; Disney & Boreham 1969; Garms 1973; Hargreaves 1925). According to Le Roux (1929) birds are the principal hosts in the Transvaal. In Tanzania Haüsermann (1969) observed swarms of *S. damnosum* and *S. vorax* around cattle and goats, but the animals were only seen to be bitten by *S. vorax.* In certain areas of Uganda north of the Kabalega (*ex* Murchison) Falls *S. damnosum* is remarkably zoophilic (Nelson 1968), and in the eastern Usambaras in Tanzania Raybould (1968) has reported that the species is non-anthropophilic. In Upper Volta Philippon, Sechan *et al.* (1968) considered that *S. damnosum* was mainly zoophilic in certain areas, probably because of the scarcity of man. Crosskey has presented a useful map of Africa showing the distribution of *S. damnosum* and the approximate limits of its man-biting populations (Smith 1973). Additional evidence that this species feeds on animals other than man is provided by the high infection rates that have sometimes been found with filaria other than *O. volvulus* (Duke 1967; Garms & Voelker 1969; Voelker & Garms 1972). De Meillon (1957) lists some of the earlier records of its zoophilic and ornithophilic tendencies, and Fallis (1964) gives a useful review of the natural hosts of Simuliidae.

As a result of the catholic feeding habits of some important onchocerciasis vectors and because of the veterinary importance of several Simuliidae, various methods have been designed to catch blackflies attracted to non-human hosts. The simplest procedure consists of catching blackflies from animals that are not enclosed in cages but are either tethered or free to roam. Sometimes animal baits are visited at intervals to collect in sweep-nets, tubes or aspirators the simuliids attracted to them, alternatively the collector remains with the animal and continually collects from it. A disadvantage of both methods, but especially the latter, is that the presence of the collector may attract blackflies not attracted to the bait animal. Conversely it is possible that the presence of one species of bait may deter the approach and/or biting by flies on the other bait animal. For example, both Vale (1974b) and Hargrove (1976) have shown that the numbers of *Glossina morsitans* attracted to an ox are markedly reduced when man is present. Due to difficulties in interpreting the numbers of flies attracted to bait animals in man's presence Shewell (1955) in Canada made a careful distinction when collecting blackflies attracted to ducklings between those biting the birds and those hovering over them. Also in Canada Jones & Richey (1956) found that although adults of *S. slossonae* and *S. congareenarum,* both ornithophilic species, and *S. jenningsi* which bites cattle, landed and crawled over their clothes and skin, none bit them. In Ghana, however, Crisp (1956) considered the presence of collectors near cattle did not bias the catch; for example 110 *S. damnosum* were collected within an hour from the belly of an ox, but the collectors were rarely bitten. Cattle were considered very useful because *S. damnosum* could be collected from them even when flies were sparse.

In England Davies (1957) collected large numbers of *S. ornatum* with aspirators from untethered cattle. Since the same number seemed to be attracted to cows when a man was collecting as when he was 5 m away, and the fact that no *S. ornatum* landed on the collectors, he concluded that man's presence had little or no effect on the catch. Blackflies landed almost exclusively on a cow's ventral surface and a single collector could collect virtually all of them. A similar distribution of blackflies landing on horses and cows was observed by Guttman (1972) in Colombia, and on reindeer in Russia by Breyev (1950), who also showed experimentally that they concentrated on the undersurfaces in response to reduced illumination. Davies (1957) found that a high proportion of *S. ornatum* landing on the cows departed within less than 10 min, in fact there was a more or less steady stream of flies arriving and departing. The time they spent on the animals decreased as the number of flies landing per unit area increased, that is there was a directly density-dependent phenomenon. Of those that landed it was estimated that only 8–25% bit. In Canada Davies (1952) found that only about 16–25% of *S. venustum* that landed on man actually bit. Also in Canada, Abdelnur (1968) collected various simuliids attracted to horses and cattle, and also aspirated those settling and feeding on birds in their nests.

In Guatemala Giaquinto (1937) conducted host preference studies as long ago as the early 1930s' by exposing simultaneously a man, horse, cow and dog. *S. ochraceum* was the commonest species caught, over 90% of which fed on man in preference to other baits. In Venezuela Lewis & de Aldecoa (1962) collected eight species of blackflies, including *S. exiguum* and *S. metallicum,* from paired baits, comprising a man and donkey or a man and turkey, and in Belize a man and mule. The numbers of *S. exiguum* caught were about equally divided between man and donkey baits, but the catch of *S. metallicum* on donkeys was about one fifth that on man. In Belize only a single *Simulium* was caught on man, but 134 were caught trying to bite a mule. In Colombia blackflies were caught simultaneously from a horse and cow stationed 5–10 m apart in a corral and two men seated on the ground in dense vegetation some 30 m away. Since nearly all the simuliids attracted to the bait animals landed on the belly, a boy seated under each animal could catch all those landing during 20-min periods each hour, from dawn to dusk (Guttman 1972). Catches on human bait were for 30 min every hour. The principal species biting all baits were *S. exiguum* (66%) and *S. metallicum* (32%), *S. callidum* only constituted about 2% of the total collection.

Large cages or traps such as stable traps or bed nets (Service 1976) have rarely been used to catch blackflies attracted to large mammals such as cattle, donkeys or goats, but Wright & DeFoliart (1970a) caught several species in bed net traps in the USA. Twenty species of animal baits, ranging from frogs, snakes, birds, rodents to deer were exposed in Gater-type bed nets, about 6 ft (1·8 m) in length, width and height. The flap-like opening of the bed net gave an entrance about one-third the size of one of the sides (Wright & DeFoliart 1970b). The commonest species caught was *S. meridionale.* Even with small mammals and birds baits have not usually been placed in traps, but exposed in wire cages, and periodically nets or boxes lowered to enclose the blackflies attracted to the baits. In Russia various types of descending nets and large cages have been used to collect blackflies attracted to large animals such as horses and reindeer (Breyev 1950; Ussova 1961). In Australia Myers (1956) using a cord and simple pulley system suspended a cone, 3 ft (0·9 m) high and 3 ft (0·9 m) in basal diameter, covered with marquisette material, over a rabbit pinioned to a base board. At intervals the cone descended and enclosed the rabbit. Blood-fed insects were collected by inserting aspirators through a cloth sleeve sown about half way up the cone. In addition to mosquitoes a few simuliids were caught, but no further details are given.

Some of the earlier attempts to catch simuliids feeding on birds were made in Canada. Bennett (1960) exposed several different bird species in 8- or 12-in (20- or 30-cm) cube cages having the top and sides made of chicken wire or heavy mesh netting (0·5 or 1 in (1·2 or 2·5 cm)), and the bottom covered with 0·5-in (1·2-cm) mesh hardware cloth. Hoods were placed over the heads of birds, except ducks and sparrows, to minimise their movements. Ducks were sufficiently inactive without hoods, and small birds such as sparrows were placed in a chicken wire cylinder to restrict their movements. These cages were positioned on a 2-ft (0·6-m) square white painted plywood board placed on the ground, on a raft in a lake or at heights of 5–25 ft (1·5–7·6 m) in trees, and after a 20–30-min exposure period they were covered with a 2-ft (0·6-m) cube cage of nylon netting. Flies were allowed a further 20–30 min to engorge, after which they were collected by inserting an aspirator through a cloth sleeve in the cage. After a 20–30-min exposure period cages which had been set at various heights in trees were carefully lowered and placed on white boards and covered with netting cages. Many blackflies were caught in these trials, and several showed distinct preferences for habitat and species of birds. For example, in 407 collections over three years 2673 *S. rugglesi* were collected from traps placed on the ground near the lake shore, but only 15 in 18 collections with traps at heights of 15 ft (4·5 m) in trees. Similarly, in 126 catches from traps placed on the forest floor, 237 *S. 'aureum',** 55 *S. decemarticulatum* and 201 *S. 'latipes'** grp. were caught but when birds were exposed at heights of 5–25 ft (1·5–7·6 m) in the forest the catch from 107 collections increased to 1088 *S. 'aureum',* 1050 *S. decemarticulatum* and 1973 *S. 'latipes'* grp. Cages baited with grouse, crows or hawks caught most blackflies, relatively few were caught in cages containing ducks. Khan & Fallis (1970) also used this method of Bennett (1960) to catch blackflies attracted to birds exposed in the tree canopy.

Two simple procedures were used by Anderson & DeFoliart (1961) for trapping blackflies attracted to a variety of wild and domesticated birds. These were confined in wire mesh cages, 24 × 12 × 12 in (61 × 30·5 × 30·5 cm) or 20 × 16 × 12 in (50 × 41 × 30·5 cm), and exposed in various habitats for 30 min, after which they were covered with a cardboard box having windows cut in the sides and top covered with cheesecloth. Cheesecloth sleeves were attached to two opposite ends of the box, and a strip of this material larger than the open bottom of the box was attached along one edge of it. Trapped simuliids flew to the windows of the box, which was lifted up and turned upside down so that the strip of cheesecloth covered the bottom. Flies were then removed with aspirators inserted through the cloth sleeves.

A better arrangement for collecting blackflies feeding on birds confined in wire mesh cages consisted of covering them with a cardboard box strengthened with a wooden frame around the open bottom. The only source of light was through a 5-in (13-cm) square hole cut from the top near a corner. A 6-in (15-cm) square framework covered with cheesecloth at the top and on three sides, and with transparent plastic on the remaining side was secured over the corner opening in the cardboard box. A sliding panel at the bottom of this 6-in (15-cm) collecting cage was partially opened to allow flies to escape into it. After 15 min the sliding panel was closed, the collecting cage replaced with an empty one, and the bird re-exposed for a further 15 min. This procedure allowed baits to be exposed for two 15-min periods each hour.

*Unfortunately references to these two species in North America do not refer to the true *S. aureum* and *S. latipes* as found in Europe, and are therefore given throughout this paper in inverted commas.

Some birds were confined to wire mesh cages fixed to a base board and raised to various heights in trees. After an exposure period a cardboard box and collecting cage sited 2–4 ft (0·6–1·2 m) above the bait was lowered over it. The entire trap was then lowered to the ground. This procedure is a modification of that used by Bennett (1960).

Seven species, including *S. 'aureum', S. johannseni, S. taeniatifrons, S. meridionale* and *S. rugglesi* were collected from these bird-baited traps, and sometimes over 700 blackflies were caught from a trap after a single exposure period. Most ornithophilic species exhibited well-marked habitat and stratification preferences. There were also significant differences in host preferences, although in many cases this seemed more related to host size than any other factor.

In Wisconsin Anderson, Trainer & DeFoliart (1962) used wire mesh cages similar to those used by Anderson & DeFoliart (1961) to expose ducks as sentinels for *Leucocytozoon simondi.* In Colombia Guttman (1972) made several attempts to collect blackflies in this type of cage baited with chickens, rabbits and hamsters, but only five simuliids were caught, consequently the method was abandoned.

Disney (1972) used a simple bait trap in Cameroon for collecting flies attracted to a chicken tethered alongside a river. A bottomless screened cage was suspended over a chicken by tying it to a pivoted wooden beam. The operator retired, but returned after a few minutes, several times each hour, and lowered the cage over the chicken. Entrapped flies were removed through a cloth sleeve in the mesh cage. A total of 526 *S. damnosum,* 787 *S. unicornutum,* 11 *S. kenyae* and 88 unidentified species, probably *S. garmsi* and/or *S. coalitum* were caught in 169 trap-hours. Invariably they were engorged with chicken blood.

In limited numbers of trials in Cameroon Thompson (in press) placed a chicken in a basket, underneath which there was a small fan to suck attracted flies into a small cage. For comparison a sheep had a fan trap tied underneath its abdomen. In the forest the chicken-baited trap caught about 90% of the number of *S. damnosum* caught at human bait, the sheep only about 1%; in savanna areas the chicken attracted only about 6% whereas the sheep attracted about 56% of the flies caught at human bait. These differences may have been due to the existence of different species of the *damnosum* complex inhabiting forest and savanna areas.

In Northern Sudan several hundred *S. griseicolle* were caught by exposing a bait chicken for 10-min periods and then lowering a bottomless wooden box (60 × 40 × 40 cm) with a small glass window (10 × 5 cm) over the bird (El Bashir, Jack & El Hadi 1976). Enclosed blackflies were caught on sticky tree-banding grease smeared on to the inner surface of the window, after 20 min the plate was removed and a new one installed.

In Ghana Crisp (1956) placed a 4-ft (1·2-m) square cage made of 2 mm metal gauze wire over bait animals, such as a hen. There were no entrance slits or cones incorporated in the trap, but small species of blackflies such as *S. adersi* and *S. griseicolle* managed to crawl through the gauze mesh. After feeding on the bait they were too large to escape through the gauze. As many as 98 *S. adersi* were recovered from the cage after a 2-h exposure. *S. damnosum* was not caught as the holes in the mesh were too small to let through even unfed animals.

Also in Ghana Odetoyinbo (1969) caught large numbers of *S. damnosum* attracted to chickens. The procedure involved removing the light tube and baffles of a Monks Wood light trap and bulb of a CDC light trap and placing a chicken with breast feathers removed and wrapped in chicken wire, except for its head and neck, immediately above the mesh screen at the top of the plastic cylinder housing the traps' fan. Traps were operated from 0600–1800 h, and blackflies attracted to the chicken were sucked down by the fan and collected in a nylon mesh cage at the bottom of the traps. A CDC-type trap baited with a chicken was placed near the Red Volta, White Volta and Sisili Rivers for 32, 21 and 15 trap-days during July–September. Totals of 2492, 2799 and 18,797 blackflies were caught in these three traps, of which about 80, 62 and 31% were *S. damnosum.* A Monks Wood modified light trap baited with a chicken was placed for 11 trap-days on the banks of the Red Volta and caught 931 blackflies, some 89% of which were *S. damnosum.* In all traps unfed females predominated, but some 11–24% were recently blood-fed having managed to engorge on the bait before being drawn down into the trap. Gravid females, a few of which had also fed on the chicken, represented 0·1–1·9% of the catch in the CDC-type trap and 13% in the modified Monks Wood trap. These traps were clearly extremely useful in these situations for sampling populations of *S. damnosum* orientated to feeding on chickens. They deserve further evaluation, especially as it seems catches would have been larger if it were not for the fact that some adults escaped through the holes in the mesh collecting bags, and the motor driving the fan in the Monks Wood trap was not operating properly (Odetoyinbo 1969).

In Alberta flocks of 30–40 domestic chickens were placed in a sentinel trap designed principally for catching mosquitoes (Shemanchuk 1969). It consisted of a small wooden chicken shed having an exit trap fitted to the front to catch a sample of the flies leaving the shed after having had the opportunity of feeding on the birds, and an inlet trap to catch some of the flies entering the shed. A run enclosed by chicken wire was provided at the rear of the shed. A total of 1624 blackflies were caught in the entry traps and 1126 in the exit traps, mostly *S. 'aureum'*, but 57 *S. griseum*, 95 *S. meridionale* and a few of another six species were also caught (Shemanchuk & Depner 1971).

Disney (1966) designed a trap for catching Phlebotominae attracted to small rodents that has become widely used for these small insects. Although there are no published references to the trap being useful for Simuliidae, it caught *Simulium* species in Belize (Disney pers. comm. 1974). Basically the trap consists of a bait cage made of wire mesh (size depending on the animal used) placed on a metal tray in the centre of a galvanised metal sheet, about 20 × 20 in (51 × 51 cm), having a 0·33-in (8-mm) high rim bent up around the perimeter. This tray is covered with castor oil. The trap is fixed under a large metal roof (36-in (91-cm) square) to afford protection against rain, and is either suspended from bushes and trees or placed on the ground. In Brazil I have seen large bait cages capable of holding sloths or monkeys surrounded by a number of 20-in (51-cm) square trays coated with castor oil. A modified version of the Disney trap was made by Thatcher (1968) for catching Phlebotominae in Panama. These traps, possibly in a modified form, deserve further evaluation against Simuliidae. One of their advantages is that insects attracted to the baits do not have to fly through various baffles or one-way entrances to arrive at the bait. Also, traps need be visited only every 1 or 2 days. The method, however, depends on insects attracted to the bait animal resting on the castor oil trays either prior to or after feeding. Phlebotomines have a characteristic feeble hopping type of flight and are readily caught in this type of trap, simuliids are stronger fliers, but their behaviour on approaching hosts probably varies according to species.

Most traps catch only a proportion of the haematophagous insects attracted to them because of their restrictive openings, and furthermore usually attract fewer insects than the same bait when not enclosed in a trap. Nevertheless it is considered that there is an overdue need for animal-baited traps to be further evaluated for trapping blackflies. The most appropriate traps may be bed nets for large animals, and suction-type traps for small mammals and birds. Several different types of bed nets have been used in studying mosquito host preferences. For blackflies the best design may be that in which a small door-like panel is removed from one, or possibly two, sides. This allows the bait animal to be seen and should give blackflies easier access than nets having more restrictive openings. It may, however, be found that with this arrangement too many escape. Modified bed nets can also be used to catch blackflies attracted to baits placed at various heights in trees.

There are a few traps in which the bait is not enclosed in a cage, but more or less exposed and freely available to biting flies. At intervals an overhead fan automatically switches on and insects attracted to the bait are sucked into a collecting cage. The chief disadvantage of such traps is that they need electricity, although portable generators can be used. Comprehensive accounts of different types of bed nets and animal-baited suction traps are given by Service (1976).

CARBON DIOXIDE TRAPS

Snoddy & Hays (1966) had little success in catching blackflies in the USA with a New Jersey light trap operated nightly for a year. They found that more blackflies were attracted to a person 'in vigorous exercise' than an inactive person, and that even more were caught if a stream of carbon dioxide was released in his clothing. These observations resulted in an evaluation of carbon dioxide as an attractant for sampling blackflies.

They selected a New Jersey light trap with the bulb removed and its large fan replaced with a small 12-V d.c. fan run from a 12-V car battery. Carbon dioxide was released at a rate of 1 lb (0·45 kg)/h from a 20-lb (9-kg) cylinder and delivered to the underneath of the trap's roof. Females of some 11 species of simuliid, including *Cnephia pecuarum, Prosimulium magnum, S. vittatum, S. venustum, S. tuberosum* and *S. decorum* were caught. Males were not caught. The largest catch was 669 simuliids in an hour, the average was 45/h. A similar trap without carbon dioxide collected very few blackflies. In Lapland Kureck (1969) caught Simuliidae including *S. rostratum* in this type of trap baited with carbon dioxide. In the USA Frommer, Carestia & Vavra (1974) released carbon dioxide from a 20-lb (9-kg) cylinder at the rate of 2 l/min underneath the roof of a CDC battery-operated light trap. With this discharge rate operating from 0900–1800 h cylinders needed replacing about every five days, whereas at the higher discharge rates used by Snoddy & Hays (1966) cylinders would only be expected to last two days. Two traps sited amongst new secondary vegetation caught over a 32-day test period 82,042 simuliids, the mean catch being 1282 blackflies/day. No details are given concerning the species caught. In later trials carbon dioxide from a 20-lb (9-kg) cylinder was discharged via a regulator and flowmeter at rates of 50, 100, 200, 500, 1000, 1500 and 1900 ml/min to seven CDC-type light traps having the light sources removed. After eight nights operation 4808 blackflies were caught, about 46% were *C. mutata* while the remainder consisted of *P. hirtipes* complex.* With a discharge rate of 500 ml/min a mean of 116·9 flies/day were trapped, smaller discharge rates caught significantly fewer adults (24·3–37·8), while little if anything was gained with higher release rates of carbon dioxide (Frommer, Schiefer & Vavra 1976). A control trap without carbon dioxide caught a mean of 0·1 blackflies/day.

In Australia host-seeking *Austrosimulium pestilens* and *A. bancrofti* were caught in carbon dioxide baited tent traps (90 × 90 × 45 cm) which were tied at each corner to sticks or shrubs (Hunter & Moorhouse 1976a). Traps having an internal cloth baffle reaching to the ground caught substantially more blackflies than traps without this baffle. In one series of experiments over 117 days four traps caught > 30,000 female, ten male and one gynandromorph of *A. bancrofti,* but only 195 female *A. pestilens.* Trap location was found to be very important. With *A. pestilens,* but not *A. bancrofti,* more adults were caught in traps placed near rivers than in those away from them and generally more adults were caught in traps placed amongst tall grass, where adults were resting, than in traps placed amongst shorter vegetation or on bare ground. Catches were also influenced by temperature, wind, light intensity and rain. When human baits were also present in the carbon dioxide traps the numbers of *A. bancrofti* caught decreased markedly, this species did not appear to bite man or any of the birds and mammals tested. Man's presence therefore seemed to deter adults entering carbon dioxide baited traps. In contrast *A. pestilens* bit man and many mammals tested, and there were large minute to minute fluctuations in the numbers caught in carbon dioxide tents when man was also present.

In Canada *S. venustum* was caught in considerable numbers on cylindrical, dark blue sticky traps baited with dry ice (Baldwin, Allen & Slater 1966; West, Baldwin & Gomery 1971). In later trials about 15 times as many *Cnephia dacotensis, S. venustum* and *S. furculatum* were caught in this type of sticky trap when a 2·5-lb (1-kg) piece of dry ice was placed on top, than in traps without it (Baldwin, West & Gomery 1975). This sized lump of dry ice ensured the release of gas for about 12 h, but the rate of release depends on environmental conditions, especially temperature. During studies on dispersal of *S. slossonae* tagged with P^{32} approximately 55,560 blackflies were caught over a three-month period on sticky plastic sheeting wrapped around 23 dark shiny blue 50-lb (22·6-kg) lard cans supplied with carbon dioxide from a 50-lb (22·6-kg) block of dry ice placed in a styro-foam box at the base of each trap (Moore & Noblet 1974). Also in Canada Golini & Davies (1971) studied the orientation of *S. venustum* to carbon dioxide. A 26-in (66-cm) diameter bicycle wheel was mounted horizontally on a 12-in (30-cm) diameter wooden disc positioned 3 ft (0·9 m) above the ground. Around the circumference of the wheel were 13 upright wooden dowels, each covered with a test tube coated with Tanglefoot. In a modified trap the sticky test tubes were replaced with an 82-in (2-m) length of 3·25-in (8·2-cm) deep sheet metal band, coated with adhesive and marked off in 24 equal sections. A wind vane clamped 3 ft (0·9 m) above the wheel ensured that the same part of the circumference was pointed in the direction of the wind. Carbon dioxide from a cylinder was released at a rate of 3000 ml/min into the centre of the bicycle wheel. Tests show that *S. venustum* flew upwind towards a source of carbon dioxide, which confirmed the hypothesis of Smith (1966) of an upwind flight of most Simuliidae to carbon dioxide. In Tanzania Fallis & Raybould (1975) also found a mainly upwind orientation by *S. adersi* and either *S. impukane* or a closely related species to carbon dioxide released near small silhouettes (p. 17).

Carbon dioxide gas released from cylinders has been used in Canada in experiments with ether extracts of the uropygial glands from loons and ducks (Bennett, Fallis & Campbell 1972; Fallis & Smith 1964; Fallis, Bennett *et al.* 1967). In nearly all trials fewer Simuliidae were attracted to carbon dioxide on its own than to the loon's uropygial glands, or to the combination of the loon's or duck's gland and carbon dioxide. In Norway sticky traps releasing 100 ml of carbon dioxide in a minute caught substantial numbers of female *S. rendalense* when they were placed immediately above the water surface of the River Renåa, but many fewer when positioned 1·3 and 2·3 m above the water and at ground level 10 m away. The catch was increased four times or more by the addition of extracts from the uropygial glands of domestic ducks, which were acceptable hosts of the species. Gland extracts alone attracted only about one-tenth of the numbers caught in carbon dioxide baited traps (Golini 1975).

*True *P. hirtipes* is a Eurasian species and does not occur in North America. What used to be called *P. hirtipes* until around late 1950s' is a complex of *S. mixtum, S. fuscum* and *S. fontanum.*

In Algonquin Park, Canada, Fallis, Bennett *et al.* (1967) investigated the attractiveness of carbon dioxide by itself and in combination with visual stimuli such as silhouettes to blackflies. In one series of experiments small 'fan traps' were used. These consisted of 4-in (10·2-cm) diameter, 5-in (12·7-cm) long cylinders housing a small 6-V fan which were suspended on the ends of four 12-ft (3·6-m) arms extending at right angles to each other and mounted on a turntable. The traps made one complete revolution every 8 min and insects near the horizontal fan inlets were sucked down into a gauze collecting bag. In some traps carbon dioxide was not emitted and these acted as controls, whereas carbon dioxide was released alongside other traps at rates of 50, 100, 200, 400 and 800 ml/min. Collections were for 16- to 32-min durations. More than 90% of the simuliid catch consisted of *S. venustum.* Many fewer flies were collected in traps without carbon dioxide (0·12 flies/min) than in traps with the gas (1·61–4·83 flies/min). The greater the discharge of gas the greater the numbers caught. Most flies were caught between 0900–1000 and 1700–1800 h. The addition of heat, supplied by hot water bottles placed near the traps, seemed to indicate that a thermal stimulus increased the catch, but difficulties were encountered in standardising the procedure and the effect of heat as a stimulus needs re-evaluation.

In other experiments comparisons were made between the number of blackflies attracted to mannequins resembling humans and coated with Tanglefoot and cylinders, 52-in (132-cm) long and 9-in (23-cm) diameter, covered with black paper, also coated with adhesive. With both types of silhouettes the catch was greatly increased (2·3–33·4 fold) by the addition of carbon dioxide (400 ml/min). When cylinders were supplied with carbon dioxide fewer flies (20–77%) landed on those placed vertically than on those placed horizontally, but the height of the horizontal cylinders was important.

In this paper the author speculated that blackflies may be divisible into four groups based on their response to various host stimuli. One group would include species that are attracted to an odour without the addition of carbon dioxide, although this might increase the catch, at present only one species, *S. euryadminiculum,* is known to belong to this group. The second group would include species such as *S. rugglesi* that are attracted to carbon dioxide alone or in combination with an odour, but not to odour alone. The third group comprises species, such as *S. venustum,* that are attracted to carbon dioxide by itself, although more may possibly be taken when heat is added. In the fourth group visual stimulus is the main attraction not carbon dioxide, examples are *S. equinum* and *S. erythrocephalum.* This classification is undoubtedly a great oversimplification, because too little is known about either the natural or artificial stimuli that attract simuliids for generalisations to be made (but see Bradbury & Bennett 1974b; Smith 1966; Thompson 1976c).

Rivosecchi (1972) describes some interesting work in Italy which showed that the species attracted to carbon dioxide traps was greatly influenced by their position. One of his traps consisted of a small cylinder into which carbon dioxide from a gas cylinder was released at the rate of 100 ml/min, flies were drawn down by a small fan into a collecting bag. When these traps were placed at heights of 4–6 m in trees they caught *'S. latipes meridionale'** and *S. fucense,* both ornithophilic species of blackflies, including *S. salopiense* (= *S. lineatum*), which were not caught by any other heights of 50 cm – 2·5 m in hedges, four other ornithophilic species, including *S. aureum* auct. were caught. When these traps were placed under bushes with a discharge rate of 260 ml gas/min three species of blackflies, including *S. salopiense* (= *S. lineatum*), which were not caught by any other method, were collected. Seven species, including *P. hirtipes,* were caught biting cattle but were never caught in any carbon dioxide traps, while four other species, including *S. equinum* and *S. nitidifrons,* were collected both biting cattle and also in carbon dioxide traps.

Very little effort has been made in Africa to evaluate the effectiveness of carbon dioxide in attracting blackflies, but recently in Upper Volta Bellec (1974) has experimented with the release of carbon dioxide from 80-kg cylinders. In one series of experiments sticky glass plates were suspended at different heights and distances from the source of the gas, while in other experiments a simple fan-type trap placed on the ground caught flies attracted to the gas. Sometimes considerable numbers (122–129) of *S. damnosum* were caught during the day. In other experiments the end of tubing emitting carbon dioxide was tied to the neck of either a black, wooden, human-shaped silhouette coated with adhesive, a cow silhouette, or a black (80 × 80 cm) wooden panel placed either away or near a human bait catcher. In six trials with the human-type silhouette the maximum daytime catches consisted of 68 *S. damnosum,* 27 *S. adersi* and 24 *S. cervicornutum,* in a single trial with the cow silhouette 119 *S. damnosum* and 35 *S. adersi* were caught, and in a single trial 44 *S. damnosum* and 15 *S. adersi* were caught on the black sticky panel. During a two-day

*There are nomenclatural difficulties with this name and it has therefore been placed in inverted commas.

catch 388 *S. damnosum* were caught at human bait and 174 on a nearby human-shaped silhouette having carbon dioxide released near it, while in another trial 103 *S. damnosum* were caught at bait and 67 *S. damnosum* and 5 *S. adersi* on a nearby 80 × 80 cm black sticky panel. In these two trials 30 and 40% of the total catches of *S. damnosum* were trapped on the silhouettes. In comparative trials with two different silhouettes of the same surface area supplied with carbon dioxide, 114 *S. damnosum* were caught on a 200 × 50 cm black panel and 82 *S. damnosum* on a human-shaped silhouette. In all trials with silhouettes only females were caught. Bellec (1974) considered that a suitable silhouette augmented with carbon dioxide would probably catch about half the *S. damnosum* normally attracted to human bait. He concluded that this trapping technique could in many instances complement human bait catches.

In Cameroon Thompson (1976c) found that in forest areas carbon dioxide by itself at an emission of 100–400 ml/min caught on average 2·7–31·3% of the numbers of *S. damnosum* attracted to man; for some reasons results were very variable. He concluded that in the forest a carbon dioxide trap might be effective in raising the efficiency of a trap baited with some sort of human odour, or worn clothing, but in savanna areas of Cameroon carbon dioxide traps would be of little use.

In Ghana Fallis (1968) suspended both white and black mesh cages, each approximately 2-ft (0·6-m) cube and open at the base, about 8–10 in (20–25 cm) above the ground. Carbon dioxide was released at the rate of 100 or 200 ml/min below the cages. In addition carbon dioxide was released below small fan traps. Although blackfly populations were relatively small during these trials a number of *S. adersi* and *S. damnosum* were caught in both types of traps. In later trials in Tanzania Fallis & Raybould (1975) studied the responses of *S. adersi* and a species that was either *S. impukane* or closely related to it to carbon dioxide and visual stimuli. Two 66-cm cube cages with open bottoms were suspended 2 m apart at a height of 30 cm. Carbon dioxide was released at a rate of 100–200 ml/min for 10–15 min through tubing positioned on the ground underneath alternate cages. In 19 collections of 10–15-min periods between 1600–1830 h 182 blackflies were collected in cages supplied with carbon dioxide, but only eight flies were trapped during the same period in the absence of the gas. In other trials carbon dioxide was combined with visual stimuli and considerable numbers of blackflies were caught (see p. 19).

Mosquito workers have baited a variety of different traps with carbon dioxide, such as stable traps, metal cylinders with inverted cones, bed nets, sticky traps, small animal-baited traps, Malaise traps, and also traps designed specifically for use with carbon dioxide, such as the conical trap of DeFoliart & Morris, the conical trap of Thompson, the canopy trap of Catts and the Plexiglass trap (Service 1976). DeFoliart & Morris (1967) reported that blackflies were caught in their traps, which were later redesigned and simplified (DeFoliart 1972). Sometimes carbon dioxide has been added, frequently in the form of dry ice, to various types of light traps (Service 1976), and in many, but not all, instances this has substantially increased the catch of certain mosquito species. More rarely carbon dioxide has been released alongside bait catches to increase the catch (Edman & Lea 1972; Harden & Poolson 1969; Vickery, Meadows & Baughman 1966).

The two common sources of carbon dioxide are cylinders and dry ice. An obvious advantage of using cylinders for releasing carbon dioxide into traps is that the discharge of gas can be set and maintained at predetermined levels, an important consideration if it is suspected that different species are attracted to different emission rates. Uniform release of gas, however, necessitates a sensitive regulatory valve system and meters to control and measure flow rates, and these together with the cylinders, are more costly and bulky than dry ice. These factors can prove a serious disadvantage if several traps are used. Recently there have been indications that some gas cylinders may contain impurities and these may be deterrents to blackflies (D. Marr. pers. comm. 1976). Dry ice on the other hand is relatively cheap and light, although in certain areas it may be more difficult to obtain than cylinders. Despite wrapping dry ice in paper or aluminium foil, or placing it in plastic bags or polystyrene containers, there is little control over the release of gas. The warmer the weather the faster the sublimation and the higher the local concentration of gas, which if excessive may deter some blackflies from entering the traps. Furthermore, host-seeking blackflies are likely to be attracted to warmth, whereas dry ice will usually lower the temperature in the vicinity of the trap.

A relatively cheap, simple and small piece of commercially available laboratory apparatus can be fitted to a gas cylinder to produce small blocks (about 75 mm across and 25 mm thick) of dry ice weighing about 4 oz (113 g). The amount of dry ice produced is approximately half that of the weight of gas in the cylinder. This apparatus enables the rapid production of a number of uniform-sized blocks, which can be made conveniently in the field for immediate use. It overcomes the need to transport large blocks of dry ice to the field for breaking up into irregular lumps. For practical purposes cylinders of more than 7 lb (3 kg) must be used, otherwise the apparatus will not become sufficiently cold for the formation of dry ice. This useful piece of equipment seems to have considerable potential in areas where supplies of dry ice are limited.

VISUAL ATTRACTION TRAPS

Gibbins (1934) reported that female *S. adersi* were caught in tsetse traps made by Chorley and placed on an island in Lake Victoria, Uganda. These traps were of four basic designs (Chorley 1933), but all were essentially visual attraction traps, consisting of dark materials covering a framework and having ventral slits or openings for flies. A few rotated in the wind. Sometimes, fat from cormorants and crocodiles, or extracts from sebaceous and other glands of animals, were added as these substances were attractive to tsetse flies. This overlooked reference probably represents the first published record of blackflies being caught in traps.

In Canada a Manitoba fly trap having a 75-cm diameter black plastic hemisphere suspended about 1 m from the ground under a plastic cone which supported a collecting jar, although designed principally for catching Tabanidae (Thorsteinson, Bracken & Hanec 1965) also collected some simuliids (Peschken 1960). In England, this type of trap with a large plastic beach ball (70 cm) painted glossy black caught Tabanidae, and a few *S. latipes* auct. (Service unpublished). Peschken & Thorsteinson (1965) found significantly more *S. venustum, S. vittatum* and *S. decorum* were attracted to a stationary black cylinder (49 cm in length, 27 cm in diameter) positioned under the conical roof of a Manitoba fly trap than to one rotating freely in the wind. Only about nine blackflies/trap were caught in the traps over 12- or 24-h periods. Sodium cyanide was placed in the collecting bottle at the top of the trap because it increased the catch threefold, probably because in its absence some trapped flies escaped. However, Hocking (1960) and Hocking & Hudson (1974) found that low concentrations of cyanide can be an insect attractant.

In other experiments significantly more blackflies were caught on flat black triangles and squares smeared with Tanglefoot and suspended 0·5 m above the ground, than on flat discs and cardboard figures cut out to represent the forms, X Y and □ (Peschken & Thorsteinson 1965). Several investigators have observed that simuliids appear to be more attracted to the edges or prominent parts of silhouettes than to central areas (Bennett, Fallis & Campbell 1972; Bradbury & Bennett 1974a; Fallis, Bennett *et al.* 1967; Wenk & Schlörer 1963).

Also in Canada Davies (1951) compared the attraction of simuliids, mainly *S. venustum,* to 6-in (15 cm) square cloths coloured dark blue, dark brown, dark green, dark red, black, medium grey and white. A black cloth and a coloured cloth were placed side by side along an observer's outstretched legs. The number of flies landing on the cloths in 2-min periods were counted. Results were expressed as a landing percentage, calculated as the number of flies landing on the coloured cloth expressed as a percentage of the total flies landing on both cloths. The lowest value (7·6%) was recorded for the white cloth, the highest for the dark blue (81·3%) and dark brown (70·5%) cloths. In later studies Davies (1961) used purple, purple-blue, blue, blue-green, green, green-yellow, yellow, yellow-red, red and red-purple cloths. One at a time was placed on a large black cloth which covered the legs of a collector seated on the ground. In 2-min catches the greatest numbers were caught from the purple-blue cloth. In other experiments Davies (1972) used a greater variety of coloured cloths and also coloured papers made according to the Munsell Color System (Nickerson 1948). Landing frequency of *S. venustum* varied inversely with the intensity of reflected light with both neutral shades (white, grey and black) and with colours. When intensity was constant, yellow, green and orange were less attractive than white and much less than maroon, purple or grey of the same intensity. A white material with a low ultraviolet reflectance attracted more *S. venustum* than a similar material with a higher ultraviolet reflectance.

Bradbury & Bennett (1974a) compared the numbers of simuliids landing on two-dimensional silhouettes (squares, rectangles, triangles, stars and circles) coloured white, yellow, red, blue and black and covered with adhesive. Carbon dioxide was released near the targets to provide a general upwind attractant. Adults of *P. mixtum/P. fuscum* complex and *C. mutata* were attracted mostly to black and red silhouettes while *S. venustum* (possible mixed with *S. tuberosum* and *S. verecundum*) was more attracted to blue targets, and *S. vittatum* almost indiscriminately to all colours except yellow. Colours reflecting the least amount of incident light attracted most blackflies. Golini (1970) also found that simuliids landed most frequently on silhouettes with low reflectance. In other trials in Canada Bradbury & Bennett (1974b) concluded that vision, including colour perception, was the most effective factor in close range orientation (0–180 cm) of *S. venustum*, and possibly other species, to silhouettes.

The important paper of Davies (1972) and those of Bradbury & Bennett (1974a, b) contain much important information on the perception of colour by simuliids and their response in the field to colour, shape and carbon dioxide.

In Upper Volta Bellec (1974) constructed silhouettes resembling a heron, a cow and a man, and also wooden panels measuring 60, 80 or 100 cm square. These silhouettes were painted black, red or striped black and red, or black and white, and coated with adhesive. After 25 days exposure, six *S. damnosum* and three *S. adersi* were caught on the human silhouette, 27 *S. damnosum,* eight *S. adersi* and five *S. cervicornutum* on the cow silhouette, 26 *S. damnosum* on the 60 × 60 cm black panels, but only three *S. damnosum* on the black and white striped panels. In other trials black and white painted cylinders were suspended along river banks, but very few blackflies were caught. Bellec (1974) concluded that silhouettes by themselves were of little use in trapping *S. damnosum,* but in combination with carbon dioxide they were the most efficient trapping device he tested. Similarly, in Tanzania Fallis & Raybould (1975) found that silhouettes alone were of little use in catching the ornithophilic species, *S. adersi,* and a species that was either *S. impukane* or closely related to it. For example, no blackflies were caught on round, rectangular or bird-shaped silhouettes made of brown or white cardboard, measuring about 420 cm^2 and coated with Tanglefoot when they were placed 6 m apart at heights of 30, 60, 90 and 150 cm. However, when carbon dioxide was released (100–200 ml/min) on alternate sides of these silhouettes substantial numbers of blackflies were trapped. More flies landed on the lee side (e.g. 3070 on silhouettes at 30 cm) of the carbon dioxide outlets than the windward side (e.g. 854). The largest numbers were caught on the lowest positioned silhouettes (1164) and fewest on those at 150 cm (115). Fallis & Raybould concluded that *S. adersi* and *S. impukane,* and probably *S. vorax,* are attracted to a host by visual stimuli, but only when there is a carbon dioxide gradient. Thompson (1976c) has studied the various stimuli that promote host orientation in *S. damnosum* in savanna and forest areas of the Cameroon (see p. 17).

In Germany Wenk & Schlörer (1963) made a number of ingenious life-like silhouettes from wood and plastic to resemble horses or birds, including a black plastic crow. The head and ears of the horse silhouette could be moved and with birds the wings, tail and head moved. With both live horses and cows and the wooden horse silhouette *S. equinum* and *S. salopiene* (*S. lineatum*) were attracted principally to the ears, whereas *S. erythrocephalum* was attracted mainly to the belly. The ornithophilic species *S. latipes* auct. was not attracted to large silhouettes but to small ones such as those mimicking birds. A bird silhouette trap that remained on the same spot but with the head, tail and wings moving failed to attract *S. latipes* auct. whereas bird silhouettes that were pulled along proved attractive. In Russia Breyev (1950) caught female *S. tuberosum* and *S. pusillum* on simple silhouettes, and Vladimirova & Popapov (1963) caught blackflies in a variety of three dimensional silhouettes in the form of pyramids, cones and rectangles covered with dark blue cloth. More recently Popapov & Bogdanova (1973) caught considerable numbers of blackflies in round and rectangular three dimensional silhouettes covered with black cloths.

In Canada Bennett, Fallis & Campbell (1972) experimented with loon-like decoys and various silhouettes for trapping *S. euryadminiculum.* All silhouettes and decoys were painted with matt polyurethane, smeared with Tanglefoot and baited with ether extracts of the loon's uropygial glands. When these decoys were floated on a lake, more than 70% of the flies were caught on the head of the decoy. There was no significant difference between the numbers caught on free floating decoys and stationary ones. Most flies landed on the leeward side. Other silhouettes, which were placed along the lake margins, consisted of vertical 5-in (13-cm) diameter cylinders, 14 or 26-in (35 or 66-cm) long and made of differently coloured cardboard, a 6-in (15-cm) tall cylinder with a 6-in (15-cm) cross section crudely representing a neck-head-beak silhouette, and differently coloured rectangles (2·5 × 4 in (6 × 10 cm)) which were used in pairs and placed on a flat surface. With the neck-head-beak silhouettes about equal numbers of blackflies landed on those painted red or black, but substantially fewer on the white or yellow silhouettes; many more flies landed on black vertical cylinders than on those painted other colours. With horizontal two dimensional targets surprisingly white was the most favoured colour, and black relatively unattractive. The reason for this was not established, but it was thought that it might be associated with a resting response of *S. euryadminiculum*.

In the USA Hansens, Bosler & Robinson (1971) compared the efficiency of sticky panels, Manitoba fly traps and the Manning trap (Decoster 1968) for trapping Tabanidae. The Manning trap was found to be the best trapping device, and was also easier and cheaper to make than Manitoba traps. Basically it consists of a wooden box 32-in (81-cm) square and 16-in (40-cm) deep elevated about 32 in (81 cm) from the ground on four wooden legs. Flies attracted to the trap pass through an inverted 'V'-shaped mesh baffle having a 1·5 in (4 cm) wide entrance slit situated on the underside of the trap, and are collected in a mesh screen cage mounted on top of the wooden box. This type of trap with the box section painted black or with contrasting black and white stripes, but not white as in the original design, might prove effective for catching simuliids. Somewhat similar traps have in fact been evaluated in Canada and elsewhere for trapping blackflies. For example, in Saskatchewan Fredeen (1961) found silhouette traps useful for catching *S. arcticum.* Three types of trap were made, a large cow silhouette trap, 4 ft (1·2 m) high, 5 ft (1·5 m) long and 2 ft (0·6 m) wide with the underside having an opening 10 ft^2 (0·9 m^2); a sheep type silhouette 1·5 ft (0·4 m) high, 2 ft (0·6 m) long, 1 ft (0·3 m) wide and having a ventral opening 2 ft^2 (0·2 m^2), finally a pyramid silhouette trap, 4·5 ft (1·3 m) high, 3-ft (0·9-m) square at the bottom of the canopy, with an opening of 9 ft^2 (0·8 m^2). All traps stood on four wooden legs with the upper two-thirds and top covered with dark brown plywood or dark blue denim cloth. The undersides remained open. Sunlight was admitted to the otherwise dark interior through a central opening in the top, which was covered with a glass collecting jar having a one-way plastic funnel. Over 97% of the catch consisted of unfed females; very few males, blood-fed and gravid females were caught. Comparative trials showed that the ratio of the numbers of *S. arcticum* caught in the cow, sheep and pyramidal silhouettes traps was 30:1:10; ratios almost identical to those obtained by multiplying trap surface area by the area of the ventral opening. Fredeen (1961) considered that a trap's efficiency was a function of its size and opening, rather than its shape, and that flies were also attracted to the shade provided by the traps. Bellec (1974) found these silhouette-type traps of Fredeen to be of no use in Upper Volta and according to him Walsh and McCrae found them unsatisfactory in Ghana. In Uganda McCrae & Manuma (1967) experimented with 'modified Fredeen traps' but apart from a bad photograph no details of the trap are given. The only blackflies caught in these traps with and without the addition of 2 kg dry ice was *S. adersi.* Results indicated that this species is not attracted to carbon dioxide, but that the traps serve solely as a visual attractant.

In Tanzania Haüsermann (1969) constructed a 'shade trap'. This consisted of a rectangular frame covered with a black cloth with a hole in the centre having a funnel leading to a collecting bottle. During seasons of high population density large numbers of *S. damnosum,* up to 100 a day, and also some adults of three unidentified species were caught; but at other times of the year few flies were trapped by this technique.

LIGHT TRAPS

It is commonly said that insects are attracted to light, but according to Robinson (1952), Verheijen (1960), Hartstack, Hollingsworth & Lindquist (1968) and de Jong (1967) the mechanism may not be that simple. Some insects become disorientated by a point source of light, and while strong fliers (e.g. moths) may have insufficient time to brake and turn away and are thus caught in light traps, weakly flying insects may come within a short distance of the light but be 'repelled at the last minute'. Such insects are rarely caught unless they are sucked into the trap with a fan.

Bowden & Church (1973) postulated the existence of a boundary around a light trap which enclosed the region of influence; beyond this distance the illumination from the light source of a trap is less than natural background illumination. The use of light as an attractant in a trap is more artificial than the use of most other attractants, because light disrupts the insect's normal behaviour. Taylor & Brown (1972) considered that much of the controversy surrounding light traps was semantic, pointing out that whether or not insects were 'attracted' to a light was not relevant for sampling purposes, the catch merely represented a congregation of insects at a point in space. They also pointed out that the volume of influence (commonly called the area of influence) of a trap depends on its design and type of light.

Little is known about the reponse of blackflies to light, but possibly certain species may initially exhibit positive phototaxis and then reaching a certain distance from the light source, varying according to the intensity of the light source, be repelled.

In Pennsylvania Frost (1949) caught 27 male and 133 female simuliids belonging to 11 species in light traps and later mentioned that simuliids were caught in Minnesota type traps (Frost 1954). Fox (1953) caught 753 *S. haematopotum,* 189 *S. quadrivittatum* and 24 *S. wolcotti* (a new species) during 1540 trap nights with two New Jersey light traps.

Peterson (1959) recorded various simuliid species biting during the night in Utah at high altitudes, but most studies have indicated that biting and oviposition cease with the onset of darkness (Davies 1950; Davies 1957), and therefore light traps would not be expected to be very useful in sampling blackflies. However, after Williams & Davies (1957) reported catching large numbers of several *Simulium* species in a Rothamsted light trap (Williams 1948) in Scotland there was some renewed interest in light traps. In Scotland the catch consisted of males, gravid and blood-fed females in addition to unfed females. Ten species were caught including mainly ornithophilic species such as *S. latipes* auct. and *S. aureum* and mammalophilic species such as *S. tuberosum, S. reptans, S. monticola* auct. (= *rheophilum*), *S. variegatum* and *S. ornatum. P. hirtipes* was an abundant local species but only seven specimens were caught in five years of trapping (Davies & Williams 1962).

Davies & Williams (1962) considered light traps were not catching host-seeking adults. Later Williams (1964) showed that only about 21% of blackflies were caught during the first quarter of the night, demonstrating that the traps were not catching only individuals flying just after dusk. In later trials both a Rothamsted light trap with a mercury-vapour bulb, and a 9-in (23-cm) diameter Johnson-Taylor suction trap (Service 1976) sampling 20,000 ft^3 (566 m^3) of air/h and sited with its inlet 1 m from the ground were operated for 36 months. The light trap caught 17,505 blackflies belonging to ten species, including 6468 *S. latipes* auct., whereas the suction trap caught only 693 *S. latipes* auct.

In a mimeographed WHO document Williams & Davies (1966) described and illustrated the Rothamsted light trap, presented modifications for its use in tropical areas, and outlined the case for evaluating light traps for catching simuliid vectors.

Lamontellerie (1963) failed to catch any *S. damnosum* during the dry season in Upper Volta when a 100-W frosted light bulb was suspended over a white tray containing water, although both sexes of *S. adersi* were caught. In later trials the trap was placed about 1–2 m from the ground and operated from sunset for about 5 h nightly (Lamontellerie 1967). From 349 night operations eight or nine species of *Simulium,* usually of both sexes, were caught including 359 *S. adersi,* 182 *S. ruficorne,* and 125 *S. alcocki* (possibly mixed with *S. cervicornutum*), but only eight male and 13 female *S. damnosum.* A certain number of blood-engorged specimens were caught. In Upper Volta Bellec (1974) caught two *S. damnosum* in four nights operation of a New Jersey trap, eight *S. damnosum* and one *S. cervicornutum* in eight nights with a Monks Wood trap and six *S. damnosum* after three nights of placing a 125-W bulb over a dish of water. Bellec (1974) considered light traps unsatisfactory for the local blackflies.

In Ghana a Rothamsted light trap employing a mercury vapour bulb caught few *S. damnosum* (Marr & Lewis 1964), and in the same country only two *S. damnosum* were caught at night by Crisp (1956). Also in Ghana Marr (1971) improvised a light trap, as follows. A 220-V table fan was secured in a 7-litre plastic bucket which had a fluorescent light tube from a Monks Wood trap fixed above. The fan was operated from a 300-W generator and the light tube from a 12-V car battery. From five nights trapping 73 male and 1184 female *S. damnosum,* four male and nine female *S. griseicolle* and eight male and nine female *S. adersi* were caught, a composition that reflected the catches taken earlier in the evening of blackflies resting on vegetation (see p. 29). The largest catch was generally between 1800–1900 h, after which numbers diminished, although there was some flight activity throughout the night. In West Africa Le Berre (1966) caught few blackflies at light in savanna areas, but in the forest about 100 *S. damnosum* were caught.

In northern Nigeria Walsh (1970) constructed a Rothamsted type of light trap using a 12-V car battery and car headlamp unit. Only five *S. damnosum* were caught in 18 nights trapping but this light source may not have been particularly suitable for blackflies. At Amani, Tanzania, preliminary trials showed that a 'quite large number' of male and female simuliids were attracted to a mercury-vapour lamp (Raybould 1966), but no further details were given. Raybould (1969) also observed late one evening large numbers of blackflies attracted to light shining through a window of a house. Within about 30 min 302 flies were collected, 166 of the 259 females were *S. vorax* and of these 152 were recently blood-fed. It was considered that they had probably fed on nearby grazing cows. Other species of *Simulium* caught were not identified.

In the dry season near a breeding site on the White Volta, Ghana 130 male and 172 female *S. damnosum* were caught in 17 trap-nights (1830–0600 h) in a Monks Wood light trap having an ultraviolet fluorescent light tube. Flies were caught during all quarters of the night, though fewer from 0300–0600 h than at other times (J. F. Walsh pers. comm. 1976). Undoubtly the most successful trials with light traps in Africa were studies carried out by Odetoyinbo (1969) in Ghana. In comparative studies he found that Monks Wood light traps with daylight fluorescent tubes were considerably better in catching blackflies than CDC-type traps, despite the former having very inefficient motors. On 27 nights during late August through September a Monks Wood trap placed on the bank of the Red Volta River caught 6325 blackflies, of which about 92% were *S. damnosum.* A CDC miniature light trap, however, operated on ten nights during September caught only 142 blackflies, 89% of which were *S. damnosum.* Males were not caught in either trap. In the Monks Wood trap the catch consisted of about 50·5% unfed, 1·7% blood-fed and 47·8% gravid females, in the CDC trap these percentages were 76·8, 2·8 and 20·4 respectively. On another ten nights a Monks Wood trap was placed in a village 4 miles (6·4 km) from the nearest *Simulium* breeding place. Eighty-seven blackflies were caught, of which 95% were *S. damnosum,* the proportions of unfed, blood-fed and gravid individuals were 40·2, 4·6 and 55·2%.

During five nights' catches at the Red Volta River site the Monks Wood trap caught 82, 247, 47, 475 and 310 (total 1161) *Simulium* from 1800–2400 h, and 130, 20, 293, 521 and 130 (total 1094) adults from 2400–0600 h. The pre-midnight catches on seven nights in the village situated 4 miles (6·4 km) from the nearest larval habitat were 23, 5, 3, 1, 8, 7 and 3 (total 50), and the post-midnight catches were 6, 20, 0, 0, 1, 3 and 1 (total 31) blackflies, mostly *S. damnosum.* These results clearly show that *S. damnosum* can be caught throughout the night, not just as might be suspected in the early hours of dusk. In discussing catches of *Culicoides* spp. in Monks Wood and CDC light traps in Kenya Walker & Boreham (1976) refer to these traps as catching blackflies. Monks Wood light traps have also been useful in England in catching blackflies, predominantly *S. latipes* auct., *S. aureum* and *S. ornatum* (Service unpublished).

Large cumbersome mains electricity-operated light traps developed for catching mosquitoes (Breyev 1958) have also caught a few *Simulium* in the Astrakhan region of Russia (Breyev 1963), and Mazokhin-Porshnyakov (1956) and Grebelskiy, Kovrov & Bychenkova (1963) evaluated the efficiency of ultraviolet lights of different strength for catching blackflies. In Canada Peterson (1959) found two male and many gravid *S. bicornis* and large numbers of gravid and newly emerged nullipars of *S. canonicolum* attracted to neon lights situated about 1 mile (1·6 km) from breeding places. In describing the value of silhouette traps for catching *S. arcticum* Fredeen (1961) mentioned that many more times as many were caught in light traps (type unspecified) than were attracted to the silhouettes. Abdelnur (1968) used an ultraviolet light trap in Canada 4 miles (6·4 km) from a river but caught relatively few simuliids, 91 female *S. venustum,* 49 female *S. decorum,* 36 female and 24 male *S. arcticum* and 18 female '*S. latipes*'.

In Lapland Kureck (1969) caught Simuliidae, mainly *P. ferrugineum* in light traps, but apart from mentioning that the largest numbers were caught between 2000–0200 h no other relevant details are given. In Norway three species of blackflies, including *P. ferrugineum,* and all considered likely to be ornithophilic, were caught flying around outdoor lamps (Raastad & Mehl 1972). In West Bengal, several unidentified *Simulium* species were caught in a portable light trap (type unspecified) using a 500-W light source (Dasgupta, Sharma *et al.* 1969). A later paper reports that 210 blackflies of both sexes and belonging to six species were caught in light traps in West Bengal (Datta & Dasgupta 1974).

Very few trials have been made in Central and South America with light traps for trapping blackflies, but in Venezuela Dalmat (1955) recorded that both sexes were attracted to a Coleman lantern.

Placing light traps near suitable baits, such as in cattle corrals or near groups of birds, etc. merits investigation. Such traps will not have to attract simuliids from far afield but catch them after they have been attracted to the area by the bait. Prevention of feeding, such as placing the baits under bed nets should increase the chance of capture, although this might reduce the numbers attracted to the baits. It is interesting to note that Jones & Richey (1956) caught a few *S. slossonae* in a light trap in the USA when this was placed near turkeys which are important hosts of this species.

A good review of the response of insects to induced lights, with particular emphasis on the physical characteristics of light sources and the factors affecting photosensitivity in insects, is presented in a series of papers published by the U.S. Department of Agriculture (1961). It is clear from these papers that many types of lamps and lights, such as infrared, luminescent plates, flickering and flashing lights etc. await evaluation.

LOON GLANDS

In Quebec, Lowther noticed that hundreds of *S. euryadminiculum* were attracted to recently killed Common Loons (*Gavia immer*), their skins and to a rock over which washings from loon skins had been poured (Lowther & Wood 1964). These findings prompted Fallis & Smith (1964) to experiment with dead loons and extracts from various tissues of their bodies. They found that dead loons attracted hundreds of *S. euryadminiculum,* but very few other *Simulium* species. Blackflies were attracted to loons even when they were concealed from view by being enclosed within screen cages. Most flies settled on the back, neck and head of loons, very few on the breast. It was considered that odour was a long-medium range attractant, but at close quarters there were also important visual responses.

When diethyl ether extracts of macerated muscles from the loon's tail and uropygial glands were poured over paper towelling and allowed to evaporate, large numbers of *S. euryadminiculum* were attracted. A few *S. rugglesi* and some other unidentified *Simulium* spp. were also caught.

S. rugglesi feeds on ducks but neither ether, acetone nor petroleum extracts of their uropygial glands attracted this species, although solvent extracts, particularly ether ones, plus the release of carbon dioxide did. A useful trapping technique consisted of attaching paper impregnated with ether extracts of duck's uropygial glands together with a tube releasing carbon dioxide to a stick protruding 6–8 in (15–20 cm) above the water of a lake. A 2-ft (0·6-m) cube cage of fine plastic netting suspended about 8–12 in (20–30 cm) above the water directly over the extract caught flies attracted to this bait combination. About 20 flies/min (apparently mostly *S. rugglesi*) were caught in the afternoons and evenings. Carbon dioxide alone usually attracted 3 or 4 flies/min, but in one test an average of 20 were caught. Extracts of uropygial glands without the addition of carbon dioxide attracted very few flies (Fallis & Smith 1964).

Many fewer flies were caught in traps baited with either carbon dioxide alone or in combination with ether extracts of the uropygial glands of ducks when traps were placed 10 ft (3·0 m) above the water than in those only 1 ft (0·3 m) over the water (Fallis & Smith 1964). Anderson & DeFoliart (1961) and Bennett (1960) found that several ornithophilic species appeared to be found in rather specific habitats, and that preferences for a particular site may sometimes be more important than host preferences in affecting spatial distribution of blackflies. As in nearly all trapping techniques trap location can be very important in determining the success or failure of traps.

Fallis & Smith (1964) found that blackflies were not attracted to ether extracts of the uropygial glands of the Ruffed Grouse (*Bonasa umbellus*), grackles (*Quiscalus quiscula*) and bantams (*Gallus gallus*). However, considerable numbers of *S. 'latipes', S. quebecense, S. croxtoni, S. 'aureum'* and *P. decemarticulatum* were caught in traps baited with carbon dioxide alone or in combination with uropygial gland extracts from these birds.

In later studies ether extracts of the uropygial glands of loons were placed on filter paper discs and suspended near fan traps (Fallis, Bennett *et al.* 1967); in some experiments carbon dioxide was released from cylinders at the rate of 200 ml/min. In four trials uropygial gland extracts attracted 110 *S. euryadminiculum,* carbon dioxide alone only 35, but when these two attractants were combined 316 flies were caught (Bennett, Fallis & Campbell 1972).

In Norway Golini (1975) found that uropygial gland extracts of domestic ducks attracted few *S. rendalense,* but when added to carbon dioxide traps this increased the catch about fourfold (see p. 15).

STICKY TRAPS

Sticky traps can be divided into two basic types, attractant and non-attractant. Examples of the former are those employing carbon dioxide, a bait animal (Disney 1966) and traps made of a particular colour or shape that attracts insects (e.g. Bellec 1976; Broadbent 1948; Snoddy 1970). With non-attractant traps insects are caught either as they alight or are blown on to the sticky surfaces. Only the former are considered here, the use of non-attractant sticky traps for catching blackflies are described later (pp. 27–28).

A variety of sticky compounds have been used including commercial tree banding resins (Bentley's Tree Grease, Stop Moth, Stickem, Deadline, Tack Trap, etc.), various greases, castor oil and other oils, mixtures of oils and greases, and commercial sticky adhesives, and sticky plastics e.g. rea-plastic. Bird repellents, such as Roost-no-More and Tanglefoot have also been used on sticky insect traps.

It is often difficult to get an adhesive of the correct viscosity and tackiness. If the mixture is too thin it tends to run down the coated surface and get washed off by rain. When the mixture is too thick many insects alighting on the sticky surface are not held and fly off again, only those blown forcibly on the surface being trapped. High temperatures may also cause greases and oils to become fluid.

In Canada West, Baldwin & Gomery (1971) recaptured *S. venustum* labelled with P^{32} on sticky traps which consisted of 50-lb (22·6-kg) lard tins painted dark blue and having six evenly spaced vertical white stripes to make them more visible in densely wooded areas. Plastic sheets smeared with Roost-no-More, and in later trials with Tanglefoot (Baldwin & Gross 1972), were fastened around the cylinders. Traps were suspended at heights of about 1·2 m above the ground from trees or stakes, and inspected every other day and the plastic sheets removed. To determine the rate and direction of dispersal the study area was divided into concentric annuli whose radii were the diameter of the inner circle (in this instance 0·4 km), where tagging and releasing was undertaken. Each annulus was divided into sectors, having areas of the inner circle, thus the first annulus was divided into eight sectors and the four following annuli into 14, 20, 25 and 30 sectors. The trapping area had a radius of 2·2 km and the 97 sticky traps were placed in the middle of each sector on the annuli. Although the traps were successful in catching Simuliidae, increased catches were obtained by placing 1-kg block of dry ice wrapped in several layers of paper towelling on top of each trap (Baldwin & Gross 1972; West, Baldwin & Gomery 1971).

Foot square plywood boards painted dark green and coated with an adhesive (Beacon Bird Repellent) were placed near the base of trees and at heights up to 9·2 m in trees growing up to 106 m away from *S. damnosum* breeding in a spillway in Ghana (Walsh 1972). These sticky boards were inspected daily (except Sunday). Only 129 female, 78 male *S. damnosum,* 21 female, 14 male *S. adersi,* one female *S. ruficorne* and four males and four females of unidentified *Simulium* spp. were caught from 1279 trap-days. Most *S. damnosum* females were nullipars. An average of 0·10 *S. damnosum* were caught on a sticky board placed near the base of the trees. The catch increased with successive heights to reach 0·26 *S. damnosum*/trap/day on boards between 7·5–9·2 m. Results suggest that *S. damnosum* may be resting high up in trees during the day and merit further investigations.

Walsh (1972) found that boards painted dark blue attracted fewer flies than those painted dark green.

During the dry season in Ghana Marr & Lewis (1964) placed castor oil papers at various points in stream beds, alongside a stream near rodent burrows and termite mounds but failed to trap any *Simulium.* Neither were they caught on coloured discs coated with adhesive.

In Upper Volta Bellec (1974) suspended glass plates (100 × 40 cm) coated with equal parts Tween 20 and 95% alcohol at different heights amongst vegetation alongside a river. From two days catches 92 gravid *S. adersi* and 14 female *S. damnosum,* including two gravid individuals, were caught. In other experiments white, pale blue, dark blue, red, green, yellow and orange coloured sticky plastic panels were placed at ground level and at a height of 40 cm amongst vegetation, mainly alongside rivers. On average they caught only 0·8 blackflies/trap/day, and were considered unsatisfactory.

In Ivory Coast Gillon (1967) caught very few blackflies from coloured sticky panels. In contrast Bellec (1976) caught large numbers of simuliids on 1 m^2 aluminium panels coated with equal parts of Tween 20 and 95% alcohol when these were placed on rocks at sites adjacent to streams in Ivory Coast breeding mainly the Soubré (80%), but also the Nile and Sirba cytotypes, of the *S. damnosum* complex. From 57 trap-days 2430 gravid and 19,007 non-gravid females, consisting of some newly emerged but mainly parous females, and 211 males *S. damnosum* and also 145 gravid and 131 non-gravid *S. unicornutum* were caught. No blood-fed females were recovered from these traps. Most *S. damnosum* of both sexes were caught between 1700–1800 h, whereas most female *S. unicornutum* were caught between 0900–1200 h. Only sticky panels placed very near streams caught blackflies, and on these there were large variations between the numbers caught by different traps and also by the same traps on different days (16·7–2117). Usually more *S. damnosum* were caught by these traps than were obtained by human and animal bait collections and by carbon dioxide traps. The parity rate of adults caught on the traps was higher than those caught at bait. It appears that they trapped females mainly just prior to or shortly after oviposition, and that the shiny reflecting surface of the panels was the attractive feature of the trap. The reflectance of lakes and other bodies of water have been noted to be attractive to blackflies in search of oviposition sites (Carlsson 1971). In Canada Golini & Davies (1975a) found that gravid females of *S. verecundum* landed and oviposited preferentially on yellow and green surfaces and least on darker colours such as purple or red. With neutral surfaces, white was the most, and dark grey and black the least, attractive surfaces, attractance varied directly with luminous reflectance. More or less similar results were obtained for gravid *S. vittatum* in Canada (Golini 1974) and *S. ornatum* in Norway (Golini & Davies 1975b).

In Canada Abdelnur (1968) caught a few simuliids, including *S. 'aureum',* on nylon gauze and paper coated with castor oil or Tanglefoot placed near birds' nests and amongst vegetation near breeding sites. In Pakistan Lewis (1973) caught *S. mediterraneum* and *S. stevensoni* on unspecified type of sticky traps. Adults of *S. meridionale* were included among many other insects that were caught on stiff yellow pieces of paper (8 × 10 in (20 × 25 cm)) coated with Tanglefoot and attached to stakes placed in grasslands in the USA (Ahring & Howell 1968).

In Australia Hunter & Moorhouse (1976b) caught *A. bancrofti* and *A. pestilens* on lengths of clear plastic sheeting 30 cm wide and coated with the adhesive Stikem Special. In most trials carbon dioxide, placed at various distances from these sticky sheets, was used as an attractant. The numbers of blackflies caught on coloured cloths and an adjacent white standard overlain with sticky plastic sheeting showed that the relative attractiveness of the different colours decreased as follows — turquoise, pink, white, purple, red, navy blue, black, light green, yellow and gold. It is unclear whether these coloured cloths were exposed alongside carbon dioxide, but I think this probable.

EXIT TRAPS

Window-type exit traps as illustrated by Peterson (1955) have been fitted in Canada to barns containing horses, cattle, pigs or chickens (Downe & Morrison 1957). When population densities were high the traps were emptied in the early morning and also at dusk, but at other times only once daily. Adults of *S. vittatum, S. venustum, S. parnassum, S. decorum, S. tuberosum, S. corbis, S. rugglesi, P. hirtipes* complex* and *C. mutata* were caught.

In Guatemala Dalmat (1950) reported large numbers of flies, mainly *S. ochraceum* but also some *S. metallicum* and *S. callidum,* resting on the muslin cloth used as window screening inside buildings and offices on plantations. These flies bit man inside the buildings. Exit traps might have been useful in collecting simuliids leaving these buildings. Lagraulet (1965) also caught considerable numbers of *S. ochraceum* biting man indoors but in this instance in a completely darkened room. In Canada certain ornithophilic simuliids, such as *S. johannseni* and *S. meridionale,* can be collected in quite large numbers from poultry sheds (Anderson & DeFoliart 1961), and in Australia Hunter & Moorhouse (1976b) collected *A. pestilens* inside buildings. In these situations entry and exit traps might have been useful in trapping those entering and leaving sheds and buildings.

MISCELLANEOUS METHODS

Meat bait and carrion

Davis & James (1957) record the first, and I think only, instance of Simuliidae being attracted to meat. Minced beef with ample quantities of tallow were placed on white paper towelling anchored to the ground. Unrefrigerated meat that had been allowed to age and putrefy seemed more attractive than fresh meat. In one year 881 male and 512 female, and in another year, 42 male and 62 female *S. venustum* were caught in cylindrical screen traps having an inverted funnel at the entrance and supported in a wooden frame over the meat bait.

Anderson & DeFoliart (1961) collected *C. taeniatifrons* from a recently road-killed Ruffed Grouse, but no information was given as to whether the corpse was in a bloody or good condition.

Sugar baits

In Upper Volta Bellec (1974) tried several simple arrangements of various mixtures of orange juice and sugar to attract blackflies on to sticky panels or into traps, but extremely few were collected. The method does not appear to be promising.

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*See nomenclatural note on p. 15.

NON-ATTRACTANT TRAPS

Blackflies are usually caught by using human or animal baits or more occasionally with some other attractant such as carbon dioxide. Even when several species are caught by the same method it is most unlikely that they will be equally attracted, consequently their populations will not be equally sampled. Several non-attractant traps have been used to sample insect populations because of the virtual impossibility of finding one attractant trap that samples all species equally.

Whereas most attractant traps are heavily biased in favour of collecting unfed females orientated to host feeding, non-attractant traps should give more representative samples of both sexes and the different physiological conditions and age groups. However, they sample the aerial population, hence the numbers caught depend not only on their population densities but also on their flight activities. Unfed females usually predominate in catches, mainly because they are usually the most active. Non-attractant traps are unlikely to be completely free from sampling bias although every effort is made to minimise this. For example, the presence of a trap may promote visual responses causing blackflies to be either attracted or repelled.

Non-attractant traps such as Malaise traps, ramp traps, rotary traps, suction traps, sticky traps and vehicle-mounted traps have been used to trap a variety of insects.

Malaise traps

Malaise traps, sometimes baited with carbon dioxide, and thereby becoming attractant traps, have been used to catch mosquitoes (Service 1976 for review), Tabanidae (Blume, Miller *et al.* 1972; Roberts 1972), and less frequently Phlebotominae and Ceratopogonidae (Easton, Price & Graham 1968). Smith, Breeland & Pickard (1965) discussed the value of Malaise traps in medical entomology but made no reference to them catching Simuliidae. In Uganda McCrae (1966) experimented with a 'window tent trap' described later by Herting (1969). This is essentially a modified Malaise trap in which insects are not caught at the top of the trap in killing jars but are collected from the back wall of the trap. McCrae recorded that it collected *S. adersi* (22 females) and *S. damnosum,* and that in one site it 'showed promise as a means of differential sampling of a population of *S. damnosum* which possesses variable biting behaviour'.

It is often assumed that Malaise traps give unbiased collections of flying insects, but probably at least some insects are attracted or repelled by them. In fact the effect of trap colour on catching Tabanidae has been investigated (Roberts 1972). I do not think Malaise traps will prove very useful for catching blackflies, although the type used by Roos (1954) over streams caught some blackflies, and might therefore be useful in studying dispersal of newly emerged and gravid females.

Ramp traps

Ramp traps (Gillies & Wilkes 1972) were devised to study the flight range and direction of mosquitoes attracted to animal baits and carbon dioxide. Mosquitoes flying near the ground are guided up wooden or netting ramps into a collecting cage. Although I do not think they will be of much general use in catching blackflies they might be valuable for trapping blackflies flying towards hosts of oviposition sites, or those dispersing from breeding sites.

Rotary traps

Various designs of rotary traps have been made to collect insects. Basically they consist of two or four conical nets mounted at the ends of horizontal arms with their openings perpendicular to the ground which are rotated at speeds varying from 1–55 rev/min. They operate from mains electricity, or from petrol-driven engines. One model was designed so that water from a stream was directed on to a water-wheel which by a system of pulleys rotated the nets (Davies 1935; Thomas & Vevai 1940). As pointed out by Taylor & Palmer (1972) rotary traps are more difficult to construct than suction traps and have no advantage over them. A water-driven trap, however, might be useful in sampling blackflies near their breeding places.

In Russia Vladimirova & Popapov (1963) suspended different types of traps, but mainly wind-orientated conical mesh nets, up to 150 m by large gas-filled balloons, and considered them especially useful for studying dispersal of insects, including simuliids.

Suction traps

Johnson-Taylor-type suction traps (Service 1976) can probably give the most reliable estimates of relative and absolute population sizes. They can also be used to study vertical distribution, diel flight activities, seasonal incidence and flight direction. Few blackflies will be caught in them when populations are low because they are non-attractant traps, consequently prolonged sampling may be necessary. It is the aerial population that is sampled by suction traps, consequently, the numbers of blackflies caught will depend on their flight activity as well as population size.

In Scotland Williams & Davies (1957) caught substantially fewer blackflies in Johnson-Taylor-type suction traps than in Rothamsted light traps using ultraviolet light, e.g. 221 in October and 87 in November compared with 1360 and 557 caught at light in these trials. In later trials 17,500 blackflies belonging to ten species were caught in a light trap operated from 1955–59, whereas a nearby suction trap operating from 1956–59 caught only 693 blackflies, almost all were female *S. latipes* auct. No simuliids were caught in suction traps during the day (Williams 1965).

In Northern Sudan Johnson-Taylor-type traps with the inlets 150 cm above the ground caught an average of 154 *S. griseicolle* from 1700–1800 h according to table 1 of the paper by El Bashir, Jack & El Hadi (1976), but according to their figure 2 a mean of 173 were caught. The mean numbers caught each hour in suction traps and in vehicle-mounted traps have been interchanged in the table and figures 2 and 3 (see p. 28). However, both these catches are large for non-attractant traps, and there must have been exceptionally large populations of this species in the area.

In Canada Fallis, Bennett *et al.* (1967) constructed what they termed 'fan traps' to catch simuliids, especially *S. venustum,* mainly in trials using carbon dioxide or some other attractant. Functioning without any added stimuli they can be regarded as suction traps. Each trap consisted of a 6-V fan having four 3-in (7·6-cm) blades mounted in a 4-in (10-cm) diameter and 5-in (13-cm) long metal casing. A netting collecting bag was fastened underneath the casing and fan which was mounted vertically so the fan inlet was horizontal. Four traps were suspended at the ends of four 12-ft (3·6-m) arms that extended out at right angles to each other from a turntable. Each trap moved through 90° every 2 min. When they (number not specified) were operated for periods of 16–32-min periods the mean capture rate was 0·12 *Simulium*/min, which represents a catch of about 80–90 flies over 12 h. The addition of 800 ml/min of carbon dioxide to the traps increased the catch to an estimated 3478/12 h.

Sticky traps

Most sticky traps used to sample simuliids have incorporated an attractant such as carbon dioxide, or have been painted various colours to attract blackflies in search of resting sites (pp. 24–25). More occasionally non-attractant sticky traps have been used to sample, by impaction, the aerial population, these are considered here.

Cylindrical sticky traps are more efficient than most flat surfaces in sampling windborne insects because eddies are not produced. The best procedure is not to coat the trap with an adhesive but to apply this to a sheet of paper or plastic which is wrapped around the trap. The sticky surface can be readily removed and replaced with a new one.

In England, three 30-cm long, 15-cm diameter metal cylinders covered with plastic covers coated with tree banding grease were supported horizontally about 5 cm above the water surface of a stream at known communal ovipositing sites. Ovipositing blackflies were caught during their low level (1–5 cm) flights over the water (Davies 1957). A few *S. aureum* were trapped, but the main catch consisted of *S. ornatum,* as many as 368 being caught on three traps within a week. Gravid flies were active only from sunset to dusk, with peak activity between 1900–2000 h, that is when the sun was setting.

In Scandinavia Carlsson (1962) used 1 m^2 transparent plastic cloths dipped in a plastic (rea-plastic) that did not harden for four days, but failed to catch any of the large numbers of *S. ornatum* that had been marked with various stains and released. Similar sticky cloths, but only about 0·5 m^2, were placed across streams with their lower edge on the water surface to study upwind and downwind dispersal. A total of 426 blackflies were caught on traps sampling upstream dispersal and 231 on traps sampling downstream dispersal. Roos (1954) used directional Malaise traps in

Sweden to catch insects flying up and down streams. He caught 18 male and 258 female blackflies dispersing upstream and six males and seven females dispersing downstream.

In Ivory Coast Bellec & Hebrard (1976) placed 100 × 50 cm glass panels, 200 × 30 and 200 × 40 cm transparent plastic sheets covered with equal parts of Tween 20 and 95% alcohol across rivers to act as flight interception traps. Most larvae of the *S. damnosum* complex collected from these streams consisted of the Soubré cytotype (80%), others were Nile and Sirba cytotypes. From 59 trap-days with the glass traps and 32 trap-days with the plastic traps, 8296 *S. damnosum,* 3790 *S. adersi,* 425 *S. unicornutum* and 167 *S. griseicolle* were caught. Females comprised 94–98% of the catch and most (71–91%) were gravid individuals, no blood-fed females were caught. Much larger numbers of blackflies were caught from the plastic than glass traps. By far the majority of blackflies were caught on sticky traps placed just above the water surface (1–30 cm), indicating that flies dispersed over water very close to the surface. Most newly emerged *S. damnosum* and *S. adersi* of both sexes were caught on the downstream side of the sticky traps, whereas most gravid females and older males were caught on the upstream sides of the traps. These interception traps were considered to be non-attractant, unlike the sticky aluminium traps developed by Bellec (1976) (see p. 24), and consequently caught blackflies by impaction as they flew up and down streams. Although this seems a likely assumption, it is nevertheless possible that the traps were not invisible to the flies, and that they served, at least in part, as resting sites.

Vehicle-mounted traps

Several traps have been designed that are fixed on vehicles, usually the roof of a car or van, but occasionally on boats and even bicycles, to catch insects as the vehicle is driven. The usefulness of these traps, and similar ones towed by aeroplanes and ships, has been discussed elsewhere in connection with catching mosquitoes (Service 1976). The best design of a vehicle trap was made specifically for catching blackflies, and is described below.

To study the flight activities and population size of British simuliids Davies & Roberts (1973) designed a trap that can be fitted to a roof rack mounted on a van. The trap has a 91·5-cm wide, 61-cm high entrance which tapers to 10·2-cm diameter at the opposite end. To ensure a smooth air-flow through the trap it is covered with polyester netting having 13·3 meshes/cm, giving about 50% open area. The lower edge of the trap is positioned 23 cm in front of the leading edge of the van's roof so as to minimise the effect of the slip stream of air over the windscreen. The volume of air sampled depends on the van's speed, the cross-sectional area of the trap, and wind speed and direction. An anemometer is fixed in the entrance of the trap to measure the volume of air sampled. Insects collected by the trap are delivered into perspex collecting tubes mounted in a turntable placed in the back of the van, which is rotated by an electric motor connected to the van's 12-V battery and an auxiliary one. At the completion of each kilometre run the driver presses a switch on the van's instrument panel causing the turntable to advance and position a new collecting tube beneath the delivery tube.

The van is driven at 48 km/h. At lower speeds blackflies may not be forced down into the collecting tubes, while at higher speeds a back pressure is set up which prevents a smooth flow of air through the trap.

In Northern Sudan large numbers of *S. griseicolle* were caught in a sweep net held vertically some 150 cm from the ground through an opening in the roof of a car driven at 20 km/h along a 750 m section of road, some 250 m from a river bank (El Bashir, Jack & El Hadi 1976). No further details are given of the catching methods, but according to table 1 in this paper a mean of 173 flies were caught from 1700–1800 h, but according to figures 2 and 3 this is the mean catch of *S. griseicolle* in suction traps (see p. 27), the mean catch in the vehicle-mounted trap being 154.

Vehicle-mounted traps sample only aerial populations of blackflies where they are actually driven, that is those flies flying over the terrain covered by the trap. There will be many situations where it is impossible to trap because of unmotorable conditions, this is one of the biggest disadvantages of these traps. The number of blackflies caught will depend on the time of catching and the blackfly flight times.

OUTDOOR RESTING SITES

Bait catches usually catch only unfed hungry female blackflies in search of blood meals. Traps employing attractants such as carbon dioxide, light or some other visual stimuli, also attract simuliids primarily concerned with host seeking, and, moreover, are usually species selective. Non-attractant traps, such as suction traps, give less biased collections and should sample all species more or less equally. However, they only sample the aerial population.

Most workers' trapping procedures are orientated to catching flying blackflies, but adults probably pass more time resting in natural shelters than in flight. Collections of resting adults should be more representative of the population as a whole than most methods. In addition to unfed females, not all of which may be concerned with blood feeding, males and both blood-fed and gravid females should be caught. The collection of blood-engorged adults is particularly useful for studying host preferences (e.g. Disney & Boreham 1969).

Many have tried to locate outdoor resting populations of Simuliidae, but often with little success (Dalmat 1955; Lamontellerie 1963; Le Berre 1966; Marr & Lewis 1964), but occasionally results have been more encouraging. For example, Hargreaves (1925), Crisp (1956) and Wanson & Henrard (1945) have collected *S. damnosum* resting amongst vegetation. In Guatemala Dalmat (1955) noticed that at night caged adults of *S. metallicum, S. callidum* and *S. ochraceum* rested near the ground at the base of plants, or even at times "slightly beneath the surface", whereas during the day they rested on branches or leaves. Crisp (1956) considered that this sort of night-time niche, which would have a high relative humidity and low temperature, should be attractive to *S. damnosum,* but none were caught when tobacco smoke was blown into rock clefts, tree holes, or holes formed by ants, rats or crocodiles in stream beds. However, on one occasion three *S. damnosum* were collected from deep down near the ground amongst shaded vegetation, but Crisp thought they might have been disturbed from other sites and only recently settled there. Although Wanson (1950) collected some simuliids from a shallow box filled with dead leaves and left outside until the morning, Crisp (1956) failed to collect any blackflies by this method even in areas where *S. damnosum* was abundant.

Disney & Boreham (1969) reported collecting 1135 blackflies in the Sudan savanna of Cameroon resting amongst vegetation along river banks, especially under leaves. Adults were also collected from the underside of tent guy ropes sited 100 m from a river. Two of the 37 *S. damnosum* collected were blood-fed and another two were males, in addition 180 female and 55 male *S. griseicolle* and 380 female and 460 male *S. schoutedeni* were caught. In Guinea savanna areas 56 female and 20 male simuliids, including some *S. damnosum* were caught from vegetation. A few *S. damnosum* were also collected from crab burrows and other small excavations in river banks. *S. damnosum* was not caught from vegetation in forest areas of Cameroon, possibly because of a greater availability of resting sites resulting in a more scattered distribution of adults, thus making them more difficult to find.

In Ghana Marr (1971) collected 4300 *S. damnosum* of both sexes during 16 days collection from vegetation near the Vea Dam. Adults were sufficiently numerous for them to be caught with aspirators, and in the evenings occasionally as many as about 440 were pooted within 30 min from a clump of grass. At other times, despite widespread searches only a few blackflies were caught. Near a spillway and drainage channel adults rested mainly on low grass, but 10–20 m away they rested up to heights of 2–3 m on Guinea corn, millet or bushes, and were found only above 5 m on a tree 37 m from the spillway. Most flies were caught from 1630 h onwards, and until about 1730 h *S. damnosum* consisted mostly of males and newly emerged nullipars, but from then until about 1815 h gravid females predominated. Their appearance coincided with times of oviposition on the spillway. By daybreak all resting blackflies had left these resting places. In addition to *S. damnosum,* 34 female *S. adersi* and four female *S. griseicolle* were collected by Marr (1971). These sites represent temporary resting places for newly emerged adults and gravid females prior to oviposition. Presumably there are other sites, probably further away from the breeding places and more diffuse, where blood-fed and unfed hungry females rest. Encouraged by these results Marr (1971) searched vegetation growing beside the Red Volta and Sisili rivers on five evenings, but collected only six female and four male *S. damnosum* and one female *S. griseicolle.* There was a more extensive growth of vegetation at these sites and consequently probably a more diffuse distribution of adults, thus reducing the chances of collecting them. In Upper Volta 73 female *S. damnosum,* mostly newly emerged unfed individuals but also females that had recently oviposited and one partially blood-fed were collected when trees, bushes and grass along rivers and in forests were sweep-netted (Philippon, Sechan *et al.* 1968).

In the Sudan Lewis (1948) found many male and female *S. griseicolle* resting during the day on corn stalks, but most of them disappeared from these sites at night.

Ussova (1963) considered that for a better understanding of blackfly behaviour it was important to discover where adults rested in between flights orientated to blood feeding, oviposition and swarming. She therefore made a special study of their resting sites. Various types of vegetation were sweep-netted in the Karelian region of Russia and both sexes of *S. reptans, S. truncatum, S. tuberosum, S. morsitans, S. argyreatum* and *S. frigidum* collected. Most adults were located on the underside of leaves and twigs of bushes and trees, more rarely on tree trunks, the most favoured sites were those protected from wind and bright sunlight. The proportion of males decreased with increasing distance from breeding sites. During the day most adults rested on vegetation at heights of 3–10 ft (0·9–3·0 m), but at night they were located as high as 15–22 ft (4·5–6·7 m) in the crowns of trees. Many fewer were found resting in woods of spruce or pine trees. Ussova considered that some species such as *S. argyreatum* may also rest in rodent burrows. More recent investigations in Russia by Patrusheva (1972) showed that nine blackfly species, but predominantly *S. truncatum,* rested in the tops of trees, especially conifers. Adults were also located resting amongst forest leaf litter and in small rodent burrows, and surprisingly in old tunnels made by wood-boring insects.

Dalmat (1955) observed adults of *S. metallicum, S. callidum* and *S. ochraceum* resting on leaves and branches of trees in Venezuela up to a height of 112 ft (34 m). He also found that they bit man at this height as well as at lower ones and at ground level.

In Canada several blackfly species were caught by sweep-netting vegetation, especially *Vaccinium* spp. from which it was believed they derived most of their sugar meals (Davies & Peterson 1956). Wolfe & Peterson (1960) frequently found both sexes of *S. venustum* resting during the daytime on the undersides of leaves of shrubs, and also on the needles of spruce and fir trees. At night, blackflies believed to be *S. venustum* were seen flying up to rest amongst the tops of spruce trees and at dawn descending again. In fact this species was caught when these trees were climbed at night and the branches shaken and the disturbed blackflies sweep-netted. Davies (1961) found that *P. fuscum* also rested on pine needles. He collected adults by beating with a stout net the lower branches of pine trees growing near streams in which the species bred. Nearly all the females were newly emerged individuals. Fredeen, Rempel & Arnason (1951) caught gravid *S. arcticum* by sweep-netting vegetation along the Saskatchewan river. During the day they clung to the undersides of leaves especially those of willow trees, and also to boulders, but at sundown they flew from daytime resting sites and swarmed low over the river and oviposited.

In Australia Mackerras & Mackerras (1948) collected large numbers of *A. pestilens* by sweep-netting vegetation. They rested predominantly on *Melaleuca* bushes, particularly *M. branchiata,* and at times of peak abundance hundreds could be collected from a single sweep. They sheltered on the leaves of these, and other bushes, shortly after emergence and returned to them after blood-feeding. Males, half-gravid and a few gravid females were also caught. Although several other simuliid species were present in the area, relatively few were found resting amongst vegetation. In later studies Hunter & Moorhouse (1976b) caught substantial numbers of *A. pestilens* including blood-fed, half-gravid and gravid females in addition to unfed ones from branches of *Casuarina* and *Eucalyptus* spp. 'Thousands of flies' were caught by sweep-netting grassy vegetation near trees harbouring resting flies. Over 50 flies were collected from a 2-m tall plastic 'Christmas tree' 30 min after it had been placed near *Eucalyptus* trees. In the same area adults of *A. bancrofti* were collected from rocks at the river's edge, from nearby tall grass and during periods of high population density newly emerged and also older adults were caught on hilltop trees, such as *Eucalyptus tesselaris* and *Alphitonia exelsa.*

The main difficulty in sampling resting populations of blackflies is locating day-time and night-time resting sites. Different species probably select different types of resting places, and within a species the resting sites may differ for the different physiological stages. Adults resting amongst vegetation will be afforded less protection against wind, sunlight and desiccation than those sheltering in rodent holes and tree holes, etc. There may therefore be seasonal changes in the selection of resting places, for example an increase in resting in more sheltered sites (e.g. rodent holes) during dry periods. Possibly some of the techniques used to collect mosquitoes may be appropriate for collecting blackflies. The following three methods may be worth evaluating.

The first consists of lowering large mosquito nets suspended within light wooden or metal frames over vegetation. Adults resting amongst the enclosed plants are induced to fly out and settle on the netting by introducing smoke or other irritants such as fine sprays of weak pyrethrum solutions, citronella oil or insect repellents. Instead of trying to collect adults from vegetation with sweep-nets small battery-operated suction sweepers could be used. Basically they consist of a collecting tube that is thrust into vegetation, and a small fan mounted at its rear to draw insects into a collecting bag. Suction sweepers designed by de Freitas, Shope & Causey (1966), Hayes, Kitaguchi & Mann (1967) and J. B. Davies (Service 1976) might prove the most useful. A larger more powerful petrol-driven aspirator (Dietrick 1961), commercially available under the name of D-vac, merits evaluation. The third method might be useful for collecting blackflies resting in trees, and consists of a commercially available smoke bomb (150 g lindane, 30 g DDVP, and other ingredients, weighing in total 600 g) in a holder mounted on a long telescopic metal stick so that the smoke can be directed towards the tops of trees. Insects are anaesthetised or killed and are collected on plastic sheets placed beneath the trees and bushes. In Japan 29,772 Diptera, comprising 8·3% of the total catch of arthropods, were collected from 384 sheets (1 m^2) placed under various trees and bushes (Yamashita & Ishii 1976).

Nectar feeding and swarming

Blackflies can sometimes be caught while visiting flowers for nectar and also when swarming for mating or oviposition. For these reasons brief accounts are presented of nectar feeding and swarming in *S. damnosum*, together with notes on methods that have been used to collect swarming adults of other simuliid species.

Nectar feeding

Lewis (1948) found that in the Sudan both sexes of *S. griseicolle* fed on sugary secretions of date flowers, and in later studies collected *S. damnosum* with pollinia on their mouthparts, nectar in their crops and pollen grains in the gut, good evidence that the species feeds on natural sugars (Lewis 1953). Also in the Sudan Hocking & Hocking (1962) found sugary fluids in the crops of *S. damnosum* attracted to human baits, and one adult of *S. griseicolle* with pollinia, probably of the genus *Ceropegia* or *Caralluma,* attached to the mouthparts. Lewis & Domoney (1966) using thin paper chromatography identified glucose, fructose and sucrose, and also a few other sugars in the crops of 82 *S. damnosum* from Ghana. They also found sugar in the crops of a mixture of nine *S. adersi* and *S. griseicolle.* Lewis (1958) reported that nulliparous *S. damnosum* biting man usually had fed on sugars first.

The sugary secretions in the crops and stomachs of wild-caught simuliids in Africa are typically clear, but greenish-yellow sugary fluids have occasionally been found. In Cameroon Disney (1970a) never observed *S. damnosum* visiting flowers, and stated that the times of sugar feeding by this species and its natural sources of sugar remain unknown. However, in Ghana Marr (1971) caught large numbers of *S. damnosum* resting in the early evenings amongst vegetation near a spillway, and observed males and parous and nulliparous females feeding avidly on plant juices.

Sugar feeding by blackflies on flower and other natural sweet secretions has been reviewed by Bequaert (1934), Hocking (1953), Davies & Peterson (1956) and Downes (1958).

Swarming

In savanna areas of Cameroon Le Berre & Wenk (1966) sighted swarms of male *S. damnosum,* but failed to find similar swarms in the forests, although Disney (1970b) observed diffuse swarming in the forest by this vector some 2–4m above the road under a tree between 1700–1900 h. *S. alcocki* was also seen swarming at Kumba. By using swarm markers previously employed by Wenk (1965), such as large black squares mounted on poles which are held vertically or horizontally to the ground Le Berre & Wenk (1966) observed a few swarms of *S. damnosum* up to 50 m from larval habitats.

In the Sudan, Gassouma (1972) observed swarms of male *S. damnosum* forming from 1000 h onwards under branches of trees, over bushes and shrubs, above the heads of people and other markers. Such swarms were widespread and around sunset they built up to about 200–300 individuals. Mating occurred in the swarms and copulating pairs fell to the ground for a fraction of a second then separated. Mating was not restricted to the evening as found by Le Berre & Wenk (1966), although its incidence at this time increased. Placing a white sheet under a swarm to collect adults falling to the ground caused a thinning out of the swarm. Nevertheless at the peak of the *S. damnosum* season up to 120 mated couples/h could be collected from the sheet. Blood-fed individuals were also present in the swarm.

In Germany Wenk (1965) caught swarms of male *S. equinum, S. salopiense* (= *S. lineatum*) and *S. erythrocephalum* and associated females by placing horizontal black squares (20 × 20 –

100 × 100 cm) on posts at heights of about 1·5–2 m. Swarms were also seen forming over, or under, tree branches. Males appeared to be attracted from a considerable distance and usually swarmed underneath the black markers and contrasting bright sky. Both sexes were caught in sweep-nets and by placing paper smeared with adhesive below a marker. Males and females were also attracted to a tethered horse, which served more as a marker than a host. Adults were caught either in small hand-nets as they swarmed around the horse or as copulating adults falling onto a white sheet spread over the ground near the horse.

In Australia mating swarms of *A. pestilens* formed during the day-time over bushes of *Callistemon viminalis* growing along the banks of a stream. Swarming ceased at dusk and flies were found resting amongst grass. Copulating pairs were caught on a white 3 × 1 m cloth placed on the ground alongside bushes (Mackerras & Mackerras 1948). A swarm of females observed during the day flying low over a stream, consisted mostly of gravid and ovipositing individuals. Interesting details concerning swarms of both sexes of *A. pestilens* over *Eucalyptus* and *Acacia* trees alongside rivers are given by Hunter & Moorhouse (1976b). No coupling pairs were recovered from a cloth placed on the ground near swarms.

Peterson (1959) observed low level flights of gravid *S. arcticum* over streams in Canada, and simultaneously slightly higher level swarms of thousands of both sexes. Males mate in flight with gravid individuals just prior to them ovipositing; similar behaviour has been observed in *S. decorum* (Davies & Peterson 1956). In Canada Corbet (1967) caught some gravid *Simulium*, which were flying close to the water, in partially submerged traps (see below).

At least under certain circumstances *S. damnosum* has communal oviposition sites such as twigs and leaves in turbulent waters at specific sites (Marr 1962; Muirhead-Thomson 1956), it might therefore be possible to use this type of aggregation behaviour to trap ovipositing adults, as done with *S. ornatum* in Britain (Davies 1957).

Davies & Peterson (1956) give many references to mating swarms in blackflies.

EMERGENCE TRAPS

There are basically two broad categories of aquatic emergence traps. Those such as funnel traps which are completely submerged in the water and those that are either positioned on the water surface or are only partially submerged. Only the latter type of traps have been used to sample simulliids, and then only infrequently.

A number of simuliids were caught on the St. Laurence River, Quebec in conical traps somewhat similar to those described by Mundie (1956) and designed to catch Trichoptera (Corbet 1966). Each trap consisted of three styrofoam floats attached to a basal plywood ring which supported a conical mesh cage having a glass collecting bottle. The rim of the trap was 8–10 cm below the water surface. To catch insects that had not yet flown into the collecting jar a circle of mesh netting supported on a wooden wing was placed under a trap. Traps were fixed to a wooden beam to stabilise them and to guy ropes stretching to the river bank. At approximately 4-h intervals the trap was pulled to the bank and emptied. About 76% of the *S. venustum* collected in these traps had mature eggs in their ovaries, while the remainder were newly parous and thus considered to have recently oviposited. This trap was clearly not catching emerging individuals but ovipositing females. A somewhat similar trap, which might be of use for catching Simuliidae, was described and illustrated by Mundie (1956). It consists of a three-sided pyramid made from heavy metal framework, with two sides covered mainly in Perspex plastic and the other with fine mesh. It was securely fastened into position with wire and remained in place even in spates when the trap was completely submerged. Insects were caught in a glass jar containing a one-way plastic funnel fitted to the top of the trap.

More useful emergence traps for Simuliidae are the box-types that either rest on or near the bottom of streams (Ide 1940; Sprules 1947), or have the lower parts submerged and are securely fixed in position. Davies & Syme (1958) caught emerging adults of *P. mixtum, P. fuscum* and *P. fontanum* in 1-ft (0·3-m) cube screened cages of the type developed by Ide (1940) and which were placed on the bottom of streams in Algonquin Park, Ontario. Similar cages were used by Hocking & Richards (1952) in Canada. Two cages trapping for 22 days caught 253 male and 178 female *P. hirtipes* complex* and a few other blackfly species. Tarshis (1973) also used box-like emergence traps resting on the bottom of streams in Algonquin Park to catch emerging *S. ornithophilum.*

*See nomenclatural note on p. 15.

Sommerman, Sailer & Esselbaugh (1955) designed a trap to catch specifically blackflies. It consists of a 2-ft (0·6-m) cube wooden bottomless box with two of the opposite sides extending 4 in (10 cm) at the bottom. The only light entering is through a glass jar inserted into a hole cut from one of the sides near the top. A small quantity of 70% alcohol in the jar, which is tilted slightly downwards, drowns and preserves the catch. The trap is positioned in a stream with the extended sides parallel to the flow of water. The trap is held in position by guy ropes or by placing heavy objects, such as rocks, on top of it.

In Ghana Thompson, Walsh & Walsh (1972) caught emerging blackflies in a cage supported over wooden sticks introduced into a stream as artificial oviposition sites and attachment sites for larvae and pupae. The cage consisted of a wooden frame about 2 m long and 1 m in width and height, with legs extended to rest on the stream bottom. The top was made of plywood, and the sides of one half were covered with cloth and on the other by mosquito netting. The cloth sides gave some protection against the sun, and also resulted in concentrating the flies at the other end of the cage thus making their collection in the morning easier. A simple cloth door suspended from the top allowed a person to enter and stand in the cage to remove the flies.

A trap that has been used to collect emerging mosquitoes and one that might prove useful for collecting blackflies, is made from 1-in (2·5-cm) tubular metal framework, covered with plastic mesh netting reinforced at the corners with canvas. A heavy duty zip fastener is sewn into one of the vertical edges to allow a collector to enter. It is easily dismantled and reassembled (Service 1976). In shallow waters the bottom edges of the framework could be held in position by pitons hammered into the stream bed, while in deeper waters guy ropes at the corners and fastened to stakes on the bank should be capable of holding the trap in position.

Recently Chandler & Highton (1975) found that a modified CDC-type light trap having a 3·8-V torch bulb and small fan operating from a 12-V car battery caught large numbers of newly emerged mosquitoes when the trap opening was placed about 10 cm above breeding places. This or a similar trap, possibly employing a fluorescent light tube, might be worthwhile evaluating for Simuliidae.

MARK-RECAPTURE TECHNIQUES FOR DISPERSAL STUDIES

The first person to study blackfly dispersal by marking adults, releasing them and then recapturing them was Dalmat (1950). In Guatemala he marked and released 9931 *S. metallicum,* 8675 *S. ochraceum* and 974 *S. callidum* by dusting them with a mixture of 1 part Safranin-Bluish, an aniline dye, and 9 parts flour. Nine marked *S. ochraceum,* eight *S. metallicum* and four *S. callidum* were recaptured 2·1–7·4 km away. Marked flies were detected by placing them in a solution of 3 parts absolute ethyl alcohol, 2 parts glycerine and 1 part chloroform. In later studies (Dalmat 1952) 60,377 *S. metallicum,* 3574 *S. ochraceum* and 2593 *S. callidum* were marked with Carmine and released. Thirty *S. metallicum* and one *S. ochraceum* were recaptured in bait catches 1·0–9·7 miles (1·6–15·6 km) from the release points. In another experiment, the first on longevity of blackflies by mark-recapture techniques, 40,083 flies were marked with six different coloured aniline dyes, each dye being used for two consecutive days. Recapture collections were started three days after the last release. Fifty-four *S. metallicum,* 29 *S. ochraceum* and eight *S. callidum* were recaught, the first being caught on the third day after release and the last after 85 days.

In other experiments using aniline dyes one *S. metallicum* was discovered to have flown 9·7 miles (15·6 km) from the release point, one *S. ochraceum* 2·9 miles (4·6 km) in 2 or 3 days and one *S. callidum* 2·7 (4·3 km) miles in 3 or 4 days (Dalmat & Gibson 1952).

The first study on blackfly dispersal using radionuclides was by Fredeen, Spinks *et al.* (1953). Larvae were kept for 24 h in a solution containing 0·2 μ Ci/ml P^{32} to produce labelled adults. In one experiment in Saskatchewan about 500,000 tagged larvae of *S. luggeri, S. venustum* and *S. vittatum* were released into a stream. Subsequently some 6000 adults were caught by sweep-netting vegetation and around herds of livestock and in light traps, but none was radioactive. Similarly, in another experiment over 300,000 tagged larvae, mainly of *S. luggeri* and *S. venustum,* were returned to the river, but only a single tagged *S. venustum,* a female, was recaught, at a house 100 yd (91·4 m) from the release site.

In Canada West, Baldwin & Gomery (1971) marked adults of *S. venustum* by placing larvae and pupae in water containing 1·9 μCi/ml P^{32} for 2 h, after which they were returned to a river to complete development and emergence. Adults were caught on sticky plastic sheets wrapped around cylinders. On removal to the laboratory these sticky sheets were covered with Saran Wrap and with X-ray film retained in its protective envelope. This autoradiographic technique (Baldwin, Allen & Slater 1966) proved very sensitive. Flies caught up to a week after labelling were kept in contact with the film for three days, but the exposure period was increased for flies caught after longer intervals, reaching ten-day exposures for flies caught four weeks after tagging. Of some estimated 18 million flies tagged 5511 were recaught, some on the furthest sticky traps, which were 35·8 km from the release and emergence site.

Bennett (1963) labelled *S. rugglesi* with P^{32} by feeding them on ducks injected intraperitoneally with 0·5 or 0·25 mCi of radionuclide. After 7·5 days the radionuclide level in the blood of the ducks was about one-third that present 1·5 h after the injections. Radioactive birds were exposed for several days in the type of cages devised by Bennett (1960) to allow natural blackfly populations to feed on the birds and become radioactive. Adults were caught feeding on unlabelled birds placed in similar cages. A total of 503 labelled and 3747 unlabelled flies were caught in these traps, the furthest marked fly was caught 2 miles (3·2 km) away over land and 5 miles (8 km) away as measured over water routes. The large recapture rate was interpreted as indicating a relatively small population of *S. rugglesi.*

An estimated 94,000 *S. euryadminiculum* adults were marked by letting wild caught flies imbibe a solution containing 1 mCi of P^{32}/50 ml water. About 127,000 flies were caught in the 'fan traps' of Fallis, Bennett *et al.* (1967), and this included 204 marked flies recaught within a 1·5 miles (2·4 km), four within 4 miles (6·4 km) and two within 5 miles (8 km) of the release sites (Bennett & Fallis 1971). Moore & Noblet (1974) tagged *S. slossonae* by feeding them on turkeys injected intraperitoneally with about 0·81–1·17 mCi P^{32}/lb body weight, and found that 96% of the 206 recaptures in carbon dioxide traps were within 4 miles (6·4 km) of the release point. Only four flies travelled 6 miles (9·6 km) and three 8 miles (12·8 km). Recently Baldwin, West & Gomery (1975) marked approximately 18 million *C. dacotensis, S. venustum* and *S. furculatum* by placing larvae collected from streams in Ontario in tubs containing about 1·2 μ Ci/ml of P^{32}. After 2 h exposure larvae were placed in a river for completion of development and adult emergence. Adults were caught on cylindrical sticky traps painted dark blue and having six white stripes, as used in earlier studies (West, Baldwin & Gomery 1971). About 2·5 lb (1 kg) of dry ice wrapped in paper towelling was placed on top of about half of the 223 traps. Autoradiographic techniques were used to identify tagged adults; blackflies with counts as low as 10–20 ct/min above background noise were detectable. A total of 5529 tagged flies were recovered representing a recapture rate of about 0·031%. A few were caught as far as 22 miles (35·4 km) away, but about 90% were recaught within 10 miles (16 km). A few crossed the Ottawa River, which is at least 1 mile (1·6 km) wide at the point nearest the release site. Traps baited with carbon dioxide caught about 15 times as many blackflies as those without this attractant.

In Ghana 3886 *S. damnosum* collected from emergence traps or in bait catches were marked with aniline dyes mixed with flour, and released (Crisp 1956). Three flies caught 12·8 km away were placed together in a single tube. When examined later although all were found to be marked, it was considered likely that this represented the recapture of only a single marked fly, the other two having become marked accidentally by being confined in the tube with the marked one. Also in Ghana Noamesi (1966) carried out mark-recapture experiments to determine the flight range of *S. damnosum.* In one experiment only 13 newly emerged flies were marked with amaranth broine, a red dust, yet among 1026 *S. damnosum* caught in bait catches four were marked. Moreover, they were caught four months after marking and about 83 km away. Another marked *S. damnosum* was recaught 4·5 months after marking about 114 km away. In further experiments some of the 19,635 *S. damnosum* caught at bait were marked with gold or silver dusts or with amaranth broine. Among 27,422 flies caught in bait catches four were marked and were caught 74 and 96 km away as measured along the river courses from the release point. These are remarkable recaptures, and I have reservation in accepting them.

Disney (1970b) marked newly emerged *S. damnosum* in Cameroon by spraying them with phenolphthalein in acetone (Peffly & LaBrecque 1956). For detection, caught flies were tipped on to filter paper that had been soaked in dilute sodium hydroxide solution containing a liquid detergent. Marked flies stained the paper and themselves a vivid purple. Recapture rates ranged from about 0·5–2·4%.

In Tanzania batches of 25 *S. damnosum* caught during human bait catches were placed in a cylinder, and carefully sprayed for 1 s with Sparvar spraypaint. Of 33,430 *S. damnosum* marked and released 312 were recaught within 9 days in bait catches performed up to 5 km from the release point, a distance that was covered by some flies in not more than 6 h. Another marked fly was caught 3·5 km away only 9·25 h after marking and release (Haüsermann 1969).

In Ghana Thompson, Walsh & Walsh (1972) marked *S. damnosum* caught in emergence cages with a mixture of 1 part Sudan III and 7 parts flour. Flies caught at bait suspected of being marked were placed between two strips of chromatography paper and a drop of acetone placed on top of each covered fly. A red halo appeared if the fly was marked with Sudan III. Out of 62,726 marked and released flies only a single marked *S. damnosum* was recaught 12 days later, having flown at least 17 km. The very low recapture rate may have been partly due to the apparently ill chosen catching sites near the release points, at which very few *S. damnosum* were caught. A very few flies showed discreet red marks on their wings and gave reddish colouration on the application of acetone. However, examination showed that there were no fine dye particles on these flies, the red colouration being due to fungal infections. In later studies in Cameroon unfed *S. damnosum* caught at bait were marked with Dayglo powders, released and recaptured over 6–7 days after marking at seven sites along a large river, ranging from 200 m to 79 km from the release point (Thompson 1976b). Marking was achieved by placing about 100 flies in an 300 ml Erlenmeyer flask that had the sides coated with Dayglo powder, and rotating it for about 30 s. Marked recaptured flies were detected by placing them on a sheet of aluminium foil painted with backboard paint and placing them under ultraviolet light. Marked individuals were also rechecked with acetone. Green and blue pigments were unsatisfactory as they could not be readily distinguished from green fluids exuded by the flies, and furthermore debris on the flies also appeared blue under ultraviolet light. Marked flies were recaptured at all seven sites. The ratios of the number of marked flies caught per man-hour at each recapture site to the recaptures per man-hour at the release site gave what was termed the 'proportional biting density'. This declined logarithmically with increasing distance from the release site. In one experiment (Kobe River) 30,000 *S. damnosum* were marked and 1·107% were recaptured, in another experiment (Ngengo River) only 1080 flies were marked and the recapture rate was 3·89%.

In other studies in the rain forest of Cameroon to determine the interval between successive blood meals of *S. damnosum* 25,084 flies were marked on the mesonotum with different coloured oil paints and released after they had fed on human baits. The recapture rate was 1·14%. In similar experiments in the Sudan-savanna 929 blood-fed females were released, but the recapture rate at bait was only 0·32%. Thompson (1976a) considered that this might have been due to a higher degree of zoophily of *S. damnosum* in the savanna region. Large unexplained variations occurred between recapture rates of flies marked in different experiments, and for some reason the recapture rate of flies marked with yellow or orange paints was consistently smaller.

In Scandinavia Carlsson (1962) marked large numbers of *S. ornatum* with Malachite Green solutions. Attempts were made to recapture marked flies by sweep-netting vegetation and by placing directional entrance traps and sticky plastic panels close to the water over rivers, but none was caught.

A useful summary of published information on the flight ranges of various Simuliidae has been presented by Le Berre (1966).

Many of the methods for marking insects with stains, dust, powders, paints and radionuclides and the techniques for detecting recaptured individuals are reviewed elsewhere (Service 1976).

CONCLUSIONS

The choice of trapping methods to be used, or further evaluated, will depend on the type of information required. Clearly different sampling techniques are required to estimate the degree of fly-man contact in epidemiological studies, to monitor seasonal changes in relative population size, to evaluate the effectiveness of control schemes and to measure the direction and intensity of adult dispersal, etc. I think a number of trapping techniques merit further investigation, especially animal-baited bed nets, carbon dioxide traps and light traps, and suction traps and non-attractant sticky traps for measuring dispersal. Not all simuliid species will respond the same way to different traps and stimuli, consequently experiments with one species leading to the discovery of an efficient trapping mechanism may have a limited application. It is also unlikely that all species within the *S. damnosum* complex will react the same towards any trapping device, furthermore there may be variations in the efficiency of traps according to season and habitat.

Within recent years several traps have been developed for agricultural pests, mainly Lepidoptera and Coleoptera, which are baited with aphrodisiac lures (Birch 1974; *Environmental Entomology,* 1972 onwards). Sex pheromones have been discovered in a few Diptera, including some medically important ones such as tsetse flies (Langley, Pimly & Carlson 1975), *Musca domestica* (Carlson, Mayer *et al.* 1971) and *M. autumnalis* (Uebel, Sonnet *et al.* 1975), but they are weakly active substances having very short-range effectiveness. Although sex and/or aggregation pheromones may exist in simuliids it seems unlikely that they will be sufficiently powerful to be usefully employed as attractants in traps. A more rewarding investigation might be to try and identify the factors responsible for attracting simuliids to their hosts, with the aim of isolating any attractants (kairomones) and incorporating them in traps.

SUMMARY

A critical review is presented of the many methods that have been employed in various parts of the world to sample adult populations of Simuliidae. Because of the great importance of members of the *Simulium damnosum* complex as vectors of onchocerciasis in Africa, and the resources and manpower being put into their control in the Volta River Basin of West Africa, particular attention has been focussed on the many problems of trapping adults of this complex. Descriptive accounts are given of the different techniques employed in human bait catches and the difficulties of interpreting the results in terms of natural fly-man contact and the epidemiology of onchocerciasis. Methods for estimating man-biting rates and comparing transmission potentials are analysed. The different methods for trapping blackflies attracted to various bait animals both outside and inside traps are evaluated. The limitations of using more biased sampling methods, such as traps baited with carbon dioxide and lights of different intensities and spectral emissions are discussed. The usefulness of visual attraction traps, including silhouettes that are made to simulate natural hosts, are evaluated. In addition, the value of a variety of other trapping devices, such as exit traps fitted to animal houses, sticky traps, and traps incorporating miscellaneous attractants such as sugar baits, carrion and extracts from the uropygial glands of the Common Loon (*Gavia immer*) are assessed.

It is emphasised that no attractant trap is able to sample all blackfly species with equal efficiency, nor even all age groups and physiological categories of a single species. For these, and other reasons, non-attractant traps, such as Malaise traps, ramp traps, rotary traps, suction traps, sticky traps and vehicle-mounted traps have been employed to catch blackflies. Unlike the other traps, vehicle-mounted ones do not catch adults at a single site but along a transect.

Methods for catching simuliids engaged in the pursuit of nectar feeding and those orientated to swarming are described, and also the use of emergence traps placed over larval habitats to sample newly emerged individuals and sticky traps placed across rivers to catch gravid females returning to oviposit. The choice of sampling methods depends much on the type and quality of information required.

In addition to the above methods for trapping various elements of the aerial population of blackflies, the techniques that have been tried to sample non-flying adults resting amongst vegetation and other natural sites are described. The procedures that have been devised to mark adults with stains, dyes, paints and radionuclides and the techniques used to recapture and detect marked adults in order to measure rates of dispersal are described and assessed.

Finally, the trapping techniques that appear to merit further evaluation are enumerated.

RÉSUMÉ

On présente un examen critique des nombreuses méthodes qui ont été employées dans différentes parties du monde pour échantillonner les populations adultes de Simuliidae. Etant donné la grande importance des membres du groupe *Simulium damnosum* comme vecteurs de l'onchocercose en Afrique, et les ressources et le personnel employés pour lutter contre ces insectes dans le bassin de la Volta en Afrique de l'Ouest, on s'est concentré surtout sur les nombreux problèmes posés par la capture des adultes de ce groupe. Les différentes techniques de capture utilisant des appâts humains sont décrites et on indique les difficultés d'interprétation des résultats en fonction du contact naturel simulie-homme et de l'épidémiologie de l'onchocercose. Des méthodes d'estimation du taux de morsure chez l'homme et de comparaison des potentiels de transmission sont analysées. On évalue les différentes méthodes de capture des simulies attirées par divers animaux utilisés comme appâts placés à l'extérieur et à l'intérieur des pièges. Les limites d'utilisation de méthodes d'échantillonnage ayant un biais plus important, notamment pièges appâtés à l'anhydride carbonique et lumières d'intensités et d'émissions spectrales diverses sont discutées. On évalue l'utilité de pièges à attraction visuelle, notamment de silhouettes ayant l'apparence des hôtes naturels. On estime en outre la valeur de toute une gamme d'autres dispositifs de capture, pièges montés sur les bâtiments abritant des animaux pour la capture des insectes en sortant, pièges gluants, pièges contenant différentes substances attractives, sucre, charogne, extraits de glandes uropygiennes de plongeon imbrin (*Gavia immer*) entre autres.

On souligne qu'aucun piège appâté ne peut échantillonner avec une efficacité égale toutes les espèces de simulies ni même tous les groupes d'âge et toutes les catégories physiologiques d'une seule espèce. Pour ces raisons, et pour d'autres, des pièges sans appâts, pièges Malaise, à rampe, rotatifs, à aspiration, gluants et montés sur véhicules ont été employés pour capturer les simulies. Contrairement aux autres pièges, ceux qui sont montés sur véhicules ne capturent pas les insectes en un site unique mais le long d'une ligne d'échantillonnage.

On décrit des méthodes de capture des simuliidés en train de se nourrir de nectar et en train d'essaimer, ainsi que l'utilisation de pièges d'émergence, placés au-dessus des habitats larvaires pour échantillonner les adultes qui viennent d'émerger, et de pièges gluants, placés en travers des rivières pour capturer les femelles gravides qui reviennent pour pondre. Le choix des méthodes d'échantillonnage dépend beaucoup du type et de la qualité des informations requises.

En plus des méthodes sus-mentionnées pour la capture des différents éléments des populations aériennes de simulies, on décrit les techniques qui ont été essayées pour échantillonner les adultes ne volant pas, au repos sur la végétation ou dans d'autres sites naturels. On décrit et on évalue les procédés mis au point pour marquer les adultes avec des colorants, teintures, peintures et radionucléides et les techniques utilisées pour recapturer et détecter les adultes marqués, de façon à mesurer le taux de dispersion.

Enfin, on donne la liste des techniques de capture qui semblent mériter une évaluation plus poussée.

ACKNOWLEDGEMENTS

I am greatly indebted to Dr R. W. Crosskey for reading a draft of the paper and for his advice and comments on blackfly nomenclature. I am also grateful to Dr B. H. Thompson and Dr C. Bellec for providing me with manuscripts of their papers that at the time of writing were still 'in press', and Dr J. A. Odetoyinbo for giving me a copy of his unpublished 1969 report on use of light traps in Ghana and letting me quote from it.

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