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THE BIOLOGY OF THE SHEEP HEADFLY *HYDROTAEA IRRITANS* (Fallen) (DIPTERA: MUSCIDAE) IN SOUTH WEST SCOTLAND

by

Andrew David Berlyn B.Sc.(Hons.)

This work was carried out at the Department of Zoology, the West of Scotland Agricultural College for the degree of Doctor of Philosophy at the University of Glasgow.

MARCH 1980

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March 1980 — A. D. BERLYN

Raw data for the work covered in Chapter Two have been lodged with the Librarian of the West of Scotland Agricultural College, Auchincruive, Ayr.

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LIST OF CONTENTS

	page
SUMMARY	1
INTRODUCTION	4
1. Hydrotaea irritans (Fallen) - a review of the literature	
Introduction	6
The Problem	7
Habitat	8
Seasonal Activity	9
Climate	10
Trapping and Attractants	11
Feeding	12
Food Sources	12
Caged Flies	14
Larval Rearing	15
Larval Description	16
Breeding Sites	16
2. The flight activity of the sheep headfly, Hydrotaea irritans (Fallen) (Diptera: Muscidae)	
ABSTRACT	18
INTRODUCTION	18
MATERIALS AND METHODS	20
RESULTS	21
Comparison Between Traps	21
Flight Periodicity	23
Seasonal Incidence and the Effect of Weather on Trap Catches	23
DISCUSSION	26
Trap Comparison	27
Flight Periodicity	27
Seasonal Incidence and the Effect of Weather on Trap Catches	28

page

3. The field biology of the adult sheep headfly, Hydrotaea irritans (Fallen) (Diptera: Muscidae), in south-western Scotland

ABSTRACT 34

INTRODUCTION 34

MATERIALS AND METHODS 35

RESULTS 37

DISCUSSION 38

4. Factors attracting the sheep headfly, Hydrotaea irritans (Fallen) (Diptera: Muscidae), with a note on the evaluation of repellents

ABSTRACT 44

INTRODUCTION 44

MATERIALS AND METHODS 44

Investigations of Previously Determined Attractants 45

Colour 45

Carbon dioxide 46

Interaction of Attractants 46

Tests of Other Potential Attractants 46

Repellent Evaluation Using Traps 47

RESULTS 48

Investigations of Previously Determined Attractants 48

Colour 48

Carbon dioxide 48

Interaction of Attractants 50

Tests of Other Potential Attractants 51

Repellent Evaluation Using Traps 51

DISCUSSION 51

page

5. The distribution of adult H. irritans in a spruce forest

ABSTRACT 56

INTRODUCTION 56

MATERIAL AND METHOD 56

RESULTS 57

DISCUSSION 57

6. The vertical distribution of adult H. irritans

ABSTRACT 60

INTRODUCTION 60

MATERIAL AND METHOD 60

RESULTS 61

DISCUSSION 61

7. The effect of diet on the longevity and egg maturation of caged H. irritans (Diptera: Muscidae)

ABSTRACT 62

INTRODUCTION 63

MATERIALS AND METHODS 63

Life-span and Egg Maturation on a Diet of Blood and Honey Solution 64

Protein Sources 65

Number of Blood Meals Required 66

Carbohydrate Sources 66

Water Requirement 67

RESULTS 67

Life-span on a Diet of Blood and Honey Solution 67

Egg Maturation on a Diet of Blood and Honey Solution 67

Protein Sources 70

Number of Blood-meals Required 72

Carbohydrate Source 72

Water Requirement 73

page

DISCUSSION 73

SUPPLEMENT TO CHAPTER 7 80

8. The oviposition behaviour of caged H. irritans

ABSTRACT 82

INTRODUCTION 82

MATERIALS AND METHODS 82

Oviposition Preferences 82

Time of Oviposition 83

RESULTS 83

Oviposition Preference 83

Time of Oviposition 83

DISCUSSION 85

9. Laboratory rearing of the larvae of H. irritans

ABSTRACT 86

INTRODUCTION 86

MATERIALS AND METHODS 86

RESULTS 87

DISCUSSION 88

10. The breeding site of H. irritans in south-western Scotland

ABSTRACT 89

INTRODUCTION 89

MATERIALS AND METHODS 89

Emergence Boxes 89

Emergence Traps 90

Field Sampling 90

RESULTS 92

Emergence Boxes 92

Emergence Traps 92

Field Sampling 92

DISCUSSION 92

BIBLIOGRAPHY 94

LIST OF TABLES

Table		page
I	Numbers of males and females of H. irritans caught in 15-min trapping periods from 1 July to 28 July in three traps	22
II	Coefficients of factors included in multiple regression equations describing activity of males and females of H. irritans recorded by a suction trap baited with carbon dioxide and a Manitoba trap	25
III	Mean numbers of males and females of Hydrotaea irritans and of Haematopota pluvialis caught in Manitoba traps with coloured spheres	49
IV	Mean transformed numbers of H. irritans attracted to Manitoba traps in which carbon dioxide was released	50
V	The geometric mean catches of H. irritans in Manitoba traps baited with various potential attractants	52
VI	The mean transformed numbers of H. irritans attracted to Manitoba traps with black spheres treated with repellents	53
VII	Mean transformed numbers of H. irritans caught in Manitoba traps positioned at different sites	58
VIII	The life-span of males and females, and the egg maturation of females, fed on blood and honey	69
IX	Numbers of eggs matured by females fed on different sources of protein	71
X	Number of eggs matured by females given different numbers of blood-meals	71
XI	The mean transformed number of eggs laid at intervals during the day	84
XII	Habitats sampled for the larvae of H. irritans	91

LIST OF FIGURES

Figure		page
1	Geometric mean numbers of *H. irritans* caught in a suction trap baited with carbon dioxide at hourly intervals during the day throughout July. Each column shows the numbers caught in a 15-min trapping period starting on the hour	31
2	Weekly geometric mean numbers of *H. irritans* caught in a suction trap baited with carbon dioxide and a Manitoba trap in 15-min trapping periods between 11.00 and 15.00 h from May to October	32
3	Seasonal activity calculated from multiple regression equations for males and females of *H. irritans* in a suction trap baited with carbon dioxide and a Manitoba trap. Activity is expressed as a proportion of the activity on 26 June	33
4	The change in reproductive condition and the proportion of blood-fed females trapped in the suction trap baited with carbon dioxide during the summer	41
5	The percentages of females with eggs in each stage caught in the suction trap baited with carbon dioxide	42
6	The relation between decline in numbers of males and female insemination. Activity is expressed as a proportion of the activity on 26 June	43
7	The apparatus used to maintain the flies alive in captivity	77
8	The total number of eggs laid each week by: (a) 30 females fed on honey and blood throughout and not paired with males; (b) 30 females fed on blood up to the time of pairing with males, and only honey subsequently; and (c) 30 females fed on blood and honey throughout and paired with males	78
9	The total number of eggs laid each week by: (a) 30 females fed on blood once only; and (b) 30 females fed on blood continuously	79

SUMMARY

The flight activity of H. irritans was investigated in Western Scotland using an unbaited suction trap, a CO_2 baited suction trap and a Manitoba trap. In addition, trapped flies were dissected to investigate their reproductive condition, their blood-feeding activity, and whether they were newly emerged. Consistently more female flies were caught than males. The seasonal activity of adults was determined from the geometric means of catches from a Manitoba trap and a suction trap baited with carbon dioxide. The activity of females was greatest in the middle of July and declined sharply in the first week of August when the first gravid females were trapped. The proportions of females in the various ovarian categories suggested that there is a preliminary phase before host-seeking begins, attraction to animals during most of the cycle and a behavioural change at the end. Females with eggs at stages I, II and III accounted for 94% of all females caught; the only females with blood in the gut were in these categories. Some males also were obviously blood-fed. Male activity reached a peak at the same time as that of the females, then declined as an increasing number of females was found to be inseminated. Six weeks from the start of the male decline all females trapped were found to have been inseminated. After this, no more males were caught. Only females with eggs in stages later than stage II of the first ovarian cycle were inseminated. H. irritans was univoltine with two but not quite three ovarian cycles during the summer. There was no difference in feeding or reproductive development between flies from the two traps. Females were most active between 10.00 and 16.00 h B.S.T., with a peak about 13.00 h. The sex ratio did not vary significantly through the day. Multiple regression equations

of climatic and seasonal factors with log catches of flies were very similar for the two types of trap. Radiant temperature, illumination, windspeed and date were shown to influence the activity of females and, with the exception of illumination, male activity also. Seasonal activity curves were plotted for both sexes in the two traps.

Modified Manitoba traps were used on a forest track to investigate the factors which attract host-seeking adult H. irritans. Carbon dioxide, coloured spheres, movement, heat, a swarm of other headflies and Haematopota pluvialis (L) were shown to be attractants. Traps with coloured spheres attracted more H. irritans than traps without spheres. Matt black, shiny black and shiny red spheres attracted more male and female H. irritans than did shiny green, white and yellow spheres. Significant increases in the number of headflies caught did not occur when carbon dioxide was released from a trap at rates above 2 litres/min. Results suggest that carbon dioxide acts as a long range headfly attractant with a visual factor becoming important near the host. Manitoba traps were also used with three headfly repellents in order to evaluate the trap's potential for testing repellents.

The extent of adult H. irritans activity in various habitats in a spruce forest was investigated using Manitoba traps. Most H. irritans were trapped in a firebreak or on a rough track. Least flies were caught within a clearing or thicket. It is suggested that in softwood plantations H. irritans uses firebreaks and tracks as flight paths and rarely flies amongst the trees.

The vertical distribution of adult H. irritans was investigated using a handy angle tower and baited suction traps. This apparatus appeared to repel the flies and no

valid results were obtained.

A method for maintaining adult H. irritans in captivity is described. Male flies lived about half as long as females. Flies required carbohydrate and water for survival. A 50% honey solution, a 50% sucrose solution, thistle flowers and aphid honeydew were all good sources of carbohydrate, unlike blood, serum, milk, sweat and mucus. Fecundity was greatest on a diet of carbohydrate with blood or serum. Fewer eggs developed in females given a diet of carbohydrate with milk, and very few eggs were developed on a diet of carbohydrate with sweat or mucus. No eggs were produced by females fed on carbohydrate alone. All males had active spermatozoa, but females were only inseminated when both they and the males with which they were paired were given blood. This insemination was low at 13.3%. Females required more than one blood meal, but not more than one every three weeks, in order to develop the maximum number of eggs.

H. irritans females laid equal numbers of eggs on peat, pasture soil, deciduous woodland soil with leaf litter, and peat mixed with cow dung. Slightly moist peat was preferred to wet peat. Most eggs were laid between 11.30 h and 21.30 h B.S.T., with a peak in the late afternoon.

Attempted methods of rearing the larvae of H. irritans in the laboratory are described. None was successful.

A variety of methods was used to determine the breeding site of H. irritans in South West Scotland. No adults of H. irritans were recovered from emergence boxes or emergence traps. By the use of heat extraction apparatus two headfly larvae were extracted from samples of pasture soil. None was extracted from litter or dung samples.

INTRODUCTION

The sheep headfly, Hydrotaea irritans (Fallen), is a common muscid fly which swarms around animals and man during the summer. This habit has probable economic significance with sheep, cattle and deer.

The headfly is not a new pest of sheep, the problem having been investigated in the late 'forties. The problem ceased when organochlorine dips were introduced, but it has since recurred, probably due to withdrawal of these dips. The flies are attracted to the heads of horned sheep and crawl down the space between the hair and the horns to the skin where they cause considerable irritation. The sheep rub and scratch their heads causing, in time, raw bleeding areas. This attracts more flies, and results in an increasing cycle of damage. Eventually, a large bloody lesion may cover the whole of a sheep's head. In addition to H. irritans, other flies have been found in fewer numbers on sheep headfly lesions. These were: Hydrotaea albipuncta (Zett.), H. armipes (Fall.), Morellia simplex (Loew) and Trichopticoides decolor (Fall.).

A survey in South West Scotland from 1972 to 1975 has shown the problem of headfly lesions on sheep to be widespread. Six hundred shepherds were questioned and the sheep headfly was considered to be a severe problem on 10.9% of farms, a moderate problem on 17.5%, and a slight problem on 33.8%. The number and severity of headfly attacks was greatest in Kirkcudbrightshire, whilst the least affected counties were Renfrewshire and Bute.

Several Danish researchers (Bahr, 1953; Nielsen et al., 1971, 1972 and Sorensen, 1974) have suggested that insects, particularly H. irritans, play a significant role in the transmission of summer-mastitis in cattle. The headfly is

normally attracted to the heads of cattle where it feeds on fluid secretions. However, when a teat is injured by trampling or a biting fly, it becomes highly attractive to headflies, and it is then that the transmission is thought to occur. Thus, H. irritans has a role in the transmission of disease as well as causing loss of condition due to the almost constant irritation of the flies to stock.

The other animal on which the headfly may become an economic pest is the Red deer, Cervus elaphus (L). It has been reported (Anon, 1974) that the headfly is likely to be a major pest of commercial deer farming. It is highly attracted to the antlers in velvet, where it settles between the hairs and feeds on blood.

In 1973, when this project began, only two papers on the biology of H. irritans had been published (Nielsen et al., 1971, 1972). This thesis is a report of investigations from 1973 to 1976 into the biology of H. irritans. Chapters 1, 3, 4 and 7 have been published in the Bulletin of Entomological Research (Berlyn, 1978a,b,c, 1979).

1. *Hydrotaea irritans* (Fallen) - a review of the literature

Introduction

Aspects of the biology of the sheep headfly, Hydrotaea irritans (Fall.) were first reported by Hammer (1941). He investigated the biology and ecology of 40 flies associated with pasturing cattle and their excrement, and H. irritans was mentioned only briefly. However, from 1953 the fly has been suspected of transmitting summer mastitis. In Denmark, Bahr (1953) studied the headfly with regard to this transmission and his results prompted research into the fly's biology by Nielsen, Nielsen & Christensen (1971, 1972) and Sorenson (1974).

Since 1973 many papers concerning the headfly have been published in Britain. This has been due to the recurrence of the problem of broken heads on sheep, which was common before the widespread use of organochlorines such as Dieldrin. Horned sheep in the border areas of Scotland and England are particularly affected. There have been three main groups investigating the biology of the headfly in Britain. At Weybridge, in the south east of England, Tarry & Kirkwood have published six papers (Tarry, 1973; Tarry & Kirkwood, 1974; Tarry, 1975; Kirkwood, 1975; Tarry & Kirkwood, 1976 and Kirkwood, 1976). Hunter (1975), Robinson & Luff (1976) and French, Wright, Wilson & Nichols (1977) all studied the headfly in Northumberland. Titchener, Berlyn & Newbold (1974, 1975) worked in the south west of Scotland.

In Russia, Makhan'ko (1973) investigated the degree of parasitism exhibited by Hydrotaea spp. including H. irritans. Lobanov (1968) published a key to the identification of Hydrotaea larvae, based on a description of H. irritans larvae by the East German, Schumann (1963).

The Problem

Hammer (1941) first reported the effect of headflies on cattle. H. irritans occurred mainly on the heads of cows, gathering around the eyes and muzzle and feeding on fluid secretions and blood. It was very common to see species of Hydrotaea with their heads close to the head of a biting Haematobia, Haematopota or Tabanus bovinus L. Nielsen et al. (1971) supported these observations and mentioned that an injured teat was particularly attractive to headflies and that the frequency of summer mastitis was highest when cattle were in localities favoured by headflies. Nielsen et al. (1972) stressed the nuisance caused by headflies when they drove off feeding biting flies. This caused the biting flies to attack again, resulting in more wounds. Bahr (1953) found that in 86% of summer mastitis cases the only fly on the teat tip was a female of H. irritans, but it was possible only to obtain a pure culture of the causative agent, Corynebacteria pyogenes, from the flies' viscera in three out of 145 flies. Sorenson (1974) also has suggested that insects, especially H. irritans, act as vectors for the causative agents of summer mastitis.

Tarry (1973) first described the effect of headfly on sheep. Irritation by the fly causes the sheep to scratch and rub its head, thus breaking the skin and producing a sore which may become secondarily infected or attacked by blowflies. Once the skin is broken it becomes even more attractive to the flies, and with the increased irritation the animal lies down and may scarcely feed. Tarry also mentioned that mastitis was frequent in many flocks. Hunter (1975) stated that in some cases severe head shaking and ear flicking caused an aural haematoma. Lambs were more severely affected than

ewes, and the incidence of lesions and the number of flies increased with flock size. He mentioned that farmers had reported losses in weight gain of 15-20 lb; although French et al. (1977) found that differences in liveweight gain between lambs with head lesions and those with no lesions were seldom significant. Titchener, Berlyn & Newbold (1974) found from a survey in the west of Scotland that headfly was a severe, moderate and slight problem on 11.6, 16.7 and 36.8% of farms respectively.

A major setback to Red deer farming may be the pestering of deer by H. irritans (Anon, 1974). The flies land on the stags' antler velvet and feed on blood. On days of high headfly activity the stags try to escape from the flies by lying in the bracken, and consequently spend little time grazing.

Habitat

Hammer (1941), Nielsen et al. (1971) and Tarry (1973) agreed that H. irritans was most abundant in woodland margins and swarmed in the open only for short periods. This was assumed to be due to a need for high humidity, although Nielsen et al. (1972) mentioned that the fly was more far-ranging in calm weather (they did not state that it required more humid weather). Headflies were most common around cattle grazing close to wooded or swampy localities (Hammer, 1941; Nielsen et al., 1971; Tarry, 1973 and Titchener et al., 1974). Moderate numbers were found on open hillsides with a deep heather mat (Tarry, 1973) and activity was slight in wood thickets (Nielsen et al., 1971). The proportion of males was higher in areas where fewer headflies were found (Tarry & Kirkwood, 1976).

Seasonal Activity

Hammer (1941) recorded the activity of H. irritans from early May until the end of October. He suggested that the few flies found in early May were accidental forerunners of the first generation which has its principal occurrence in June and emerges until July, and that a second generation did not appear until August. He acknowledged, without detailing it, that an entirely different possibility existed. Seguy (1923) recorded headflies from June to September, and Ringdahl (1925) recorded them from June to October.

Nielsen et al. (1971) found headflies were very common from the middle of June until early September. Tarry (1973) made regular timed catches (his method was not described) throughout 1972 and 1973 at two trapping sites in Surrey and found that flies were active between late June and late September in 1972 and early September in 1973. (He mentioned that they emerged two to three weeks later in Northumberland). The male flies appeared first, but disappeared as female numbers began to rise. Tarry suggested that a sudden population fall in late July 1973 which did not occur in 1972 was due to predation of headfly larvae by Polietes and Morellia larvae. He disagreed with Hammer by suggesting, on the basis of changes in sex ratios and reproductive stages, that only a single generation occurs each year. Trapping data of Titchener et al (1974) showed numbers to be at their height in July, with a decline through August and little activity in September. Male flies were trapped only in July. French (1977) reported that headfly could be common from the end of June until September, but cold and wet or hot and dry weather might cause a fall in activity.

The change in reproductive condition over the summer was investigated by some of the workers. Hammer (1941) found that five female headflies dissected at the end of June and 18 of 19 dissected at the end of July had undeveloped ovaries. He assumed that these were all newly emerged first generation flies.

Tarry (1973) first found spermatozoa in the spermathecae of trapped females about a week after the drop in numbers of males caught. Kirkwood (1976) gave the surprising result that in 1973 and 1975 the last males were caught seven and two days respectively before the first fertilized female was caught. However, in 1974 males were caught for 15 days after the first catch of fertilized females.

Gruhl (1924) has seen H. irritans suspended in the air on its mating flight above woodland paths.

Climate

Hammer (1941) stated that the activity of H. irritans was dependent on temperature, humidity and light, and that the fly was unable to tolerate the low humidity of open fields for long periods. Nielsen et al (1972) measured headfly activity and climatic factors for 24 hour periods on 30 occasions. They found that H. irritans was active from 04.00-22.00 h, with subcrepuscular peaks and fluctuations throughout the day. Activity was delayed when the morning temperature was below 12^{o}C. Emphasis was placed on the difficulty of attributing peaks of activity to climatic factors, and no direct correlation between climate and numbers was found, although several generalisations were made. Light was said to be the primary stimulus for activity, but fly numbers fluctuated independently of temperature, probably as a result of cattle movements. Activity was negligible

in cold and changing weather or at wind speeds exceeding 6 m/sec when the fly sheltered on plants, cattle or wind-breaks. Activity was highest before and after a thunderstorm or shower, but was reduced by a downpour of rain.

On the basis of his timed weekly catches, Tarry (1973) suggested that there was a level of humidity and temperature below which activity was negligible. High temperatures with high humidity were said to give high activity except during a strong wind. However, Tarry & Kirkwood (1976) concluded that humidity is not critical although it has an optimum between 70 and 80%.

Titchener et al. (1974) found headflies most numerous between 10.00 and 16.00 h. There was a significant relationship between the numbers of flies caught and temperature, with minimum and maximum thresholds of 11 and 22^{o}C respectively.

Trapping and Attractants

Nielsen et al.(1971, 1972), Tarry & Kirkwood (1974, 1976) made use of the headfly's attraction to man in order to trap it using standardized netting. Titchener et al. (1974) trapped large numbers of H. irritans using suction traps baited with carbon dioxide, although Tarry & Kirkwood (1976) were unsuccessful in an attempt to assess adult numbers using several kinds of unspecified traps. Kirkwood (1976) described a mechanical device that was used to catch headflies. It consisted of two nets positioned on revolving booms so that each acted as an attractant for, and caught the flies following, the other. The trap was developed from an observation that H. irritans will follow a moving object.

The carbon dioxide-baited trap and the trap using revolving nets demonstrate two stimuli, carbon dioxide and

movement, in the attraction of the headfly to its host.

Feeding

Makhan'ko (1973) studied the degree of parasitism developed in various species of adult Hydrotaea. On the basis of comparative development of teeth the genus was arranged in groups. One group, containing H. irritans, consisted of species able to scratch out wounds to produce blood. They had strongly sclerotized teeth set in one row and a curved discal sclerite. H. irritans had the most highly developed prestomal teeth.

Tarry (1975) presented the shaved abdomen of a guinea-pig to headflies which, within two to three hours, penetrated the epidermis entirely so that blood was available. A spot of blood placed on unbroken skin accelerated this process. He concluded that although H. irritans is unable to penetrate skin directly it is a very efficient scraper.

Food Sources

Hammer (1941), Nielsen et al. (1972) and Tarry (1973) described H. irritans as a facultative blood sucker, commonly feeding on eye and muzzle secretions and saliva, but being highly attracted to blood from wounds. Tarry (1975) used the serological technique developed for mosquitos to determine the main blood sources of adult headflies collected from different areas in Northumberland. He found that about 20% of headflies had recently fed on blood and of these 73.6% contained cattle blood, 19.3% contained sheep blood and 10.6% contained rabbit blood. These figures add up to more than 100%, presumably indicating that the flies have fed on more than one species. Tarry suggested on the basis of these results that treatment of cattle with an insecticide would have a greater effect on fly numbers than would treatment of

sheep. The paper would have been more informative had the figures quoted in the text corresponded with the figures in the table. In another year (Tarry & Kirkwood, 1976), 55.8% of headflies tested had recently ingested blood. Of the flies tested, 5% gave a reaction for sheep blood, 29% for cattle blood, 2.5% for rabbit blood, and 18% gave a slight response to a generalised ungulate precipitin test. (It should be noted that these figures do not, in fact, add up to 55.8%.) It is most surprising that Tarry & Kirkwood did not record deer blood in the gut of H. irritans, in view of the large numbers of headflies feeding on domestic Red deer (Anon, 1974). Tarry & Kirkwood do not mention whether the bovid blood which was recorded far more often than sheep blood, even in sheep rearing areas, could have been confused with deer blood.

The effect of different protein meals on the development of the ovaries was studied by Kirkwood (1976). Flies were caught at the start of the season and provided with bovine serum, horse serum, milk, egg white or no protein source. All flies were provided with 50% sucrose solution. The rate of development did not vary with the different proteins, but the eggs of the flies from which protein was withheld did not develop beyond stage II. Kirkwood identified seven stages in the ovarian cycle. These were based on the six stages in Musca vetustissima Walker, described by Tyndale-Biscoe & Hughes (1969) with an additional stage (stage II) early in the cycle.

Muller (1881) caught H. irritans on several species of flowering plants, and Greenberg (1972) reported adult headflies on inflorescences of daucaceous plants infested with aphids.

Caged Flies

Nielsen et al. (1971) fed headflies on blood in outdoor cages. A variety of potential breeding media was offered to the flies, but the first eggs were laid in a moist cotton-wool plug. Large numbers of eggs were laid in moist Sphagnum moss that was offered subsequently.

Tarry (1973) provided flies with water, sugar, honey and blood and maintained them in cages suspended over moist peat under sheltered outdoor conditions. In addition to the peat, other media were offered for oviposition. Males died within four to five weeks whereas 20%of the females first collected survived for 10 weeks. Oviposition was observed from the third week in July. All caged females given blood laid eggs, but these were only viable if the female had been fertilized. Tarry & Kirkwood (1976) reported that female flies taken from the field during August and then caged showed maturation of eggs at about the tenth day after being fed blood, compared to the 35 days taken by flies collected before the end of June. This indicated either a period of ovarian development that did not require additional protein, or that the flies collected in August had already had a protein feed.

Tarry (1973) and Tarry & Kirkwood (1976) both mention that a choice of oviposition media was offered to the flies, but the outcome was not reported. A similar choice was offered to wild flies in woodland and clearings, but no headflies laid eggs on them (Tarry & Kirkwood, 1976). Robinson & Luff (1976) offered a choice of soil, cow dung, leaf litter or peat to flies. There was no obvious preference for a particular oviposition medium, although generally more eggs were laid on the moister media.

Larval Rearing

Tarry (1973) obtained white larvae from eggs laid by his caged flies. The eggs hatched within five days to give second instar larvae. These larvae became parchment yellow when they moulted to their third instar. As they grew they required small larvae on which to feed. (Hammer (1941) reported a larva of H. irritans which sucked out the body contents of a Rhyphus larva.) The larvae appeared to diapause in November, becoming active again the following March, and began to pupate in mid May. No adults emerged, although Tarry & Kirkwood (1976) were more successful two years later when one imago emerged on 17 June.

Robinson & Luff (1976) found that eggs laid by caged flies hatched after five to seven days at 20°C to give the second instar larvae which moulted to the third instar after three to five days! They placed the larvae in Drosophila cultures, but none survived for more than three months. Sixteen larvae collected from the field were kept at 19°C and remained active, readily feeding on Calliphora or Musca domestica L. larvae, with no sign of a diapause. The larvae pupated between December and April to give adult headflies.

Kirkwood (1976) was more successful with the rearing, although his caged adults failed to mate and he required field flies to provide fertilized viable eggs. About 1,400 headfly larvae, hatched from these eggs, were established in peat cultures. These larvae were each given a continuous supply of at least 100 second or third instar larvae of Musca domestica or Lucilia sericata (Meigen). The headfly larvae finished growing by January and stopped feeding on 14 March. They entered pupation from 6 May to 12 June and this lasted from 25-32 days. From a total of 348 pupae, 185

flies emerged from 4 June to 9 July.

Larval Description

A description of H. irritans larvae was first published by Schumann (1963), who described larvae he had found in dung. Lobanov (1968) produced a key to the larvae of eight species of Hydrotaea, but his information on H. irritans was taken from Schumann. Tarry & Kirkwood (1974) figured the cephalopharyngeal skeleton of a laboratory-reared headfly larva bud did not describe the larval body in any detail.

Robinson & Luff (1976), however, described in detail third instar headfly larvae that had been collected from the field. They claimed that the previous descriptions were of young third instar larvae which differ in important details from mature larvae. They also included descriptions of the eggs, second instar larvae, pupae, changes in the mouthparts during growth, and features by which field-collected larvae can be identified.

Breeding Sites

Hammer (1941) reported that a small percentage of Hydrotaea larvae found during the winter, just below the surface of cow dung, was H. irritans, and suggested that the fly also develops in the manure and runs of small wild animals, or in decaying vegetable matter.

Nielsen et al. (1971) carried out intensive sampling using emergence traps. They set up 940 traps in a variety of habitats, but only two flies were caught. One was from a trap in a meadow, the other from a trap set on a cowpat. Tarry (1973) found no larvae in soil samples examined in the laboratory, but Tarry & Kirkwood (1976) had more success and found eight H. irritans larvae in soil from open woodland sites, and two in soil from pastures. Skidmore (1973) records

dung as the larval habitat of H. irritans, although information regarding quantities etc. was not given.

Robinson & Luff (1976) collected many samples of soil, peat, litter and moss from areas of Northumberland infested with H. irritans. They found that the main breeding site was the soil beneath either pasture or long grass, with cow dung and bracken litter as very minor habitats. The mean density of larvae in pasture soil was 1.93/m^2, which corresponds well with an unpublished estimate of adult density by French. Sampling indicated that larvae were absent from the centre of fields, but occurred near the wooded margins.

Control

Protection by repellents, avoidance of severely affected pastures and the introduction of relatively immune breeds or crosses were the three headfly control measures suggested by Tarry (1973). In chemical control trials on Blackface sheep, Titchener et al. (1974) found that crotoxyphos as a commercial or an experimental cream gave considerable protection against headfly. The experimental cream contained more crotoxyphos and was more effective. A crotoxyphos spray was ineffective. A new insecticide dip provided significant control in one out of three trials (Titchener et al., 1975).

French et al. (1977) found no difference between the commercial and experimental crotoxyphos creams. Of the various repellents they tested, crotoxyphos cream and Marshall's "anticap" gave the best results. The insecticide dip provided some protection, but other repellents were of no value.

2. The flight activity of the sheep headfly, Hydrotaea irritans (Fallen) (Diptera: Muscidae)

ABSTRACT

The flight activity of Hydrotaea irritans (Fall.) was investigated in western Scotland using an unbaited suction trap, a carbon-dioxide-baited suction trap and a Manitoba trap. Consistently more female flies were caught than males. Trapping experiments showed that carbon dioxide and visual or thermal stimuli influence long-range attraction and short-range orientation in host-seeking flies. The seasonal activity of adults was determined from the geometric means of catches from a suction trap baited with carbon dioxide and a Manitoba trap. H. irritans was shown to be univoltine. The activity of females was greatest in the middle of July and declined sharply in the first week of August. Male activity reached a peak at the same time as that of the females, then declined until no males were caught after mid-August. Females were most active between 10.00 and 18.00 h B.S.T., with a peak about 13.00 h. There was no variation in sex ratio during the day. Multiple regression equations of climatic and seasonal factors with log catches of flies were very similar for the two types of trap. Radiant temperature, illumination, wind speed and date were shown to influence activity of females and, with the exception of illumination, male activity also. Seasonal activity curves calculated from the regression equations were plotted for both sexes in the two traps.

INTRODUCTION

The sheep headfly, Hydrotaea irritans (Fallen), is a Palaearctic fly well known for its irritating habit of

swarming round the heads of man and animals in the summer. Its association with cattle and suspected role in the transmission of summer mastitis led to several investigations in Denmark (Hammer, 1941; Bahr, 1953; Nielsen *et al.*, 1971, 1972). More recently, attention has been focused on the fly owing to the 'broken heads' syndrome in certain breeds of horned sheep in the border areas of Scotland and England (Tarry, 1973; Tarry & Kirkwood, 1974; Titchener, 1975). The irritation of swarming adults of *H. irritans* causes the sheep to scratch and rub their heads against objects. The lacerations then result in intensified attack by the flies, and the wounds become greatly extended by more self-inflicted damage. The flies may also cause damage with their prestomal teeth (Makhan'ko, 1973). A lesion may eventually cover the whole upper head, leaving a large scar when the wound heals during the winter. Sheep strike can occur on the wound.

To investigate the field biology of *H. irritans* and to compare flight activity in different areas, it is necessary to trap the fly by a method that can be standardised. The adults are readily attracted to man, and for this reason only hand nets have previously been used to catch them (Tarry, 1973; Tarry & Kirkwood, 1974). This method is unsatisfactory, as the attractiveness of different individuals varies. Kettle (1969) showed that, depending on their health and on the amount of clothing worn, different collectors caught different numbers of *Culicoides* spp. In the present investigations, a comparison was made of different trapping methods and the use of these to study various aspects of the flight activity of *H. irritans*.

MATERIALS AND METHODS

The trapping site was a field containing blackface sheep on a Lanarkshire (Scotland) farm with a severe *H. irritans* problem. The field (Nat. Grid. ref. NS 827336) was bordered on its north, south and west sides by mixed woodland and on the east side by a road. The traps were aligned 20 m apart along a south-facing stone wall to obtain the most direct sunlight.

The following traps were tested:

1. a black suction trap 0.3 m in diameter and 1.3 m high. It was made to the specifications of Johnson (1950) except that it lacked the catch-segregating mechanism and the cone was enclosed in a metal wind shield. The fan speed was set at 'boost';

2. an identical suction trap with the addition of a length of rubber tubing with an outlet 0.4 m above the fan. Through this tube was released carbon dioxide at a rate of 2 litres/min. Previous experiments by the author (see Anon., 1974) had shown that carbon dioxide attracted *H. irritans*;

3. a Manitoba trap constructed following the design of Thorsteinson *et al*. (1965). The trap comprised a black sphere (0.5 m in diameter) suspended beneath a polythene collecting cone, which was supported by a tripod. Flies were attracted to the sphere, flew upwards to escape, and were then trapped in a container at the cone's apex; and

4. an animal trap, based on the description by Morris & Morris (1949), and a sticky trap. Negligible numbers of flies were caught in them.

The suction trap baited with carbon dioxide was operated once a week during May, September and October, 1974, and two

or three times a week during June, July and August, for 15 min starting on each hour, between 11.00 and 15.00 h B.S.T. and often from before dawn until after dusk. The change in fly activity throughout the season was based on a standard catching period of 11.00-15.00 h. The Manitoba trap was operated concurrently with the carbon-dioxide-baited suction trap from 26 June until the end of August. The unbaited suction trap was operated concurrently throughout July.

The following meteorological factors were recorded during each 15-min trapping period: maximum air temperature and maximum relative humidity in the shade (from three readings) measured with a whirling hygrometer, maximum radiant temperature using a thermometer laid horizontally on a white board placed out of the shade, maximum illumination by measuring the light reflected from a horizontal grey board with a Weston Master V exposure meter (held 0.5 m above the board), barometric pressure using an aneroid barometer, and wind speed using an anemometer over the whole period.

RESULTS

Comparison Between Traps

Analysis of transformed (log catch + 1) male and female catches in July showed highly significant ($P < 0.001$) differences between trap means (Table I). The suction trap baited with carbon dioxide caught more flies than the Manitoba trap, which in turn caught more than the unbaited suction trap. This shows that *H. irritans* is highly attracted to carbon dioxide. The catches in the Manitoba trap indicate a response to a visual or thermal stimulus, colour or heat absorption accounting for the attraction to the black ball beneath the trap.

Table I. Numbers of males and females of *H. irritans* caught in 15-min trapping periods from 1 July to 28 July in three traps

	Mean transformed numbers	Geometric mean	Max. no. caught in any trapping period
Females			
Suction trap baited with CO_2	4.17	63.6	1271
Manitoba trap	3.36	27.7	186
Unbaited suction trap	1.43	3.2	51
*F value (2,88) = 148.41; $P < 0.001$			
**SED = 0.186			
Males			
Suction trap baited with CO_2	2.44	10.4	94
Manitoba trap	1.59	3.9	29
Unbaited suction trap	0.42	0.5	7
*F value (2,88) = 75.02; $P < 0.001$			
**SED = 0.165			

*Analysis based on mean transformed numbers
**SED = standard error of the difference

Analysis of transformed (arcsin) percentages of male flies in catches during the first week of July showed a significant difference ($P < 0.01$) between the catches in the suction trap baited with carbon dioxide (24.9%) and those in the Manitoba trap (30.9%). Low catches of flies causing large variation in the sex ratios of the unbaited suction trap catches prevented analysis. After the first week of July, the percentages of males caught were too low for analysis.

Flight Periodicity

The geometric means of the numbers of H. irritans caught in the suction trap baited with carbon dioxide in each catching period during July (Fig. 1) show that H. irritans was caught mainly between 10.00 and 18.00 h B.S.T., with a peak about 13.00 h. Before 08.00 h and after 22.00 h no flies were found in the traps. Analysis of the transformed (log catch + 1) data confirmed there was significant variation ($P < 0.001$) in activity of both males and females during the day, but there was no variation in sex ratio. Further analysis was impossible due to the variation in activity between days. August trap catches were low, varying greatly between the start and end of the month, and were not included in the analysis.

Seasonal Incidence and the Effect of Weather on Trap Catches

Weekly geometric means were calculated for catches of all males and females caught in the suction trap baited with carbon dioxide and the Manitoba trap between 11.00 and 15.00 h each week. The means were plotted to give a seasonal distribution of activity for each sex in the two traps (Fig. 2). Males were never as numerous as females and none was caught after the middle of August.

There were considerable fluctuations in activity between weeks. These were mostly due to weather. Multiple regression analyses were used on all trap catches of females between 26 June and 29 August and of males between 26 June and 14 August. These determined which meteorological and seasonal factors were strongly associated with variations in numbers of H. irritans trapped. Climatic factors are strongly inter-related. This could have resulted in an indirect relationship appearing direct if a single regression analysis had been used in preference to a multiple regression analysis.

A separate regression equation was derived for each sex in both traps. The dependent variable was $\log_e(n + 1)$, n being the number of males or females caught in each trapping period. The independent variables were radiant temperature (t), relative humidity (h), wind speed (w), illumination (i) and barometric pressure (p). Air temperature was excluded as it was very highly correlated with radiant temperature, which produced a better fit to the data. Quadratic terms were included for H. irritans seasonal activity by using day number from 26 June (D) and D^2, and for systematic variations in catch throughout the day by using time of day (T) and T^2. Two-factor and second order terms (e.g., tb, iw, t^2) were considered, but only t^2 merited inclusion. One variable at a time was entered into the regression, provided that its presence produced a significantly better fit to the data. All other variables in the regression were then checked using partial t tests to determine whether they could be omitted without a significant reduction in fit. The process was continued until no significantly better fit could be obtained.

The resulting equations with the percentage variation expained (R^2) are shown in Table II. Coefficients for time

Table II. Coefficients of factors included in multiple regression equations describing activity of males and females of *H. irritans* recorded by a suction trap baited with carbon dioxide and a Manitoba trap

	Coefficients								
	Constant	D	D^2	t	t^2	i	w	R^2	Number of observations
Females									
Suction trap baited with CO_2	-6.0363	0.1489	-0.0025	0.7916	-0.0167	5.78×10^{-5}	-0.6273	61.2%	230
Manitoba trap	-4.8098	0.1025	-0.0018	0.5865	-0.0132	7.04×10^{-5}	-0.5265	53.3%	224
Males									
Suction trap baited with CO_2	-3.5727	0.0983	-0.0028	0.4342	-0.0074	-	-0.2552	56.3%	198
Manitoba trap	-2.2968	0.0287	-0.0012	0.3255	-0.0062	-	-0.2375	45.3%	192

of day, relative humidity and barometric pressure were not included in the final regression equations. These equations apply only to the following range of conditions from which they were derived:

radiant temperature	9-30°C,
air temperature	9-21°C,
illumination	1.1-176000 lux,
relative humidity	53-100%,
wind speed	0.3-4.5 m/s, and
barometric pressure	989-1017 mb

From the regression equations, seasonal activity curves were plotted for males and females in the two traps (Fig. 3). These show activity during the summer, excluding variation associated with the climatic factors included in the equations. The date of optimum female activity indicated by the regression equations for both traps was 25 July; that for males in the Manitoba trap occurred on 8 July, five days before that in the suction trap baited with carbon dioxide. The optimum radiant temperatures for fly activity derived from the regression equations were 23.7°C for females and 29.3°C for males in the suction trap baited with carbon dioxide and 22.3°C for females and 26.1°C for males in the Manitoba trap. The minimum threshold value of radiant temperature was 11°C for both sexes in each trap.

DISCUSSION

It is important to remember that nearly all the flies trapped in this study are those responding to baited traps, i.e., host-seeking hungry flies. They are not representative of the adult population as a whole.

Trap Comparison

Kellogg & Wright (1962) showed that, with Aedes aegypti (L.), carbon dioxide is associated with an initial activation leading to a general search. In the case of H. irritans, carbon dioxide probably acts as a long-range attractant or activator, and a visual or thermal factor is used at short range for 'homing-in'. It had been noticed in other studies that sweeping a net around the head appeared to attract far more H. irritans than a net held stationary above the head.

It had been hoped that the unbaited suction trap would act as a non-selective trap, sampling the entire active population of H. irritans. However, it caught far more adults than a suction trap camouflaged with bracken fronds, which was compared with it briefly, and it seems likely that the black casing of the unbaited suction trap attracted flies in the same way as the Manitoba trap.

A reduction in the population of H. irritans by artificial means such as intensive trapping might provide effective control. In the United States, Wilson (1968) used sticky traps baited with carbon dioxide to reduce populations of tabanids infesting cattle. Manitoba traps with or without carbon dioxide may have a similar use for control of H. irritans.

Flight Periodicity

The exclusion of time of day (T and T^2) as an independent factor in the multiple regressions shows that the peak at 13.00 h seen in Fig. 1 is associated with climatic factors. Time of day does not act as an intrinsic factor regulating activity. Nielsen et al. (1972), working in Denmark, recorded activity peaks at dawn and dusk. Such sub-crepuscular activity was probably due to the temperature regularly exceeding the optimum through the day. This

seldom occurred in Scotland and is not apparent in Fig. 1. In contrast to the Danish findings, H. irritans was not caught in the traps between 22.00 and 08.00 h, probably because the traps were in the shade between these times.

Seasonal Incidence and the Effect of Weather on Trap Catches

Similar work over several summers is required before the regression equations in Table II could be considered accurate enough for predictive purposes. However, they give good indications of the nature of fly activity under various meteorological conditions and are consistent both in the sign and magnitude of the coefficients and in the climatic factors included.

The unexplained variation could be attributed to the following causes. There were a large number of observations for each sex and trap. The traps do not measure activity precisely, and some accuracy was inevitably lost owing to rapidly changing weather conditions within the trapping periods. The analyses take no account of possible adaptations of the flies to the weather (Digby, 1958), short term migration in and out of the population, or the movement of nearby potential hosts.

Although the inclusion of coefficients for climatic factors in the multiple regression equations does not indicate a causal relationship, other observations tend to confirm that these factors do have an influence on fly activity. Johnson (1969) stated that the warming up of large insects is often achieved by the absorption of radiant heat from the sun. Hughes et al. (1972) found that the activity level of Musca vetustissima Walker rose and fell with air temperature during the day, but radiant heat activated the fly for short periods. Thus, it was not surprising to find that radiant temperature

was associated with a large proportion of the variation in trap catches of H. irritans. Reduction in activity at high temperatures as shown by H. irritans often occurs among flies; for example, activity of M. vetustissima is reduced at temperatures over 35°C (Hughes et al., 1972). The inclusion of a coefficient for illumination in the regression equations confirms the suggestions of Hammer (1941) and Nielsen et al. (1971), who thought that light was an important stimulus for activity of H. irritans. The role of illumination distinct from that of radiant temperature is, however, difficult to understand.

The inclusion of a coefficient for wind speed was to be expected, in view of the dramatic effect of gusts of wind on fly numbers swarming round hosts. Nielsen et al. (1972) stated that activity of H. irritans was negligible at wind speeds above 6 m/s.

The exclusion from the regression equations of a coefficient for relative humidity conflicts with the findings of Hammer (1941) and Tarry & Kirkwood (1976), who suggested that there is an optimum level of humidity. Norris (1966) showed little evidence of an effect of relative humidity on trap response patterns of M. vetustissima.

Rain had an effect that could not be shown in the regression analyses. Light rain had little effect, but activity ceased in heavy rain. Few flies would, in any case, be active in the cool, cloudy conditions associated with rain.

Few studies have satisfactorily shown barometric pressure to exert a significant influence on the flight activity of insects, although Burnett & Hays (1974) found that it was the meteorological factor exerting the greatest influence on tabanid activity.

It is reassuring that the dates of peak female activity, as indicated by the regression equations, are consistent for the two traps. The same consistency is not shown with the males.

Hammer (1941) suggested that there were two generations of H. irritans each year in Denmark, the first emerging in the spring until late July and the second throughout August. The present results show only one main female peak and a very short period of male activity. This suggests that the fly is univoltine, which is in accord with the findings of Tarry & Kirkwood (1976) in southern England.

Fig. 1 Geometric mean numbers of H. irritans caught in a suction trap baited with carbon dioxide at hourly intervals during the day throughout July. Each column shows the numbers caught in a 15-min trapping period starting on the hour.

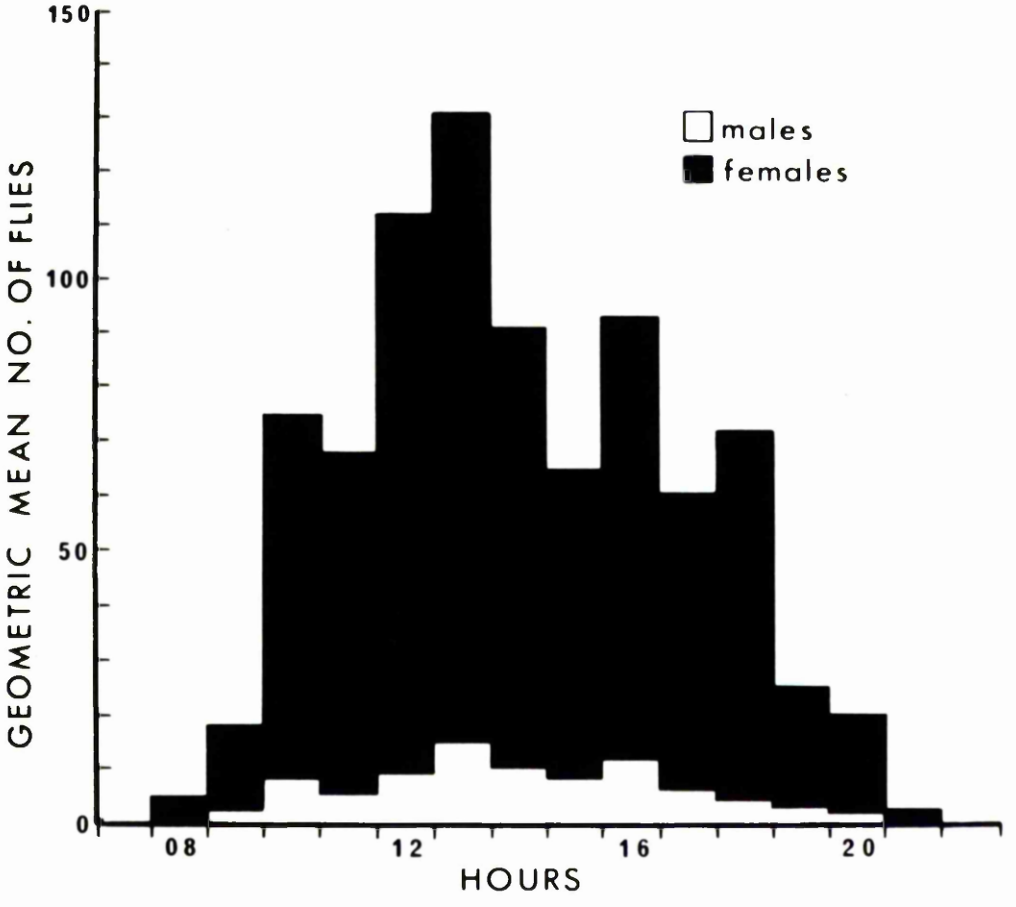

150
100
50
0
GEOMETRIC MEAN NO. OF FLIES
males
females
08
12
16
20
HOURS

Fig. 2 Weekly geometric mean numbers of H. irritans caught in a suction trap baited with carbon dioxide and a Manitoba trap in 15-min trapping periods between 11.00 and 15.00 h from May to October.

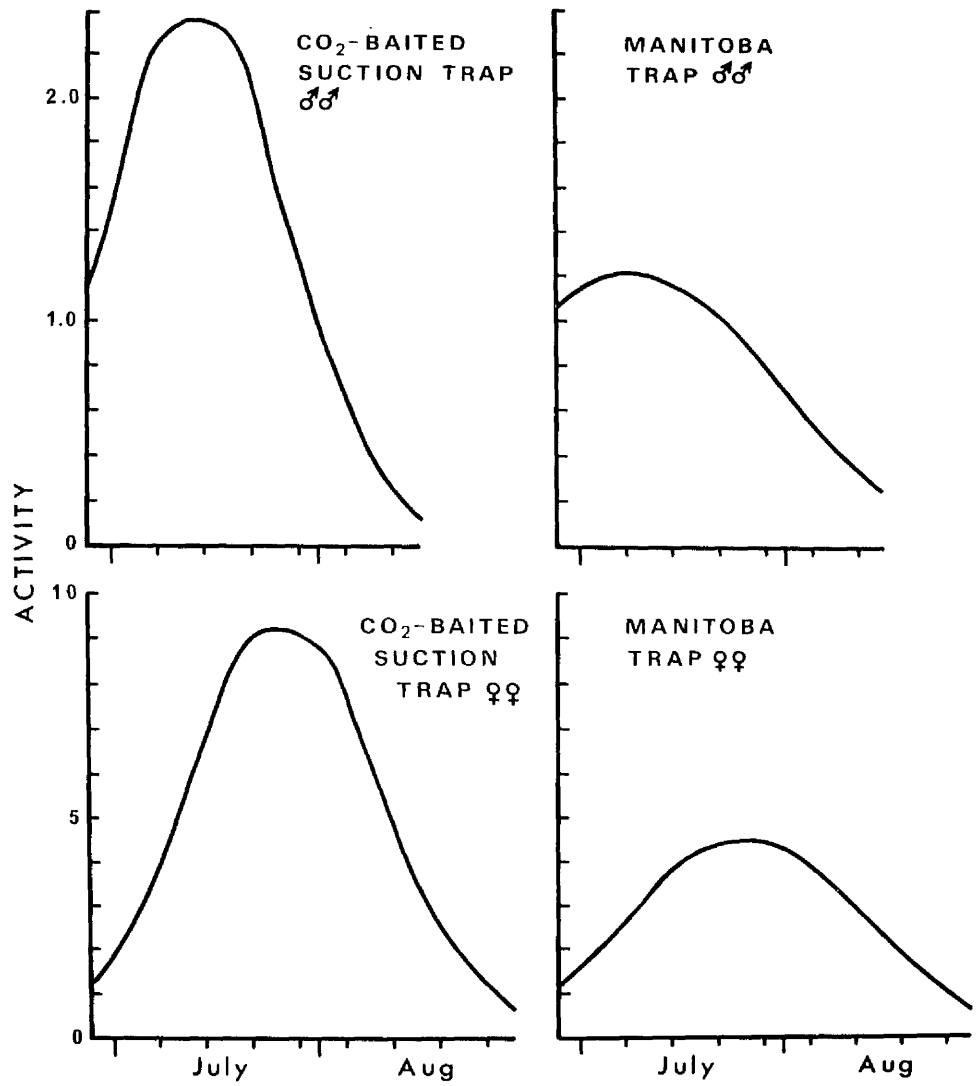
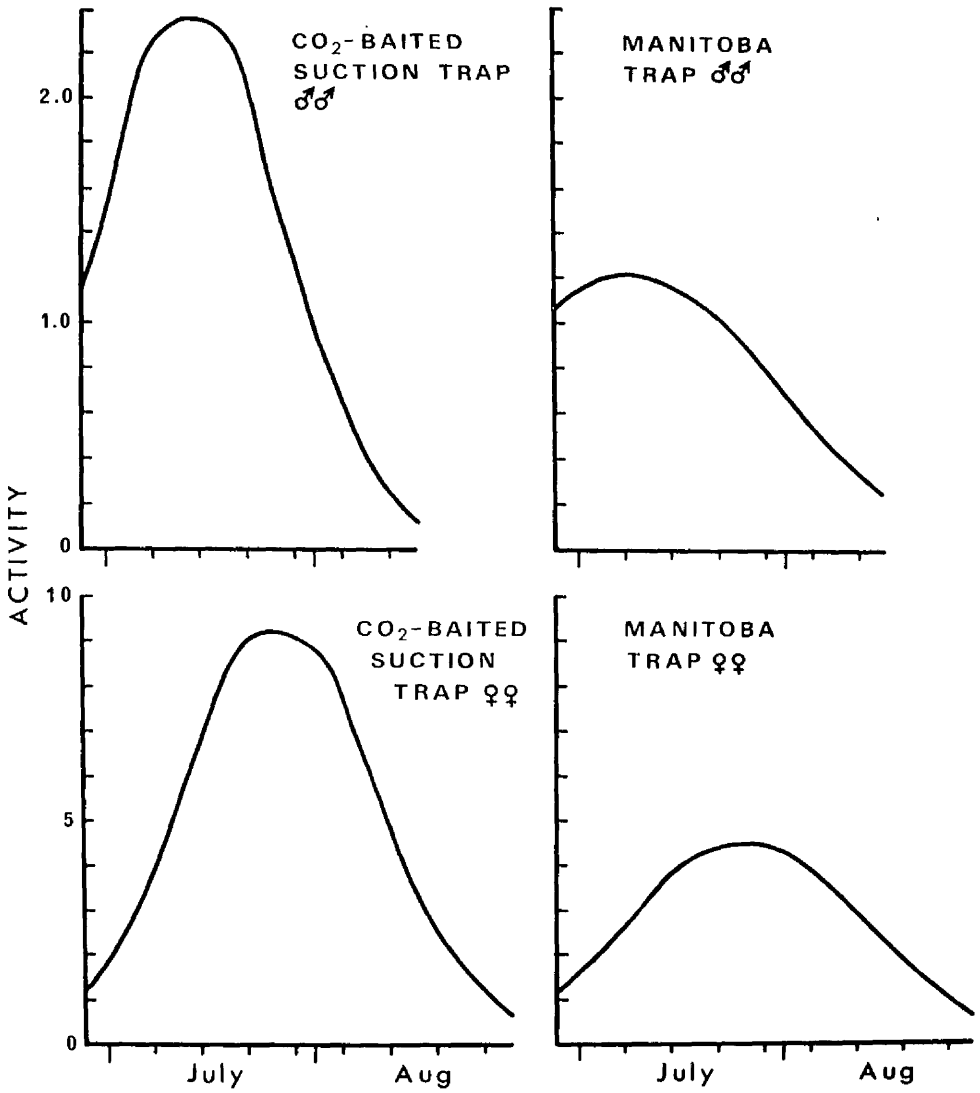

ACTIVITY
2.0
1.0
0
CO_2-BAITED SUCTION TRAP ♂♂
MANITOBA TRAP ♂♂
10
5
0
CO_2-BAITED SUCTION TRAP ♀♀
MANITOBA TRAP ♀♀
July
Aug
July
Aug

Fig. 3 Seasonal activity calculated from multiple regression equations for males and females of H. irritans in a suction trap baited with carbon dioxide and a Manitoba trap. Activity is expressed as a proportion of the activity on 26 June.


ACTIVITY
2.0
1.0
0
CO_2-BAITED SUCTION TRAP ♂♂
MANITOBA TRAP ♂♂
10
5
0
CO_2-BAITED SUCTION TRAP ♀♀
MANITOBA TRAP ♀♀
July
Aug
July
Aug

3. The field biology of the adult sheep headfly, *Hydrotaea irritans* (Fallen) (Diptera: Muscidae), in south-western Scotland

ABSTRACT

Adults of Hydrotaea irritans (Fall.) in south-western Scotland were caught in a Manitoba trap and a black suction trap baited with carbon dioxide. Trapped flies were dissected to investigate their reproductive condition, their blood feeding activity and whether they were newly emerged. Trapping of the first gravid females in August was accompanied by a sharp decline in adult activity. The proportions of females in the various ovarian categories suggested that there is a preliminary phase before host-seeking begins, attraction to animals during most of the cycle and a behavioural change at the end. Females with eggs at stages I, II and III accounted for 94% of all females caught; the only females with blood in the gut were in these categories. Some males also were obviously blood-fed. There was a single mating period lasting five weeks. Inseminated females were first trapped in the third week of July, when the numbers of males started to decline, and within five weeks all females trapped were found to have been inseminated. After this, no more males were caught. Only females with eggs in stages later than stage II of the first ovarian cycle were inseminated. H. irritans was univoltine, with two but not three complete ovarian cycles during the summer. There was no difference in feeding or reproductive development between flies from the two traps.

INTRODUCTION

The sheep headfly, Hydrotaea irritans (Fallen), is common throughout Britain, causing discomfort to man and animals. In the border area between Scotland and England,

the fly causes lesions on the heads of horned sheep. It is also thought to be associated with the transmission of cattle diseases such as summer mastitis and New Forest disease (pink eye). These problems have been discussed in detail by Tarry & Kirkwood (1974, 1976), Titchener (1975) and Berlyn (1978a).

A thorough knowledge of the fly's biology is required before effective long-term control measures can be introduced. To this end, research has been undertaken in Britain and Denmark (Nielsen et al., 1971, 1972; Tarry & Kirkwood, 1974, 1976; Robinson & Luff, 1976; Berlyn, 1978a). Tarry & Kirkwood (1976) in southern England routinely dissected field-caught flies to observe the degree of development of the reproductive system and the presence of a blood-meal in the digestive tract. These aspects of the fly's biology are covered in this chapter, in greater detail, in south-western Scotland.

MATERIALS AND METHODS

An unbiased, non-attractive method of trapping H. irritans has not yet been found. However, the previous chapter describes two methods of bait-trapping that can be standardised. The work reported in this chapter is a continuation of that work, the location, operation and types of traps being the same. Briefly, one trap was a black suction trap, 0.3 m in diameter and 1.3 m high, baited with carbon dioxide released at the rate of 2 litres/min. The other trap was a Manitoba trap (Thorsteinson et al., 1965). This comprised a black sphere suspended beneath a polyethylene collecting cone, which was supported by a tripod. Flies were attracted to the sphere, flew upwards to escape and were

trapped in a container at the cone's apex.

The trapping site was a field in Lanarkshire, Scotland. The suction trap baited with carbon dioxide was operated once a week during May, September and October 1974 and two or three times a week during June, July and August. On these days it ran for five periods of 15 min starting on each hour. The Manitoba trap was operated concurrently with the suction trap in July and August, and the results from the two traps could thus be compared for this limited period.

A preliminary investigation showed that there was no difference in the reproductive status of females caught at different times during the day. Accordingly, a random sample of 20 females caught weekly by each trap was dissected to determine reproductive condition. Egg development was classified according to the six stages described for Musca vetustissima Walker by Tyndale-Biscoe & Hughes (1969). In stage 0, the follicle consists of similar cuboid cells. In stage I, the oocyte can just be seen at the proximal end of the follicle. In stage II, the yolk is evident at the base of the oocyte. In stage III, the yolk occupies one-third to three-quarters of the elongating follicle, while in stage IV the yolk fills almost the entire egg. In stage V, the eggs are fully developed. When the eggs are laid, the eggs of the next batch are already in stage II. Flies were categorised according to the most mature eggs in the ovary unless these eggs were obviously relict ones. Flies were also examined for the presence of sperm in the spermathecae, blood in the gut (having a characteristic red clotted appearance) and floating fat spheres.

RESULTS

Dissections of the flies caught in the suction trap showed (Fig. 4) that females with eggs that had developed beyond stage 0 were first caught after 17 June. Development was gradual and the first mature eggs were observed in the week starting 5 August. No stage-0 eggs were seen after 8 July, and no stage-I eggs after 12 August. Eggs in all other stages were seen throughout the summer. There appeared to be two peaks of gravid, or almost gravid, females, with the start of a third peak indicated by the relatively large number of flies with stage-III eggs caught in the last week of trapping. The first inseminated females caught, in the third week of July, had stage-III eggs. The single mating period appeared to be about five weeks. Females with floating spherical fat globules in the body cavity were caught until 21 July. If the biology of *H. irritans* is similar to that of *M. vetustissima*, it may be assumed that such flies were newly emerged (Tyndale-Biscoe & Hughes, 1969). Weekly variation in blood feeding, as determined by blood in the gut, was significant (χ^2 test; $P < 0.01$). The majority of females with blood in the gut were caught in August, some time after the peak in trap catches and the first appearance of gravid females but coinciding with the most severe damage in sheep.

Blood was found only in females with eggs in stages I, II and III. The percentage of females with eggs in each stage caught weekly, weighted by the geometric mean number of females caught each week, shows that females with eggs in stages I, II and III accounted for over 94% of all females caught (Fig. 5). Gravid (stage V) females accounted for only 0.5% of the total catch of females. Similarly, few flies were

caught with eggs in stages 0 and IV.

There were no significant differences in the presence of blood and immature eggs between flies caught in the two traps. The two traps were thus apparently sampling the same component of the population.

DISCUSSION

The black sphere in the Manitoba trap and the blackness and carbon dioxide of the suction trap influenced the component of the H. irritans population that was being caught. These baits are often used to attract host-seeking haematophagous flies. Thus, the trapped flies do not represent the entire population of H. irritans, merely those responding to the stimuli eliciting food-searching behaviour. If it is assumed that egg stages II to V last approximately the same length of time, as with M. vetustissima (Tyndale-Biscoe & Hughes, 1969), then it would appear that females with eggs in stages IV and V were not often trapped, probably because these flies do not seek a protein meal. Thus, it is not surprising that the first gravid females were caught in the week that the maximum decline in the activity of females occurred, as caclulated from multiple regression equations (Berlyn, 1978a). Service (1973), when trapping Chrysops caecutiens (L.) with ordinary suction traps, also found gravid females accounted for a very low proportion (0.6%) of the total catch. The low numbers of gravid H. irritans females caught suggests that host-seeking behaviour becomes secondary to the search for an oviposition site. Hughes (1974) found that in baited catches of females of M. vetustissima there was a constant pattern of declining numbers of females caught in the successive egg stages, flies

with eggs in stage IV always being the most under-represented. More M. vetustissima with eggs in stage V (gravid) than in stage IV were caught, because the flies were again attracted to the traps, this time seeking a potential source of faeces for oviposition.

Unlike most specialised blood-sucking Diptera, H. irritans appears to take blood-meals throughout much of its ovarian cycle (eggs in stages I-III). It is surprising that females with blood already present in the gut are attracted to the traps. Some M. vetustissima caught in protein-baited traps in the field also had blood in the gut (Hughes, 1974). This similarity between the two species of flies is striking yet not easily explained. Both species feed primarily on body fluids, seeking low protein sources such as tears, saliva, sweat, etc., but will readily take a blood-meal if one is available. The constant urge to take protein meals may be due to the fly having adapted to taking many low concentration protein meals as opposed to one or two high protein meals.

Males also were attracted to the traps in large numbers, and some had blood in the gut. Most muscid males do not require a protein meal before spermatogenesis and subsequent copulation (Tyndale-Biscoe, 1971). This appears to be the case with H. irritans. The first males caught, in June, had sperm in the testes, and it seems unlikely that they could have taken a blood-meal so early in the season, before the females start attacking sheep. It seems probable that the males are attracted to animals only because these provide the females' aggregation sites at which mating can occur.

Berlyn (1978a) used regression analysis to produce an equation from which a male seasonal activity curve up to 14

August could be calculated. This enabled variation associated with climatic factors to be excluded, leaving a curve showing potential activity of males. This shows that the number of males declined markedly in the third week of July, when the first inseminated females were caught (Fig. 6). If the curve is extrapolated beyond 14 August, it indicates extremely low numbers of males. In practice, the last male was caught in the week starting 12 August, after which only inseminated females were trapped. Males kept in an outdoor insectary lived well into October after successful copulation earlier in the season (Berlyn, unpublished). It therefore seems likely that males stay alive but are no longer attracted to the baited traps after copulation. The first inseminated females all had eggs at stage III, suggesting that females are not receptive to mating before this stage. In this case, the inseminated females with eggs at stage II that were trapped in August must have been in at least their second ovarian cycle. The occurrence of several ovarian cycles was also indicated by two peaks of almost gravid females and the presence of relict eggs in inseminated flies with eggs in stages later than stage II.

A discrete period of emergence with a separate distinct mating period shows that H. irritans is univoltine in Scotland, confirming the observations of Tarry & Kirkwood (1976) in southern England.

Fig. 4 The change in reproductive condition and the proportion of blood-fed females trapped in the suction trap baited with carbon dioxide during the summer.

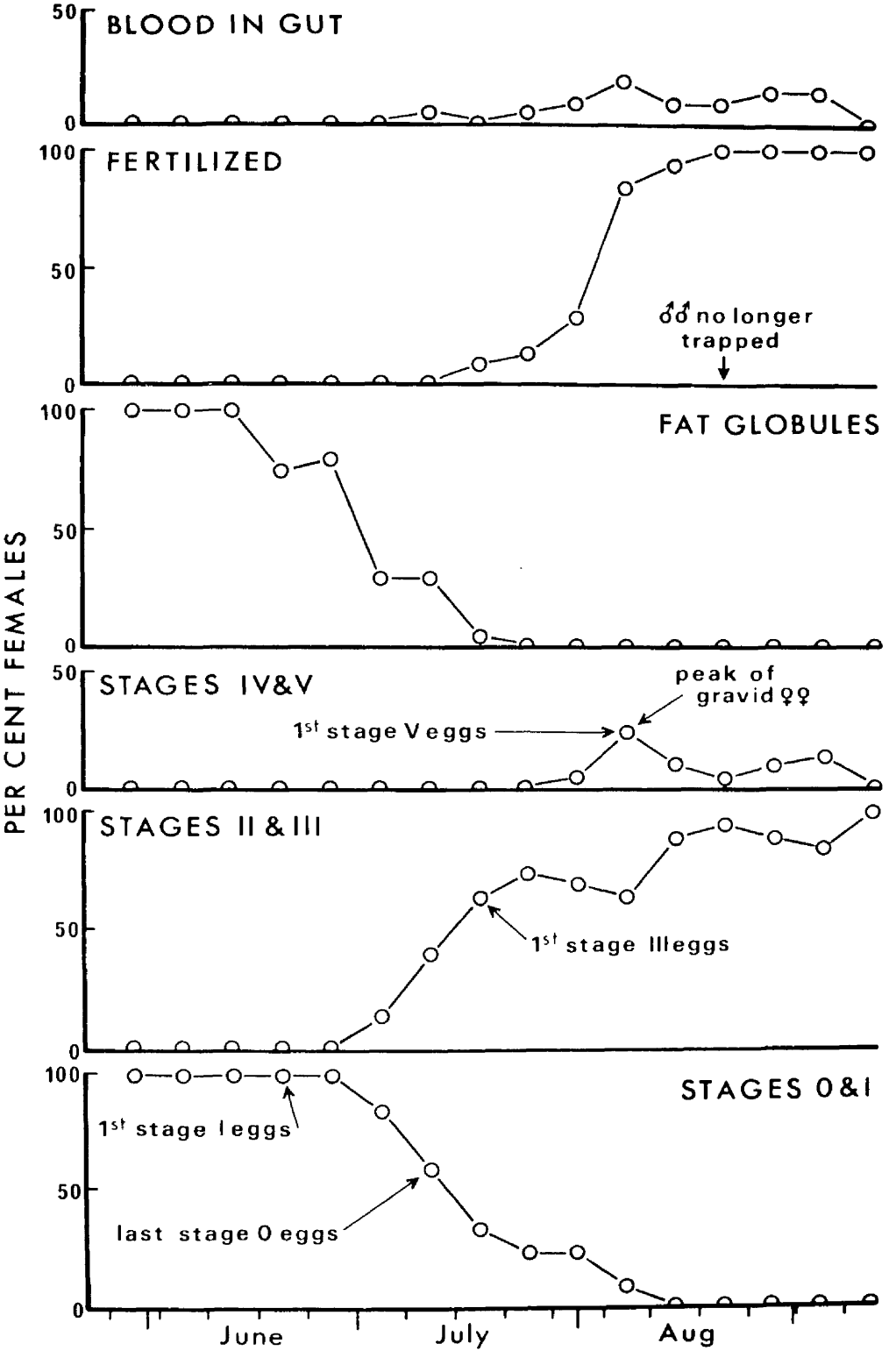

BLOOD IN GUT
FERTILIZED
♂♂ no longer trapped
FAT GLOBULES
STAGES IV&V
peak of gravid ♀♀
1st stage V eggs
STAGES II & III
1st stage III eggs
STAGES 0&I
1st stage I eggs
last stage 0 eggs
PER CENT FEMALES
50
0
100
50
0
June
July
Aug

Fig. 5 The percentages of females with eggs in each stage caught in the suction trap baited with carbon dioxide.

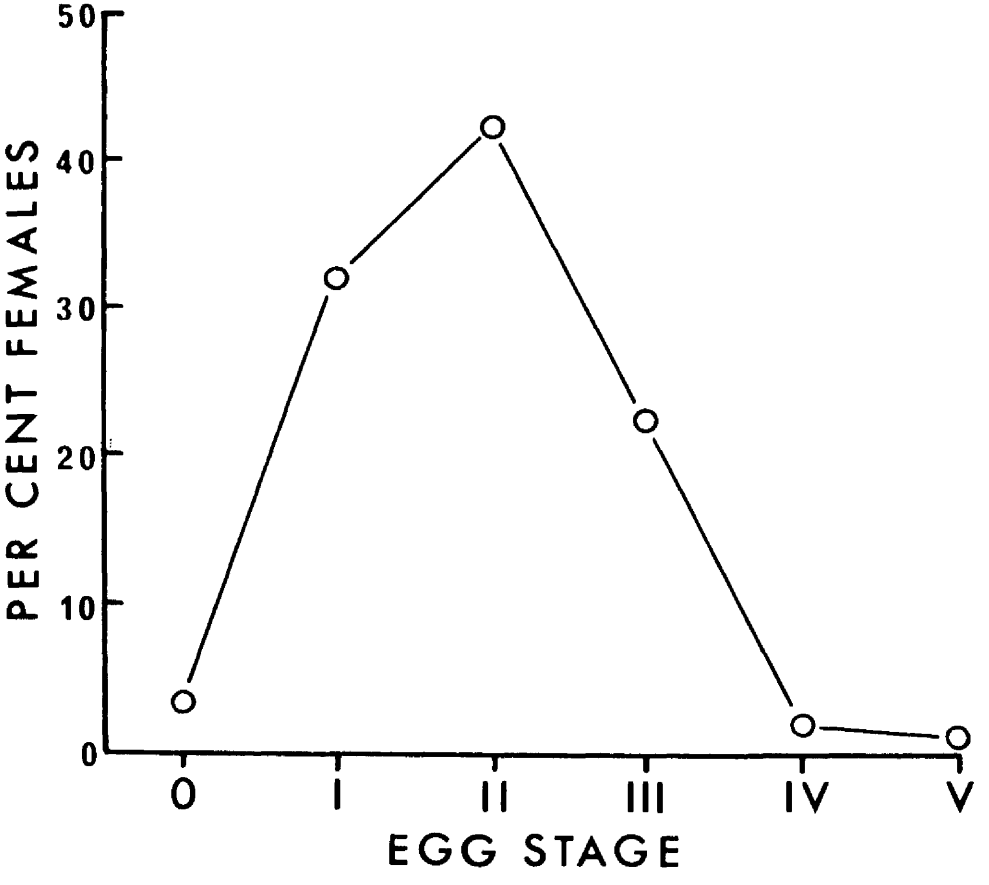
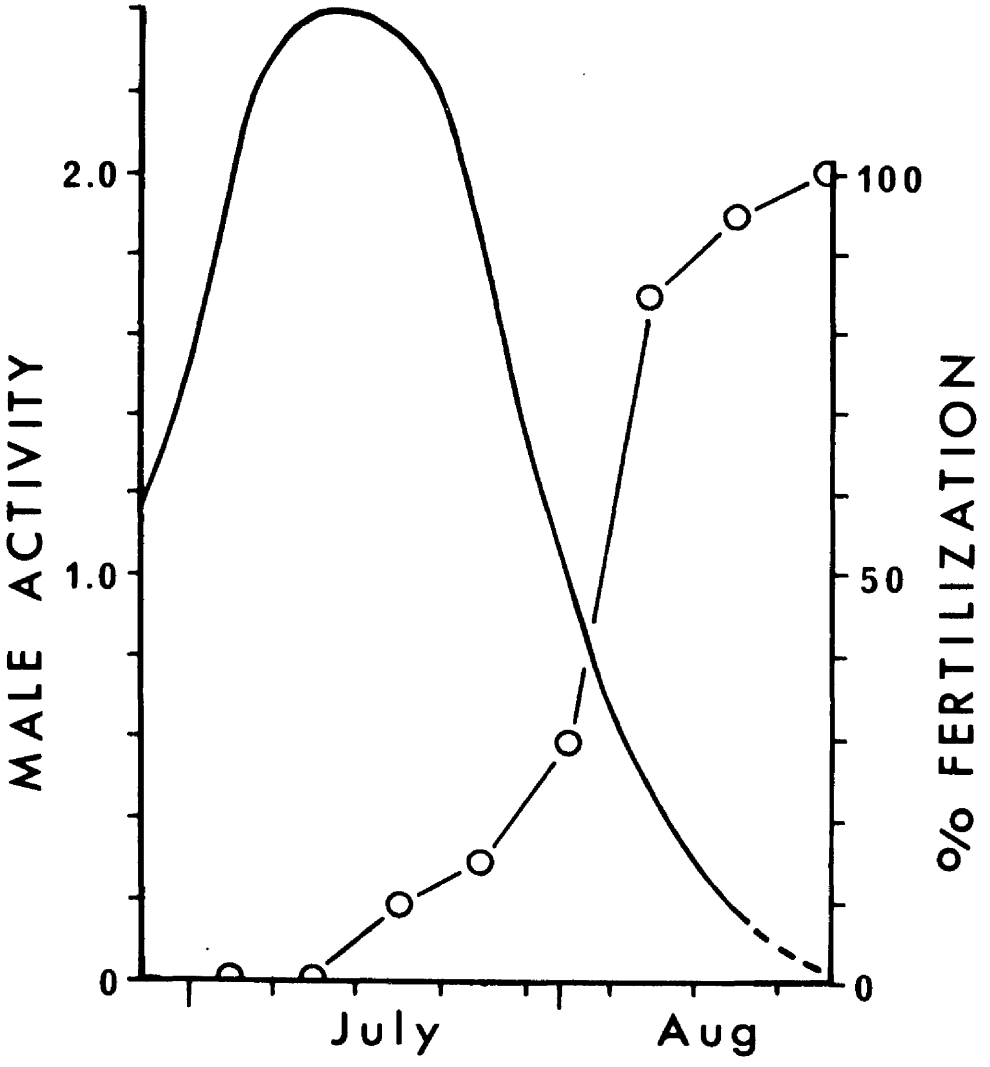

50
40
30
20
10
0
PER CENT FEMALES
0
I
II
III
IV
V
EGG STAGE

Fig. 6 The relation between decline in numbers of males and female insemination. Activity is expressed as a proportion of the activity on 26 June.


MALE ACTIVITY
2.0
1.0
0
% FERTILIZATION
100
50
0
July
Aug

4. Factors attracting the sheep headfly, Hydrotaea irritans (Fallen) (Diptera: Muscidae), with a note on the evaluation of repellents

ABSTRACT

An investigation using modified Manitoba traps on a forest track in Scotland showed that carbon dioxide, coloured spheres, movement, heat, Haematopota pluvialis (L.) and a swarm of other adults of Hydrotaea irritans (Fall.) were attractive. Traps with coloured spheres attracted more flies than traps without spheres. Matt black, shiny black and shiny red spheres attracted more males and females than did shiny green, white or yellow spheres. Significant increases in the number of flies caught did not occur when carbon dioxide was released from a trap at rates above 2 litres/min. Carbon dioxide seems to act as a long-range attractant, with vision becoming important near the host. Manitoba traps were also used with three repellents for H. irritans in order to evaluate the trap's potential for testing repellents.

INTRODUCTION

Berlyn (1978a) (Chapter 2) has shown that the sheep headfly, Hydrotaea irritans (Fallen), is attracted to a suction trap baited with carbon dioxide and to a Manitoba trap baited with a black sphere.

In the present investigation, in the summer of 1976, further use has been made of Manitoba traps to study the various factors that attract H. irritans. In addition, a means of evaluating repellents for H. irritans using Manitoba traps was attempted.

MATERIALS AND METHODS

Manitoba traps modified from those described by

Thorsteinson et al. (1965) were constructed. The framework and support consisted of a collapsible metal tripod with legs 2 m long hinged at their upper ends to the sides of a vertical metal pipe 9 cm long and with an internal diameter of 7.5 cm. A rigid polythene tube, 11 cm long and 7 cm in diameter, was attached to the open apex of a transparent polyethylene cone with a base circumference of 3.5 m. The shape of the cone was maintained by a metal ring 3.6 m in diameter hung from the base of the cone. The tube, with the cone suspended from it, was secured inside the vertical metal pipe so that a 2-cm cuff extended out of the top. A removable polyethylene bag was taped to this cuff. Thus, a polyethylene canopy, with its base 0.65 m from the ground, was supported from a metal tripod with a polyethylene collecting bag at its apex. Attractants were hung beneath the canopy, and adults of H. irritans that were attracted, once under the cone, flew upwards and were trapped in the removable bag.

The work site was a 12-m wide rough track well inside the Ayrshire (Scotland) spruce forest (O.S. grid reference NS 384969).

Investigations of Previously Determined Attractants

Colour. Six plastic spheres (0.5 m in diameter) coloured matt black, shiny black, shiny red, shiny green, shiny yellow and shiny white, were suspended below traps. A seventh trap without a sphere acted as a control. The reflectances of the sphere colours were measured using a Weston Master V exposure meter and expressed as a percentage of the reading for the white one. The numbers of H. irritans caught in each trap were recorded. As Haematopota pluvialis (L.) was also caught in large numbers in the traps, its numbers were also recorded for comparison. The traps

were aligned 6 m apart, and the spheres were randomly interchanged before each of the 28 replicates. This work was completed in two days in early July.

Carbon dioxide. Three traps with suspended red spheres were aligned 6 m apart. Carbon dioxide was released from the middle trap at 0.5, 2.0, 3.0, 4.0 or 5.0 litres/min. The two end traps were the controls. Carbon dioxide was released at a constant rate of 2 litres/min from one of the control traps, and none was released from the other. There were five replicates for each rate of release. The numbers of flies caught were compared between the different rates of carbon dioxide release.

Interaction of Attractants

This experiment was included to clarify the roles of olfactory and visual stimuli in attraction. Four traps were aligned 2 m apart. Red spheres were suspended from these traps except for one end trap, from which carbon dioxide was released at a rate of 2 litres/min. The trap with carbon dioxide was interchanged with the other end trap (with a red sphere) before each of the ten replicates. The numbers of flies caught in each trap were compared.

The traps with red spheres were termed Red 1, Red 2, Red 3; the trap nearest the trap with carbon dioxide always being Red 1 and the furthest trap being Red 3.

Tests of Other Potential Attractants

Potential attractants were suspended, in turn, below the canopy of a trap, and the number of H. irritans caught was compared with the number caught in a control trap.

The positions of the attractants and their controls were interchanged before each new replicate. The potential attractants tested and their controls were as follows:

1. Heat - a hot fan heater was compared with a cold fan heater.

2. Movement - a moving red sphere was compared with a stationary red sphere. An operator positioned equidistant from each trap used a piece of string 15 m long to rock the sphere.

3. A swarm of H. irritans - a white net cage containing about 500 flies was compared with an empty cage.

4. Blood - cotton wool soaked in sheep's blood was compared with cotton wool soaked in red dye.

5. Sheep odour - an ether extract was obtained by wiping cotton wool soaked in ether across the fleece of a sheep; the ether was then evaporated off, and cotton wool soaked in ether extract was compared with cotton wool soaked in pure ether.

6. Sheep odour and red spheres - a red sphere was hung below each trap in addition to cotton wool soaked in ether extract of sheep (see no. 5); the red spheres were included in case the substance being tested acted only as a short-range attractant and a more widespread stimulus was required in addition.

7. Indole solution and red spheres - cotton wool soaked in 2% indole solution was compared with cotton wool soaked in distilled water; red spheres were also hung beneath the traps.

8. Ammonia solution and red spheres - cotton wool soaked in 2% ammonia solution was compared with cotton wool soaked in distilled water; red spheres were also hung beneath the traps.

Repellent Evaluation Using Traps

Four traps with suspended black spheres were aligned

6 m apart along a grassy fire break. Three repellents for H. irritans, a white cream containing citronella (Willington Medicals Ltd.), a dark cream containing 0.5% crotoxyphos in a tar base and a clear cream containing 0.5% crotoxyphos in a clear base (Robert Young & Co. Ltd.), were spread separately over three of the spheres in equal amounts. The fourth trap, without a repellent, constituted a control. Subsequently, on days when flies were active the traps' catches were compared to determine the persistence of the repellents. There were five replicates on each of these days, the traps being randomly rearranged before each replicate.

RESULTS

Investigations of Previously Determined Attractants

Colour. Analysis of transformed (log catch + 1) data showed that there were significant differences in attraction between spheres of different colours (Table III). The order of attraction to the different colours was similar for both males and females of H. irritans. The colours that attracted the greatest numbers were matt black, shiny black and red. Traps with white, green and yellow spheres caught fewer flies, but significantly more than the trap without a sphere. Unlike the females, males were significantly ($P < 0.01$) more attracted to matt black than to shiny black. The numbers of flies attracted to the spheres were inversely proportional to the reflectances as measured by the exposure meter, with the exception of the white sphere.

Haematopota pluvialis was also attracted mostly by the black spheres.

Carbon dioxide. For each replicate, the catch of the

Table III. Mean numbers of males and females of *Hydrotaea irritans* and of *Haematopota pluvialis* caught in Manitoba traps with coloured spheres

Colour	Reflectance as % of white	Mean transformed catch of *H. irritans* Males	Females	Mean catch of *H. pluvialis*
Matt black	63.9	2.68	4.26	2.32
Shiny black	66.7	2.26	4.09	2.82
Red	69.4	1.97	3.47	1.50
White	100.0	1.23	2.30	1.11
Green	75.0	0.90	2.58	0.39
Yellow	88.9	0.78	1.97	0.82
No sphere	-	0.49	1.37	0.32
SED (162 d.f.)		0.14	0.15	0.37

Note: Vertical lines indicate mean catch values that are not significantly different at $P < 0.05$.

trap with varying rates of release of carbon dioxide was transformed (log catch + 1) and expressed as a percentage of the transformed catch of the control trap in which carbon dioxide was released at 2 litres/min. The trap with no output of carbon dioxide could not be used as the control as it did not catch sufficient flies.

When carbon dioxide was released from the trap at 0.5 litres/min, significantly ($P < 0.01$) fewer Hydrotaea irritans were trapped than when it was released at rates of 2 litres/min or more (Table IV). There was no significant difference in attraction between the higher rates of release.

Table IV. Mean transformed numbers of H. irritans attracted to Manitoba traps in which carbon dioxide was released

Rate of CO_2 release (litres/min)	Mean transformed numbers as % of control*
0.5	83.4
2.0	102.4
3.0	102.3
4.0	106.7
5.0	107.1

S.E.D. (20 d.f.) = 6.26

*CO_2 was released from the control trap at 2 litres/min

Interaction of Attractants

Analysis of transformed (log catch + 1) data showed that H. irritans was most attracted ($P < 0.05$) to the trap (Red 1) next to the trap with a carbon dioxide output. Attraction to the traps declined with an increase in distance from the carbon dioxide release point. The catch in the trap baited with carbon dioxide was less than that in Red 1

but not significantly different from that in Red 2.

Tests of Other Potential Attractants

Analysis of transformed (log catch + 1) data showed that of the factors examined only heat, movement and a swarm of Hydrotaea irritans caused significant attraction of H. irritans (Table V).

An incidental observation was made during the experiment on colour attraction. Large numbers of the tabanid Haematopota pluvialis were attracted to the black spheres. On landing, the H. pluvialis were immediately closely surrounded by individuals of Hydrotaea irritans, which thrust their heads close to a tabanid's proboscis. Thus, the tabanids were acting as attractants.

Repellent Evaluation Using Traps

All figures were transformed (log catch + 1), and the daily mean catches in traps with spheres treated with repellent materials are shown in Table VI. The day after their application (day 1) all three repellents provided a significant ($P < 0.01$) reduction in attraction of H. irritans. From day 2 until day 15, only the two repellents containing crotoxyphos provided a significant ($P < 0.01$) reduction in the numbers of flies attracted. Moreover, on days 9, 12 and 15, the trap with white citronella cream was significantly ($P < 0.05$) more attractive than the control.

DISCUSSION

A previous chapter has already shown that H. irritans is attracted by carbon dioxide and black spheres. The present results show that it is also attracted to other colours, heat, movement, Haematopota pluvialis, and a swarm

Table V. The geometric mean catches of *H. irritans* in Manitoba traps baited with various potential attractants

Potential attractant	Geometric mean catch		Number of replicates	t value	Significance
	Attractant	Control			
Heat	39.2	23.6	14	2.87	$P < 0.05$
Movement	33.1	14.1	12	6.49	$P < 0.001$
Swarm of *H. irritans*	69.6	29.2	10	4.47	$P < 0.01$
Blood	17.5	8.8	12	1.85	n.s.
Sheep odour	3.9	8.4	5	1.94	n.s.
Sheep odour and red spheres	31.7	23.1	10	1.66	n.s.
Indole soln. and red spheres	8.4	12.8	8	1.26	n.s.
Ammonia soln. and red spheres	7.6	9.1	6	0.40	n.s.

n.s. = not significant

Table VI. The mean transformed numbers of *H. irritans* attracted to Manitoba traps with black spheres treated with repellents

Repellent	Days after application of repellents 1	2	3	5	9	12	15	17	Mean
Clear cream containing 0.5% crotoxyphos	1.19	1.68	1.56	2.92	2.71	1.94	1.21	1.71	1.86
Dark cream containing 0.5% crotoxyphos	2.29	1.82	1.99	2.59	3.29	2.84	1.69	2.26	2.35
White cream containing citronella	3.08	4.92	4.95	5.05	4.82	4.95	4.15	2.94	4.36
Control	5.64	4.34	4.44	4.61	4.03	3.92	2.33	2.41	3.97
SED (12 d.f.)	0.514	0.420	0.525	0.361	0.310	0.452	0.393	0.416	*0.203

*(117 d.f.)

of Hydrotaea irritans.

As dark and least reflective colours are most attractive to many haematophagous flies (Brett, 1938; Davies, 1951; Barrass, 1960; Pospisil & Zdarek, 1965) it was not surprising that black and red spheres attracted the most H. irritans. The white sphere attracted more flies than expected in view of its very high reflectance, although this appears to be a common phenomenon among haematophagous flies (Brown, 1954; Bracken et al., 1962; Gatehouse & Lewis, 1973). The attraction shown by H. irritans to colours of high and low reflectance is probably because they contrast with the background. Green and yellow spheres, with medium reflectances, did not provide sufficient contrast.

The interaction of colour and carbon dioxide suggested that the latter is of primary importance at the start of the search for a host (it may activate a resting fly or promote taxic behaviour from random flight) and that visual stimuli become more important once the host is in sight, although carbon dioxide probably still exerts a confirming influence. This would explain why the red trap nearest the trap baited with carbon dioxide caught far more flies than the trap baited with carbon dioxide, most flies requiring the final visual stimulus provided by the red sphere.

Heat, in addition to its general use in host-seeking, may also attract H. irritans to deer antler velvet where the flies feed in large numbers (Anon. 1974). The antlers are at a higher temperature than the rest of the body surface due to the large peripheral blood supply of the velvet.

The association between non-biting muscid species (especially Hydrotaea spp.) and biting flies, reported by

Tashiro & Schwardt (1953) and Garcia & Radovsky (1962), is also exhibited by H. irritans in its attraction to Haematopota pluvialis. Nielsen et al. (1972) pointed out that Hydrotaea irritans often feeds simultaneously with biting flies on cattle, and this association may be of considerable importance in the transmission of summer mastitis as many bite wounds are found on the teats of infected cattle.

The attraction of haematophagous flies to others of the same species is less common. The attraction of H. irritans may be due to the black appearance of a swarm, or the noise of swarming flies (noise was not tested as an attractant) or perhaps a pheromonal stimulus. As a swarm of H. irritans indicates the presence of a host or food source, an individual fly will gain an advantage in being attracted to the swarm. Also, as a swarm grows, sheep are increasingly irritated and are more likely to scratch their heads, breaking the skin and causing blood to flow. The swarm as a whole may thus benefit from additional members.

The apparent lack of attraction to host odour and blood is not easily explained. Host odour (in addition to carbon dioxide) is a common attractant for haematophagous flies, but perhaps this is unnecessary for H. irritans because of their marked response to carbon dioxide. Normal attraction to bloody wounds and sweating areas on mammals must be due to a localised response that did not show up significantly in the trap experiments.

The use of Manitoba traps for the preliminary testing of repellents for H. irritans must be given serious consideration in view of the increasingly high cost of animal trials.

5. The distribution of adult *H. irritans* in a spruce forest

ABSTRACT

The extent of activity of adults sheep headfly, Hydrotaea irritans (Fall.), in various habitats in a spruce forest was investigated using Manitoba traps. Most headflies were trapped in a firebreak or on a rough track. Least flies were caught within a clearing or thicket. It is suggested that in softwood plantations headflies use firebreaks and tracks as flight paths and rarely fly amongst the trees.

INTRODUCTION

Hammer (1941), Nielsen, Nielsen & Christensen (1971) and Tarry (1973) all stated that Hydrotaea irritans (Fall.) was most active near woodland. Nielsen et al. (1971) reported that it was less active in thickets. However, no data were given to support these suggestions. The present investigation was a brief attempt to determine in which habitats of a spruce forest the headfly was most active.

MATERIAL AND METHOD

An Ayrshire spruce forest (O.S. grid reference NS 384969) was the site of the investigation. Five Manitoba traps were constructed according to Berlyn (1978c) and erected separately at five sites in the forest within 500 m of one another.

The five sites were:

1. An area of unthinned spruce trees within the forest.
2. Halfway across a 6 m wide firebreak.
3. Halfway across a 16.5 m wide forest track.

4. The centre of a round clearing 13 m in diameter surrounded by trees, but separated from a track by only one row of trees on part of its perimeter.

5. Halfway across a stretch of open land, 130 m wide, between two plantations in the middle of the forest.

The traps were left in position for ten days and the number of flies caught in each was recorded daily. The traps were operating concurrently.

RESULTS

Analysis was on transformed ($\log_e$ catch + 1) values and the results are shown in Table VII. The greatest numbers of headflies were trapped on the track and the firebreak. Fewer flies were caught in the Manitoba traps in the open stretch of land and in the circular clearing, while least flies were caught within the trees.

DISCUSSION

The results confirm the findings of Hammer (1941), Nielsen *et al.* (1971) and Tarry (1973) that the activity of *H. irritans* is greatest along woodland margins. Nielsen *et al.* (1971) also found that activity was slight in thickets. The large numbers of headflies caught on the margin of the wood suggest that the flies use the firebreaks and tracks as flight paths. The few flies caught in the clearing, despite its close proximity to a track, show that few flies enter the wood. (However, the writer has observed that different behaviour is exhibited in deciduous woodland.) Thus, sufficient headfly control may be obtained by insecticidal spraying of the outmost trees of the forest.

Table VII Mean transformed numbers of *H. irritans* caught in Manitoba traps positioned at different sites.

Geometric means are given in parentheses.

Site	Mean transformed no. of headflies
Dense trees	0.138 (0.15)
Clearing	1.492 (3.45)
Open land	2.467 (10.79)
Track	3.459 (30.79)
Firebreak	3.615 (36.15)

SED (36 d.f.) = 0.374

The numbers of flies caught in the open stretch of land do not necessarily indicate an avoidance of open land, as suggested by Hammer (1941). Trees on the edges of woodland are the resting sites of headflies. If there is more open land adjacent to a woodland margin, flying headflies will become more dispersed and a trap here will catch fewer flies than one in a narrow firebreak. Alternatively, the headflies may fly alongside the forest, only leaving it when a potential host is detected. A Manitoba trap without the long range stimulus of carbon dioxide would thus catch fewer flies when sited further from the forest.

6. The vertical distribution of adult *H. irritans*

ABSTRACT

The vertical distribution of the sheep headfly, Hydrotaea irritans (Fall.) was investigated. The apparatus used appeared to repel the flies and no valid results were obtained.

INTRODUCTION

The purpose of the present investigation was to determine if the height above the ground of a suction trap affected the number of H. irritans (Fall.) caught. In addition, it was hoped to detect whether different components of the population (as determined by sex or ovarian development) were trapped at different heights, and whether flight height varied throughout the day.

MATERIAL AND METHOD

A 3 m high handy angle tower was erected above a deep trench at the side of a field bordered by a wood containing headflies. A carbon dioxide-baited suction trap constructed according to Berlyn (1978a) could be suspended from the tower or placed in the trench. In the latter position the fan intake was level with the ground. A plank of wood covered the trench. At one end there was a hole for the trap fan intake, and at the other end there was a vent through which air could be channelled away from the fan output, thus preventing turbulence around the trap.

Additionally, the trap was suspended from the tower in three positions such that its intake was 1, 2 and 3 m above ground level.

The trap was operated for five periods of 10 minutes in

each position. A carbon dioxide-baited suction trap, with its intake 1 m above ground level, was operated simultaneously as a control 20 m away at the side of the field. The number of headflies caught in each trapping interval in each trap was recorded.

RESULTS

A total of over 1,000 headflies was caught in the control trap, but only 15 were caught in the experimental trap and statistical analysis of the results was impossible.

DISCUSSION

Although the present results were of no value, it would be useful to determine the vertical distribution of the headfly. Further experimental possibilities include the suspension of a suction trap by a rope from a high branch of a tree. In the present experiment the tower appeared to have acted as a repellent.

Chapter 7: The effect of dieton the longevity and egg maturation of caged *H. irritans* (Diptera: Muscidae)

ABSTRACT

A method for maintaining adults of Hydrotaea irritans (Fall.) in captivity in groups, pairs or singly is described. Male flies lived about half as long as females. Flies required carbohydrate and water for survival. A 50% honey solution, a 50% sucrose solution, thistle flowers and aphid honeydew all met the energy requirements of H. irritans, unlike blood, serum, milk, sweat, dung and mucus. The number of eggs matured was greatest on a diet of carbohydrate with blood or serum. Fewer eggs developed in flies given a diet of carbohydrate with milk, and very few on a diet of carbohydrate with horse sweat, cow sweat, dung or mucus. No eggs were matured by females fed on carbohydrate alone. All males had active spermatozoa whether or not they were fed on blood, but females were only inseminated after both they and the males with which they were kept had been given blood. The insemination rate was low at 13.3%. Females required more than one blood-meal, but not more than one every third week, in order to develop the maximum number of eggs.

INTRODUCTION

The adult sheep headfly, *Hydrotaea irritans* (Fallen), is attracted in large numbers to animals. It congregates mainly around the head, apparently feeding on sweat, lacrymal fluid, mucus secretions of the muzzle and blood from wounds. In the case of horned sheep, it may feed on blood which is produced when the skin on the head is broken by the sheep's repeated scratching and rubbing to alleviate irritation caused by the fly. *H. irritans* has also been observed feeding on wounds and on possible secretions of the teats of cattle.

In the present investigation, the effects of various food sources on the life-span and egg maturation of *H. irritans* were studied.

MATERIALS AND METHODS

Flies were enclosed either singly or in pairs in vertical open-ended glass cylinders 4.5 cm in diameter and 10 cm tall (Fig. 7). Two small plastic tubes 0.5 cm in diameter and 4 cm tall were glued to the inside wall of the cylinder and filled with the appropriate food. The top end of each glass cylinder was covered with nylon netting secured by an elastic band. The bottom end was placed in a plastic tub containing moist peat. Holes were made in the bottoms of these tubs, which were placed, with others, on water-filled trays. This ensured that the moisture content of the peat remained constant and that all flies had equal access to water. Larger glass cylinders 5 cm by 10 cm contained groups of five flies.

The flies were kept in an outdoor insectary, the walls

of which consisted of alternating vertical strips of polyethylene and nylon gauze. This enabled the flies to live in conditions approximating to those in the field. The roof was constructed from transparent PVC sheeting.

No mass-rearing technique had been developed for H. irritans, so the flies used in these experiments were caught in June at the start of seasonal activity. A sample of flies was dissected and the guts of males and females were examined for the presence of blood. None was found. As blood is noticeable in the gut for several days after a feed (unpublished observation) and the flies were caught on their first day of apparent host-seeking activity, it may be assumed that they had not obtained a blood meal before capture. Further examination revealed an absence of spermatozoa in the spermathecae indicating that the females were virgins. Active spermatozoa was found in the males' testes. Once caught, flies were kept in net cages and given a 50% honey solution until the experiments began.

Life-span and Egg Maturation on a Diet of Blood and Honey Solution

The treatments were set up on 25 June. Flies were kept individually in cylinders and fed on their respective diets until 21 July, when the majority of males and females were paired. The food then given to each pair was that part of the two diets previously common to both flies.

Treatments consisted of the following combinations of flies fed on different diets:

(1) 30 females given blood and honey solution, paired with 30 males given blood and honey solution and thereafter fed on blood and honey solution;

(2) 30 females given blood and honey solution, paired

with 30 males given honey solution only and thereafter fed on honey solution only;

(3) 30 females given blood and honey solution and not paired;

(4) 30 females given honey solution only, paired with males given blood and honey solution and thereafter both sexes fed on honey solution only; and

(5) 30 flies of both sexes fed on blood only and 30 flies of both sexes not given food other than water. No flies from these treatments lived lived long enough to be paired.

Dead flies and the number of eggs laid were recorded and removed from the cylinders twice a week. Dead females were dissected and examined for the presence of sperm in the spermathecae, and the numbers of mature unlaid eggs were recorded.

Protein Sources

Groups of five flies were kept in the larger glass cylinders. Ten groups of flies were allocated to each of the following seven protein sources:

(1) defibrinated sheep's blood;

(2) horse serum;

(3) pasteurised milk;

(4) horse sweat;

(5) a 2% solution of cow sweat;

(6) cow dung; and

(7) mucus (cotton wool wipings of the nose and muzzle of dairy cattle).

Five groups fed on each protein source were given honey solution in addition. The amount of food available to the

flies was not restricted. Control treatments comprised five groups of flies fed on honey solution alone and five groups not fed at all.

Dead flies and the numbers of eggs laid were recorded and removed from the cylinders twice a week. Dead females were dissected, and the number of mature unlaid eggs they contained was recorded.

Number of Blood Meals Required

Five groups of five flies were fed at each of the following intervals:

(1) blood continuously available (to save unnecessary duplication, this was the same treatment and flies as for treatment (1) of the previous experiment);

(2) one blood-meal each week;

(3) one blood-meal at the start of the experiment on 25 June and once every third week subsequently; and

(4) one blood-meal at the start of the experiment and no more.

All flies were given unlimited honey solution in addition to their protein allowance. The numbers of eggs laid were recorded and removed twice a week. Dead flies were dissected, and the numbers of mature eggs they contained were recorded.

Carbohydrate Sources

Five groups of five female flies were given unlimited honey solution, and five groups were given unlimited 50% sucrose solution. The numbers of dead flies were recorded daily.

In the second experiment, the possible natural sources of carbohydrate were investigated. Greenberg (1971) mentioned that H. irritans adults aggregate on the

inflorescences of daucacious plants infested with aphids. Berlyn (unpublished observation) noticed many adult H. irritans on the thistle Cirsium palustre. To investigate some possible natural sources of carbohydrate available to H. irritans, five groups of five flies were allowed access to thistle inflorescences (the inflorescences were not replaced as they died) and five groups had access to Phragmites communis leaves covered in aphids. Five control groups were given Phragmites leaves with no aphids. The numbers of dead flies were recorded daily.

Water Requirement

Flies were kept in groups of five with dry peat. Six groups of flies were each given an inflorescence of the thistle C. palustre and cattle saliva. Six groups were each given a thistle inflorescence and water. Six groups were each given a thistle inflorescence only, and six groups were given nothing. The numbers of dead flies were recorded daily. The thistle inflorescences were not replaced as they died.

RESULTS

Life-span on a Diet of Blood and Honey Solution

There were significant differences in the mean life-spans of both males and females fed on different diets (Table VIII).

Egg Maturation on a Diet of Blood and Honey Solution

The number of eggs laid plus the number of mature eggs dissected from dead gravid females was regarded as the total number of eggs matured by each fly.

Females fed on blood and honey solution throughout, whether paired or not, matured similar numbers of eggs (TableVIII). Females that were not fed on blood after pairing matured significantly fewer eggs while females that were never fed on blood developed no mature eggs. Dissection showed that eggs in this latter treatment were developed only to stage III while all other treatments exhibited mature eggs (the description of the egg stages follows that described for Musca vetustissima Walker by Tyndale-Biscoe & Hughes (1969)). Females given no food or only blood died before any egg development occurred.

Egg laying trends in the three treatments are shown in Fig. 8 . Females fed on blood and honey throughout and paired with males are probably most typical of flies in the field. In this treatment, the first eggs were laid on 18 July, in the fourth week after the flies were first offered blood. Berlyn (1978b), trapping field flies, found the first gravid females in the fourth week after blood was first identified in the gut of trapped flies. With caged flies the majority of eggs were laid by 12 September although small numbers were laid until 22 November, obviously a more extended oviposition period than that in the field. The number of ovarian cycles undergone should have been apparent from the individually caged female flies. Unfortunately, the cycles merged into one another due to continuous oviposition throughout the summer. However, when the treatment as a whole is considered, three egg-laying peaks are discernible in the last week of July, the third week of August and the second week of September (Fig. 8). These may indicate three ovarian cycles.

Inseminated females were found only in the treatment

Table VIII The life-span of males and females, and the egg maturation of females, fed on blood and honey

	Diet before pairing		Diet after pairing		Mean life-span (days)	Mean $\log_e(n+1)$ no. of eggs matured
	Blood	Honey	Blood	Honey		
Females	-	+	-	+	149.4	0
	+	+	-	+	107.3	1.94
	+	+	not paired		113.7	3.27
	+	+	+	+	104.6	3.04
	+	-	not paired		1.8	0
	-	-	not paired		2.3	0
	SED				9.99 (174 d.f.)	0.32 (87 d.f.)
Males	+	+	-	+	83.8	-
	+	+	+	+	67.0	-
	-	+	-	+	66.2	-
	+	-	not paired		1.4	-
	-	-	not paired		1.8	-
	SED				4.75 (145 d.f.)	-

\+ indicates inclusion in diet
\- " absence from diet
Vertical lines indicate values not significantly different at $P < 0.05$.

where both males and females were offered blood. Some eggs in this treatment produced larvae. Only 13.3% of the females were inseminated. Like most muscid flies, the uninseminated females developed and laid sterile eggs. Males of all treatments contained active spermatozoa. Males that achieved successful copulation lived as long as other males on that diet.

No relationship between size of fly and the number of eggs matured was found in females fed on blood and honey solution when measured across the frontal lobe of the head (the region between the eyes).

Protein Sources

As all the flies of one of the five groups fed on blood and honey solution died within the first week of the experiment, only four groups of flies could be included in the analysis.

Analysis, using $\log_e(\underline{n} + 1)$ values, of the protein treatments with the addition of honey solution showed there were highly significant differences in the numbers of eggs developed to maturity between flies in the different treatments (Table IX). The mean numbers of eggs laid by flies in each treatment were greater than that laid by flies fed on honey solution alone, which was nil. Flies fed on blood, serum and milk produced significantly ($P < 0.05$) more eggs than flies on the other treatments, and milk was significantly inferior ($P < 0.05$) to blood and serum as a protein source. The rate of development also varied greatly; females given horse sweat took 40 days longer to lay the first eggs than did flies fed on blood or serum.

There were no significant differences between the

Table IX Numbers of eggs matured by females fed on different sources of protein

Protein source	Number of replications	Mean $\log_e$ no. of eggs matured	Geometric mean no. of eggs matured
Blood	4	5.01	149.1
Serum	5	4.79	119.5
Milk	5	3.27	25.2
Mucus	5	1.58	3.9
Horse sweat	5	1.57	3.8
Cowdung	5	0.93	1.5
Cow sweat	5	0.69	1.0

SED (27 d.f.) when comparing protein sources other than blood = 0.599

when comparing blood treatment with any other = 0.635

Vertical lines indicate values not significantly different at $P < 0.05$.

Table X Number of eggs matured by females given different numbers of blood-meals

No. of blood-meals offered	Mean $\log_e$ no. of eggs matured	Geometric mean no. of eggs matured
1. Blood continuously available	5.01	148.9
2. One each week	4.99	145.9
3. One each third week	4.92	136.0
4. One only	3.89	47.9

SED (15 d.f.) comparing 1 with any other 0.267

Comparing 2,3&4 0.251

Vertical lines indicate values not singificantly different at $P < 0.05$.

life-spans of females fed on different protein sources without honey solution. Females fed on the protein sources did not live significantly longer than females that were not fed at all, indicating that the protein sources (with the small amount of associated carbohydrate and fat) were not contributing sufficiently to the energy requirements of the flies. Neither was any part of the protein meal being oxidised directly for this purpose.

Number of Blood-meals Required

The numbers of mature eggs produced by females in the different treatments are shown in Table X. Females fed on blood once only, at the start of the season, laid about one-third of the number of eggs laid by others given blood continuously. Analysis using $\log_e(n + 1)$ values, showed this was a significant reduction. The results from the other treatments were not significantly different from one another indicating that for maximum egg maturation females require no more than four or five good sized blood-meals during the summer.

The three ovarian cycles present in females fed on blood continuously were not apparent in those fed on blood once only (Fig. 9). Instead, there appeared to be only one ovarian cycle, with oviposition commencing a week later and with fewer eggs laid at its peak. It is noticeable that, except for one slight difference, the egg laying peaks of the continuously blood fed females occur at exactly the same time as those of the individually caged females.

Carbohydrate Source

Analysis showed no significant difference in mean life-span between females fed on honey and those fed on sucrose

solution. Flies in this experiment lived for a much shorter period than expected as a result of infection with the parasitic fungus Entomophthora muscae, from which many died.

Females given thistle inflorescences lived significantly longer (mean = 7.88 days) than those given access to aphid honeydew (mean = 4.04 days)m which in turn lived significantly longer than females given no obvious food source (mean = 1.76 days; SED (72 d.f.) = 1.14). The aphids left the Phragmites after a few days, and this may account for the difference in life-span between flies given aphid honeydew and those given thistle inflorescences. Flies in neither of these treatments lived for long because the carbohydrate sources were not replenished.

Water Requirement

The life-span of females given water (mean = 2.86 days) and cattle saliva (mean = 2.73 days) in addition to thistle inflorescences were significantly greater than those of flies given thistle inflorescences alone (mean = 1.86 days) and no food or water (mean = 1.70 days; SED (116 d.f.) = 0.08).

DISCUSSION

A source of protein is certainly required for the successful development of eggs by H. irritans, and the results clearly show the advantages of a blood or serum meal. Kirkwood (1976) found that the rate of egg development did not vary in H. irritans females fed on blood, serum, milk or egg white, and that the choice of protein was not critical. However, the present results show that although milk supported egg development it was markedly inferior to blood or serum. This was to be expected with a specialised blood-feeder.

Even Lucilia cuprina (Wiedemann,), a general feeder, exhibits slower egg development on casein, milk, yeast and egg albumen than on liver (Webber, 1958). The other natural protein sources tested on H. irritans (sweat, dung and mucus), which Kirkwood did not try, appear to be of little use as protein sources, although better than a carbohydrate source alone. This is in contrast to M. vetustissima which can utilise vegetable or dung protein if continuously supplied (Tyndale-Biscoe & Hughes, 1969). It is possible that H. irritans feeds on facial secretions to provide its water requirements.

That caged females require more than one blood-meal but less than one every three weeks must be extended to the field situation with care. Captive flies were able to imbibe blood freely with no constraints upon them. In the field, they would be subject to climatic variations, host movements, competition with other flies, etc., and it is unlikely that they could ever ingest such large quantities of blood in one meal as they did in the insectary. However, the result could explain the ability of H. irritans to live within extensive Scottish forests where virtually the only mammals available for a blood-meal are widely dispersed deer and rabbits (the natural hosts of the fly in Britain). The fly would not have the opportunity to feed on such animals frequently.

The role of blood in the reproductive biology of the male is not clear. From the start of the season, before a blood-meal, males had active spermatozoa in their testes. Nevertheless, the absence of any insemination in treatments where the male had no access to blood must be of significance. Mammals, the natural source of blood, may be regarded as

aggregation sites, and blood feeding by males may be a behavioural mechanism whereby they come into contact with the females. Females of Glossina pallidipes (Austen) are inseminated near the host while seeking their first blood-meal (Saunders, 1962). This explains the 'following swarm' of 'sexually appetitive' males which follows a host (Fiske, 1920). It is known that odours of aggregation sites can stimulate male sexual behaviour; males of L. cuprina are stimulated by the odour of sheep liver (Shorey, Bartell & Barton Browne, 1969). Stimulation of male H. irritans by aggregation site odours could be the reason for the restriction of insemination to treatments in which both males and females were given blood. The low level of insemination in these treatments must have a different cause and could possibly be explained by behaviour similar to that of G. morsitans (Westwood) where most effective pairing is obtained with older non-virgin males and young females, and where the male to female ratio is important; a ratio of 2:1 with older males gave insemination rates of about 90% (Southon & Cockings, 1963). Alternatively, considerable space may be required in order to perform a successful mating flight.

Not all haematophagous flies require a carbohydrate source in addition to blood. Bursell (1970) stated that Glossina oxidises directly a part of the proline and glutamate intake of each blood-meal to meet current energy requirements. This is evidently not the case with H. irritans and in addition, the 0.1% carbohydrate content of blood must be too low for noticeable use. The blood meal, then, must be taken solely for a reproductive purpose, while thistle flowers and aphid honeydew provide probable natural carbohydrate sources.

Females feeding on blood and honey solution had a shorter life than females feeding only on honey solution, probably due to egg development using resources from the fly and inducing earlier senescence. Blood appears to have had no effect on the production of spermatozoa by males, which is possibly why it did not reduce length of life.

Fig. 7 . Glass cylinder apparatus in which flies were kept.

a - nylon netting secured by elastic band

b - plastic tube

c - glass cylinder

d - plastic tub

e - moist peat

f - tray of water

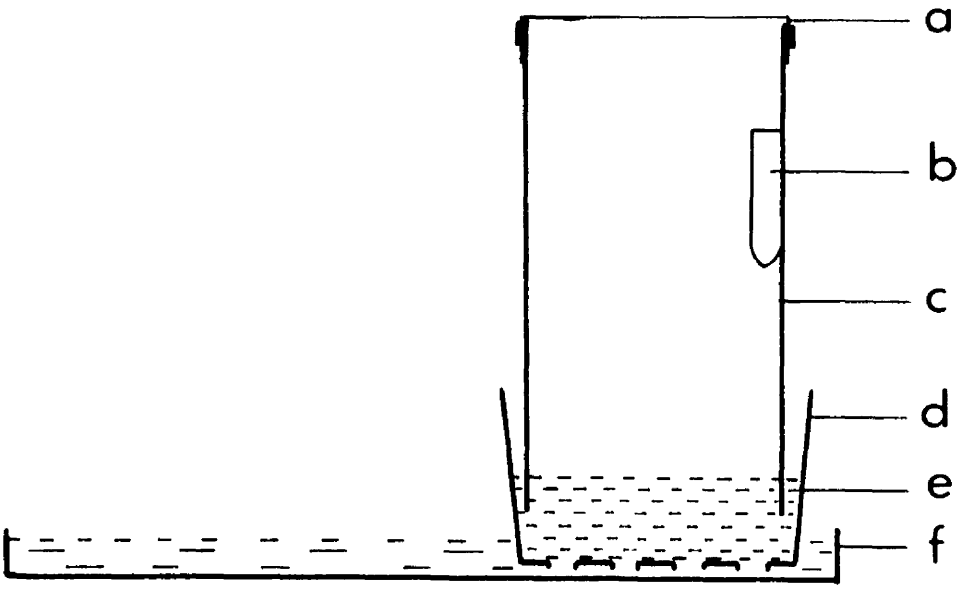

a
b
c
d
e
f

Fig. 8 . The total number of eggs laid each week by:

(a) 30 females fed on honey and blood throughout and not paired with males;

(b) 30 females fed on blood up to the time of pairing with males, and only honey subsequently; and

(c) 30 females fed on blood and honey throughout and paired with males.

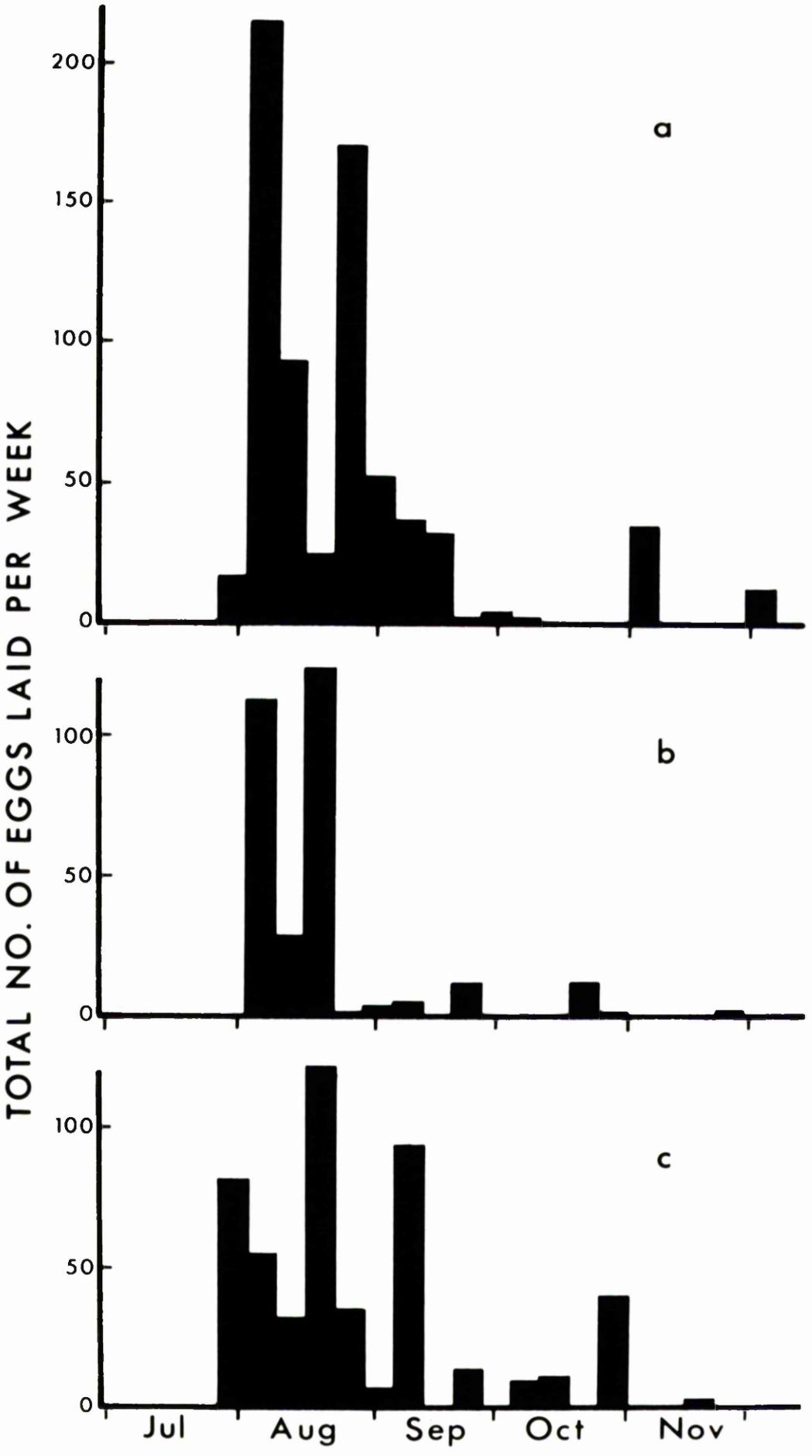
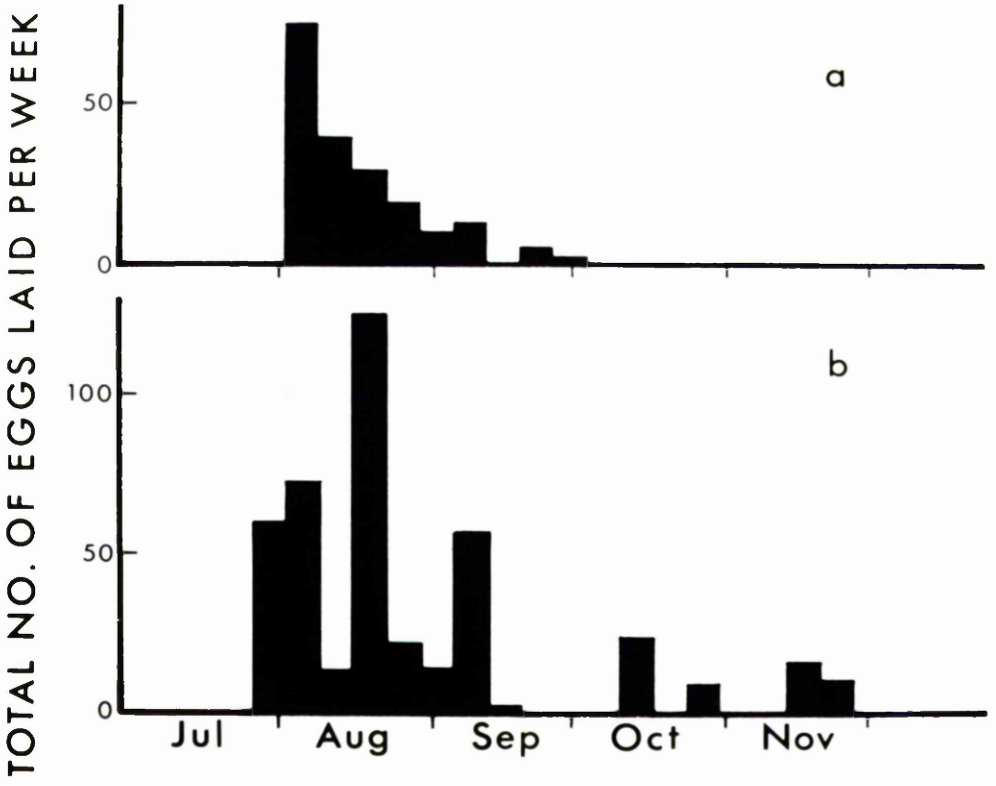

TOTAL NO. OF EGGS LAID PER WEEK
200
150
100
50
0
a
100
50
0
b
100
50
0
c
Jul
Aug
Sep
Oct
Nov

Fig. 9. The total number of eggs laid each week by:

(a) 30 females fed on blood once only; and

(b) 30 females fed on blood continuously.


TOTAL NO. OF EGGS LAID PER WEEK
50
0
a
100
50
0
b
Jul
Aug
Sep
Oct
Nov

Supplement to Chapter 7

SUPPLEMENT TO CHAPTER 7

It was stated earlier that H. irritans is highly attracted to the antler velvet of Red deer where it settles between the hairs and feeds on blood. At times of high headfly activity the antlers appear black and the velvet cannot be seen through the mass of feeding flies.

Although the precise method is unknown, the fly feeds on the extensive peripheral blood supply of the velvet. At an experimental Red deer farm in Kincardineshire a Red deer stag was immobilised and the hairs were shaved off the antler velvet, exposing a large number of small pustules. These are likely to have been septic midge bites as large numbers of midges, Culicoides impunctatus Goetghebur, feed in the velvet. Also present were small holes about 1 mm in diameter which could have been caused by the well developed prestomal teeth of H. irritans rasping at these pustules (where the skin is weaker). Thus the headfly could create an open wound and obtain a blood meal. Tarry (1975) demonstrated that in the laboratory H. irritans could penetrate entirely the shaved epidermis of a guinea-pig by scraping with its greatly enlarged prestomal teeth.

Female headflies were trapped with sweepnets from two Ayrshire woodland sites in July 1975. Stairaird Wood was a small mixed wood with no part of it more than 250 m from pasture containing cattle. Carrick Forest was a very large spruce forest, the area where the flies were caught being at least 1250 m from grazing land. Both areas had large populations of feral Roe deer. The flies were sent to D. W. Tarry at Weybridge Central Veterinary Laboratory for serological tests which gave the following results.

22.5% of flies caught at Stairaird Wood had recently taken a blood meal. Of these, 51.9% had fed on cattle blood and 48.1% on unidentified bovid blood. The latter signifies a faint bovid reaction but no sheep reaction, and is assumed by Tarry to signify generally an older cattle feed. However, there is no reason why it could not signify a meal of deer blood.

21.7% of flies caught in the Carrick Forest were recently blood fed. Of these, 40% had fed on cattle blood and 60% on unidentified bovid blood.

In view of the large numbers of H. irritans feeding on Red deer velvet at the Red deer farm it seems probable that the "unidentified bovid blood" is, in fact, deer blood.

8. The oviposition behaviour of caged *H. irritans*

ABSTRACT

Sheep headflies, Hydrotaea irritans (Fall.), laid equal numbers of eggs on peat, pasture soil, deciduous woodland soil with leaf litter, and peat mixed with cow dung. None was laid on rotten wood or cow dung. Slightly moist peat was preferred to wet peat. Most eggs were laid between 11.30 and 21.30 h B.S.T., with a peak in late afternoon.

INTRODUCTION

Robinson & Luff (1976) found the highest numbers of the larvae of the sheep headfly, Hydrotaea irritans (Fall.), beneath pasture and long grass. After extensive searches, Tarry & Kirkwood (1976) found eight larvae from grouped open woodland sites, but only two from pasture.

The present paper reports an attempt to ascertain the preferred oviposition medium of the headfly. It was hoped that this would indicate a habitat particularly suitable for extensive field sampling of the larvae. Time of day at which oviposition occurred was also investigated.

MATERIALS AND METHODS

Oviposition Preferences

About 500 headflies were kept in a cage (40 x 25 x 25 cm) made from mosquito netting. The cage was hung in the outdoor insectary described in chapter 7. A tray containing fresh moist peat, pasture soil, deciduous woodland soil with leaf litter, cow dung mixed with peat, cowdung and rotten wood was placed underneath the cage daily. The surface area exposed to the flies for egg laying was the same for each medium. The numbers of eggs laid were recorded daily by manual sifting through the media. Each day constituted one of 25 replicates.

A further experiment tested the preference for egg laying on moist or wet peat. Unlike the wet peat, water could not be squeezed from a handful of moist peat. Flies were offered this choice for ten days, and the numbers of eggs laid were recorded daily.

Time of Oviposition

About 500 headflies were kept in a mosquito net cage (40 x 25 x 25 cm). A tray of moist peat was placed underneath the cage for oviposition. The number of eggs laid on the peat was recorded at 09.00 h B.S.T. and thereafter every 2½ hours until 21.30 h. Newly dampened peat was given to the flies after each recording to prevent a "drying out" effect through the day. The experiment lasted ten days.

RESULTS

Oviposition Preference

Headflies laid no eggs on the rotten wood and only two eggs (a mean of 0.08) on the cow dung. The numbers of eggs laid on the other media were not significantly different from one another, with an overall daily mean of eight eggs laid on each medium.

A total of 203 eggs was laid on the moist peat, but none was laid on the wet peat.

Time of Oviposition

Analysis of transformed ($\log_e$ catch + 1) values indicated highly significant differences in the numbers of eggs laid throughout the the day (Table XI). Most eggs were laid between 11.30 and 21.30 h B.S.T, with a peak in the period 16.30-19.00 h.

Table XI The mean transformed number of eggs laid at intervals during the day

Time interval (h)	Mean transformed number of eggs laid
09.01-11.30	0.43
11.31-14.00	1.00
14.01-16.30	1.53
16.31-19.00	2.80
19.01-21.30	1.81
21.31-09.00	0.18

SED (9 d.f.) = 0.387

DISCUSSION

The oviposition of *H. irritans* indicatesa wide tolerance of oviposition sites. It is surprising that cow dung was not used for oviposition, as previous authors (Hammer, 1941; Schumann, 1963; Skidmore, 1973) mention only dung as a known breeding site for *H. irritans*.

The time of day for peak headfly oviposition may be of significance when a control method is devised.

9. Laboratory rearing of the larvae of *H. irritans*

ABSTRACT

Various attempted methods of rearing the larvae of the sheep headfly, Hydrotaea irritans (Fall.) in the laboratory are described. None was successful.

INTRODUCTION

Research into the biology of the sheep headfly, Hydrotaea irritans (Fall.) can be done most effectively by studying caged laboratory reared flies. However, until recently a method of rearing the larvae of H. irritans had not been described, and the present investigation was an attempt to rear the larvae to adults.

MATERIALS AND METHODS

In September, caged female headflies laid fertilized eggs on moist sterile peat, provided for this purpose below the cages. The eggs hatched within a week to give small white second instar larvae. (The first instar is spent within the egg.) The second instar larvae either did not feed or fed saprophagously within the peat. After about a week the larvae moulted to become yellow, final third instar, larvae. These were equipped with a highly developed stabbing cephalopharyngeal skeleton, and required live larvae on which to feed. Several methods were used in an attempt to culture these third instar larvae.

1. One hundred larvae were placed separately on petri dishes containing a layer of Oxoid agar No. 3, and maintained at room temperature. The agar was necessary to prevent the larvae desiccating. Four Drosophila larvae were placed in each petri dish every two days. The headfly larvae were

transferred to new petri dishes each week.

2. One hundred larvae were placed separately in 4.5 x 7.5 cm plastic tubes three-quarters filled with peat. About 15 fungus gnat (Sciarid) larvae were added to each tube each week. The tubes were maintained at room temperature.

3. One hundred larvae were added to a mass culture of Musca domestica larvae. The culture medium, containing bran, grass meal, yeast, soya flour, cod-liver oil, malt and vermiculite, was maintained at room temperature.

In early December, half the larvae from the first two methods were placed in the dark in a refrigerator at 2°C. During this time the agar was not renewed and the larvae were not fed. Once a fortnight live larvae from each method were removed from the refrigerator and re-established at room temperature.

RESULTS

None of the larvae pupated. The most successful method was that of using petri dishes containing agar and feeding the larvae on Drosophila larvae. In this group, one larva survived until April, but died before pupating. All larvae in the group fed on Sciarid larvae died by January. The larvae added as a group to the M. domestica culture died within a month.

About a third of the larvae placed in the cold died under these conditions. The others, when removed from the cold, failed to resume feeding and died within a week of removal.

When feeding, the headfly larvae stabbed the prey with their cephalopharyngeal hooks. The prey larvae were immediately motionless, presumably paralysed. (By contrast, if a Drosophila larva was pricked with a very sharp needle, it

wriggled.) The H. irritans larvae then extracted the body contents of the prey larvae for about 30 minutes.

The larvae stopped feeding and growing after December.

DISCUSSION

Robinson & Luff (1976) also found problems in rearing larvae. They placed about 80 larvae in Drosophila cultures but all died within three months.

Tarry & Kirkwood (1976) obtained a headfly adult by keeping H. irritans larvae in a culture of Stomoxys calcitrans (L) larvae and culture medium mixed with fine leaf litter. They reported that by December the larvae had almost completed larval growth and became inactive until the following March. Kirkwood (1976) had success by rearing larvae in peat cultures and feeding them on young M. domestica or Lucilia sericata (Meigen) larvae each week. The larvae attained full growth by January, and continued to feed until mid March. Some of the larvae pupated and adults were obtained. This method is still not completely satisfactory and more work is required before it is as refined as the mass rearing of M. domestica or S. calcitrans.

10. The breeding site of *H. irritans* in south-western Scotland

ABSTRACT

A variety of methods was used to determine the breeding site of the sheep headfly, Hydrotaea irritans (Fall.), in South West Scotland. No headfly adults were recovered from emergence boxes and emergence traps. By the use of heat extraction apparatus two headfly larvae were extracted from samples of pasture soil. None was extracted from litter or dung samples.

INTRODUCTION

Hammer (1941) and Skidmore (1973) stated that dung was the breeding site of the sheep headfly, Hydrotaea irritans (Fall.). However, Nielsen, Nielsen & Christensen (1971) and Tarry (1973) did not find headfly larvae numerous in this habitat. Until recently, larvae of the headfly had not been found anywhere in appreciable numbers, and the present account is of an attempt from 1973 to 1975 to find the breeding site.

MATERIALS AND METHODS

Emergence Boxes

In the winter of 1973, cowpats were taken from fields infested with headflies during the summer, and were placed in 20 biscuit tins, each 23 x 22 x 22 cm. A hole, diameter 15 cm, was cut in each tin lid and an inverted polythene funnel was placed over it. An inverted 7.5 x 2.5 cm glass tube was fitted over the end of the funnel. Any flies emerging from the dung were attracted to the light shining down the funnel and were caught in the glass tube.

Emergence Traps

In spring, from 1974 to 1976, a total of 100 emergence traps were erected in equal numbers in woodland and on pasture, both with large populations of adult headflies. Each trap comprised four 2 x 2 cm posts inserted firmly in the ground at the corners of a 1 m square, with a height of about 20 cm above the ground. Nylon mosquito netting was stretched over the posts, and was fastened to them by drawing pins, allowing no gap between the netting and the ground. Any fly emerging in the trap was easily seen through the netting, and could be removed with a pooter for identification.

Field Sampling

Samples were taken in 1974 and 1975 from many different habitats in the South West of Scotland (Table XII). The ages of the cowpats being sampled were determined using the following procedure in 1974. Every fortnight from April to September each new cowpat in an area of a field containing cattle was marked with a coloured peg. A different colour code was used each fortnight. During the following winter the cowpats, with the 8 cm deep patch of soil beneath, were removed and any larvae were extracted.

The fauna was initially extracted from the samples by hand. However, this time-consuming method was rejected, and instead the samples were washed and the animals were extracted by flotation. This too required constant manual operation, and the high amount of organic matter and clay in the samples made washing and flotation difficult. Accordingly, a system of Tullgren funnels was designed. The bottoms of 50, 5 litre paint tins were removed and 3 mesh (metric) gauze was substituted. A hole was cut in each of the tins' lids into which a light bulb holder containing a 60W bulb

Table XII Habitats sampled for the larvae of *H. irritans*

Habitat		Number of samples	Amount taken per sample
Litter:	Bracken	150	0.09m^2 taken to soil layer
	Mixed woodland	80	" " " " "
	Spruce	5	" " " " "
Soil:	Rough pasture	100	" 15 cm deep
	Woodland	55	" " "
Dung:	Cow	200	Complete cowpat + soil beneath down to 8 cm
	Sheep	50	Individual faeces
Peat (with no vegetation cover)		25	0.09m^2 15 cm deep
Sphagnum moss		5	" taken to soil layer
Rotten wood		5	Sticks

was fitted. The paint tins were suspended over trays of water, by their handles, from a handy angle rack. The lids were placed on the tins so that the light bulbs, which were wired to the mains, shone inside the tins. The samples were put inside the tins and the heat from the bulbs drove the animals downwards to the mesh, where they fell into the trays of water. The paint tins were easily removed from the rack for filling and emptying. Samples were usually left under the heat for three days. The tins each contained about half a sample, which was always broken up.

RESULTS

Emergence Boxes

No headflies emerged from the cowpats in the boxes, although some *Hydrotaea albipuncta* Zetterstedt adults were observed.

Emergence Traps

No headflies emerged under these traps although many flies including muscids and tabanids were found.

Field Sampling

The paint tin extraction apparatus worked effectively; many species of muscid larvae were found. However, only two *H. irritans* larvae, from two samples of pasture soil were extracted using this apparatus. This was equivalent to a density of $0.0012/m^2$. No other headfly larvae were found in any other samples, by any extraction method.

DISCUSSION

The extraction of only two *H. irritans* larvae is unlikely to be due to the method being unsuitable for *H. irritans*

larvae, because many types of larvae were extracted and headfly larvae, being predacious, are fast moving and should be able to avoid desiccation. Headfly larvae may in fact be very widely dispersed and their true density indicated by the results. Alternatively, pasture may not be the main breeding site of the headfly in South West Scotland, but this seems unlikely in view of the negative results of the samples taken from the other habitats. Robinson & Luff (1976) found many headfly larvae in soil beneath pasture, equivalent to a density of $1.93/m^2$. This is far greater than that indicated by the present results, and the contrast cannot be explained.

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APPENDIX

Plate I. A headfly lesion on the head of a Blackface sheep

Plate II. A close-up of feeding female H. irritans on the velvet of a Red deer stag

Plate III. The effect of *H. irritans* adults on Red deer

(a) Adults swarming on antler velvet

(b) A stag sheltering in the bracken

(c) Close-up of antler velvet showing a bare patch at the fork

(d) Close-up of antler velvet showing small holes probably caused by *H. irritans*

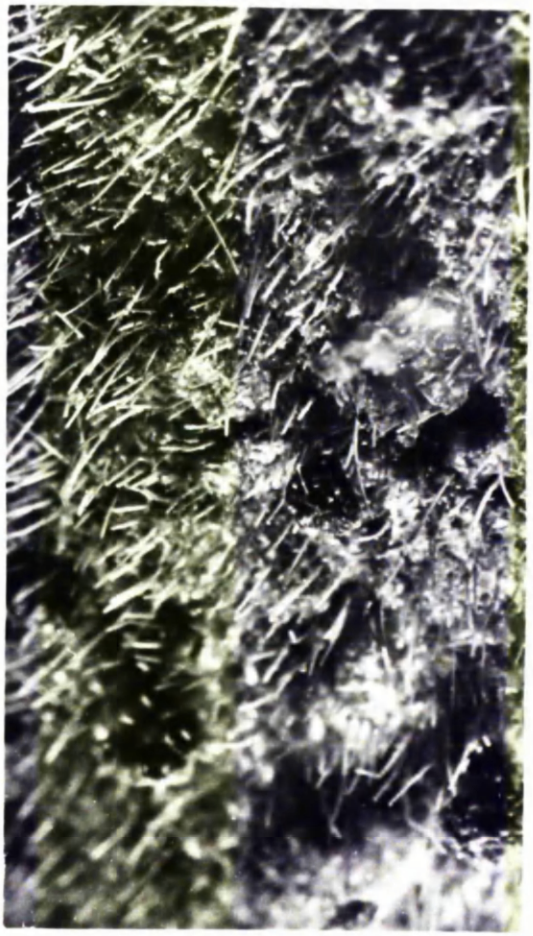
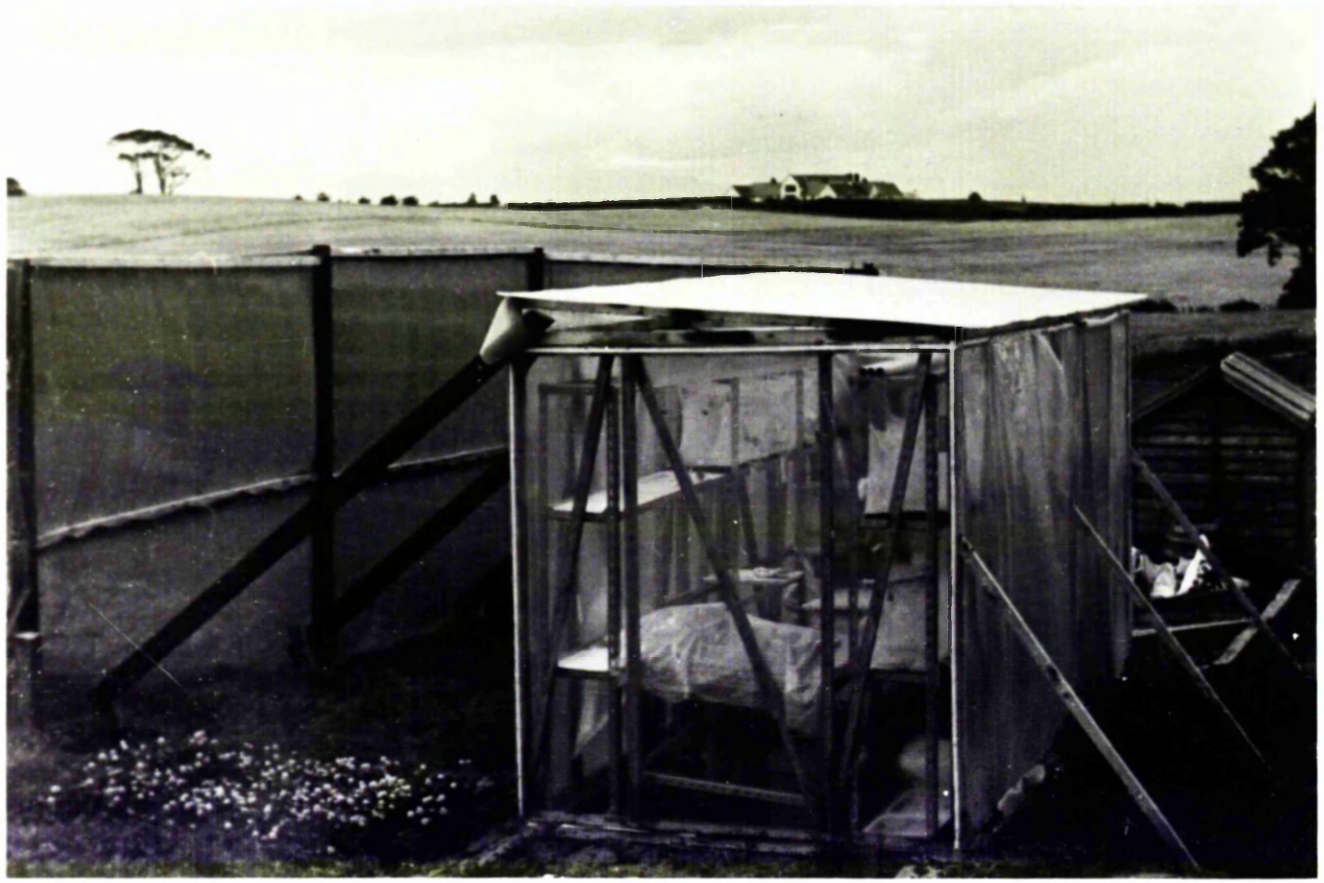


Plate IV. Manitoba trap

Plate V. Detail of top of Manitoba trap



Trap Comparison

The numbers of male and female flies caught in each trapping period from 1 July - 28 July were transformed ($\log_e$(catch + 1)), and the following analyses of variance were obtained.

Female flies

Source	d.f.	Sum of squares	Mean square	F	P
Traps	2	231.944	115.972	148.41	0.001
Catches	44	117.210	2.664	3.41	
Error	88	68.764	0.781		
Total	134	417.918			

SED = 2/n x error mean square = 0.186

Male flies

Source	d.f.	Sum of squares	Mean square	F	P
Traps	2	91.904	45.952	75.02	0.001
Catches	44	56.115	1.275	2.08	
Error	88	53.899	0.613		
Total	134	201.918			

Flight Periodicity

The number of male and female flies caught each trapping period in July were transformed ($\log_e$(catch + 1)) and the following analyses of variance were obtained.

Female flies - comparing hourly intervals between 08.00-22.00h.

Source	d.f.	Sum of squares	Mean square	F	P
Hours	13	144.792	11.138	3.826	0.001
Error	117	340.542	2.911		
Total	130	485.334			

Male flies - comparing hourly intervals between 09.00-21.00h.

Source	d.f.	Sum of squares	Mean square	F	P
Hours	11	36.213	3.292	2.205	0.05
Error	108	161.282	1.493		
Total	119	197.495			

Regression Analyses

Single and multiple regression equations were derived for each sex in both traps. The dependent variable was $\log_e$(catch + 1), and the independent variables were day number (D) and D^2, time of day (T) and T^2, air temperature (a.t), direct temperature (t) and t^2, relative humidity (h), windspeed (w), illumination (i), barometric pressure (p) and rain (r).

Single regression equations

CO_2-baited suction trap (females)

		Estimate	S.E.	t
Day	Constant	2.9959	0.238	12.43
	D	0.0075	0.0067	1.12
$(Day)^2$	Constant	3.2471	0.179	18.13
	D^2	-0.00005	0.0001	-0.50
Time of day	Constant	3.7337	0.511	7.31
	T	0.0392	0.035	-1.11
$(Time\ of\ day)^2$	Constant	3.6472	0.283	12.87
	T^2	-0.0022	0.0012	-1.83
Air temperature	Constant	-2.2875	0.686	-3.34
	a.t	0.3817	0.047	8.09
Direct temperature	Constant	-1.1319	0.350	-3.24
	t	-.2533	0.0197	12.84
$(Direct\ temperature)^2$	Constant	1.1664	0.202	5.78
	t^2	0.0064	0.0006	11.53
Relative humidity	Constant	7.8414	0.752	10.43
	h	-0.0681	0.010	-6.27
Windspeed	Constant	3.6282	0.268	13.52
	w	0.3050	0.163	-1.87
Illumination	Constant	1.4830	0.191	7.75
	i	0.0008	0.00002	10.57
Barometric pressure	Constant	-77.306	2.23	-3.47
	p	0.0803	0.022	3.61
Rain	Constant	3.3870	0.123	27.56
	r	-0.8175	0.143	-5.73

CO_2-baited suction trap (males)

		Estimate	S.E.	t
Day	Constant	1.7127	0.174	9.87
	D	-0.0176	0.006	-2.82
$(Day)^2$	Constant	1.6735	0.129	12.95
	D^2	-0.00049	0.00012	-4.00
Time of day	Constant	1.6937	0.363	4.67
	T	-0.0279	0.025	-1.14
$(Time\ of\ day)^2$	Constant	1.6189	0.205	7.91
	T^2	-0.0015	0.0008	-1.77
Air temperature	Constant	-1.4661	0.497	-2.95
	a.t	0.1947	0.035	5.64
Direct temperature	Constant	-0.7096	0.277	-2.56
	t	0.1175	0.016	7.55
$(Direct\ temperature)^2$	Constant	0.3799	0.160	2.37
	t^2	0.0029	0.0004	6.66
Relative humidity	Constant	3.6059	0.551	6.55
	h	-0.0304	0.007	-4.25
Windspeed	Constant	1.3254	0.202	6.55
	w	-0.0220	0.126	-0.18
Illumination	Constant	0.3978	0.149	2.68
	i	0.00009	0.00001	7.19
Barometric pressure	Constant	-44.2820	16.000	-2.77
	p	0.0455	0.016	2.85
Rain	Constant	1.3691	0.093	14.77
	r	-0.4514	0.151	-3.00

Manitoba trap (females)

Day	Constant	1.7834	0.192	9.30
	D	0.0008	0.005	0.15
$(Day)^2$	Constant	1.9437	0.143	13.64
	D^2	-0.0001	0.00008	-1.31
Time of day	Constant	2.8737	0.396	7.26
	T	-0.0762	0.027	-2.78
$(Time\ of\ day)^2$	Constant	2.4856	0.218	11.41
	T^2	-0.0033	0.0009	-3.47
Air temperature	Constant	-1.8298	0.555	-3.30
	a.t	0.2543	0.038	6.64

		Estimate	S.E.	t
Direct temperature	Constant	-1.1486	0.294	-3.91
	t	0.1740	0.017	10.48
(Direct temperature)^2	Constant	0.4310	0.167	2.57
	t^2	0.0044	0.0005	9.51
Relative humidity	Constant	4.6600	0.615	7.58
	h	-0.0370	0.008	-4.70
Windspeed	Constant	2.2322	0.209	10.68
	w	-0.2937	0.128	-2.29
Illumination	Constant	0.5150	0.151	3.41
	i	0.00014	0.00001	10.23
Barometric pressure	Constant	-36.1660	17.800	-2.03
	p	0.0379	0.018	2.13
Rain	Constant	1.9342	0.100	19.44
	r	-0.4916	0.114	-4.31

Manitoba trap (males)

Day	Constant	1.0933	0.122	8.98
	D	-0.0645	0.004	-3.81
(Day)^2	Constant	0.9900	0.091	10.92
	D^2	-0.0004	0.00008	-4.41
Time of day	Constant	1.2465	0.248	5.02
	T	-0.0390	0.017	-2.31
(Time of day)^2	Constant	1.0491	0.139	7.53
	T^2	-0.0017	0.0006	-2.86
Air temperature	Constant	-0.8642	0.352	-2.46
	a.t	0.1101	0.025	4.49
Direct temperature	Constant	-0.4120	0.201	-2.05
	t	0.0650	0.011	5.74
(Direct temperature)^2	Constant	0.2068	0.115	1.79
	t^2	0.0015	0.0003	4.92
Relative humidity	Constant	1.8534	0.394	4.71
	h	-0.0152	0.005	-2.98
Windspeed	Constant	0.8465	0.139	6.08
	w	-0.1091	0.088	-1.24
Illumination	Constant	0.1601	0.106	1.51
	i	0.00006	0.000009	6.02
Barometric pressure	Constant	-16.6620	11.300	-1.48
	p	0.0173	0.011	1.54
Rain	Constant	0.7236	0.066	11.03
	r	-0.1820	0.105	-1.73

Female multiple regression analyses

CO_2-baited suction trap (i) Regression coefficients

	Estimate	S.E.	T
Constant	-6.0363	1.10000	- 5.50
D	0.1489	0.01540	9.66
D^2	-0.0025	0.00023	-10.72
t	0.7916	0.12300	6.46
i	5.78×10^{-5}	0.00002	2.85
t^2	-0.0167	0.00306	- 5.45
W	-0.6273	0.10100	- 6.19

(ii) Analysis of variance

Source of variation	d.f.	Sum of squares	Mean square
Regression	6	490.4	81.736
Residual	223	297.9	1.336
Total	229	788.3	

Manitoba trap (i) Regression coefficients

	Estimate	S.E.	T
Constant	-4.8098	0.97200	- 4.95
D	0.1025	0.01400	7.33
D^2	-0.0018	0.00021	- 8.54
t	0.5865	0.10900	5.40
i	7.04×10^{-5}	0.00002	3.90
t^2	-0.0132	0.00271	- 4.85
W	-0.5265	0.09090	- 5.79

(ii) Analysis of variance

Source of variation	d.f.	Sum of squares	Mean square
Regression	6	272.5	45.414
Residual	217	226.6	1.044
Total	223	499.1	

Male multiple regression analyses

CO_2-baited suction trap (i) Regression coefficients

	Estimate	S.E.	T
Constant	-3.5727	0.6140	- 5.81
D	0.0983	0.0162	6.06
D^2	-0.0028	0.0003	- 8.51
t	0.4342	0.0705	6.16
t^2	-0.0074	0.0019	- 3.86
W	-0.2552	0.0861	- 2.96

(ii) Analysis of variance

Source of variation	d.f.	Sum of squares	Mean square
Regression	5	185.4	37.089
Residual	192	137.8	0.718
Total	197	323.3	

Manitoba trap (i) Regression coefficients

	Estimate	S.E.	T
Constant	-2.2968	0.4730	- 4.86
D	0.0287	0.0127	2.26
D^2	-0.0012	0.0003	- 4.61
t	0.3255	0.0542	6.00
t^2	-0.0062	0.0015	- 4.23
W	-0.2375	0.0674	- 3.52

(ii) Analysis of variance

Source of variation	d.f.	Sum of squares	Mean square
Regression	5	68.93	13.786
Residual	186	78.57	0.422
Total	191	147.50	

Host-seeking Attractants

Numbers of flies trapped were transformed to $\log_e$ (catch + 1) values. The results of the potential attractants were compared with those of their controls using a t-test:

$$t = \frac{X}{(S^2/N)}$$

Colour and Attraction

Numbers of flies caught in each trap were transformed to $\log_e$(catch + 1) values, and the following analyses of variance were obtained:

Females

Source of variation	d.f.	SS	MS	F
Times	27	28.817	1.067	3.63
Colours	6	203.374	33.896	115.20
Residual	162	47.657	0.294	
Total	195	279.848		

SED = 0.145

Colour	Mean $\log_e$ no. females
Matt black	4.262
Shiny black	4.090
Shiny red	3.469
Shiny green	2.581
Shiny white	2.297
Shiny yellow	1.969
No sphere	1.368

Males

Source of variation	d.f.	SS	MS	F
Times	27	41.482	1.540	5.93
Colours	6	116.577	19.430	74.80
Residual	162	42.082	0.260	
Total	195	200.241		

SED = 0.136

Colour	Mean $\log_e$ no. males
Matt black	2.681
Shiny black	2.262
Shiny red	1.968
Shiny white	1.227
Shiny green	0.903
Shiny yellow	0.782
No sphere	0.487

The untransformed numbers of clegs, Haematopota pluvialis L, caught in each trap gave the following analysis of variance.

Source of variation	d.f.	SS	MS	F
Times	27	39.673	1.469	0.77
Colours	6	152.316	25.386	13.22
Residual	162	311.112	2.759	
Total	195	503.102		

SED = 0.370

Colour	Mean catch
Shiny black	2.82
Matt black	2.32
Shiny red	1.50
Shiny white	1.11
Shiny yellow	0.82
Shiny green	0.39
No sphere	0.32

CO_2 Concentration and Attraction

Numbers of headflies caught in the CO_2-baited control trap and in the trap with varying rates of CO_2 were transformed to $\log_e$(catch + 1) values. The catches of the trap with varying CO_2 rates were expressed as percentages of the CO_2-baited control trap and the following analysis of variance was obtained.

Source of variation	d.f.	SS	MS	F
CO_2 concentration	4	1906.59	476.65	4.86
Residual	20	1959.12	97.96	
Total	24	3865.70		

SED = 6.26

Rate of CO_2 output (litres/min)	Mean transformed numbers as % of control
0.5	83.4
2.0	102.4
3.0	102.3
4.0	106.7
5.0	107.1

Interaction of Attractants

Numbers of headflies caught in three Manitoba traps baited with red spheres, and one trap baited with CO_2, were transformed to $\log_e$(catch + 1) values. The following analysis of variance was obtained.

Source of variation	d.f.	SS	MS	F
Time	9	7.535	0.837	4.55
Traps	3	13.922	4.641	26.20
Residual	27	4.972	0.184	
Total	39	26.429		

SED = 0.192

	Trap			
	CO_2	Red 1	Red 2	Red 3
Mean transformed catch	3.90	4.91	3.58	3.37

Repellent Evaluation

Numbers of H. irritans caught in each trap were transformed to $\log_e$(catch + 1) values, and the following analyses of variance were obtained.

Day 1

Source of variation	d.f.	SS	MS	F
Times	4	5.518	1.380	2.09
Repellents	3	53.713	17.904	27.06
Residual	12	7.941	0.662	
Total	19	67.173		

SED = 0.514

Repellent	Mean transformed catch
Clear	1.19
Dark	2.29
White	3.08
Control	5.64

Day 2

Source of variation	d.f.	SS	MS	F
Times	4	9.026	2.256	5.12
Repellents	3	42.287	14.096	31.99
Residual	12	5.287	0.441	
Total	19	56.599		

SED = 0.420

Repellent	Mean transformed catch
Clear	1.68
Dark	1.82
White	4.92
Control	4.34

Day 3

Source of variation	d.f.	SS	MS	F
Times	4	2.741	0.685	0.99
Repellents	3	43.682	14.561	21.14
Residual	12	8.264	0.689	
Total	19	54.687		

SED = 0.525

Repellent	Mean transformed catch
Clear	1.56
Dark	1.99
White	4.95
Control	4.44

Day 5

Source of variation	d.f.	SS	MS	F
Times	4	3.423	0.856	2.63
Repellents	3	22.254	7.418	22.77
Residual	12	3.910	0.326	
Total	19	29.587		

SED = 0.361

Repellent	Mean transformed catch
Clear	2.92
Dark	2.59
White	5.05
Control	4.61

Day 9

Source of variation	d.f.	SS	MS	F
Times	4	16.228	4.057	16.94
Repellents	3	12.583	4.194	17.51
Residual	12	2.875	0.240	
Total	19	31.686		

SED = 0.310

Repellent	Mean transformed catch
Clear	2.71
Dark	3.29
White	4.82
Control	4.03

Day 12

Source of variation	d.f.	SS	MS	F
Times	4	2.538	0.635	1.24
Repellents	3	25.677	8.559	16.78
Residual	12	6.123	0.510	
Total	19	34.338		

SED = 0.452

Repellent	Mean transformed catch
Clear	1.94
Dark	2.84
White	4.95
Control	3.92

Day 15

Source of variation	d.f.	SS	MS	F
Times	4	6.1293	1.5323	3.97
Repellents	3	24.8260	8.2753	21.45
Residual	12	4.6298	0.3858	
Total	19	35.5851		

SED = 0.393

Repellent	Mean transformed catch
Clear	1.21
Dark	1.69
White	4.15
Control	2.33

Day 17

Source of variation	d.f.	SS	MS	F
Times	4	2.619	0.655	1.52
Repellents	3	3.846	1.282	2.97
Residual	12	5.180	0.432	
Total	19	11.646		

Repellent	Mean transformed catch
Clear	1.71
Dark	2.26
White	2.94
Control	2.41

Overall daily mean

Source of variation	d.f.	SS	MS	F
Times	39	91.087	2.336	2.84
Repellents	3	176.789	58.930	71.61
Residual	117	96.288	0.823	
Total	159	364.164		

SED = 0.203

Repellent	Mean transformed catch
Clear	1.86
Dark	2.35
White	4.36
Control	3.97

APPENDIX TO CHAPTER 5

Distribution of Adult *H. irritans*

The numbers of headflies caught in the traps at the different sites were transformed to $\log_e$(catch + 1). The following analysis of variance was obtained.

Source	d.f.	Sum of squares	Mean square	F
Time	9	18.630	2.070	0.098
Traps	4	84.488	21.122	60.086
Error	36	12.564	0.349	
Total	49	115.682		

APPENDIX TO CHAPTER #7

Longevity on Diets with Blood and Honey

The longevity of each fly was determined and the following analyses of variance were obtained:

Analysis of variance - females

Source of variation	d.f.	SS	MS	F
Diet	5	583882	116776	77.8
Residual	174	261001	1500	
Total	179	844883		

SED = 9.99

Diet	Mean longevity (days)
Honey only	149.37
Blood and honey	104.63
Blood and honey then honey only	107.27
Blood and honey (not paired with males)	113.73
Blood only	1.77
No food	2.27

Analysis of variance - males

Source of variation	d.f.	SS	MS	F
Diet	4	185961	46490	137
Residual	145	49168	339	
Total	149	235129		

SED = 4.75

Diet	Mean longevity (days)
Honey only	66.17
Blood and honey	67.03
Blood and honey then honey only	83.80
Blood only	1.40
No food	1.83

Oviposition Preferences

The numbers of eggs laid on each substrate each day were transformed to $\log_e$(catch + 1) and the following analysis of variance was obtained. The dung and wood substrates were excluded from the analysis.

Source	d.f.	Sum of squares	Mean square	F	P
Times	24	1.638	0.06	0.20	ns
Substrates	3	0.907	0.30	0.65	ns
Error	72	33.074	0.46		
Total	99	35.619			

Time of Day for Oviposition

The number of eggs laid in each period each day were transformed to $\log_e$(catch + 1) and the following analysis of variance was obtained.

Source	d.f.	Sum of squares	Mean square	F	P
Days	9	27.164	3.018	4.02	0.001
Times	5	46.684	9.337	12.45	0.001
Residual	45	33.148	0.750		
Total	59	107.597			

SED = $2/n \times$ error mean square = 0.387

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Factors attracting the sheep headfly, *Hydrotaea irritans* (Fallén) (Diptera: Muscidae), with a note on the evaluation of repellents

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Abstract

An investigation using modified Manitoba traps on a forest track in Scotland showed that carbon dioxide, coloured spheres, movement, heat, *Haematopota pluvialis* (L.) and a swarm of other adults of *Hydrotaea irritans* (Fall.) were attractive. Traps with coloured spheres attracted more flies than traps without spheres. Matt black, shiny black and shiny red spheres attracted more males and females than did shiny green, white or yellow spheres. Significant increases in the number of flies caught did not occur when carbon dioxide was released from a trap at rates above 2 litres/min. Carbon dioxide seems to act as a long-range attractant, with vision becoming important near the host. Manitoba traps were also used with three repellents for *H. irritans* in order to evaluate the trap's potential for testing repellents.

Introduction

Berlyn (1978) has shown that the sheep headfly, *Hydrotaea irritans* (Fallén), is attracted to a suction trap baited with carbon dioxide and to a Manitoba trap baited with a black sphere.

In the present investigation, in the summer of 1976, further use has been made of Manitoba traps to study the various factors that attract *H. irritans*. In addition, a means of evaluating repellents for *H. irritans* using Manitoba traps was attempted.

Materials and methods

Manitoba traps modified from those described by Thorsteinson *et al.* (1965) were constructed. The framework and support consisted of a collapsible metal tripod with legs 2 m long hinged at their upper ends to the sides of a vertical metal pipe 9 cm long and with an internal diameter of 7·5 cm. A rigid polythene tube, 11 cm long and 7 cm in diameter, was attached to the open apex of a transparent polyethylene cone with a base circumference of 3·5 m. The shape of the cone was maintained by a metal ring 3·6 m in diameter hung from the base of the cone. The tube, with the cone suspended from it, was secured inside the vertical metal pipe so that a 2-cm cuff extended out of the top. A removable polyethylene bag was taped to this cuff. Thus, a polyethylene canopy, with its base 0·65 m from the ground, was supported from a metal tripod with a polyethylene collecting bag at its apex. Attractants were hung

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beneath the canopy, and adults of *H. irritans* that were attracted, once under the cone, flew upwards and were trapped in the removable bag.

The work site was a 12-m wide rough track well inside the Ayrshire (Scotland) spruce forest (O.S. grid reference NS 384969).

Investigations of previously determined attractants

Colour. Six plastic spheres (0·5 m in diameter), coloured matt black, shiny black, shiny red, shiny green, shiny yellow and shiny white, were suspended below traps. A seventh trap without a sphere acted as a control. The reflectances of the sphere colours were measured using a Weston Master V exposure meter and expressed as a percentage of the reading for the white one. The numbers of *H. irritans* caught in each trap were recorded. As *Haematopota pluvialis* (L.) was also caught in large numbers in the traps, its numbers were also recorded for comparison. The traps were aligned 6 m apart, and the spheres were randomly interchanged before each of the 28 replicates. This work was completed in two days in early July.

Carbon dioxide. Three traps with suspended red spheres were aligned 6 m apart. Carbon dioxide was released from the middle trap at 0·5, 2·0, 3·0, 4·0 or 5·0 litres/min. The two end traps were the controls. Carbon dioxide was released at a constant rate of 2 litres/min from one of the control traps, and none was released from the other. There were five replicates for each rate of release. The numbers of flies caught were compared between the different rates of carbon dioxide release.

Interaction of attractants

This experiment was included to clarify the roles of olfactory and visual stimuli in attraction. Four traps were aligned 2 m apart. Red spheres were suspended from these traps except for one end trap, from which carbon dioxide was released at a rate of 2 litres/min. The trap with carbon dioxide was interchanged with the other end trap (with a red sphere) before each of the ten replicates. The numbers of flies caught in each trap were compared.

The traps with red spheres were termed Red 1, Red 2, Red 3; the trap nearest the trap with carbon dioxide always being Red 1 and the furthest trap being Red 3.

Tests of other potential attractants

Potential attractants were suspended, in turn, below the canopy of a trap, and the number of *H. irritans* caught was compared with the number caught in a control trap.

The positions of the attractants and their controls were interchanged before each new replicate. The potential attractants tested and their controls were as follows:

1. Heat—a hot fan heater was compared with a cold fan heater.
2. Movement—a moving red sphere was compared with a stationary red sphere. An operator positioned equidistant from each trap used a piece of string 15 m long to rock the sphere.
3. A swarm of *H. irritans*—a white net cage containing about 500 flies was compared with an empty cage.
4. Blood—cotton wool soaked in sheep's blood was compared with cotton wool soaked in red dye.
5. Sheep odour—an ether extract was obtained by wiping cotton wool soaked in ether across fhe fleece of a sheep; the ether was then evaporated off, and cotton wool soaked in ether extract was compared with cotton wool soaked in pure ether.
6. Sheep odour and red spheres—a red sphere was hung below each trap in addition to cotton wool soaked in ether extract of sheep (see no. 5); the red spheres were included in case the substance being tested acted only as a short-range attractant and a more widespread stimulus was required in addition.
7. Indole solution and red spheres—cotton wool soaked in 2% indole solution was

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compared with cotton wool soaked in distilled water; red spheres were also hung beneath the traps.

8. Ammonia solution and red spheres—cotton wool soaked in 2% ammonia solution was compared with cotton wool soaked in distilled water; red spheres were also hung beneath the traps.

Repellent evaluation using traps

Four traps with suspended black spheres were aligned 6 m apart along a grassy fire break. Three repellents for *H. irritans*, a white cream containing citronella (Willington Medicals Ltd.), a dark cream containing 0·5% crotoxyphos in a tar base and a clear cream containing 0·5% crotoxyphos in a clear base (Robert Young & Co. Ltd.), were spread separately over three of the spheres in equal amounts. The fourth trap, without a repellent, constituted a control. Subsequently, on days when flies were active the traps' catches were compared to determine the persistence of the repellents. There were five replicates on each of these days, the traps being randomly rearranged before each replicate.

Results

Investigations of previously determined attractants

Colour. Analysis of transformed (log catch+1) data showed that there were significant differences in attraction between spheres of different colours (Table I). The

TABLE I. *Mean numbers of males and females of* Hydrotaea irritans *and of* Haematopota pluvialis *caught in Manitoba traps with coloured spheres*

Colour	Reflectance as % of white	Mean transformed catch of *H. irritans* males	Mean transformed catch of *H. irritans* females	Mean catch of *H. pluvialis*
Matt black	63·9	2·68	4·26	2·32
Shiny black	66·7	2·26	4·09	2·82
Red	69·4	1·97	3·47	1·50
White	100·0	1·23	2·30	1·11
Green	75·0	0·90	2·58	0·39
Yellow	88·9	0·78	1·97	0·82
No sphere	—	0·49	1·37	0·32
s.e.d. (162 d.f.)		0·14	0·15	0·37

Note: Vertical lines indicate mean catch values that are not significantly different at $P < 0·05$.

order of attraction to the different colours was similar for both males and females of *H. irritans*. The colours that attracted the greatest numbers were matt black, shiny black and red. Traps with white, green and yellow spheres caught fewer flies, but significantly more than the trap without a sphere. Unlike the females, males were significantly ($P<0·01$) more attracted to matt black than to shiny black. The numbers of flies attracted to the spheres were inversely proportional to the reflectances as measured by the exposure meter, with the exception of the white sphere.

Haematopota pluvialis was also attracted mostly by the black spheres.

Carbon dioxide. For each replicate, the catch of the trap with varying rates of release of carbon dioxide was transformed (log catch+1) and expressed as a percentage of the transformed catch of the control trap in which carbon dioxide was released at 2 litres/min. The trap with no output of carbon dioxide could not be used as the control as it did not catch sufficient flies.

When carbon dioxide was released from the trap at 0·5 litres/min, significantly ($P<0·01$) fewer *Hydrotaea irritans* were trapped than when it was released at rates of

2 litres/min or more (Table II). There was no significant difference in attraction between the higher rates of release.

TABLE II. *Mean transformed numbers of* H. irritans *attracted to Manitoba traps in which carbon dioxide was released*

Rate of CO_2 release (litres/min)	Mean transformed numbers as % of control*
0·5	83·4
2·0	102·4
3·0	102·3
4·0	106·7
5·0	107·1

s.e.d. (20 d.f.) = 6·26

* CO_2 was released from the control trap at 2 litres/min

Interaction of attractants

Analysis of transformed (log catch+1) data showed that *H. irritans* was most attracted ($P<0·05$) to the trap (Red 1) next to the trap with a carbon dioxide output. Attraction to the traps declined with an increase in distance from the carbon dioxide release point. The catch in the trap baited with carbon dioxide was less than that in Red 1 but not significantly different from that in Red 2.

Tests of other potential attractants

Analysis of transformed (log catch+1) data showed that of the factors examined only heat, movement and a swarm of *Hydrotaea irritans* caused significant attraction of *H. irritans* (Table III).

TABLE III. *The geometric mean catches of* H. irritans *in Manitoba traps baited with various potential attractants*

Potential attractant	Geometric mean catch: Attractant	Geometric mean catch: Control	No. of replicates	*t* value	Significance
Heat	39·2	23·6	14	2·87	$P<0·05$
Movement	33·1	14·1	12	6·49	$P<0·001$
Swarm of *H. irritans*	69·6	29·2	10	4·47	$P<0·01$
Blood	17·5	8·8	12	1·85	n.s.
Sheep odour	3·9	8·4	5	1·94	n.s.
Sheep odour and red spheres	31·7	23·1	10	1·66	n.s.
Indole soln. and red spheres	8·4	12·8	8	1·26	n.s.
Ammonia soln. and red spheres	7·6	9·1	6	0·40	n.s.

n.s. = not significant.

An incidental observation was made during the experiment on colour attraction. Large numbers of the tabanid *Haematopota pluvialis* were attracted to the black spheres. On landing, the *H. pluvialis* were immediately closely surrounded by individuals of *Hydrotaea irritans*, which thrust their heads close to a tabanid's proboscis. Thus, the tabanids were acting as attractants.

Repellent evaluation using traps

All figures were transformed (log catch+1), and the daily mean catches in traps with spheres treated with repellent materials are shown in Table IV. The day after

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their application (day 1) all three repellents provided a significant ($P<0{\cdot}01$) reduction in attraction of *H. irritans*. From day 2 until day 15, only the two repellents containing crotoxyphos provided a significant ($P<0{\cdot}01$) reduction in the numbers of flies attracted. Moreover, on days 9, 12 and 15, the trap with white citronella cream was significantly ($P<0{\cdot}05$) more attractive than the control.

TABLE IV. *The mean transformed numbers of* H. irritans *attracted to Manitoba traps with black spheres treated with repellents*

	Days after application of repellents								
Repellent	1	2	3	5	9	12	15	17	Mean
Clear cream containing 0·5% crotoxyphos	1·19	1·68	1·56	2·92	2·71	1·94	1·21	1·71	1·86
Dark cream containing 0·5% crotoxyphos	2·29	1·82	1·99	2·59	3·29	2·84	1·69	2·26	2·35
White cream containing citronella	3·08	4·92	4·95	5·05	4·82	4·95	4·15	2·94	4·36
Control	5·64	4·34	4·44	4·61	4·03	3·92	2·33	2·41	3·97
s.e.d. (12 d.f.)	0·514	0·420	0·525	0·361	0·310	0·452	0·393	0·416	*0·203

* (117 d.f.)

Discussion

Berlyn (1978) has already shown that *H. irritans* is attracted by carbon dioxide and black spheres. The present results show that it is also attracted to other colours, heat, movement, *Haematopota pluvialis*, and a swarm of *Hydrotaea irritans*.

As dark and least reflective colours are most attractive to many haematophagous flies (Brett, 1938; Davies, 1951; Barrass, 1960; Pospíšil & Ždárek, 1965) it was not suprising that black and red spheres attracted the most *H. irritans*. The white sphere attracted more flies than expected in view of its very high reflectance, although this appears to be a common phenomenon among haematophagous flies (Brown, 1954; Bracken *et al.*, 1962; Gatehouse & Lewis, 1973). The attraction shown by *H. irritans* to colours of high and low reflectance is probably because they contrast with the background. Green and yellow spheres, with medium reflectances, did not provide sufficient contrast.

The interaction of colour and carbon dioxide suggested that the latter is of primary importance at the start of the search for a host (it may activate a resting fly or promote taxic behaviour from random flight) and that visual stimula become more important once the host is in sight, although carbon dioxide probably still exerts a confirming influence. This would explain why the red trap nearest the trap baited with carbon dioxide caught far more flies than the trap baited with carbon dioxide, most flies requiring the final visual stimulus provided by the red sphere.

Heat, in addition to its general use in host-seeking, may also attract *H. irritans* to deer antler velvet where the flies feed in large numbers (Anon., 1974). The antlers are at a higher temperature than the rest of the body surface due to the large peripheral blood supply of the velvet.

The association between non-biting muscid species (especially *Hydrotaea* spp.) and biting flies, reported by Tashiro & Schwardt (1953) and Garcia & Radovsky (1962), is also exhibited by *H. irritans* in its attraction to *Haematopota pluvialis*. Nielsen *et al.* (1972) pointed out that *Hydrotaea irritans* often feeds simultaneously with biting flies on cattle, and this association may be of considerable importance in the transmission of summer mastitis as many bite wounds are found on the teats of infected cattle.

The attraction of haematophagous flies to others of the same species is less common. The attraction of *H. irritans* may be due to the black appearance of a swarm, or the

noise of swarming flies (noise was not tested as an attractant) or perhaps a pheromonal stimulus. As a swarm of *H. irritans* indicates the presence of a host or food source, an individual fly will gain an advantage in being attracted to the swarm. Also, as a swarm grows, sheep are increasingly irritated and are more likely to scratch their heads, breaking the skin and causing blood to flow. The swarm as a whole may thus benefit from additional members.

The apparent lack of attraction to host odour and blood is not easily explained. Host odour (in addition to carbon dioxide) is a common attractant for haematophagous flies, but perhaps this is unnecessary for *H. irritans* because of their marked response to carbon dioxide. Normal attraction to bloody wounds and sweating areas on mammals must be due to a localised response that did not show up significantly in the trap experiments.

The use of Manitoba traps for the preliminary testing of repellents for *H. irritans* must be given serious consideration in view of the increasingly high cost of animal trials.

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The flight activity of the sheep headfly, *Hydrotaea irritans* (Fallén) (Diptera: Muscidae)

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Abstract

The flight activity of *Hydrotaea irritans* (Fall.) was investigated in western Scotland using an unbaited suction trap, a carbon-dioxide-baited suction trap and a Manitoba trap. Consistently more female flies were caught than males. Trapping experiments showed that carbon dioxide and visual or thermal stimuli influence long-range attraction and short-range orientation in host-seeking flies. The seasonal activity of adults was determined from the geometric means of catches from a suction trap baited with carbon dioxide and a Manitoba trap. *H. irritans* was shown to be univoltine. The activity of females was greatest in the middle of July and declined sharply in the first week of August. Male activity reached a peak at the same time as that of the females, then declined until no males were caught after mid-August. Females were most active between 10.00 and 18.00 h B.S.T., with a peak about 13.00 h. There was no variation in sex ratio during the day. Multiple regression equations of climatic and seasonal factors with log catches of flies were very similar for the two types of trap. Radiant temperature, illumination, wind speed and date were shown to influence activity of females and, with the exception of illumination, male activity also. Seasonal activity curves calculated from the regression equations were plotted for both sexes in the two traps.

Introduction

The sheep headfly, *Hydrotaea irritans* (Fallén), is a Palaearctic fly well known for its irritating habit of swarming round the heads of man and animals in the summer. Its association with cattle and suspected role in the transmission of summer mastitis led to several investigations in Denmark (Hammer, 1941; Bahr, 1953; Nielsen *et al.*, 1971, 1972). More recently, attention has been focused on the fly owing to the 'broken heads' syndrome in certain breeds of horned sheep in the border areas of Scotland and England (Tarry, 1974?; Tarry & Kirkwood, 1974; Titchener, 1975). The irritation of swarming adults of *H. irritans* causes the sheep to scratch and rub their heads against objects. The lacerations then result in intensified attack by the flies, and the wounds become greatly extended by more self-inflicted damage. The flies may also cause damage with their prestomal teeth (Makhan'ko, 1973). A lesion may eventually cover the whole upper head, leaving a large scar when the wound heals during the winter. Sheep strike can occur on the wound.

To investigate the field biology of *H. irritans* and to compare flight activity in different areas, it is necessary to trap the fly by a method that can be standardised. The adults are readily attracted to man, and for this reason only hand nets have previously been used to catch them (Tarry, 1974?; Tarry & Kirkwood, 1974). This method is unsatisfactory, as the attractiveness of different individuals varies. Kettle (1969) showed that, depending on their health and on the amount of clothing worn, different collectors caught different numbers of *Culicoides* spp. In the present investigations, a comparison was made of different trapping methods and the use of these to study various aspects of the flight activity of *H. irritans*.

Material and methods

The trapping site was a field containing blackface sheep on a Lanarkshire (Scotland) farm with a severe *H. irritans* problem. The field (Nat. Grid. ref. NS 827336) was bordered on its north, south and west sides by mixed woodland and on the east side by a road. The traps were aligned 20 m apart along a south-facing stone wall to obtain the most direct sunlight.

The following traps were tested:

1, a black suction trap 0·3 m in diameter and 1·3 m high. It was made to the specifications of Johnson (1950) except that it lacked the catch-segregating mechanism and the cone was enclosed in a metal wind shield. The fan speed was set at 'boost';

2, an identical suction trap with the addition of a length of rubber tubing with an outlet 0·4 m above the fan. Through this tube was released carbon dioxide at a rate of 2 litres/min. Previous experiments by the author (see Anon., 1974) had shown that carbon dioxide attracted *H. irritans*;

3, a Manitoba trap constructed following the design of Thorsteinson *et al.* (1965). The trap comprised a black sphere (0·5 m in diameter) suspended beneath a polythene collecting cone, which was supported by a tripod. Flies were attracted to the sphere, flew upwards to escape, and were then trapped in a container at the cone's apex; and

4, an animal trap, based on the description by Morris & Morris (1949), and a sticky trap. Negligible numbers of flies were caught in them.

The suction trap baited with carbon dioxide was operated once a week during May, September and October 1974, and two or three times a week during June, July and August, for 15 min starting on each hour, between 11.00 and 15.00 h B.S.T. and often from before dawn until after dusk. The change in fly activity throughout the season was based on a standard catching period of 11.00–15.00 h. The Manitoba trap was operated concurrently with the carbon-dioxide-baited suction trap from 26 June until the end of August. The unbaited suction trap was operated concurrently throughout July.

The following meteorological factors were recorded during each 15-min trapping period: maximum air temperature and maximum relative humidity in the shade measured with a whirling hygrometer, maximum radiant temperature using a thermometer laid horizontally on a white board placed out of the shade, maximum illumination by measuring the light reflected from a horizontal grey board with a Weston Master V exposure meter, barometric pressure using an aneroid barometer, and wind speed using an anemometer over the whole period.

Results

Comparison between traps

Analysis of transformed (log catch+1) male and female catches in July showed highly significant ($P<0·001$) differences between trap means (Table I). The suction trap baited with carbon dioxide caught more flies than the Manitoba trap, which in turn caught more than the unbaited suction trap. This shows that *H. irritans* is highly attracted to carbon dioxide. The catches in the Manitoba trap indicate a response to

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TABLE I. *Numbers of males and females of* H. irritans *caught in 15-min trapping periods from 1 July to 28 July in three traps*

	Mean transformed numbers	Geometric mean	Max. no. caught in any trapping period
Females			
Suction trap baited with carbon dioxide	4·17	63·6	1271
Manitoba trap	3·36	27·7	186
Unbaited suction trap	1·43	3·2	51
*F value (2,88) = 148·41; $P < 0·001$			
**SED = 0·186			
Males			
Suction trap baited with carbon dioxide	2·44	10·4	94
Manitoba trap	1·59	3·9	29
Unbaited suction trap	0·42	0·5	7
*F value (2,88) = 75·02; $P < 0·001$			
**SED = 0·165			

*Analysis based on mean transformed numbers.
**SED = standard error of the difference.

a visual or thermal stimulus, colour or heat absorption accounting for the attraction to the black ball beneath the trap.

Analysis of transformed (arcsin) percentages of male flies in catches during the

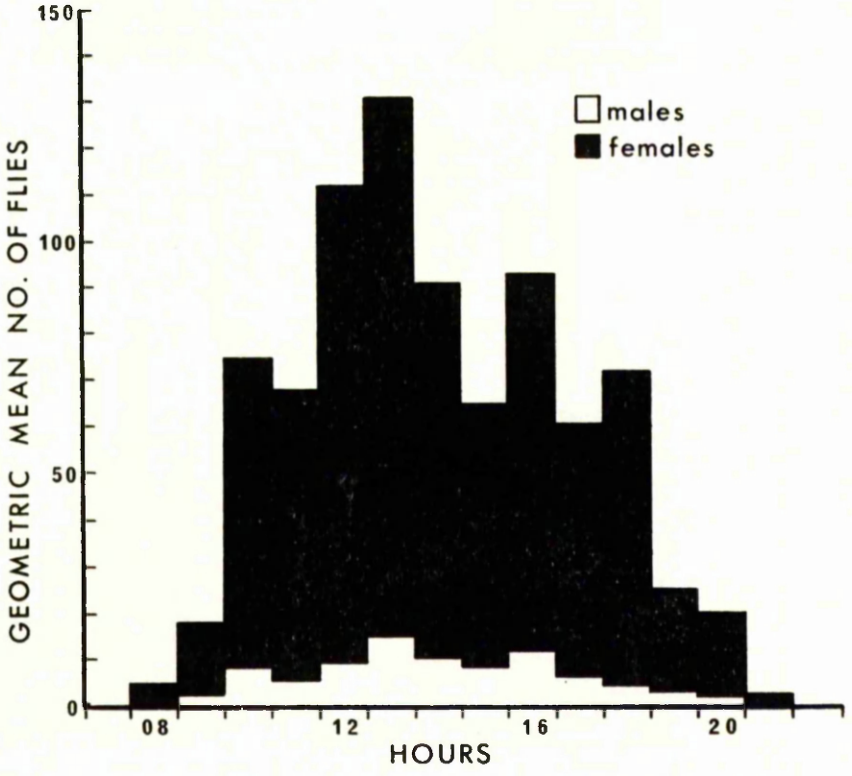

Fig. 1.—Geometric mean numbers of *H. irritans* caught in a suction trap baited with carbon dioxide at hourly intervals during the day throughout July. Each column shows the numbers caught in a 15-min trapping period starting on the hour.

first week of July showed a significant difference ($P<0{\cdot}01$) between the catches in the suction trap baited with carbon dioxide (24·9%) and those in the Manitoba trap (30·9%). Low catches of flies causing large variation in the sex ratios of the unbaited suction trap catches prevented analysis. After the first week of July, the percentages of males caught were too low for analysis.

Flight periodicity

The geometric means of the numbers of *H. irritans* caught in the suction trap baited with carbon dioxide in each catching period during July (Fig. 1) show that *H. irritans* was caught mainly between 10.00 and 18.00 h B.S.T., with a peak about 13.00 h. Before 08.00 h and after 22.00 h no flies were found in the traps. Analysis

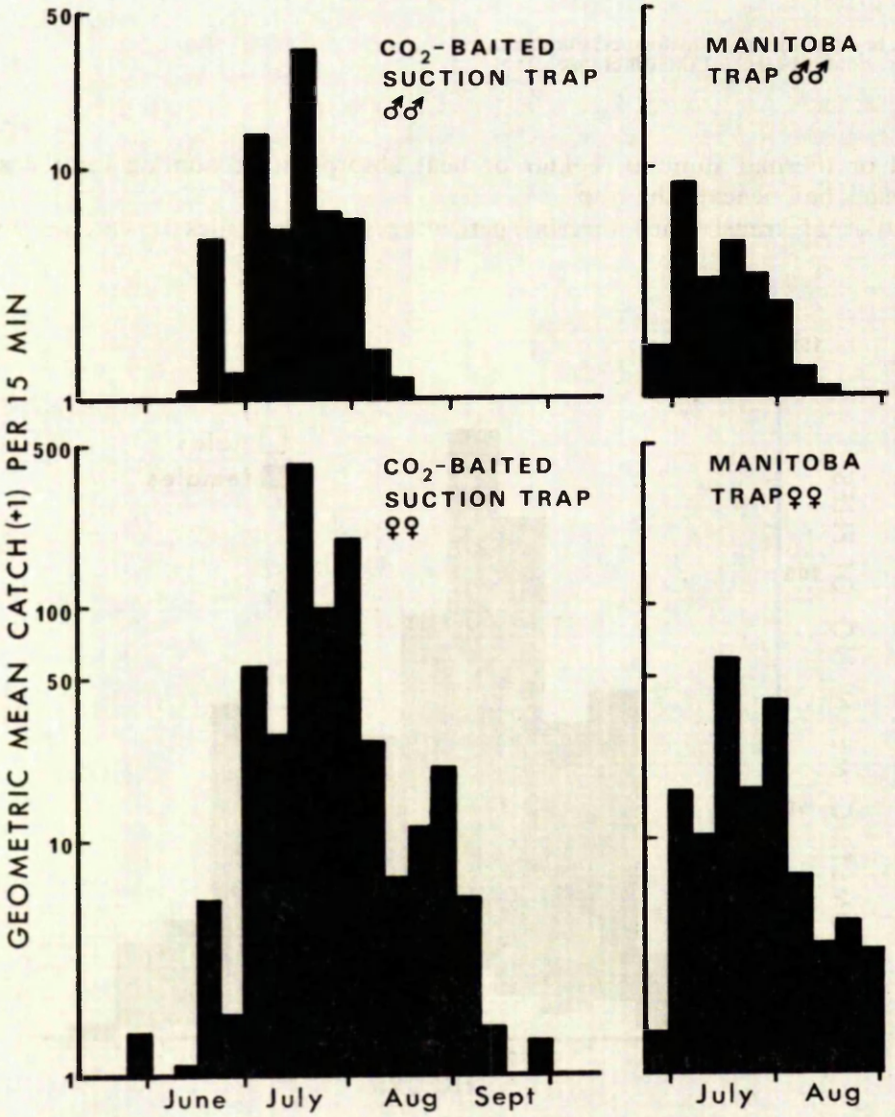

Fig. 2.—Weekly geometric mean numbers of *H. irritans* caught in a suction trap baited with carbon dioxide and a Manitoba trap in 15-min trapping periods between 11.00 and 15.00 h from May to October.

of the transformed (log catch+1) data confirmed there was significant variation ($P<0{\cdot}001$) in activity of both males and females during the day, but there was no variation in sex ratio. Further analysis was impossible due to the variation in activity between days. August trap catches were low, varying greatly between the start and end of the month, and were not included in the analysis.

Seasonal incidence and the effect of weather on trap catches

Weekly geometric means were calculated for catches of all males and females caught in the suction trap baited with carbon dioxide and the Manitoba trap between 11.00 and 15.00 h each week. The means were plotted to give a seasonal distribution of activity for each sex in the two traps (Fig. 2). Males were never as numerous as females and none was caught after the middle of August.

There were considerable fluctuations in activity between weeks. These were mostly due to weather. Multiple regression analyses were used on all trap catches of females between 26 June and 29 August and of males between 26 June and 14 August. These determined which meteorological and seasonal factors were strongly associated with variations in numbers of *H. irritans* trapped. Climatic factors are strongly inter-related. This could have resulted in an indirect relationship appearing direct if a single regression analysis had been used in preference to a multiple regression analysis.

A separate regression equation was derived for each sex in both traps. The dependent variable was $\log_e (n+1)$, n being the number of males or females caught in each trapping period. The independent variables were radiant temperature (t), relative humidity (h), wind speed (w), illumination (i) and barometric pressure (p). Air temperature was excluded as it was very highly correlated with radiant temperature, which produced a better fit to the data. Quadratic terms were included for *H. irritans* seasonal activity by using day number from 26 June (D) and D^2, and for systematic variations in catch throughout the day by using time of day (T) and T^2. Two-factor and second order terms (*e.g.*, tb, iw, t^2) were considered, but only t^2 merited inclusion. One variable at a time was entered into the regression, provided that its presence produced a significantly better fit to the data. All other variables in the regression were then checked using partial t tests to determine whether they could be omitted without a significant reduction in fit. The process was continued until no significantly better fit could be obtained.

The resulting equations with the percentage variation explained (R^2) are shown in Table II. Coefficients for time of day, relative humidity and barometric pressure were not included in the final regression equations. These equations apply only to the following range of conditions from which they were derived:

radiant temperature	9–30°C,
air temperature	9–21°C,
illumination	1·1–176000 lux,
relative humidity	53–100%,
wind speed	0·3–4·5 m/s, and
barometric pressure	989–1017 mb

From the regression equations, seasonal activity curves were plotted for males and females in the two traps (Fig. 3). These show activity during the summer, excluding variation associated with the climatic factors included in the equations. The date of optimum female activity indicated by the regression equations for both traps was 25 July; that for males in the Manitoba trap occurred on 8 July, five days before that in the suction trap baited with carbon dioxide. The optimum radiant temperatures for fly activity derived from the regression equations were 23·7°C for females and 29·3°C for males in the suction trap baited with carbon dioxide and 22·3°C for females and 26·1°C for males in the Manitoba trap. The minimum threshold value of radiant temperature was 11°C for both sexes in each trap.

TABLE II. *Coefficients of factors included in multiple regression equations describing activity of males and females of* H. irritans *recorded by a suction trap baited with carbon dioxide and a Manitoba trap*

	Coefficients							R^2	No. of observations
	Constant	D	D^2	t	t^2	i	w		
Females									
Suction trap baited with carbon dioxide	−6·0363	0·1489	−0·0025	0·7916	−0·0167	$5{\cdot}78\times10^{-5}$	−0·6273	61·2%	230
Manitoba trap	−4·8098	0·1025	−0·0018	0·5865	−0·0132	$7{\cdot}04\times10^{-5}$	−0·5265	53·3%	224
Males									
Suction trap baited with carbon dioxide	−3·5727	0·0983	−0·0028	0·4342	−0·0074	—	−0·2552	56·3%	198
Manitoba trap	−2·2968	0·0287	−0·0012	0·3255	−0·0062	—	−0·2375	45·3%	192

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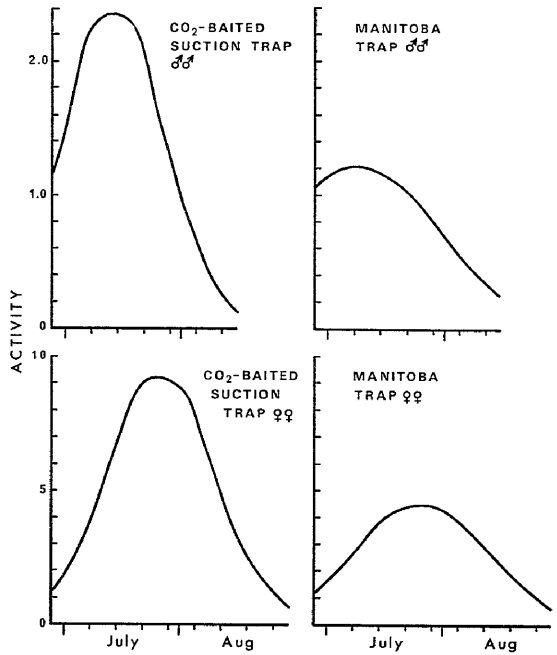

Fig. 3.—Seasonal activity calculated from multiple regression equations for males and females of *H. irritans* in a suction trap baited with carbon dioxide and a Manitoba trap. Activity is expressed as a proportion of the activity on 26 June.

Discussion

It is important to remember that nearly all the flies trapped in this study are those responding to baited traps, *i.e.*, host-seeking hungry flies. They are not representative of the adult population as a whole.

Trap comparison

Kellogg & Wright (1962) showed that, with *Aedes aegypti* (L.), carbon dioxide is associated with an initial activation leading to a general search. In the case of *H. irritans*, carbon dioxide probably acts as a long-range attractant or activator, and a visual or thermal factor is used at short range for 'homing-in'. It had been noticed in other studies that sweeping a net around the head appeared to attract far more *H. irritans* than a net held stationary above the head.

It had been hoped that the unbaited suction trap would act as a non-selective trap, sampling the entire active population of *H. irritans*. However, it caught far more adults than a suction trap camouflaged with bracken fronds, which was compared with it briefly, and it seems likely that the black casing of the unbaited suction trap attracted flies in the same way as the Manitoba trap.

A reduction in the population of *H. irritans* by artificial means such as intensive

trapping might provide effective control. In the United States, Wilson (1968) used sticky traps baited with carbon dioxide to reduce populations of tabanids infesting cattle. Manitoba traps with or without carbon dioxide may have a similar use for control of *H. irritans*.

Flight periodicity

The exclusion of time of day (T & T^2) as an independent factor in the multiple regressions shows that the peak at 13.00 h seen in Fig. 1 is associated with climatic factors. Time of day does not act as an intrinsic factor regulating activity. Nielsen *et al.* (1972), working in Denmark, recorded activity peaks at dawn and dusk. Such sub-crepuscular activity was probably due to the temperature regularly exceeding the optimum through the day. This seldom occurred in Scotland and is not apparent in Fig. 1. In contrast to the Danish findings, *H. irritans* was not caught in the traps between 22.00 and 08.00 h, probably because the traps were in the shade between these times.

Seasonal incidence and the effect of weather on trap catches

Similar work over several summers is required before the regression equations in Table II could be considered accurate enough for predictive purposes. However, they give good indications of the nature of fly activity under various meteorological conditions and are consistent both in the sign and magnitude of the coefficients and in the climatic factors included.

The unexplained variation could be attributed to the following causes. There were a large number of observations for each sex and trap. The traps do not measure activity precisely, and some accuracy was inevitably lost owing to rapidly changing weather conditions within the trapping periods. The analyses take no account of possible adaptations of the flies to the weather (Digby, 1958), short term migration in and out of the population, or the movement of nearby potential hosts.

Although the inclusion of coefficients for climatic factors in the multiple regression equations does not indicate a causal relationship, other observations tend to confirm that these factors do have an influence on fly activity. Johnson (1969) stated that the warming up of large insects is often achieved by the absorption of radiant heat from the sun. Hughes *et al.* (1972) found that the activity level of *Musca vetustissima* Walker rose and fell with air temperature during the day, but radiant heat activated the fly for short periods. Thus, it was not surprising to find that radiant temperature was associated with a large proportion of the variation in trap catches of *H. irritans*. Reduction in activity at high temperatures as shown by *H. irritans* often occurs among flies; for example, activity of *M. vetustissima* is reduced at temperatures over 35°C (Hughes *et al.*, 1972). The inclusion of a coefficient for illumination in the regression equations confirms the suggestions of Hammer (1941) and Nielsen *et al.* (1971), who thought that light was an important stimulus for activity of *H. irritans*. The role of illumination distinct from that of radiant temperature is, however, difficult to understand.

The inclusion of a coefficient for wind speed was to be expected, in view of the dramatic effect of gusts of wind on fly numbers swarming round hosts. Nielsen *et al.* (1972) stated that activity of *H. irritans* was negligible at wind speeds above 6 m/s.

The exclusion from the regression equations of a coefficient for relative humidity conflicts with the findings of Hammer (1941) and Tarry & Kirkwood (1976), who suggested that there is an optimum level of humidity. Norris (1966) showed little evidence of an effect of relative humidity on trap response patterns of *M. vetustissima*.

Rain had an effect that could not be shown in the regression analyses. Light rain had little effect, but activity ceased in heavy rain. Few flies would, in any case, be active in the cool, cloudy conditions associated with rain.

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Few studies have satisfactorily shown barometric pressure to exert a significant influence on the flight activity of insects, although Burnett & Hays (1974) found that it was the meteorological factor exerting the greatest influence on tabanid activity.

It is reassuring that the dates of peak female activity, as indicated by the regression equations, are consistent for the two traps. The same consistency is not shown with the males.

Hammer (1941) suggested that there were two generations of *H. irritans* each year in Denmark, the first emerging in the spring until late July and the second throughout August. The present results show only one main female peak and a very short period of male activity. This suggests that the fly is univoltine, which is in accord with the findings of Tarry & Kirkwood (1976) in southern England.

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The effect of diet on the life-span and egg maturation of caged adult sheep headflies, *Hydrotaea irritans* (Fallén) (Diptera: Muscidae)

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Abstract

A method for maintaining adults of *Hydrotaea irritans* (Fall.) in captivity in groups, pairs or singly, is described. Male flies lived about half as long as females. Flies required carbohydrate and water for survival. A 50% honey solution, a 50% sucrose solution, thistle flowers and aphid honeydew all met the energy requirements of *H. irritans*, unlike blood, serum, milk, sweat, dung and mucus. The number of eggs matured was greatest on a diet of carbohydrate with blood or serum. Fewer eggs developed in flies given a diet of carbohydrate with milk, and very few on a diet of carbohydrate with horse sweat, cow sweat, dung or mucus. No eggs were matured by females fed on carbohydrate alone. All males had active spermatozoa whether or not they were fed on blood, but females were only inseminated after both they and the males with which they were kept had been given blood. The insemination rate was low at 13·3%. Females required more than one blood-meal, but not more than one every third week, in order to develop the maximum number of eggs.

Introduction

The adult sheep headfly, *Hydrotaea irritans* (Fallén), is attracted in large numbers to animals. It congregates mainly around the head, apparently feeding on sweat, lacrymal fluid, mucus secretions of the muzzle and blood from wounds. In the case of horned sheep, it may feed on blood which is produced when the skin on the head is broken by the sheep's repeated scratching and rubbing to alleviate irritation caused by the fly. *H. irritans* has also been observed feeding on wounds and on possible secretions of the teats of cattle.

In the present investigation, the effects of various food sources on the life-span and egg maturation of *H. irritans* were studied.

Materials and methods

Flies were enclosed either singly or in pairs in vertical open-ended glass cylinders 4·5 cm in diameter and 10 cm tall (Fig. 1). Two small plastic tubes 0·5 cm in diameter and 4 cm tall were glued to the inside wall of the cylinder and filled with the appropriate food. The top end of each glass cylinder was covered with nylon netting secured by an elastic band. The bottom end was placed in a plastic tub containing moist peat. Holes were made in the bottoms of these tubs, which were placed, with others, on water-filled

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trays. This ensured that the moisture content of the peat remained constant and that all flies had equal access to water. Larger glass cylinders 5×10 cm contained groups of five flies.

The flies were kept in an outdoor insectary, the walls of which consisted of alternating vertical strips of polyethylene and nylon gauze. This enabled the flies to live in conditions approximating to those in the field. The roof was constructed from transparent PVC sheeting.

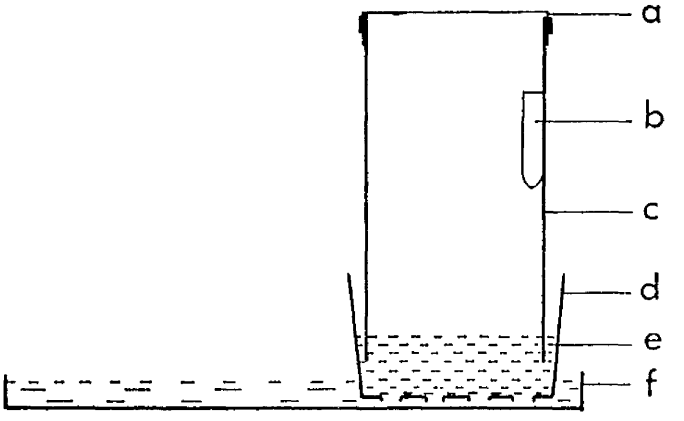

Fig. 1.—Glass cylinder apparatus in which flies were kept. (*a*, nylon netting secured by elastic band; *b*, plastic tube; *c*, glass cylinder; *d*, plastic tub; *e*, moist peat; *f*, tray of water.)

No mass-rearing technique had been developed for *H. irritans*, so the flies used in these experiments were caught in June at the start of seasonal activity. A sample of flies was dissected and the guts of males and females were examined for the presence of blood. None was found. As blood is noticeable in the gut for several days after a feed (unpublished observation) and the flies were caught on their first day of apparent host-seeking activity, it may be assumed that they had not obtained a blood-meal before capture. Further examination revealed an absence of spermatozoa in the spermathecae, indicating that the females were virgins. Active spermatozoa were found in the males' testes. Once caught, flies were kept in net cages and given a 50% honey solution until the experiments began.

Life-span and egg maturation on a diet of blood and honey solution

The treatments were set up on 25 June. Flies were kept individually in cylinders and fed on their respective diets until 21 July, when the majority of males and females were paired. The food then given to each pair was that part of the two diets previously common to both flies.

Treatments consisted of the following combinations of flies fed on different diets:

(1) 30 females given blood and honey solution, paired with 30 males given blood and honey solution and thereafter fed on blood and honey solution;
(2) 30 females given blood and honey solution paired with 30 males given honey solution only and thereafter fed on honey solution only;
(3) 30 females given blood and honey solution and not paired;
(4) 30 females given honey solution only, paired with males given blood and honey solution and thereafter both sexes fed on honey solution only; and
(5) 30 flies of both sexes fed on blood only and 30 flies of both sexes not given food other than water. No flies from these treatments lived long enough to be paired.

Dead flies and the number of eggs laid were recorded and removed from the cylinders twice a week. Dead females were dissected and examined for the presence of sperm in the spermathecae, and the numbers of mature unlaid eggs were recorded.

Protein sources

Groups of five females were kept in the larger glass cylinders. Ten groups of flies were allocated to each of the following seven protein sources:

(1) defibrinated sheep's blood;
(2) horse serum;
(3) pasteurised milk;
(4) horse sweat;
(5) a 2% solution of cow sweat;
(6) cow dung; and
(7) mucus (cotton wool wipings of the nose and muzzle of dairy cattle).

Five groups fed on each protein source were given honey solution in addition. The amount of food available to the flies was not restricted. Control treatments comprised five groups of flies fed on honey solution alone and five groups not fed at all.

Dead flies and the numbers of eggs laid were recorded and removed from the cylinders twice a week. Dead females were dissected, and the number of mature unlaid eggs they contained was recorded.

Number of blood-meals required

Five groups of five female flies were fed at each of the following intervals:

(1) blood continuously available (to save unnecessary duplication, this was the same treatment and flies as for treatment 1 of the previous experiment);
(2) one blood-meal each week;
(3) one blood-meal at the start of the experiment on 25 June and once every third week subsequently; and
(4) one blood-meal at the start of the experiment and no more.

All flies were given unlimited honey solution in addition to their protein allowance. The numbers of eggs laid were recorded and removed twice a week. Dead flies were dissected, and the numbers of mature eggs they contained were recorded.

Carbohydrate sources

Five groups of five female flies were given unlimited honey solution, and five groups were given unlimited 50% sucrose solution. The numbers of dead flies were recorded daily.

In the second experiment, the possible natural sources of carbohydrate were investigated. Greenberg (1971) mentioned that *H. irritans* adults aggregate on the inflorescences of daucacious plants infested with aphids. Berlyn (unpublished observation) noticed many adult *H. irritans* on the thistle *Cirsium palustre*. To investigate some possible natural sources of carbohydrate available to *H. irritans*, five groups of five flies were allowed access to thistle inflorescences (the inflorescences were not replaced as they died) and five groups had access to *Phragmites communis* leaves covered in aphids. Five control groups were given *Phragmites* leaves with no aphids. The numbers of dead flies were recorded daily.

Water requirement

Flies were kept in groups of five with dry peat. Six groups of flies were each given an inflorescence of the thistle *C. palustre* and cattle saliva. Six groups were each given a thistle inflorescence and water. Six groups were each given a thistle inflorescence

only, and six groups were given nothing. The numbers of dead flies were recorded daily. The thistle inflorescences were not replaced as they died.

Results

Life-span on a diet of blood and honey solution

There were significant differences in the mean life-spans of both males and females fed on different diets (Table I).

TABLE I. *The life-spans of males and females, and the egg maturation of females, fed on blood and honey*

Diet before pairing		Diet after pairing		Mean life-span	Mean $\log_e (n+1)$
Blood	Honey	Blood	Honey	(days)	no. of eggs matured (eggs)
FEMALES					
–	+	–	+	149.4	0
+	+	–	+	107.3	1.94
+	+	not paired		113.7	3.27
+	+	+	+	104.6	3.04
+	–	not paired		1.8	0
–	–	not paired		2.3	0
S.E.D.				9.99 (174d.f.)	0.32(87d.f.)
MALES					
+	+	–	+	83.8	–
+	+	+	+	67.0	–
–	+	–	+	66.2	–
+	–	not paired		1.4	–
–	–	not paired		1.8	–
S.E.D.				4.75(145d.f.)	

\+ indicates inclusion in diet.
– indicates absence.
Vertical lines indicate values not significantly different at $P<0.05$.

Egg maturation on a diet of blood and honey solution

The number of eggs laid plus the number of mature eggs dissected from dead gravid females was regarded as the total number of eggs matured by each fly.

Females fed on blood and honey solution throughout, whether paired or not, matured similar numbers of eggs (Table I). Females that were not fed on blood after pairing matured significantly fewer eggs, while females that were never fed on blood developed no mature eggs. Dissection showed that eggs in this latter treatment were developed only to stage III, while all other treatments resulted in mature eggs (the description of the egg stages follows that described for *Musca vetustissima* Walker by Tyndale-Biscoe & Hughes (1969)). Females given no food or only blood died before any egg development occurred.

Egg-laying trends in the three treatments are shown in Fig. 2. Females fed on blood and honey throughout and paired with males are probably most typical of flies in the field. In this treatment the first eggs were laid on 18 July, in the fourth week after the flies were first offered blood. Berlyn (1978), trapping field flies, found the first gravid females in the fourth week after blood was first identified in the gut of trapped flies. With caged flies, the majority of eggs were laid by 12 September, although small numbers were laid until 22 November, obviously a more extended oviposition period than that in the field. The number of ovarian cycles undergone should have been apparent from the individually caged female flies. Unfortunately, the cycles merged into one another due to continuous oviposition throughout the summer. However, when the treatment as a whole is considered, three egg-laying peaks are

discernible, in the last week of July, the third week of August and the second week of September (Fig. 2). These may indicate three ovarian cycles.

Inseminated females were found only in the treatment where both males and females were offered blood. Some eggs in this treatment produced larvae. Only 13·3% of the females were inseminated. Like most muscid flies, the uninseminated females developed and laid sterile eggs. Males of all treatments contained active spermatozoa. Males that achieved successful copulation lived as long as other males on that diet.

No relationship between size of fly and the number of eggs matured was found in females fed on blood and honey solution when measured across the frontal lobe of the head (the region between the eyes).

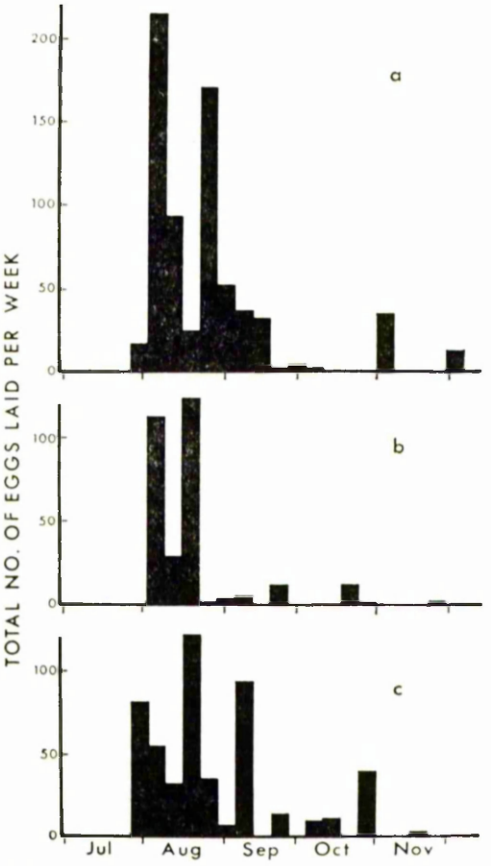

Fig. 2.—The total number of eggs laid each week by (a) 30 females fed on honey solution and blood throughout and not paired with males, (b) 30 females fed on blood up to the time of pairing with males, and only honey solution subsequently, and (c) 30 females fed on blood and honey solution throughout and paired with males.

Protein sources

As all the flies of one of the five groups fed on blood and honey solution died within the first week of the experiment, only four groups of flies could be included in the analysis.

Analysis, using $\log_e (n+1)$ values, of the protein treatments with the addition of honey solution showed there were highly significant differences in the numbers of eggs developed to maturity between females in the different treatments (Table II). The mean

TABLE II. *Numbers of eggs matured by females fed on different sources of protein*

Protein source	No. of replications	Mean $\log_e$ no. of eggs matured.	Geometric mean no. of eggs matured
Blood	4	5.01	149.1
Serum	5	4.79	119.5
Milk	5	3.27	25.2
Mucus	5	1.58	3.9
Horse sweat	5	1.57	3.8
Cowdung	5	0.93	1.5
Cow sweat	5	0.69	1.0

S.E.D. (27d.f.) comparing protein sources other than blood 0.599
comparing blood treatment with any other 0.635
Vertical lines indicate values not significantly different at $P<0.05$

numbers of eggs laid by flies in each treatment were greater than that laid by flies fed on honey solution alone, which was nil. Flies fed on blood, serum and milk produced significantly ($P<0{\cdot}05$) more eggs than flies on the other treatments, and milk was significantly inferior ($P<0{\cdot}05$) to blood and serum as a protein source. The rate of development also varied greatly; females given horse sweat took 40 days longer to lay the first eggs than did flies fed on blood or serum.

There were no significant differences between the life-spans of females fed on different protein sources without honey solution. Females fed on the protein sources did not live significantly longer than females that were not fed at all, indicating that the protein sources (with the small amount of associated carbohydrate and fat) were not contributing sufficiently to the energy requirements of the flies. Neither was any part of the protein meal being oxidised directly for this purpose.

Number of blood-meals required

The numbers of mature eggs produced by females in the different treatments are shown in Table III. Females fed on blood once only, at the start of the season, laid

TABLE III. *No. of eggs matured by females given different numbers of blood-meals*

No. of blood-meals offered	Mean $\log_e$ no. of eggs matured	Geometric mean no. of eggs matured
1. Blood continuously available	5.01	149.1
2. One each week	4.99	145.9
3. One each third week	4.92	136.0
4. One only	3.89	47.9
S.E.D. (15d.f.) comparing 1 with any other	0.267	
comparing 2, 3 & 4	0.251	

Vertical lines indicate values not significantly different at $P<0.05$

about one-third of the number of eggs laid by others given blood continuously. Analysis, using $\log_e (n+1)$ values, showed this was a significant reduction. The results from the

other treatments were not significantly different from one another, indicating that for maximum egg maturation females require no more than four or five good-sized blood-meals during the summer.

The three ovarian cycles present in females fed on blood continuously were not apparent in those fed on blood once only (Fig. 3). Instead, there appeared to be only one ovarian cycle, with oviposition commencing a week later and with fewer eggs laid at its peak. It is noticeable that, except for one slight difference, the egg laying peaks of the continuously blood-fed females occur at exactly the same time as those of the individually caged females.

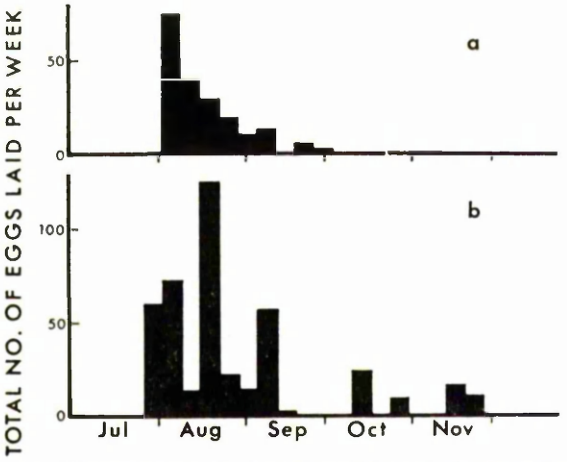

Fig. 3.—The total number of eggs laid each week by (a) 30 females fed on blood once only, and (b) 30 females fed on blood continuously.

Carbohydrate source

Analysis showed no significant difference in mean life-span between females fed on honey solution and those fed on sugar solution. Flies in this experiment lived for a much shorter period than expected, as a result of infection with the parasitic fungus *Entomophthora muscae*, from which many died.

Females given thistle inflorescences lived significantly longer (mean=7·88 days) than those given access to aphid honeydew (mean=4·04 days), which in turn lived significantly longer than females given no obvious food source (mean=1·76 days; S.E.D. (72 d.f.)=1·14). The aphids left the *Phragmites* after a few days, and this may account for the difference in life-span between flies given aphid honeydew and those given thistle inflorescences. Flies in neither of these treatments lived for long because the carbohydrate sources were not replenished.

Water requirement

The life-spans of females given water (mean=2·86 days) and cattle saliva (mean=2·73 days) in addition to thistle inflorescences were significantly greater than those of flies given thistle inflorescences alone (mean=1·86 days) and no food or water (mean=1·70 days; S.E.D. (116 d.f.)=0·08).

Discussion

A source of protein is certainly required for the successful development of eggs by *H. irritans*, and the results clearly show the advantages of a blood or serum meal. Kirkwood (1976) found that the rate of egg development did not vary in *H. irritans*

females fed on blood, serum, milk or egg white, and that the choice of protein was not critical. However, the present results show that although milk supported egg development it was markedly inferior to blood or serum. This was to be expected with a specialised blood-feeder. Even *Lucilia cuprina* (Wiedemann), a general feeder, exhibits slower egg development on casein, milk, yeast and egg albumin than on liver (Webber, 1957). The other natural protein sources tested on *H. irritans* (sweat, dung and mucus), which Kirkwood did not try, appear to be of little use as protein sources, although better than a carbohydrate source alone. This is in contrast to *M. vetustissima*, which can utilise vegetable or dung protein if continuously supplied (Tyndale-Biscoe & Hughes, 1969). It is possible that *H. irritans* feeds on facial secretions to provide its water requirements.

That caged females require more than one blood-meal but less than one every three weeks must be extended to the field situation with care. Captive flies were able to imbibe blood freely with no constraints upon them. In the field, they would be subject to climatic variations, host movements, competition with other flies, etc., and it is unlikely that they could ever ingest such large quantities of blood in one meal as they did in the insectary. However, the result could explain the ability of *H. irritans* to live within extensive Scottish forests where virtually the only mammals available for a blood-meal are widely dispersed deer and rabbits (the natural hosts of the fly in Britain). The fly would not have the opportunity to feed on such animals frequently.

The role of blood in the reproductive biology of the male is not clear. From the start of the season, before a blood-meal, males had active spermatozoa in their testes. Nevertheless, the absence of any insemination in treatments where the male had no access to blood must be of significance. Mammals, the natural source of blood, may be regarded as aggregation sites, and blood feeding by males may be a behavioural mechanism whereby they come into contact with the females. Females of *Glossina pallidipes* Austen are inseminated near the host while seeking their first blood-meal (Saunders, 1962). This explains the 'following swarm' of 'sexually appetitive' males which follows a host (Fiske, 1920). It is known that odours of aggregation sites can stimulate male sexual behaviour; males of *L. cuprina* are stimulated by the odour of sheep liver (Shorey, Bartell & Barton Browne, 1969). Stimulation of male *H. irritans* by aggregation site odours could be the reason for the restriction of insemination to treatments in which both males and females were given blood. The low level of insemination in these treatments must have a different cause, and could possibly be explained by behaviour similar to that of *G. morsitans* Westwood where most effective pairing is obtained with older non-virgin males and young females, and where the male to female ratio is important; a ratio of 2:1 with older males gave insemination rates of about 90% (Southon & Cockings, 1963). Alternatively, considerable space may be required in order to perform a successful mating flight.

Not all haematophagous flies require a carbohydrate source in addition to blood. Bursell (1970) stated that *Glossina* oxidises directly a part of the proline and glutamate intake of each blood-meal to meet current energy requirements. This is evidently not the case with *H. irritans* and in addition, the 0·1% carbohydrate content of blood must be too low for noticeable use. The blood-meal, then, must be taken solely for a reproductive purpose, while thistle flowers and aphid honeydew provide probable natural carbohydrate sources.

Females feeding on blood and honey had a shorter life than females feeding only on honey solution, probably due to egg development using resources from the fly and inducing earlier senescence. Blood appears to have had no effect on the production of spermatozoa by males, which is possibly why it did not reduce length of life.

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Proceedings of the 8th British Insecticide Conference (1975)

THE PREVALENCE AND CONTROL OF THE SHEEP HEADFLY, HYDROTAEA IRRITANS

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Summary A survey has shown that during the last five years headfly, Hydrotaea irritans, has become a serious pest of sheep in South-West Scotland. Attacks occur mainly on horned breeds of sheep during July and August and are particularly severe on those farms situated close to forests or woodland.

In field trials crotoxyphos gave some protection against headfly. This compound proved to be more effective in a cream containing tar than when used as a spray. The new insecticide 1, 1 - bis (p - ethoxyphenyl) - 2 - nitropropane provided a significant measure of headfly control for the whole of the test period in one of three trials carried out with this compound.

Résumé Une inspection a montré que pendent les cinq derniers ans Hydrotaea irritans a devenu un insecte nuisible des moutons au sud-ouest d'Écosse. Les moutons cornés sont les victimes principales des attaques, quelles ont lieu pendant Juillet et Aôut et sont exceptionnellement grave si la ferme est à proximité d'une forêt où d'un bois.

Aux essais de champ crotoxyphos offrit quelque protection contre H. irritans. Ce composé s'est révélé de faire de l'effet meilleur comme une crème avec gourdon que comme un embrun. Le nouvel insecticide 1, 1, bis (p - ethoxyphenyl) - 2 - nitropropane munit une mesure importante de pouvoir sur les mouches pendant toute la durée de l'épreuve à un de trois essais effectué avec ce produit chimique.

INTRODUCTION

The headfly, Hydrotaea irritans is widely distributed throughout Britain and Europe. During the last five years this fly has been shown to be responsible for the phenomenon of broken heads on certain sheep breeds in the border areas of Scotland and the counties of Northumberland and Durham (Hunter, 1972 ; Tarry, 1973 ; Titchener et al, 1974).

The object of the present investigation was to determine the prevalence and severity of headfly attacks in the West College area and to aid in the development of possible control measures.

METHOD AND MATERIALS

Survey

To determine the prevalence and severity of headfly attacks a survey was carried out in South-West Scotland during the period 1972 to 1974. An even sample distribution was obtained by sampling at least four farms in each 10 km ordnance survey grid square of the area.

Chemical Trials

Trials were conducted on commercial Blackface flocks with a severe headfly problem. Ewe and wether lambs were used for trial work. Whilst attacks were more frequent and severe on tup lambs these could not be used in trials since they were not present in sufficient numbers for valid statistical comparisons. Ewes were included in one trial as they had been particularly seriously affected by headfly in previous years.

Treatments used were :

Flymort 24 (Tuco Chemical Company). A 1% crotoxyphos spray used over the head and body at approximately 2 week intervals.

Headfly repellent dark quality (Robert Young & Co.). A cream containing 0.05% crotoxyphos and pine tar oil. Applications were made at approximately 2 week intervals around the base of the horns.

"C" fluid. The headfly repellent with an increased crotoxyphos content of 0.5%.

GH74 (Wellcome Research Laboratories). The new insecticide 1, 1 bis (p - ethoxyphenyl) - 2 - nitropropane used as a 0.125% dip. Two dippings were carried out with a 4 week interval between them.

Treatments started during the last week in June/first week in July before any broken heads had occurred in the flocks. Trials were then continued until the 3rd week of August. Visual assessment was made of the number and severity of headfly lesions. Statistical analysis of the trial results was by means of the X^2 test.

RESULTS

Survey

A total of 600 farms were sampled in the survey. Sheep headfly was considered to be a severe problem on 10.9%, a moderate problem on 17.5% and a slight problem on 33.8%. On 37.8% of farms there had been no headfly attacks. The number and severity of headfly attacks showed considerable variation in different shires (Table 1).

Kirkcudbrightshire was the most seriously affected by headfly. Headfly was also a problem in Dumfriesshire and Lanarkshire as well as in some parts of Ayrshire and Wigtownshire. Whilst most headfly attacks occurred on Blackface and other horned breeds some attacks occurred in Border Leicester, Cheviot and Suffolk flocks. Farms situated close to woodland or forestry suffered particularly badly from headfly.

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Table 1

Percentage of headfly attacks by Shires in South-West Scotland

Shire	None	Slight	Moderate	Severe
Ayrshire	47.0	32.1	15.5	5.4
Dumfriesshire	31.7	34.5	23.5	10.3
Kirkoudbright-shire	10.7	39.8	24.3	25.2
Lanarkshire	47.4	29.5	12.6	10.5
Renfrewshire & Bute	50.0	35.3	11.8	2.9
Wigtownshire	50.8	32.8	8.2	8.2

Chemical trials

Two available commercial preparations for headfly control, Flymort 24 and Headfly repellent (dark quality) were compared in 1973. The results are given in Table 2.

Table 2

Incidence of broken heads on lambs

Untreated Controls	Flymort 24	Headfly repellent
Trial 1, 1973		
1st observation		
9/110 = 8.2%	4/50 = 8%	0/100 = 0%
2nd observation		
26/110 = 23.6%	4/50 = 8%	0/100 = 0%
3rd observation		
26/110 = 23.6%	5/50 = 10%	1/100 = 1%

A significant degree of protection was afforded by Flymort 24 by the 2nd observation ($X^2 = 4.54$, $p < 0.05$). By the 3rd observation, however, the protection afforded by Flymort 24 was less conclusive and only approached significance at the 5% level ($X^2 = 3.3\%$, $p < 0.10$). Headfly repellent provided significantly more protection than Flymort 24 on the 1st, 2nd (significance probability 2.26%) and 3rd (significance probability 3.20%) observations.

Trials were carried out in 1973 and 1974 to compare the effectiveness of Headfly repellent with an improved repellent known as "C" fluid. The results of these trials are given in Table 3.

Table 3

Incidence of broken heads

Headfly repellent	"C" fluid	X^2 (1 d .f.)
Trial 2, 1973		
Lambs 14/98 = 14.3%	6/104 = 5.8%	3.20 ($p < 0.10$)
Trial 3, 1974		
Lambs 3/43 = 7.0%	0/74 = 0%	2.87 ($p < 0.10$)
Trial 4, 1974		
Lambs 66/218 = 30.3%	41/210 = 19.5%	6.59 ($p < 0.02$)
Ewes 92/320 = 28.8%	54/328 = 16.5%	14.0 ($p < 0.001$)

In trials 2 and 3 there was a reduction of headfly lesions in the groups where "C" fluid was used which approached significance at the 5% level. In the 4th trial the protection afforded by "C" fluid was significantly better than that of the commercial repellent especially in ewes.

The efficacy of the new dip GH74 against headfly was also tested in 1974. The results of these trials are given in Table 4.

Table 4

Percentage incidence of broken heads on lambs treated with GH74

Untreated controls	GH74	X^2 (1 d .f.)
Trial 5, 1974		
1st observation		
33/96 = 34.4%	65/340 = 19.1%	9.14 ($p < 0.01$)
2nd observation		
34/96 = 35.4%	51/340 = 15.0%	18.60 ($p < 0.001$)
Trial 6, 1974		
1st observation		
85/250 = 34.0%	27/200 = 13.5%	23.89 ($p < 0.001$)
2nd observation		
73/250 = 29.2%	46/200 = 23.0%	1.89 ($p < 0.20$)
Trial 7, 1974		
1st observation		
53/177 = 29.9%	13/73 = 17.8%	3.32 ($p < 0.10$)

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By the first observation a significant degree of protection was afforded by GH74 in trials 5 and 6 but not, however, in Trial 7 where protection only approached significance at the 5% level. In the two trials where a second observation was made only in trial 5 was a significant degree of protection afforded by GH74.

DISCUSSION

Most farmers attribute the recent appearance of the headfly problem to the withdrawal of dieldrin and other persistent organochlorine dips. Treatment of heads with, or dipping in dieldrin has not prevented headfly attack (Titchener, 1975a). There is the possibility, however, that when dieldrin was widely used on farms it was having an indirect environmental effect on headfly numbers (Titchener, 1975b).

Advisory experience shows there is an urgent need to find a solution to the headfly problem. In the West College area recent reports show the incidence of headfly attacks to be increasing and the problem to be spreading northwards into Argyll and Perthshire. Whilst the environmental effects of dieldrin on wildlife and the residue hazard in sheep fat preclude bringing back dieldrin there is at present only one commercial compound, the dark quality headfly repellent, that affords any protection against headfly attacks. This repellent, however, does not afford complete protection and very frequent treatments, every 3 or 4 days, are required in severe headfly areas. Many breeders also object to its use since they feel it stains the head.

Of the new compounds tested, with the exception perhaps of "C" fluid, none are likely to be commercially developed. Even more disturbing is the fact that there are few candidate chemicals available for headfly control. One of the peculiar difficulties of the headfly problem is that all attempts to rear headflies artificially have, so far, failed with the result that large scale screening of potential headfly compounds is not yet possible. This has made applications for Animal Test Certificates a most unattractive financial gamble when the limited potential of the headfly market in relation to world sales is considered.

Recently it has proved possible to keep headflies, captured from field populations, alive for long periods in outdoor insectaries and it is hoped to extend this work to the testing of chemicals under conditions of simulated headfly attack. This could lead to a useful preliminary screening procedure but is, however, likely to prove difficult when it is remembered that most of the damage to sheep that occurs is apparently self-inflicted by the rubbing and scratching of the affected parts.

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