BIOLOGY AND MANAGEMENT OF THE FACE FLY

MUSCA AUTUMNALIS DEGEER (DIPTERA:MUSCIDAE) IN NORTH AMERICA

by

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Biology and control of the face fly, Musca autumnalis DeGeer (Diptera: Muscidae) - A Review

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Abstract

The face fly, Musca autumnalis DeGeer, completes its life cycle in 16-21 days under field conditions. After mating, females actively and selectively seek protein from the mucous membranes and secretions of the eye and nose of cattle. Females are facultatively haematophagous. Face flies are among the first insects to arrive at freshly dropped dung, on which they feed and oviposit. Dung that has been dropped in open sunny areas is the preferred oviposition site. Generally 20-26 eggs are laid per ovarian cycle, with most females completing 2-3 cycles in a lifetime. Males occasionally are found feeding on cattle; however, much of their time is spent resting on objects in the surrounding pasture.

After its introduction to North America from Europe, the face fly spread rapidly across the continent, often appearing in explosive numbers. Initial reports on the adverse effects of the face fly on livestock productivity were exaggerated; research now indicates that face flies are more of an aesthetic problem to producers than a problem to cattle. Nevertheless, the face fly can transmit eyeworms and the causal organism of pinkeye. Recently, in Sweden, the face fly has been identified as the intermediate host of a filarial nematode which could have a significant impact on livestock. Despite a lack of scientific data on the economic importance of the face fly, considerable time and effort has been devoted toward finding suitable control

methods for it. Many insecticides, insecticide formulations and application techniques have been tested with less than satisfactory results. One promising control method involves the use of pesticides incorporated into sustained-release boluses. A control measure of this nature, if practiced over a large area, holds considerable potential for suppression of face fly populations as well as those of other dung-breeding pests.

Numerous parasites and predators affect various life stages of the face fly. However only the nematode, Heterotylenchus autumnalis Nickle, shows any potential as a biocontrol agent.

Dedication

I dedicate this manuscript to the memory of my mother.

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Table of Contents

List of tables

BIOLOGY AND MANAGEMENT OF THE FACE FLY

MUSCA AUTUMNALIS DEGEER (DIPTERA:MUSCIDAE) IN NORTH AMERICA

1.0 Introduction

The face fly, Musca autumnalis DeGeer (Diptera:Muscidae) known in Europe as the autumn-fly (Oldroyd 1964), was first discovered in North America in Nova Scotia in 1952 (Vockeroth 1953).

It is synonymous with: M. continua Robineau-Desvoidy; M. corvina Port. nec F.; M. floralis Robineau-Desvoidy; M. grisella Robineau-Desvoidy; M. ludicifacies Robineau- Desvoidy; M. nigripes Panz. nec F.; M. ovipara Port. (Keilin); M. prashadii Patt.; M. rustica Robineau-Desvoidy; and M. tau Sch. (West 1951). Four subspecies have been described: M. autumnalis autumnalis DeGeer; M. autumnalis pseudocorvina van E.; M. autumnalis somalorum Bezzi; and M. autumnalis ugandae van E. M. a. autumnalis is the typical Palearctic subspecies, and is at present causing concern in North America (West 1951; Vockeroth 1953). The remaining subspecies are generally confined to the Ethiopian zone (West 1951).

In Europe the face fly is apparently of little economic consequence (James and Harwood 1969) but, within a relatively short period of time since its introduction into North America from Europe it became a major livestock pest (Vockeroth 1953; Pickens and Miller 1980). Its rapid spread across the continent has been accompanied by numerous complaints from livestock producers about increasing incidences of livestock eye disorders, cattle annoyance, and lost grazing by cattle

disturbed by face flies, (U.S.D.A. 1959; Dobson and Matthew 1960; Teskey 1960,1969; Decker 1961; Holdsworth 1962; Benson and Wingo 1963; Ode and Matthysse 1964).

The face fly has been found throughout southern Canada (Depner 1969) and the continental United States except Arizona, New Mexico, Texas and Florida (Morgan 1981; Wright 1985).

Although the face fly gained considerable notoriety upon its spread in North America, it is now considered, in my opinion, to be a pest of little consequence. However, because face flies feed on body wounds and mucous membranes of cattle, they are potentially serious vectors of disease.

2.0 General description of the life cycle

The life cycle of the face fly under field conditions generally requires 16-21 days (Hammer 1941; Wang 1964; Teskey 1969). After mating, females lay their eggs in freshly dropped, undisturbed cattle dung (Teskey 1969). Females usually complete 2-3 ovarian cycles (Thomas et al. 1972), laying approximately 20-26 eggs per cycle (Wang 1964; Killough and McClellan 1965). Eggs generally hatch within a day (Hammer 1941). Depending on temperature, larvae will complete their development within 3-5 days (Wang 1964; Teskey 1969). When mature, the third-instar larvae leave the fecal pat in search of a suitable pupation site. The pupal period is also dependent on temperature and

lasts from 8-10 days. As seasonal temperatures and photoperiods decrease, face flies begin to enter diapause (Stoffolano and Matthysse 1967; Valder et al. 1969; Caldwell and Wright 1978) and begin to seek out buildings in which to hibernate. In the spring adults emerge from the overwintering sites and mate (Caldwell and Wright 1981). Males are left behind as females disperse to the surrounding areas. Females generally oviposit 2-5 days after mating (Hammer 1941; Wang 1964; Teskey 1969).

2.1 Description of life stages

Egg: The egg of the face fly is yellowish-white and is ca 3.1 mm long and 0.5 mm wide (Hammer 1941; Wang 1964). It is distinctive because of the greyish-black, respiratory mast projecting from its anterior portion. This mast is ca 0.7 mm long, 0.1 mm wide, grooved dorsally and somewhat curved at the tip.

Larvae: The 12-segmented larvae are typically muscoid in shape, tapered toward the anterior, with a truncated posterior end (Wang 1964). Each of the 3 instars can be distinguished on the basis of size, the presence or absence of spiracles and details of the cephalopharyngeal skeleton (Wang 1964). First instar larvae average 3.0 mm in length and 0.6 mm in width. They are whitish, with black sclerotized spines. Second instar larvae

are from 5.0 to 6.7 mm long and 0.8 to 1.3 mm wide. A pair of lateral spiracles, each bearing 7-9 finger-like openings are evident on the first thoracic segment. Third instar larvae range from 8.0 to 13.7 mm in length and average 2 mm in width. They are light yellowish, turning deeper yellow prior to pupation (Wang 1964).

Pupa: The pupa is enclosed in a nearly cylindrical puparium, averaging 6.5 mm in length and 2.6 mm in width. Pupae are first yellowish, gradually hardening and turning to a opaque whitish grey (Wang 1964; Fraenkel and Hsiao 1967). The manner in which the pupal case hardens is unusual in that calcium salts are used rather than phenolic cross-linking compounds (Grodowitz and Broce 1983). Fraenkel and Hsiao (1967) reported that the face fly puparium consists of 65 - 80% calcium carbonate.

Adults: The following descriptions of the adults are condensed from Teskey (1960) and Wang (1964). Vockeroth (1953) provides a key to help separate the face fly from the house fly, Musca domestica L., which also annoys cattle.

Males average 6.2 mm in length and 2.2 mm in width. Eyes are bare, separated above by less than the width of the ocellar triangle. The lower portion of the vertex is silvery and the genae white. The thorax is bluish-grey, lightly pollinose with 4 broad, black stripes. The abdomen is reddish orange, except for the first 2 tergites which are black. From this base a

broad median black stripe extends poseteriorly.

Females average 7.5 mm in length and 2.2 mm in width. The vertex is nearly as wide as the eye, with the orbital stripe at least half as wide as the median frontal stripe. The genae and thorax are grey, the latter with 4 dark stripes. The dorsal surface of the abdomen is silvery, with the anterior tergum dark orange ventrolaterally. Tergites 3 and 4 are marked by a narrow median black stripe. The sternites are black and slightly pollinose.

3.0 Spatial and temporal occurrence

In Europe and North America, face flies are generally present in pastures from May to October (Hammer 1941; Teskey 1960,1969). They are consistently located about the heads and occasionally the flanks of cattle (Hillerton et al. 1984). When particularly abundant, face flies are also found on the brisket, shoulders and sides of the animal, or wherever saliva, blood (Bruce et al. 1960) or excrement (Teskey 1969) are found. Hammer (1941) originally reported that populations of face flies declined between generations so that throughout the summer there was a series of peaks of abundance. Ode and Matthysse (1967); Teskey (1969) and Krafsur et al. (1985b) all noted, however, that after the initial appearance of first generation flies in June, successive generations resulted in a steady

increase to maximum abundance of flies by August, indicating an overlapping of populations.

Males and females exhibit distinct differences in habits. Their distribution and behaviour in the field is affected by a number of factors, including temperature, light intensity, rainfall, wind velocity, humidity, cloud cover, physiological condition of the fly, location of food sources, and cattle behaviour (Peterson and Meyer 1978). Adults of both sexes are generally more abundant in pastures with water and shade as opposed to drier more open pastures (Hammer 1941; Depner 1969). In addition, Pickens and Nafus (1982) noted that fly populations were higher in valleys than on hills.

Male flies are typically most abundant along forest margins (Hansens and Valiela 1967), near intersecting lines of trees (Pickens and Nafus 1982), and resting on conspicuous objects in the pasture (Hammer 1941; Treece 1960; Dobson and Matthew 1960; Ode and Matthysse 1967; Teskey 1969). Trap catches have also shown that male face flies are not commonly found in open areas of pasture (Hansens and Valiela 1967; Pickens and Nafus 1982), and are rarely found on cattle or dung. In pastures without cattle, males are most prevalent in northern exposures followed in descending order, as indicated by numbers caught on traps, by eastern, southern and western exposures (Peterson and Meyer 1978). Male activity is maximal 3 h after sunrise (Teskey 1969; Peterson and Meyer 1978). Ideal trap sites are typically areas protected from the wind, where temperatures increase

through the 16-19°C range and a minimum of 5 h of sunlight is received per day (Peterson and Meyer 1978).

Female face flies are much more common than males in open areas, although both sexes are equally abundant along forest margins (Hansens and Valiela 1967; Pickens and Nafus 1982). Female activity and abundance in the pasture is strongly influenced by the location of cattle, with topography and vegetation playing lesser roles. Numbers of face flies can increase as much as 10 fold when cattle are introduced into an area (Hansens and Valiela 1967) .

Although extremely high numbers of face flies can occur on cattle, they may represent only a small fraction of the total population. Jones (1963), concluded from field cage studies, that only 4% of the test flies were on cattle at any one time. Ode and Matthysse (1967) hypothesized that face flies spend a great deal of time during the day resting on vegetation and prominent objects throughout the pasture and only visit cattle periodically. Morgan (1981), without providing data, claimed that face flies spend 75% of their time on vegetation and 25% on cattle. Miller and Treece (1968b) were able to recover only about 2% of tagged and released female face flies on cattle.

A number of authors have reported on the factors which initiate or terminate activity of face flies. Killough (1965), noted that face flies were generally quite active in the field at light intensities exceeding 5380 lx, and that once light intensity dropped to 646-753 lx, activity ceased. Ode and

Matthyse (1967) stated that maximal activity did not necessarily coincide with maximum light intensities. Face flies were active as long as temperatures exceeded ca 15°C; although activity fluctuated throughout the day, populations were generally most active from 1000-1700 h. Hillerton et al. (1984) similarly found fly activity to be greatest from mid-morning to late afternoon. Hansens and Valiela (1967) found flies to be most active at temperatures of 27-29°C, with maximum activity occurring when light intensities exceeded 75320 lx. Activity generally peaked at 1200 h, with minimal activity occurring at temperatures below 18°C. Cessation of activity was believed to occur when light intensity dropped below 10760 lx. Teskey (1969) found that face flies did not commence daily activity until temperatures exceeded 14°C, and that they were most active in the 26-28°C range. Activity generally increased throughout the day and peaked in early afternoon. Teskey (1969), although admitting that light intensity may well control the initiation and cessation of activity, observed only the latter, noting a decline in activity once light intensity dropped to the 108-538 lx range in the evening. Temperature as a limiting factor in the evening was not discussed. Partial cloud cover had no observable effects on activity (Ode and Matthysse 1967; Teskey 1969); however, under sustained overcast conditions, activity was reduced (Teskey 1969).

Wind speeds in excess of 16 km/h, as well as rain, will either terminate or substantially reduce activity of face flies

(Benson and Wingo 1963; Hansens and Valiela 1967; Teskey 1969; Engroff et al. 1972). Precipitation lasting several hours will at times reduce fly numbers on cattle for up to 24 h, despite ideal conditions afterwards (Teskey 1969).

Controversy also surrounds opinions of how relative humidity influences fly activity. Benson and Wingo (1963) and Teskey (1969) both noted that during periods of high R. H., face flies were not very abundant on cattle. However Teskey (1969) noted that often this relationship was contradictory and at times highly variable in the R. H. range of 40-96%. He did suggest that when R. H. and temperature were favourable to the water balance of flies (as is the case in the morning) that flies would visit cattle less frequently for fluid replenishment. Thus, greater attraction to cattle would occur in drier, warmer parts of the day. Roberts and Pitts (1971) found that when laboratory-reared 5 day old flies were offered a choice between low and high R. H. they preferred the former. Pretest conditioning in wet or dry conditioning chambers appeared to influence only the intensity of the response. Engroff et al. (1972) concluded that the effects of R. H. on activity could not be separated from factors such as temperature and wind speed. Attempts to correlate vapour pressure deficits with activity yielded no conclusive findings (Hansens and Valiela 1967; Teskey 1969).

Dispersal of face flies was studied by Fales et al. (1964) who found that marked flies could travel at least 1.2 km in 2

days. Later studies expanded this range to 3.2 km in one day, 6 km in 5 days (Killough et al. 1965) and 12 km in 5 days (Ode and Matthysse 1967). The extent to which wind contributed to dispersal was not considered in these studies. The above authors are in agreement that much of this dispersal was cattle-directed. Dispersal between pastures or herds was apparently not influenced by the time of day, type of site, fly age or sex, provided that light and temperature requirements were optimal for flight (Ode and Matthysse 1967). Pickens and Nafus (1982), however, found that dispersal was influenced by topography. They recaptured marked flies most commonly on farms connected to the release site by rivers and forest borders. Trap catches indicated that marked flies tended to avoid flight over wide open fields. Face fly dispersal was obviously not random.

The face fly's highly dispersive nature is further proven by the rapidity of its spread in North America; in 1958 the fly was confined to New York, Maine and Virginia. By 1960 it had travelled as far west as Nebraska (Jones and Medley 1963).

Once daily activity has ceased, face flies will spend the night resting on vegetation surrounding a pasture (Killough et al. 1965; Ode and Matthysse 1967; Teskey 1969).

4.0 Diapause and overwintering

In the fall, adult face flies enter a true facultative diapause characterized by fat body hypertrophy, cessation of ovarian development, and lack of mating (Hammer 1941; Benson and Wingo 1963; Stoffolano and Matthysse 1967). Male sexual development is apparently unaffected by the factors that induce diapause (Teskey 1969). Several researchers have made the general observation that as temperatures and photoperiods decreased, the numbers of face flies entering diapause increased (Stoffolano and Matthysse 1967; Valder et al. 1969; Caldwell and Wright 1978). Steve and Lilly (1965) reported that face flies retired to their overwintering habitat shortly after the first full frost. Under laboratory conditions, maximum diapause induction occurs when flies are exposed to total darkness at 18°C (Stoffolano and Matthysse 1967; Caldwell and Wright 1978). Valder et al. (1969), concluded that most flies enter and complete diapause when exposed to temperatures <16°C in conjunction with photoperiods of <12 h.

Once in diapause, both sexes undergo a period of carbohydrate feeding which ultimately leads to the hypertrophy of their fat bodies (Stoffolano 1968a; Schmidtmann and Redfern 1985). This occurrence requires about 2 weeks under laboratory conditions of 18°C and 12 h photoperiods (Stoffolano 1968a). Although face flies are not normally attracted to cattle during this time (Stoffolano 1968a; Krafsur et al. 1986) some

reseachers have noted otherwise (Schmidtmann and Redfern 1985). The adaptive advantage of such an attraction is unclear, as protein is not required for oogenesis and only nectar is used to develop fat bodies.

Laboratory-reared males tend to enter diapause more readily than females (Stoffolano and Matthysse 1967; Valder et al. 1969; Caldwell and Wright 1978); adults of both sexes are sensitive to diapause-inducing stimuli only during the first 2 days after ecdysis (Valder et al. 1969).

Approximately 20 days' exposure to fall conditions is required by adult flies to fully enter diapause. No other life stage was found to respond to diapause-inducing factors (Valder et al. 1969).

Large numbers of face flies may overwinter in homes, granaries and public buildings (Hammer 1941; Kearns 1942; Vockeroth 1953; Dobson and Matthew 1960; Goble 1961,1964; Matthew 1961; McNay 1962,1963b; Benson and Wingo 1963; Teskey 1969; Strickland et al. 1970; Caldwell and Wright 1981; Peterson and Meyer 1982). This habit first drew attention to the face fly in North America (Vockeroth 1953). In these structures face flies cluster in groups in attics, around windows, in closets, roof spaces and on ceilings and walls (Strickland et al. 1970).

Face flies are frequently found in the tallest buildings in the vicinity (Strickland et al. 1970) and are also highly attracted to white, 2-story frame structures (Spencer and

Poorbaugh 1972; Benson and Wingo 1963). There is apparently no correlation between overwintering site and the proximity of cattle (Benson and Wingo 1963; Strickland et al. 1970). A number of researchers have noted that face flies tend to overwinter in the same structure year after year (Kearns 1942; Oldroyd 1964; Stoffolano and Matthysse 1967; Strickland et al. 1970; Caldwell and Wright 1981). This tendency may be due to certain building attributes such as situation, aspect, or roof shape (Oldroyd 1964) or it may be due to an olfactory response similar to that of the "fly factor theory" described by Barnhard and Chadwick (1953) (Stoffolano and Matthysse 1967). This theory claims that flies are attracted to certain areas by the accumulation of fly feces or speckings.

Once attracted to an overwintering site, face flies typically settle on the exterior southwest portion of the building, sunning themselves until nightfall, when they enter the structure by way of cracks and crevices (Oldroyd 1964). This habit continues as long as temperatures permit. The sex ratio of overwintering flies is approximately equal (Benson and Wingo 1963; Ode and Matthysse 1967; Peterson and Meyer 1982).

There has been little mention in the literature of overwintering sites in the wild. Kearns (1942) found small numbers overwintering in hollow trees, and Caldwell and Wright (1981) found them in animal burrows.

In eastern North America, face flies generally leave their overwintering site toward the end of April (Benson and Wingo

1963; Ode and Matthysse 1967; Teskey 1969; Caldwell and Wright 1975). Termination of diapause is thought to be prompted by gradual increases in temperature and photoperiod (Valder et al. 1969). In the laboratory, male face flies required 20 days of temperatures above 4.4°C before becoming active (Valder et al. 1969). Within a week of emerging, most flies will have mated (Caldwell and Wright 1981). Females then disperse to outlying areas, leaving males presumably to die, since males are not found in the field until first generation progeny have developed (Hammer 1941; Ode and Matthysse 1967). Upon emerging in the spring face flies behave as a uniform cohort, exhibiting well-synchronized mating, dispersal and oviposition (Krafsur et al. 1985a).

5.0 Host selection and preference

The exact mechanisms by which females are attracted to cattle are poorly understood (Teskey 1960). Hammer (1941) believed the attractant to be an odor. Pechuman and Burton (1969) noted that when dry ice was used in Malaise traps designed to catch tabanids, numerous face flies were captured, even though the nearest herd of cattle was at least 1.6 km away. Similarly, Caldwell and Wright (1981) noted that face flies were attracted to CO_2-baited traps; however, once cattle were placed in the pasture no flies were captured. Hammer (1941) repeatedly

observed that face flies left cattle to feed on human blood. Teskey (1960) observed feeding face flies leaving cattle in favour of the scent of his perspiration.

Although face flies feed on and annoy a wide variety of mammals, cattle are the principal host (Hammer 1941; Teskey 1960,1969; Pickens and Miller 1980). Horses are reportedly as attractive as cattle (Teskey 1960,1969; McNay 1961; Dorsey 1966; Annon. 1969,1970,1971; Allan 1970; Gregory and Wright 1973; Morgan 1981), although their feces are not suitable for oviposition (Bay et al. 1968). Bison also suffer considerable annoyance from face flies; reports on eye disorders and occassional blindness have surfaced from Montana only since the arrival of the face fly (Burger and Anderson 1970). The face fly has also been noted to irritate deer (Teskey 1969; Burger and Anderson 1970), sheep (Roadhouse 1960; Treece 1960; Teskey 1969), hogs (Teskey 1969), yaks (McNay 1961) and even humans (Dobson and Matthew 1960; Teskey 1960; Treece 1960; Spencer and Poorbaugh 1972).

Attraction of face flies to cattle is often characterized by a high variation in numbers of flies per animal (Hansens and Valiela 1967; Ode and Matthysse 1967), possibly reflecting differing degrees of host attractiveness. However, the factors involved are poorly defined and understood (Schmidtmann and Berkebile 1985).

Host characteristics such as age, physiological condition, and color, as well as certain pasture-related phenomena, such as

location in the pasture, aggregation, posture, and even management practices, can contribute to the attractiveness of the host to face flies (Teskey 1969; Hansen and Valiela 1967; Schmidtmann and Berkebile 1985).

Several researchers have noted that older cattle (possibly because they are less active and excitable than younger animals) are afflicted with greater numbers of face flies than are younger cattle (Ode and Matthysse 1967). Schmidtmann and Berkebile (1985) concluded that older cows were more susceptible to attack than younger cows because they aggregated less. However, Hansen and Valiela (1967) and Teskey (1969) found no correlation between age and susceptibility to attack. Teskey (1969) did note that new-born calves attracted considerably more face flies than mature cattle, possibly because of the remnants of amniotic fluid and afterbirth still adhering to the calf. These calves, in comparison to mature cattle, remained more attractive to flies for up to 3 weeks. The reason for this differential attraction was not discussed.

Teskey (1969) found no correlation between cattle color and attractiveness to face flies; however, others report that face flies prefer cattle with dark or spotted coats over those with light-colored coats (Frishman and Matthysse 1966; Hansens and Valiela 1967; Ode and Matthysse 1967; Engroff et al. 1972). When attractiveness studies were conducted based on facial color alone, no correlation was found (Schmidtmann and Berkebile 1985). Pickens (1983) provides a detailed discussion on the

color responses of the face fly.

Contrary to the findings of Engroff et al. (1972), cattle apparently attract more flies when they are near wooded, slightly-shaded areas than in open, sunny areas (Benson and Wingo 1963; Hansens and Valiela 1967; Depner 1969). This differential attraction seems unusual, as adult face flies are strongly photo-positive (Wang 1964). However, it may be explained by the high number of resting areas in shaded or wooded locations. Unless ovipositing, face flies may also avoid open areas where wind and other environmental factors may interfere with their flight.

Individual cattle as opposed to those in close proximity to other cattle also attract more face flies (Hansens and Valiela 1967; Teskey 1969; Schmidtmann and Valla 1982; Schmidtmann 1985b; Schmidtmann and Berkebile 1985). Teskey (1969) points out that when face flies are particularly bothersome, cattle will congregate into compact groups, typically with their heads to the centre. Those in the centre of such groups do gain some protection, but those on the periphery often have fly counts about the face higher than when standing alone.

Animals lying down or standing idle as opposed to grazing are also subject to greater face fly annoyance (Benson and Wingo 1963; Hansens and Valiela 1967; Teskey 1969; Engroff et al. 1972). Such cattle provide greater opportunity for flies to feed than those grazing, especially in tall grass which can brush flies from the face.

Beef cattle tend to be generally more heavily infested with face flies than dairy cattle (Teskey 1969). This differential infestation rate can be explained by management practices in the dairy cattle industry. Dairy cattle are much cleaner, they are removed from the pasture daily for milking purposes, and are frequently moved to fresh pasture, thus constantly subjecting local face fly populations to re-distribution pressures.

6.0 Feeding activities and nutrional requirements

The feeding requirements and food preferences of male and female face flies differ substantially. Nectar or some other source rich in carbohydrates is necessary for the survival of adults of both sexes, while protein is necessary for egg development (Wang 1964; Turner and Hair 1967; Valder and Hopkins 1968; Teskey 1969).

Laboratory-reared males, when given food choices, showed a significant preference for carbohydrates (malt or glucose) followed in descending order by milk or blood and dung (Stoffolano 1968a; Miller and Treece 1968b). Diet preferences were not influenced by age, nor did feeding preferences change throughout the day. Stoffolano (1968a) points out that although males will feed on blood and dung under laboratory conditions, these food sources have not been adequately confirmed in the field. Occasionally, males have been observed feeding on bovine

lacrimal secretions (Hower and Cheng 1972). Treece (1960) reported males to be attracted to "blood boards" placed among cattle in the field; however, only 17% of captured flies were males.

The hypothesis that males rarely feed on cattle or dung is strengthened by the following observations. Females have been found to outnumber males 10:1 (Ode and Matthysse 1967; Teskey 1969), 15:1 (Dobson and Matthew 1960), 17:1 (Kaya et al. 1979) and 20:1 (Cheng et al. 1962) on cattle and 10:1 (Teskey 1969) and 50:1 (Kaya et al. 1979) on dung. From the literature, it can be concluded that males thrive primarily on nectar, and those that frequent cattle may do so in search of sexually receptive females. It is not known what role protein plays in the sexual maturation of males. Kaya et al. (1979) noted that only males less than 8 days old frequented cattle. The significance of this observation needs clarification.

In addition to nectar, females also feed on the mucus membranes and secretions exuded from the eyes, nose and mouths of cattle, as well as on perspiration, strings of saliva and dung liquids (Hammer 1941; Teskey 1969). Females are also facultatively haematophagous, frequently obtaining blood from bites inflicted by biting flies. Their requirements are in direct relationship to ovarian development (Stoffolano 1968a; Miller and Treece 1968b; Bay and Pitts 1976; Kaya et al. 1979). Females commonly feed on cattle during the early stages of egg development, switching to dung when development is

almost complete (Miller and Treece 1968b; Kaya et al. 1979; Van Geem and Broce 1985). They feed most actively on dung one day before and 2 days after peak oviposition (Miller and Treece 1968b). Hammer (1941) and Teskey (1969) noted, however, that females also feed on dung during oviposition. Van Geem and Broce (1985) concluded that since females visit dung only in the late stages of ovarian development, it was not as viable a protein source as other available sources. However, face flies are still capable of maturating eggs when only dung is available (Kaya and Moon 1980; Van Geem and Broce 1985). Once all eggs are laid, this feeding cycle is again repeated.

Van Geem and Broce (1985) studied the significance of bovine protein food sources on face fly ovarian development and concluded that nasal discharges and eye secretions were the primary sources of protein sought and used by the female for vitellogenesis. They proposed that the most valuable protein sources, as measured by their ability to promote the fastest egg development, were blood, followed by eye secretions, nasal discharges and dung. They tested saliva but found it to be generally not a good protein source, an observation similarly noted by Valder and Hopkins (1968).

Wang (1964) concluded that the inclusion of blood in the diets of laboratory-reared females both accelerated ovarian development and increased fecundity. Contrary to these findings, Lodha et al. (1970b) found that the addition of blood to diets increased only egg hatchability.

Larvae of the face fly are coprophagous and derive their nutrional requirements from living bacteria and other microorganisms in the dung (Hammer 1941). They thrive best in feces which have a moisture content of approximately 85%; they are unlikely to survive at moisture extremes <65 or >95% (Bay et al. 1969).

Larvae survive best in the feces of cattle maintained on low-roughage, grain-supplemented diets followed by alfalfa hay diets (Bay et al. 1969). Feces produced by cattle on strict roughage diets supported minimal larval development. It was initially believed that the dry nature of this type of feces affected larval survival. However, when moisture levels were corrected, survival did not improve, thus indicating that the chemical composition of the dung affected survival (Bay et al. 1969).

7.0 Mating behaviour

In the laboratory mating most commonly occurs within 2-7 days after eclosion. (Wang 1964; Teskey 1969; Lodha et al. 1970a; Chaudhury and Ball 1973). Males are sexually mature within 36-48 h post eclosion (Teskey 1969; Lodha et al. 1970a); females will not mate until at least 42 h post eclosion, when vitellogenesis can be initiated, after a protein meal. Female face flies emerging from diapause, however, will

mate without having obtained protein. One can speculate that a common endocrine mechanism may be involved in both the termination of diapause and the acquisition of a protein meal that triggers mating behaviour and vitellogenesis. The greatest mating activity does not occur until 4 days of age, when eggs are almost completely developed (Chaudhury and Ball 1973). If protein is not available, egg development is slowed and females do not mate (Chaudhury and Ball 1973). A positive correlation between age and frequency of mating, from the 2nd through the 6th day, was reported by Lodha et al. (1970a), who also noted that the mating activity of face flies increased significantly with the amount of light.

Although spermatozoa can be effectively transferred in as little as 6 min (Lodha et al. 1970a), copulation normally requires an hour or more (Wang 1964; Teskey 1969). Males are capable of multiple matings. Females normally mate only once; occasionally they have been observed to mate with 2 or 3 different males (Wang 1964; Teskey 1969; Lodha et al. 1970a). Lodha et al. (1970b) reported that a single mating was sufficient to sustain normal egg production for at least 3 ovarian cycles and that additional matings did not enhance fecundity. Unmated female face flies will oviposit as readily as mated females; however, their eggs are not viable (Benson and Wingo 1963; Killough and McClellan 1965). Experimental studies have shown that females that mate more than once probably do so because they did not receive spermatozoa in the initial mating

(Killough and McClellan 1969). Such females will continue to mate until fertilized.

In the field, conspicuous objects such as fence posts, tree stumps, etc., serve as mating sites (Hammer 1941; Teskey 1969). From these vantage points males actively seek out anything that flies nearby. Once a responsive female face fly is encountered, the 2 then fall to the ground to complete mating (Hammer 1941). Teskey (1969) and Lodha et al. (1970a) both noted that mating activity was highest in the morning, followed by a distinct late afternoon decline. Face flies have also been noted copulating on the sunny side of farm buildings after spring emergence (Benson and Wingo 1963; Ode and Matthysse 1967).

Chaudhury et al. 1972 reported the discovery of a sex pheromone in the extract of mature virgin (5-6 day-old) female face flies. They speculated that this pheromone not only attracted males to females but also provided the sexual stimulus for copulation. Ubel et al. (1975), described the most active components of the extract to be the straight-chain monoalkenes (Z)-14-nonacosene, (Z)-13-nonacosene, and (Z)-13-heptocosene. These compounds are found in the extracts of both sexes; however, sexually mature males contain higher proportions of nonacosene and heptacosene, a difference that apparently accounts for the ability of male face flies to distinguish females from males (Ubel et al. 1975).

8.0 Oviposition

Face flies prefer to oviposit in undisturbed bovine droppings deposited in open sunny areas and will avoid feces which have been trampled, heaped (Ebling 1975),or dropped in shaded areas, tall grass or heavily travelled portions of pasture (Teskey 1969; Kaya and Moon 1978). Although face flies will lay their eggs in the feces of bison and swine (Bay et al. 1968), they prefer the feces of cattle, because of their ideal texture and moisture content (Teskey 1969; Bay et al. 1968). Teskey (1969) noted that face flies preferred to oviposit in the droppings of dairy cattle as opposed to beef cattle because feces of the former are generally less viscous. The feces of mature cattle, because they are not as dry as the feces produced by younger cattle, are also more favourable to ovipositing flies. The feces of horses, sheep, deer and other large ungulates are not considered ideal for oviposition because of either their coarse texture, pelleted forms or lower moisture contents (Bay et al. 1968).

Differences in cattle diet can influence the acceptability of droppings for oviposition. Gravid females preferred the feces of cattle maintained on alfalfa diets as opposed to corn silage (Treece 1966; Ruprah and Treece 1968). However, when females were not offered a choice between the above 2 types of droppings, oviposition still occurred without any deleterious effect on larval development.

Field (Hammer 1941; Teskey 1969) and laboratory (Wang 1964) observations in general agree on the oviposition behaviour of females. Within 2-5 days of mating, females begin to oviposit. Oviposition generally occurs throughout the day, but peaks in the morning and late afternoon have been noted (Sanders and Dobson 1966). Gravid females are immediately attracted to fresh droppings and upon arrival will creep over the dung's surface, imbibing fluids while searching for suitable oviposition sites. The antennae of the face fly act as the primary receptor organ for detecting the odor of feces (Bay and Pitts 1976). Although odor alone may stimulate oviposition, gustatory stimulation of the tarsi, proboscis and ovipositor is required to elicit maximum oviposition. Olfactory sensilla have been found on the ovipositer, but their function is not clearly understood (Hooper et al. 1972). Maximum attraction to fresh dung usually declines after 20-30 min, due to the inevitable crusting over of the dung's surface, even under humid conditions (Hammer 1941; Teskey 1969). More eggs are laid towards the centre of the fecal pat than near the peripheries (Hower and Cheng 1968b). Teskey (1969) also made the observation that females tend to deposit eggs in areas of the pat previously oviposited in, and suggested that a fly factor similar to that described by Barnhart and Chadwick (1953) for house flies may be involved. This tendency could also occur if these areas were the only suitable oviposition sites on the fecal pat.

Eggs are individually laid with the respiratory stalk

extending upwards (Bay et al. 1968; Degrugillier and Grosz 1981), either singly on smooth surfaces, or in clusters of 5-8 in cracks or crevices where accumulated moisture has prevented crust formation (Teskey 1969). Individual flies do not lay their full complement of eggs in any one fecal pat, although several hundred eggs per dropping are not uncommon when face flies are abundant (Teskey 1960,1969). Maximum survival as measured by pupal weight and adult emergence occurs, provided that there is a minimum of 2.0 g of feces per face fly larva (Bay et al. 1970). Moon (1980) stated that when the total number of coprophagous larvae inhabiting the fecal pat exceeded ca 278/kg of feces, face fly larvae are put under stress. As a result, larvae either fail to pupate or suffer from lower fecundity as adults.

The ovaries of the face fly are polytrophic; they develop in 7 stages and all eggs in each cycle mature together even though they are laid at different times (Teskey 1969). Under laboratory conditons, females are capable of completing 4-6 ovarian cycles, each about 3-4 days apart and will lay 20-26 eggs per cycle (Wang 1964; Killough and McClellan 1965; Miller and Treece 1968a; Teskey 1969). Most females will lay 30-128 eggs during their lifetime (Wang 1964), although Killough and McClellan (1965) and Teskey (1969) both recorded maxima of 230 eggs per lifetime. Approximately one-half of the flies collected throughout the summer were nulliparous (Thomas et al. 1972). The remainder was composed of equal numbers of

uniparous and biparous flies with a small fraction being triparous. It was concluded then that most females completed only 2 gonotrophic cycles during their lifetimes. Krafsur et al. (1985) similarly noted that the proportion of field-collected multiparous flies was low, and suggested that this was due to the increasing rate of mortality with age. Treece (1964) noted that females produced 80% of their total eggs in their first 3 weeks of adult life, even though they could still produce eggs at 7 weeks.

Hammer (1941) concluded that eggs laid in the morning and late afternoons in the field hatched within 10 and 23 h, respectively. Egg hatch in the laboratory at 25°C occurs within 16 h (Wang 1964; Treece 1964).

Newly-hatched larvae are negatively phototactic and thus will immediately begin to tunnel to just below the dung's surface (Wang 1964; Teskey 1969), where the first instar larvae remain due to respiratory requirements. As the larvae develop, they begin to migrate to all portions of the fecal pat. Teskey (1969) noted that although larvae during their first 2 instars moved randomly throughout the dung (within the limitations of their respiratory requirements) those in the 3rd and final instar tended to cluster in certain areas of the dung, a phenomenon also noted by Valiela (1969). Larval development, depending on temperature, is usually complete in the field within 3-5 days (Wang 1964; Teskey 1969; Wingo et al. 1974; Moon 1983). Wang (1964) indicated that in the laboratory, larval

development could be completed in as little as 2.5 days at 37°C, but may take as long as 21 days at 11°C.

When mature, larvae leave their fecal habitat in search of a suitable pupation site. The puparium is typically found slightly beneath the soil surface, under organic matter, or within grass crowns (Teskey 1969; Jones 1969). Depending on ground cover and temperature, larvae may migrate up to 10 m before a suitable pupation site is found (Jones 1969). Migration from the fecal pat was thought to occur just before sunrise (Hammer 1941). However, Teskey (1969) observed migration throughout the day and suggested that night migration was also possible. The pupal period in the field is normally completed within 8-10 days (Wang 1964; Teskey 1969). In the laboratory at 20 and 37°C, pupae required 12 and 5 days, respectively, to complete development (Wang 1964).

9.0 The face fly and its role in reducing livestock productivity

As the face fly spread across North America, reports were common of numbers in excess of 100 flies per animal (U.S.D.A. 1959,1961,1963,1969; Dobson and Matthew 1960; Bruce et al. 1960; Ode and Matthysse 1964a) or 50 flies per face (U.S.D.A. 1959,1961,1969; Dobson and Matthew 1960; Teskey and Allan 1963; Ode and Matthysse 1964a; Turner 1965; Wrich

1970; Wright 1971). More recent counts, although still highly variable, are generally much lower (Del Fosse and Balsbaugh 1974; Barlow and Surgeoner 1979; Surgeoner and Moolenbeek 1979). DeFoliart (1963) noted that fewer than 5 flies per face caused little annoyance, 5-10 per face caused noticeable annoyance and >10 per face caused considerable annoyance. Annoyance levels are now generally accepted to be ca 10 flies per face (DeFoliart 1963; Hansens and Granett 1963; Houser and Wingo 1967; Ode and Matthysse 1967; Schmidtmann and Valla 1982). Teskey (1969) observed that cattle aggregated for protection only when densities exceeded 30 flies per face. Schmidtmann and Valla (1982) reported that only 9-12 flies per face were required to elicit this response. Recently, Hall (1984) recommended that because of the face flies' ability to damage eye tissues while feeding (Shugart et al. 1979; Van Geem and Broce 1985) an economic damage threshold of one face fly per eye per month be adopted.

Initially, reports on the economic impact of the face fly on dairy and beef operations were either non-existent, misleading, or lacking in scientific credibility. Numerous authors, including Pickens and Miller (1980) and Kanga (1984), cite the findings of Peterson and Borcherding (1962) and Hansens and Swift (1963), which stated that face fly annoyance to cattle resulted in weight loss of 114 g per day and a 25% decrease in milk production, respectively. The observations of Peterson and Borcherding (1962) were published in a newspaper editorial,

which referred to the broad spectrum of flies that attack and annoy cattle, rather than face flies alone. Hansens and Swift (1963) put forth their hypothesis in an extension leaflet without providing any data. In addition to these sources, a number of others (U.S.D.A. 1959,1961,1965; Anon. 1960; Treece 1960; Rousell 1965; Smith 1966) have made similar undocumented assertions. In 1965, the U.S.D.A (1965) estimated the annual economic losses attributed to the face fly to be $68 million, ca $42 million from weight losses in the beef industry, and $26 million from reduced milk production. However as Steelman (1976) points out, these estimates are extremely high and no specific data relating the effects of face fly on livestock productivity were presented.

It was reported in 1980 that annual losses in the livestock industry in the United States attributed to all livestock insects (including ticks and mites) amounted to ca $2.7 billion. Of this total, which included costs of control, the face fly was deemed responsible for $140 million (Anon 1980). In 1977, cattle production losses attributable to face flies in the United States, reportedly totalled $53.2 million (Drummond et al. 1981). However, it was pointed out that this figure was extrapolated from data obtained using limited tests, and small numbers of animals in specific areas.

Recent research on the quantitative effect of face flies on weight gains and milk production in beef and dairy operations indicated that the face fly does not exert a suppressive

influence. Schmidtmann et al. (1981) conducted a 2 yr study and found that even though population levels of 10-11 flies per face significantly reduced grazing times, weight gains were not adversely affected. Similarly, Arends et al. (1982b), found that populations as high as 12-17 flies per face did not affect weight gains, the amount of feed consumed, or feed conversion ratios, when compared to fly-free beef cattle. There was, however, visible evidence of annoyance, eye redness and lacrimation. McMillan et al. (1982), found that even though populations of face flies and horn flies, Hematobia irritans L., were effectively controlled by insecticide-impregnated eartags, no significant increases in milk production resulted. Cheng and Kesler (1962) conducted a 3 yr trial in which they controlled a broad spectrum of flies attacking dairy herds, and concluded that fly control did not increase milk production. They stated that if a dairy operation is properly managed, the costs of fly control may not be recovered.

Schmidtmann et al. (1984) provide further evidence that protecting dairy cattle from face flies results in little, if any, change in milk quantity or quality. They suggest that the rationale behind expending energy, labour and capital to protect cattle from face flies needs further evaluation.

It should be noted, however, that in the study by Arends et al. (1982b) beef cattle were provided with optimum feed under feedlot conditions. More studies on the influence of face fly annoyance on beef cattle under rangeland conditions are needed.

Only with such studies can it be shown conclusively that the face fly is indeed simply a tolerable annoyance.

It is interesting to note that Wright (1985) claims that in the absence of pinkeye, large numbers of face flies on cattle may be more of an aesthetic problem to producers than a real production problem.

10.0 The face fly as a mechanical vector of pinkeye

The association of the face fly with numerous bovine occular pathogens and the damage that results are often used to justify the cost of control programs (Hall 1984). Infectious bovine keratoconjunctivitis (IBK or pinkeye) is regarded as an important and frequent disease of cattle (Hall 1984). Although insects were suspected of being able to transmit the disease (Allen 1919), it has only recently been shown that it can be mechanically transmitted by face flies (Steve and Lilly 1965). This association has identified what is possibly the only significant threat this pest has to the livestock industry (Hall 1984). Outbreaks of pinkeye, however, would not be eliminated with the eradication of the face fly.

Pinkeye can be simply described as reddened teary eyes (Davidson 1986). In more scientific terms, pinkeye is described as an inflammation of the cornea and conjunctiva that can prevail in a subacute, acute or chronic ulcerative form (Jones

and Little 1923; Baldwin 1945; Jackson 1953; Steve and Lilly 1965; Brown and Adkins 1972). Typical signs of the disease include photophobia, corneal ulceration and opacity, lacrimation and general discomfort (Jones and Little 1923; Baldwin 1945; Jackson 1953; Scott 1957). The disease may regress spontaneously or progress to the extent that the cornea becomes perforated, resulting in blindness (Allen 1919; Baldwin 1945; Wilcox 1970).

Cattle afflicted with pinkeye eat less, and prefer to remain in shaded areas. Calves suffer similar pain and discomfort, and when suffering from impaired vision or blindness, are unable to nurse or graze properly, resulting in weight loss (Killinger et al. 1977). Afflicted cattle are more injury prone due to temporary or permanent blindness. If blindness is permanent, the value of the livestock is greatly reduced (Baldwin 1945; Steve and Lilly 1965). Although cattle of all ages and breeds are susceptible (Baldwin 1945; Jackson 1953), the incidence of pinkeye is highest in animals <2 yr old (Baldwin 1945; Hughes and Pugh 1970). It is more common among Hereford and Jersey breeds and less common in Aberdeen Angus and Brahma and Aberdeen Angus-Hereford crosses (Jackson 1953). Thrift and Overfield (1974) found that certain sire groups of cattle expressed more resistance to pinkeye than others, suggesting that perhaps genetics could be manipulated to reduce the occurrence of the disease.

Of the numerous suspected causal organisms of pinkeye in

cattle, Moraxella bovis (Hauduroy) (Eubacteriales: Brucellaceae) has been the most commonly proposed etiological agent (Henson and Grumbles 1960; Wilcox 1970; Hubbert and Hermann 1970). The disease can be transmitted by flies, by direct contact between individuals, or by fomites contaminated from lacrimal or nasal discharges (Steve and Lilly 1965; Hubbert and Hermann 1970). Further proof of transmission by direct contact is attested to by the observation that bulls, noted for their particular habit of contacting numerous individuals in a herd, have higher incidences of the disease than cows (Thrift and Overfield 1974; Ward and Nielson 1979).

Many authorities believe that the bovine eye becomes predisposed to pinkeye infection by irritants such as grass, sunlight, wind, dust, pollen or flies (Baldwin 1945; Jackson 1953; Wilcox 1968; Baptista 1979, Arends et al. 1982a; Davidson 1986).

Steve and Lilly (1965) were among the first to demonstrate that IBK could be transmitted by face flies. They not only isolated the pathogen from flies that contacted diseased cattle, they were also able to show that the disease organism could survive on topically contaminated flies for at least 4 days. These results were supported by Berkebile et al. (1981b). Additional research by Brown and Adkins (1972), Arends et al. (1982a), and Arends et al. (1984) demonstrated that face flies could transmit M. bovis from artificial media to the eyes of susceptible cattle. That face fly feeding can predispose

eyes to infection has been revealed by Shugart et al. (1979) and Van Geem and Broce (1985). Although a strong correlation between large face fly populations and the incidence of pinkeye has been reported (Cheng 1967; Gerhardt and Cook 1976; Gerhardt et al. 1976,1982), actual field studies are somewhat lacking. Using blood boards, Berkebile et al. (1981a) collected ca 5000 flies over a 2-year period and found <1% to be positive carriers of the bacterium, despite high levels of pinkeye in the experimental herds. They concluded that the face fly played a limited role in the dissemination of this disease. Gerhardt et al. (1982), however, isolated M. bovis from ca 9% of 200 flies collected from the faces of cattle. The discrepancies between the 2 studies may be due in part to the methods of sampling employed.

Until recently, much of the research dealing with the recovery of M. bovis from face flies and their role in its transmission, failed to distinguish between external and internal contamination of the fly. Based on Steve and Lilly's (1965) hypothesis, most researchers assumed that the bacterium was rapidly destroyed in the fly's digestive tract, and thus dealt strictly with external contamination. In contrast Burton (1966) detected limited survival of the pathogen in the digestive tract. The fact that face flies frequently regurgitate while feeding (Glass and Gerhardt 1984), in conjunction with evidence presented by Simpson (1981), Glass et al. (1982) and Glass and Gerhardt (1983) that the bacterium

could survive in the fly's digestive tract, support the assumption that face flies are effective vectors of pinkeye. The pathogen can survive for at least 48 h in the alimentry canal (Glass et al. 1982), and it is now believed that regurgitation of the bacteria from the crop of the face fly into the eyes of cattle is the most probable avenue of pathogen transfer (Glass and Gerhardt 1984). Overwintering face flies were not found to harbour the pinkeye pathogen (Steve and Lilly 1965; Staples et al. 1981).

Although pinkeye is seldom fatal, it is responsible for significant economic losses through reduced weight gains, lower milk yields, veterinary bills, treatment costs (medications plus producer input), and ultimately lower sale prices (Hetland 1983; Hall 1984). In 205-day, pre-weaning, feeding trials, Thrift and Overfield (1974) found 17 and 18 kg weight advantage, respectively, for bulls and heifers free of pinkeye compared to those afflicted. Once weaned, bulls that had not suffered from pinkeye in their pre-weaning period gained significantly more weight per day, and had higher year end weights than those animals suffering from pinkeye. Similar, but not significant, trends were observed with heifers. Killinger et al. (1977) also conducted feeding trials and reported that calves suffering unilateral pinkeye experienced weight losses of ca 5 kg over a 205 day period, resulting in a monetary loss of $4.40. Those suffering bilateral infections lost ca 16 kg which amounted to a loss of $14.00 per calf. These results were corroborated by

Ward and Nielson (1979) and Cobb et al. (1976).

Although a number of diseases, including pinkeye, can result in reduced productivity during early growth periods, compensatory growth could make up for these losses (Thomas et al. 1978). Compensatory growth, however, usually takes place at the expense of the farmer, who must supply additional feed during winter months.

Recent literature dealing with the effects of pinkeye on milk production is lacking. Baldwin (1945) claimed that milk production could drop by as much as 25% when cattle are affected by pinkeye. It may well be possible that the intensive husbandry associated with dairy farming results in dairy cattle being less likely to remain infected with pinkeye as compared to free-ranging beef cattle, which tend to receive less frequent attention. However, in Saskatchewan, beef cattle are frequently put into community pastures, where herd managers regularly treat for ailments such as pinkeye and foot rot.

The reproductive performance of bulls may also be affected by pinkeye infections. Cows exposed to a bull free of pinkeye had a 40% higher conception rate than a similar group sired by a bull with pinkeye (Thrift and Overfield 1979). This particular bull was blind in one eye as a result of the disease, which may have affected its breeding performance. A lack of recent literature in this area indicates that further clarification of these observations is warranted.

Once affected by pinkeye, cattle should be treated with

antibiotics to prevent further spread of the disease. Treatments are generally carried out only during the crisis stage of the disease, while convalescing cattle are not treated. Glass and Gerhardt (1983) suggest that all stages of the disease be treated. Cattle not treated require 2-6 weeks to recover, and then only 95% do so; cattle that are treated recover within 5-10 days with an almost 100% success rate (Scott 1957). Vaccines developed to immunize cattle against the disease produce less than adequate results (Davidson 1986). Additional details regarding treatments for pinkeye are provided by Hetland (1983) and Ward and Nielson (1979).

11.0 The significance of face flies as vectors of eyeworms

Nematodes belonging to the family Thelaziidae (Order Spirurvidea) are the principal parasites that infect the eyes of cattle (Soulsby 1965). They also live in the eyes and associated tissues of a number of other mammals (Krafsur and Church 1985). Until recently, the only eyeworm known to exist in North America was Thelazia californiensis Price, an endemic species, which is confined primarily to the western United States (Krafsur and Church 1985) where it parasitizes the eyes of a wide variety of mammals (Burnett et al. 1957). The first report of an exotic Thelazia species originated in Ontario, where T. lacrymalis (Gurlt) was isolated from the eyes of horses

(Barker 1970).

Thelazia spp. require intermediate hosts of the genus Musca for their development and transmission (Levine 1980). Thus the recent arrival of the face fly made it possible for eyeworms to be transmitted. The only other member of the genus Musca in North America is M. domestica, which is not a suitable host for eyeworms (Geden and Stoffolano 1981).

Eyeworm, Thelazia spp., larvae were first found in face flies in Massachusetts (Chitwood and Stoffolano 1971). At that time it was thought that the infection was accidental. However, continued surveillance in the state provided additional evidence that the face fly served as both the invertebrate host and vector (Branch and Stoffolano 1974). These findings confirmed Sabrosky's (1959) initial warning that the face fly had the potential to serve as an intermediate host for eyeworms in North America, because it is a known vector for T. rhodesii, (Desmarest), a mammalian eyeworm in the U.S.S.R.

The first documented report of bovine thelaziasis is from Kentucky, where T. skrjabini (Ershov) and T. gulosa (Railliet and Henry) were discovered in the eyes of cattle (Lyons and Drudge 1975a, 1976). These same 2 nematodes have since been discovered in the eyes of cattle in Tennessee (Patton and Marbury 1978), Massachusetts (Geden and Stoffolano 1980,1981), Winconsin (Gutierres et al. 1980), Ontario (Moolenbeek and Surgeoner 1980), Indiana (Ladouceur and Kazacos 1981) and Iowa (Krafsur and Church 1985). In addition to these findings,

Frechette (1976) reported isolating Thelazia sp. in a herd of dairy cattle in Quebec, and the equine eyeworm, T. lacrymalis, was found infecting cattle in Ontario (Moolenbeek and Surgeoner 1980). These eyeworms had never previously been reported to occur in North America, except for T. gulosa, which was found infecting the eyes of an imported giraffe (Walker and Becklund 1971). In addition to the numerous reports of bovine thelaziasis, there have been almost as many reports regarding equine thelaziasis, including reports of T. lacrymalis in the eyes of horses in Maryland (Walker and Becklund 1971), Kentucky (Lyons and Drudge 1975b; Lyons et al. 1976), Quebec (Frechette et al. 1976) and Tennessee (Patton and Marbury 1978). An unidentified species of the same genus was recovered from a horse in Washington (Grant et al. 1973).

European studies indicate that T. gulosa is commonly found infesting the lachrymal duct, the nasolachrymal canal or the 3rd eyelid of cattle (Soulsby 1965). T. skrjabini is found primarily in the lachrymal duct of the 3rd eyelid in cattle, and T. lacrymalis has been reported to occur mainly in the conjunctival sac and lachrymal duct of horses (Soulsby 1969). Although there are numerous accounts of bovine eyeworm infections, only a few reports exist in which face flies were found to be infected. Chitwood and Stoffolano (1971) found a parasitism rate of <1% (1 of 155 flies collected from blood boards), and Branch and Stoffolano (1974) on 15 separate occasions collected a total of 2363 flies; parasitism rates

varied from 0-3.6%. Lyons et al. (1976), noted parasitism levels of ca 1.4% (12 of 866) in flies collected in sweep nets from the heads of horses. More recent estimates of Thelazia prevelance among face flies collected around cattle approximate 2-3% (Geden and Stoffolano 1977,1981; Moolenbeek and Surgeoner 1980; Krafsur and Church 1985). It is believed that the face fly is the only suitable vector of these exotic eyeworms (Geden and Stoffolano 1982).

Some researchers have hypothesized that thelaziasis of cattle and horses has been present for some time but remained unrecognized until recently (Krafsur and Church 1985). Possibly, many of the reported cases of pinkeye infection may have in fact been due to eyeworms; the 2 diseases have similar symptoms and eyeworms are usually hard for farmers and researchers alike to detect (Stoffolano 1970a).

The following description of the life cycle has been condensed from Soulsby (1965), Stoffolano (1970a) and Levine (1980). The face fly, while feeding on lachrymal secretions of infected cattle, ingests first instar larval nematodes. Once ingested, the nematodes penetrate the gut wall and enter the hemocoel. Here, they develop into second stage larvae and eventually into the third and infective stage. Development within the fly takes 15-30 days. Upon reaching the infective stage, the larvae migrate through the thorax and head capsule into the proboscis and are liberated as the fly feeds on the bovine eye. They then enter either the lacrimal duct or the

conjunctival sac of the eye, where they develop into adults 7-19 mm in length. After mating, adult female nematodes lay fully embryonated eggs into the eye fluids to repeat the cycle. The developmental cycle in the eye takes 20-40 days. Thelazia spp. can survive in the eyes of cattle for months, which may explain the survival of the nematode during winter, since they were not found in face flies in reproductive diapause in the fall, nor among nulliparous overwintered flies in the spring (Krafsur and Church 1985). Sexually mature nematodes have been isolated from cattle in winter and spring. The time frame and factors involved in the process of infected cattle becoming infectious to face flies is not known (Krafsur and Church 1985).

Thelazia infections in North America have been found upon post-mortem investigation to be primarily subclinical in nature (Geden and Stoffolano 1980). However, mild infections which cause lacrimation, conjunctivitis, eye discharge and photophobia may eventually lead to progressive keratitis, which can result in ulceration of the cornea or in opacity followed by blindness (Soulsby 1965; Levine 1980). The extent to which thelaziasis affects the productivity of beef and dairy cattle has not yet been investigated. One can only assume that productivity might be affected in a manner similar to cattle affected by pinkeye, as the 2 disorders exhibit similar symptoms. To reduce the incidence of bovine and equine thelaziasis, one can reduce fly populations and treat affected animals in winter (Levine 1980). Because of the relatively recent discoveries of these eyeworms,

it would seem necessary that additional efforts be made to determine their range, prevalence, and economic impact.

12.0 Relationship of the face fly to other diseases

The filarial nematode, Parafilaria bovicola Tubangui (Filaroidea: Filariidae), hitherto regarded as a tropical and subtropical parasite, has recently been discovered in Sweden (Bech-Nielsen et al. 1982). Subsequent investigations established that the intermediate host was M. autumnalis and that this fly could transmit this parasite experimentally via the intraconjunctival route. This nematode causes cutaneous bleeding which produces bruise-like lesions in the subcutaneous surfaces of carcasses (Soulsby 1965; Bech-Nielsen et al. 1982). It was estimated that this filarial disease caused an estimated $1 million damage to the Swedish livestock industry in 1981, and that, if the disease went unchecked, damage by 1990 could exceed $8 million per year (Bech-Nielsen et al. 1982). The authors point out that since the face fly also occurs in North America, the possibility exists for P. bovicola eventually to become established in this area as well.

It has been suggested that because of its close association with cattle, the face fly has the potential of transmitting bovine mastitis (Greenburg 1973). However, as Hillerton et al. (1984) point out, the face fly is an unlikely vector in that

it rarely visits the undersides of cattle. The face fly has also been shown to be capable of in-vitro transfer of hog cholera virus (Morgan and Miller 1976). This observation is interesting, as face flies are attracted to swine (Teskey 1969).

13.0 Human annoyance

The face fly, because of its overwintering habits, is considered by some to be an extreme annoyance. That it overwinters in homes and other buildings has been well documented (see Section 4.0). Its presence in dwellings can at times be overwhelming; Strickland et al. (1970) found almost 400,000 face flies hibernating in a 7.6 m^2 attic in California. A hibernation habit of this sort can lead to any one or all of the following nuisances. The presence and clustering of numerous flies in and on walls and crevices, especially windows, results in the accumulation of dead flies and fly specks. Flies that become active during warm spells can be bothersome to building occupants, particularly in the spring. Finally, the build up of dead flies almost inevitably leads to infestations of dermestid beetles (Matthew et al. 1960; Strickland et al. 1970). There have been numerous reports regarding outbreaks of the larder beetle, Dermestes lardarius L., in association with infestations of cluster flies, Pollenia rudis (F.), and face flies (MacNay 1963a,1965; Rich and Neilson 1973).

The face fly can also harbour microorganisms that can cause human disease. Staples et al. (1981), found face flies harbouring the following bacteria: Bacillus spp., Diplococcus spp., Enterobacter spp., Escherichia spp., Herellea spp., Mima spp., Pasteurella spp., Staphylococcus spp., Streptococcus spp., and Yersinia spp.

14.0 Biological control agents and their potential for face fly control

Following its introduction to North America, the face fly was quite successful in utilizing cattle dung as a breeding habitat (Turner et al. 1968). Because of this abundant resource, and the lack of natural control agents, an initial wave of face flies spread across the continent virtually unchecked (Nickle 1974; Schmidtmann 1977). It soon became evident that very little information existed on its ecology in the Old World (Drea 1966). Hammer (1941) did report on a number of predators and parasites (Table 1) associated with the face fly in Denmark. However, it was only the serious nature of the North American invasion that prompted more intensive investigation (Drea 1966). Numerous reports have now been published (Table 1) on potential natural controls in North America, while only a few have been reported from the Old World.

It is generally accepted that hymenopterous parasitoids

Table 1. Predators, parasites and other organisms known to attack or affect M. autumnalis

Organism	Life stage affected [a]	References
COLEOPTERA		
Histeridae		
Atholus americanus Paykull	L	Thomas et al. 1983.
Hister abbreviatus F.	E	Kessler and Balsbaugh 1972.
H. unicolor L.	L	Hammer 1941.
Phelister subrotundatus Say	L	Thomas et al. 1983.
Hydrophilidae		
Sphaeridium scarabaeoides L.	L	Hammer 1941; Rummel 1971; Thomas et al. 1983.
Scarabaeidae		
Geotrupes stercovarius L.	DD	Hammer 1941.
Onthophagus gazella (F.)	DD	Lancaster et al. 1976.
Staphylinidae		
Aleochara bimaculata Gravenhorst	E, L, P	Thomas and Wingo 1968; Wingo et al. 1967; Kessler and Balsbaugh 1972; Thomas et al. 1983.
A. tristis Gravenhorst	E, L, P	Drea 1966; Jones 1967; Wingo et al. 1967.
Aleochara spp.	------	Turner et al. 1968.

Organism	Life stage affected [a]	References
Amischa analis Gravenhorst	E, L	Thomas et al. 1983.
Aphodius spp.	DD	Hammer 1941.
Falagria dissecta Erickson	E, L	Thomas et al. 1983.
Ontholestes cinqulatus Gravenhorst	A	Teskey 1969.
Oxyteles suspectus Casey	E, L	Thomas et al. 1983.
Philanthus cruentatus Gmelin	E, L	Valiela 1969; Kessler and Balsbaugh 1971; Wingo et al. 1974; Thomas et al. 1983.
P. rectangulus Sharp	L	Kessler and Balsbaugh 1972; Wingo et al. 1983; Thomas et al. 1983.
P. varians Paykull	L	Thomas et al. 1983.
Platystethus americanus	E, L	Thomas et al. 1983.
Rhipiphoridae		
Rhipiphorus sp.	A	Lyons et al. 1976.
DIPTERA		
Asilidae		
Asilus crabroniformis L.	A	Hammer 1941.

Organism	Life stage affected [a]	References
Sarcophagidae		
Ravinia lherminiere Robineau-Desvoidy	E, L	Pickens 1981.
Scatophago stercovaria L.	A	Teskey 1969.
HYMENOPTERA		
Braconidae		
Aphaerta pallipes Say	L to P	Blickle 1961, 1965; Benson and Wingo 1963; Houser and Wingo 1967; Burton and Turner 1968; Thomas and Wingo 1968; Turner *et al.* 1968; Teskey 1969; Wingo 1970; Gary and Wingo 1971; Hayes and Turner 1971; Rummel 1971; Kessler and Balsbaugh 1972; Wylie 1973; Figg *et al.* 1983b.
Alysia sp.	L to P	Thomas and Wingo 1968.
Eucoilidae		
Eucoila impatiens Say	L to P	Thomas and Wingo 1968; Rummel 1971; Hayes and Turner 1971.
Eucoila sp.	L to P	Figg *et al.* 1983.
Eucoila sp.	L to P	Blickle 1961, 1965.
Figitidae		
Xyalophora quinquelineata Say	L to P	Blickle 1961.

Organism	Life stage affected [a]	References
Xyalophora sp.	L to P	Teskey 1969.
Pteromalidae		
Eupteromalus dubius Ashmead	P	Wylie 1973, 1976.
Musidifurax raptor Girault and Saunders	P	Burton and Turner 1968, 1970: Thomas and Wingo 1968; Turner *et al*. 1968; Wylie 1973.
Muscidifurax sp.	P	Figg *et al*. 1983a.
Nasomia vitripennis Walker	P	Hair and Turner 1965.
Spalangia niger Latreille	L to P	Wylie 1973.
Sphecidae		
Bembix pruinosa Fox	A	Sabrosky 1956.
Mellinus sp.	A	Hammer 1941.
Vespidae		
Vespula germanica (F.)	A	Schmidtmann 1977.
Vespa spp.	A	Schmidtmann 1977.
Vespa sp.	A	Hammer 1941.
ORTHOPTERA		
Gryllidae		
Allonemobius fasciatus DeGeer	E	Wingo *et al*. 1974.

Organism	Life stage affected [a]	References
ACARINA		
Dermanyssidae		
Macrocheles muscaedomesticae Scopoli	E	Singh et al. 1966.
EUBACTERIALES		
Bacillaceae		
Bacillus thuringiensis Berliner	L to P	Ode and Matthysse 1964b; Cantwell et al. 1964; Yendol and Miller 1967; Hower and Cheng 1968a; Kanga 1984.
ENTOMOPHTHORALES		
Entomophtharaceae		
Entomophthora muscae Cohn (Fres.)	A	Pickens and Miller 1980.
Entomophthora sp.	A	Gregory and Wright 1973.
AVES		
Charadriidae		
Charadrius vociferus L. (Killdeer)	L, DD	Valiela 1969.
Icteridae		
Molothrus ater Grinnell (Cowbird)	L, DD	Valiela 1969.

Organism	Life stage affected [a]	References
Sturnella major L. (Meadowlark)	L, DD	Valiela 1969.
Sturnidae		
Sturnus vulgaris L. (Starling)	L, DD	Hammer 1941; Valiela 1969.

[a] E = egg; L = larvae; P = pupae; A = adult; DD = disturbs dung

under field conditions cause limited mortality among immature face flies (Blickle 1961; Thomas and Wingo 1968; Valiela 1969; Turner et al. 1968; Hayes and Turner 1971). Aphaerta pallipes Say, a parasitoid of at least 20 species of Nearctic Diptera (Wingo 1970) was one of the first native parasites found in face fly larvae (Blickle 1961). Considerable effort (Table 1) was directed towards this parasitoid in hopes of exploiting it as a biological control agent. Despite high levels of parasitism, however, successful eclosion of A. pallipes adults from face fly puparia rarely occurs (Benson and Wingo 1963; Houser and Wingo 1967; Thomas and Wingo 1968; Turner et al. 1968; Kessler and Balsbaugh 1972; Figg et al. 1983b). It is believed that A. pallipes, in conjunction with a number of other hymenopteran parasitoids, is incapable of emerging from the face fly puparium because of the puparium's brittle calcified nature (Fraenkel and Hsiao 1967; Wingo 1967; Grodowitz and Broce 1983). The puparium is apparently so hard that pupal parasites such as Muscidifurax raptor Girault and Sanders, can penetrate only via the spiracles (Fraenkel and Hsiao 1967). Laboratory selection of a strain of A. pallipes that can successfully emerge from the puparia has met with limited success (Thomas and Wingo 1968; Wingo 1970). Only the imported staphylinid, Aleochara tristis Gravenhorst, is able to emerge consistently from the puparium (Jones 1967; Burton and Turner 1968). However, the potential for this staphylinid as a biological control agent is limited because of its poor searching capacity (Wingo et

al. 1967). Large numbers of A. tristis were introduced into California in an attempt to provide better natural control of face flies (U.S.D.A. 1969). The success of this introduction is not known.

Predators and other biotic factors seem to play a more significant role than parasitism in mortality of immature stages of the face fly. Valiela (1969) noted that predators reduced field populations of face flies by as much as 50%. Thomas et al. (1983), in similar studies observed that predation mortalities exceeded 80%. Although a number of beetle species have been observed to prey on face flies, only the members of Staphylinidae, Histeridae and Hydrophilidae are considered important primary predators of dung-inhabiting flies (Hammer 1941; Thomas and Morgan 1972; Wingo et al. 1974; Thomas et al. 1983).

Scarabaeids are also considered important in that their activities disrupt oviposition (Hammer 1941) and enhance the dessication of the fecal pat (Moon 1980). Two species of African Scarabaeinae have been released in California in an attempt to displace face flies and other copraphagous pests from dung pats (Moon 1980). The success of this attempted manipulation of a non-pest species to compete directly with the face fly for a common resource is not known (Moon 1980).

Rich and Neilson (1973) and Nickle (1974), although not providing suitable references, hypothesized that face fly populations would eventually be checked by the nematode parasite

Heterotylenchus autumnalis Nickle (Nematoda:Sphaerulariidae). This nematode was first discovered in New York in 1965 (Stoffolano and Nickle 1967). It is believed that H. autumnalis followed the westward spread of the face fly by a time lag of 2 summers (Nickle 1974,1978). The nematode is of Palearctic origin, and was presumably carried by its host to North America (Stoffolano 1968b,1969). It is not known whether healthy flies were introduced first followed by a later introduction of infected flies, or if the 2 were introduced together. Due to a bias for sampling flies on cattle, these nematodes may have escaped early detection as infected females are most common on dung (Thomas et al. 1972; Krafsur et al. 1983). It is also possible that the nematode was present in North America prior to the host's introduction; however, no other suitable host has been mentioned in the literature.

Nematode-infected females behave in a manner similar to nulliparous healthy flies until their ovaries are invaded, resulting in the necessity to oviposit (Krafsur et al. 1983). These sterilized females deposit free-living male and female nematodes into the fecal pat (Stoffolano 1967). Here they develop into adults. After mating, males die and females begin searching for a suitable host. All larval stages of the face fly are susceptible to parasitism (Stoffolano 1970b). The exact mechanisms by which female nematodes contact their host remains unexplained, as they do not readily disperse.

After having penetrated the cuticle of the larvae, the

gamogenetic female develops and later matures in the adult fly. Eggs are then laid in the hemolymph, where they develop into parthenogenetic females, which in turn lay thousands of eggs of both sexes. Eventually the resultant immature nematodes invade the ovaries, thus completing the life cycle (Jones and Perdue 1967; Stoffolano 1967,1970b).

Parasitized females become reproductively sterilized; infected males, although they are dead-end hosts, are still capable of mating and inseminating females (Stoffolano 1970b; Nappi 1973). Infected females can apparently complete at least one gonotrophic cycle before becoming sterile (Treece and Miller 1968; Krafsur et al. 1983). Jones and Perdue (1967) and Stoffolano (1970b) reported that only females >11-days-old were capable of depositing nematodes. Treece and Miller (1968) recorded females as young as 8 days transmitting nematodes. Thus parasitized females could complete at least 1 gonotrophic cycle in that they mate within 3-7 days after eclosion and lay eggs 2-5 days afterwards. However Kaya and Moon (1978) found that infected females produced few, if any eggs.

Infected flies behave normally until their ovaries are invaded. Levels of parasitism were always higher among flies collected from dung than among flies collected from cattle (Thomas et al. 1972; Krafsur et al. 1983). Kaya et al. (1979) observed infected flies to frequent cattle for nutrition only until the juvenile nematodes invaded their ovaries. Once their ovaries become distended, females become irreversibly attracted

to dung (Kaya et al. 1979). As rapidly as nematodes are deposited, juveniles invade the ovaries, keeping them constantly distended. Thus, for the duration of their lives the female face flies continue to deposit nematodes (Kaya et al. 1979).

The effectiveness of the nematode as a biocontrol agent has been questioned by a number of authors who noted that parasitism levels were not density dependent. Jones and Perdue (1967) were unable to increase infection levels beyond 30% amongst laboratory flies. Thomas et al. (1972) noted that despite fluctuating fly densities, parasitism levels remained somewhat constant. Kaya and Moon (1978) compared different larval densities in manure to infection levels and found that they were not related. They also noted that infection levels in progeny were less than half the levels found in parents. Flies bearing 1 or 2 gamogenetic nematodes were less abundant in field samples than flies that were either healthy or infected with 3 or more gamogenetic nematodes. These authors hypothesized that larvae were differentially susceptible to infection, or that face fly eggs or nematodes or both are deposited in clusters, resulting in superinfections. Clustering of eggs has been observed by Teskey (1969), thus strengthening the latter hypothesis. Kaya and Moon (1978) concluded that nematode infections are not random.

The nematode has been shown to overwinter effectively within the host (Table 2). Infection levels are approximately equal in each sex and overwintering, infected flies contained

Table 2. Levels of nematode parasitism among face flies collected by different sampling methods

Sampling Method [a]	Location	Numbers Collected (% Parasitized)			Reference
		Females	Males	Sexes not separated	
I	New York State	2800(23)	677(23)		Stoffolano and Nickle 1966
I	New England states	4958(6)	556(7)		Stoffolano 1968b
I	France	863(2)	25(12)		Stoffolano 1969
I	Massachusetts			155(25)	Chitwood and Stoffolano 1971
I	Ontario			19297(2)	Wright 1972a
II	Nebraska			2116(2)	Jones and Perdue 1967
II	Mississippi	1819(16)	1196(18)		Robinson and Combs 1976
II	California			3273(23)	Kaya and Moon 1978
II	Iowa	569(5)			Krafsur et al. 1983
III	Nebraska			1433(22)	Jones and Perdue 1967
III	Missouri	2747(40)			Thomas and Puttler 1970
III	Missouri	2655(30)			Thomas et al. 1972
III	Missouri	498(41)			Kaya and Moon 1978
III	Iowa	25(4)			Krafsur et al. 1983

Sampling Method [a]	Location	Numbers Collected (% Parasitized)			Reference
		Females	Males	Sexes not separated	
III	Iowa, 1978	882(9)			Krafsur et al. 1983
III	Iowa, 1979	1680(7)			Krafsur et al. 1983
III	Iowa, 1980			1583(19)	Krafsur et al. 1983
IV	Nebraska			1893(20)	Jones and Perdue 1967
IV	Mississippi	274(21)	363(16)		Robinson and Combs 1976
IV	California			105(20)	Kaya and Moon 1978
IV	Iowa, 1979	426(8)			Krafsur et al. 1983
V	Missouri	200(7)			Thomas et al. 1972
V	Kentucky (from horses only)			866(2)	Lyons et al. 1976
V	California	651(23)	681(31)		Kaya and Moon 1978
VI	Iowa, 1977	54(0)			Krafsur et al. 1983
VI	Iowa, 1978	978(3)			Krafsur et al. 1983
VI	Iowa, 1980			2931(5)	Krafsur et al. 1983
III and VI	South Dakota			19297(2)	Kessler and Balsbaugh 1972

[a] Sampling Methods as follows:

I Sweep net samples taken from blood boards placed near cattle.
II Flies collected and reared from fecal pats in pastures.
III Sweep net samples taken from around dung.
IV Flies collected from overwintering sites.
V Sweep net samples taken from the faces of cattle.
VI Sweep net samples taken from the faces of cattle and from resting places.

only gamogenetic and parthenogenetic nematodes (Kaya and Moon 1978). Nematodes deprived of protein do not develop past the gamogenetic stage (Kaya and Moon 1980). Since pre-diapausing flies do not normally visit cattle and thus do not obtain protein, one can conclude that protein deprivation is the mechanism by which nematode development is temporarily arrested. The extent to which nematodes have influenced and are affecting current fly populations is not clear. Nickle (1974) states that 25-30% of the general fly population is infected. An examination of the available data (Table 2) lends some support to this statement. However, a proper analysis is not possible because of the bias introduced in different sampling methods. Sweep net samples taken from dung would tend to be biased toward infected flies that are differentially attracted to dung. Samples taken from cattle would capture only those flies which have not yet "nemaposited", and samples of larval flies obtained from manure may have a substantially different infection rate from adult flies. Samples taken from blood boards may also be biased as these were placed among cattle. Thus it would seem that only those samples taken of overwintering flies would be indicative of actual infection levels.

The nematode, however, is at present the only effective biocontrol agent of the face fly (Stoffolano 1971). It appears to be host-specific (Stoffolano 1970b), has a life cycle synchronized with the fly (Stoffolano 1967), and is effectively distributed by its host. It has also been mass reared and

released among nematode-free populations in California and Montana (Nickle 1978). In 1969, ca 10,000 nematode-infested pupae were released in California (U.S.D.A. 1969). Nickle (1978) claims that the release of these nematodes into field populations of healthy flies resulted in sterilization of 25-50% of the population.

The manipulation of currently-known biocontrol agents has been largely unsuccessful. Therefore there is a need to intensify a search for natural predators and parasites of the face fly throughout its range in the Old World (Wright 1985).

15.0 Face fly control with pesticides

The explosive nature with which face flies first appeared as they advanced across North America (Boyer et al. 1975) presented livestock producers with a problem that required immediate attention. Researchers immediately began testing numerous insecticides, repellents, attractants and combinations thereof (Table 3) in an attempt to provide some form of control. Initial and subsequent attempts at finding ideal insecticidal controls have been somewhat inadequate, despite the numerous insecticides, formulations and control methods tested (Table 3). Therefore, it was hypothesized that the face fly had a lower susceptibility to insecticides than did other dipteran livestock pests. However, numerous laboratory studies with field and

Table 3. The effectiveness of various pesticides and formulations applied for face fly control

Abbreviations for efficacy are: **E** [a] = Effective; **NE** = Not effective; **INA** = Information not available

Abbreviations for mode of applications and/or formulation are: **A** = Aerosol; **BO** = Brush or wipe on; **BR** = Back rubber; **D** = Dust; **DB** = Dust bag; **ET** = Ear tags; **FR** = Face rubber; **MB** = Mineral block; **PVC** = Polyvinyl chloride protected; **Sp** = Spray; **Su** = Sugar additive; **SuB** = Sugar bait; **SyB** = Syrup bait; **WP** = Wettable powder

All % figures indicate amount of active ingredient used. Weight values are in mg/kg body weight unless noted otherwise.

Chemical [b]	Manual application entire animal	Facial treatments	Oral application	Self application devices
Amitraz		**NE**: 10%, **ET** (Hall and Fischer 1984)		
Amitraz (10% and 20% + Peremethrin 10%)		**NE**: **ET** (Hall and Fischer 1984)		
Azinphos-methyl		**E**: 25% **WP**, **D** (Dorsey et al. 1966)		**E**: 2% and 10% **D**, **DB** and **FR** (Dorsey et al. 1966) **E**: 2% **BR** (Dorsey et al. 1966) **E**: 25% **WP**, **DB** (Hair and Adkins 1965)
Bacillus thuringiensis Berliner			**E**: 36mg (Cantwell et al. 1964) **E**: 370mg (Hower and Cheng 1968a)	

Chemical [b]	Manual application entire animal	Facial treatments	Oral application	Self application devices
Bacillus thuringiensis (cont'd.)			**E:** 35mg (Ode and Matthysse 1964b)	
			E: 18mg (Yendol and Miller 1967)	
Barthrin	**NE:** 1% and 2% **Sp** + **Su** (Fales et al. 1968)	**NE:** 0.5% **D** (Ode and Matthysse 1964a)	**E:** 10mg (Ode and Matthysse 1964a)	
Bayer (Bayer) S-940*			**NE:** 2.0mg (Treece 1964)	
Bayer 22408*			**E:** 0.5 and 1.0mg (Anthony et al. 1961)	
			E: 0.25mg and 1.0mg (Ode and Matthysse 1964b)	
			E: 0.25mg (Treece 1962)	
Bayer 29493*			**NE:** 0.5mg, **E:** 2.0mg (Treece 1962)	
Bayer 37344*	**NE:** 1% **Sp** + **Su** (Granett et al. 1962)			**E:** 5% **D, DB** (Turner 1965)
	NE: 5.0% **D** (Granett et al. 1962)			
Bromophos	**NE:** 0.5% **Sp** + **Su** (Fales et al. 1968)			

Chemical [b]	Manual application entire animal	Facial treatment	Oral application	Self application devices
Carbaryl	**E:** 0.75% **Sp** (Defoliart 1963) **NE:** 3% **D** (Fales et al. 1968)	**NE:** 50% **WP, D** (Benson and Wingo 1963)	**NE:** 5mg **Wp, E:** 10mg **WP** (Ode and Matthysse 1964b)	**E:** 50% **D, DB** (Hair and Adkins 1965) **NE:** 5% **D, DB** (Hair and Adkins 1965; Roberts 1965) **NE:** 50% **WP, DB** (Roberts 1965)
Carbaryl (1%) + piperonyl butoxide (1%)		**NE: Sp** (Granett and Hansens 1961)		
Carbophenothion				**NE:** 1% **BR** (Roberts 1963)
Coumaphos	**E:** 0.25% **Sp** (Defoliart 1963) **NE:** 0.25 and 0.5% **Sp** (Ode and Matthysse 1964a)	**NE:** 0.5% **Sp** (Granett and Hansens 1961)	**E:** 0.5mg and 1.0mg (Anthony et al. 1961) **NE:** 0.5mg and 1.0mg (Dorsey et al. 1966) **E:** 0.5mg (Jones and Medley 1963) **E:** 2% **MB** (Knapp 1965b) **E:** 1.0mg and 2.5mg (Ode and Matthysse 1964b)	**NE:** 5% **D, DB** (Fales et al. 1968; Kolach 1969; Turner 1965) **E:** 5% **D, Fr** (Gerhardt et al. 1976) **E:** 5% **D, DB** (Hair and Adkins 1965; Seawright and Adkins 1968) **E:** 25% **WP, DB** (Hair and Adkins 1965)

Chemical [b]	Manual application entire animal	Facial treatment	Oral application	Self application devices
Coumaphos (cont'd.)			**E**: 0.25mg (Treece 1962, 1964)	**NE**: 1% **D, DB** (Kolach 1969; Williams et al. 1981; Wright 1972c) **E**: 1% **D, DB** (Poindexter and Adkins 1970; Wrich 1970)
Coumaphos (2.5%) + Trichlorfon (0.5%)		**NE: BO** (Ode and Matthysse 1964a)		
Crag Fly Repellent* (CFR) (Union Carbide)		**NE**: 5% **BO** (Fales et al. 1961b) **E**: 5% and 20%, **BO** (Granett and Hansens 1961) **NE**: 10% **Sp** (Granett and Hansens 1961)		**NE**: 5% **BR, R** (Dobson and Huber 1961)
CFR (5.0%) + Diazinon (0.5%)		**NE: Sp** (Granett and Hansens 1961)		
CFR (5.0%) + Dimethoate (1%)		**NE: Sp** (Granett and Hansens 1961)		
CFR (5%) + GC 4072* (0.5%) (Allied Chemical Corp.)		**NE: Sp** (Granett and Hansens 1961)		
CFR (5%) + Malathion (0.5%)		**NE: BO** (Granett and Hansens 1961)		

Chemical [b]	Manual application entire animal	Facial treatments	Oral application	Self application devices
CFR (5% + 10%) + Methoxychlor (0.5% and 1% respectively)		**E: BO** (Granett and Hansens 1961)		
CFR (5%) + Naled (1%)	**NE: Sp** (Granett et al. 1962)			
CFR (5%) + Synergized Pyrethroids (0.03%)	**E: Sp** (Granett et al. 1962			
CFR (5%) + Synergized Pyrethroids (0.25%)		**NE: Sp** (Granett and Hansens 1961)		
CFR (8%) + Synergized Pyrethroids (0.06%)		**E: BO** (Matthysse 1961)		
CFR (8% + 16%) + Synergized Pyrethroids (0.06%)		**NE: Sp** (Ode and Matthysse 1964a)		
CFR (16%) + Synergized Pyrethroids (1%)	**NE: Sp** (Ode and Matthysse 1964a)	**NE: A** (Matthysse 1961)		
CFR (5%) + Trichlorfon (2%)		**NE: Sp** (Granett and Hansens 1961)		

Chemical [b]	Manual application entire animal	Facial treatments	Oral application	Self application devices
CFR (5%) + MGK 264* (2%) + MGK R1207* (2%) (McLaughlin Gormley King Co.)		**NE: BO** (Granett and Hansens 1961)		
CFR (10%) + MGK 264* (0.4%) + Synergized Pyrethroids (0.12%)		**NE: Sp** (Granett and Hansens 1961)		
Crotoxyphos	**E:** 0.75% **Sp** (Defoliart 1963)	**E:** 2% **Sp** (Cheng et al. 1965)		**NE:** 1% **BR** (Barlow and Surgeoner, 1979; Roberts 1963)
	E: 1% **Sp** + **Su** (Fales et al. 1968)	**E:** 5% **D** (Dorsey et al. 1966)		**NE:** 0.75% **BR** (Dorsey et al. 1966)
	E: 2% **Sp** (Fales et al. 1968)	**NE:** 1% **SyB** and 2% **SyB** (Teskey and Allen 1963)		**E:** 1% **BR** (Hair and Adkins 1965)
	E: 2% **Sp** + **Su** (Hansens and Granett 1963)			**NE:** 3% **D, DB** (Kessler and Berndt 1971; Wright 1973a)
				E: 3% **D, DB** (Poindexter and Adkins 1970)
Crotoxyphos (1%) + DDVP (0.25%)	**E: Sp** (Fales et al. 1968)			**NE: BR** (Barlow and Surgeoner 1979; Wright 1971)
	NE: 0.5% **Sp** (Gerhardt and Cook 1976)			

Chemical [b]	Manual application entire animal	Facial treatments	Oral application	Self application devices
Crufomate			**NE**: 1mg and 5mg (Treece 1962)	
Cypermethrin		**E**: 8% **ET** (Flannigan and Surgeoner 1984d) **E**: 8.6% **ET** (Surgeoner and Gilhen 1982a)		
DDT	**NE**: 0.5% **WP, Sp** (Benson and Wingo 1963) **NE**: **INA, Sp** (Bruce et al. 1960) **E**: 50% **WP** (Dobson and Huber 1961)			**NE**: 5.0% **BR** (Benson and Wingo 1963; Roberts et al. 1963) **E**: 5.0% **BR** (Dobson and Huber 1961)
DDT (0.5%) + Lindane (0.03%)	**E**: **WP** (Benson and Wingo 1963)			
DDT (2.0%) + Methoxychlor (2%)				**E**: **D, DB** (Poindexter and Adkins 1970)
DDT (5%) + Tabatrex				**E**: **BR, INA** (Dobson and Huber 1961)

Chemical	Manual application entire animal	Facial treatments	Oral application	Self application devices
Decamethrin		**E:** 1.5% **ET** (Williams and Westby 1980)		
DDVP	**NE:** 0.5% **Sp** (Fales et al. 1968) **E:** 0.5% **Sp + Su** (Fales et al. 1968) **NE:** 0.5% **D, E:** 1% and 2% **D** (Granett et al. 1962) **E:** 0.25% **Sp** (Granett et al. 1962) **NE:** 0.5% **Sp + Su** (Hansens and Granett 1963)	**E:** 0.1% **SyB** (Bruce et al. 1960) **NE:** 0.15% **Sp** (Dorsey et al. 1966) **NE:** 0.1% **SuB** (Fales et al. 1961b) **NE:** 0.2% and 0.5% **SyB** (Granett and Hansens 1961) **NE:** 0.25% **Sp** (Granett et al. 1962) **E:** 0.5% **SyB** (Holdsworth 1962; Teskey and Allan 1963; Teskey and Heming 1962; Granett et al. 1962)	**E:** 0.5mg (Jones 1963) **NE:** 5mg (Lloyd and Matthysse 1970) **E:** 5mg **PVC** (Lloyd and Matthysse 1970) **E:** 0.5 and 4.0mg **PVC** (Pitts and Hopkins 1964) **NE:** 1mg and 2mg (Treece 1962)	**NE:** 2.5% **ear bag** (Boxler et al. 1977) **NE:** 1% **BR** (Dobson and Huber 1961)
DDVP (0.5%) + Silikil dust		**NE:** **D** (Granett and Hansens 1961)		

Chemical [b]	Manual application entire animal	Facial treatments	Oral application	Self application devices
Diazinon	**NE:** 0.25% **Sp + Su** (Granett et al. 1962) **NE:** 2% **D** (Granett et al. 1962; Hansens and Granett 1963)	**NE:** 1% **SyB** (Bruce et al. 1960) **NE:** 0.5% **Sp** (Granett and Hansens 1961) **NE:** 0.5% **Sp + Su** (Granett and Hansens 1961)	**NE:** 5mg, **E:** 5mg **PVC** (Llovd and Matthysse 1970) **NE:** 1mg (Ode and **Matthysse 1964b)**	**NE:** 1 and 2% **BR** (Dorsey et al. 1966) **NE:** 2% **BR** (Hair and Adkins 1965) **E:** 2% **D, DB** (Hair and Adkins 1965)
Diflubenzuron			**E:** 0.25mg and 0.5mg (Miller 1974)	
Dimethoate		**E:** 1% **SyB** (Benson and Wingo 1963) **E:** 1% and 2% **SyB** (Bruce et al. 1960; Granett and Hansens 1961) **NE:** 0.5% **SuB** (Granett and Hansens 1961) **NE:** 1% **Sp** (Granett and Hansens 1961) **NE:** 2% **BO** (Granett and Hansens 1961)	**E:** 5mg **PVC** (Lloyd and Matthysse 1970)	**NE:** 1% **BR** (Dobson and Huber 1961; Hair and Adkins 1965) **NE:** 2% **BR**, 2% **FR** (Dorsey et al. 1966) **NE:** 5% **D, DB** (Hair and Adkins 1965)

Chemical [b]	Manual application entire animal	Facial treatments	Oral application	Self application devices
Dimethoate (cont'd.)		**E:** 2% **BO** (Ode and Matthysse 1964a)		
Dimethoate (1%) + DDVP (0.5%)		**E: SyB** (Benson and Wingo 1963)		
Dimethoate (1%) + DDVp (0.2%)		**E: SyB** (Bruce et al. 1960)		
Dimethrin	**NE:** 2% **Sp + Su** (Fales et al. 1968)		**NE:** 2mg and 5mg, **E:** 10mg (Ode and Matthysse 1964b)	
			NE: 1mg and 5mg (Treece 1962)	
Dimetilan	**E:** 1% **Sp + Su** (Fales et al. 1968)	**E:** 50% **D** (Dorsey et al. 1966)	**NE:** 5mg, **E:** 5mg **PVC** (Lloyd and Matthysse 1970)	**NE:** 2% **D, DB** (Fales et al. 1968)
	E: 0.5% **Sp + Su** (Hansens and Granett 1963)			**E:** 2% **D, DB** (Hair and Adkins 1965; Seawright and Adkins 1968; Turner 1965)
Dioxathion	**NE:** 0.25% **Sp** (Benson and Wingo 1963)			**NE:** 1.5% **BR** (Benson and Wingo 1963)
Dioxathion (10.5%) + DDVP (1%)	**NE: Sp** (Wright 1972b)			

Chemical [b]	Manual application entire animal	Facial treatments	Oral application	Self application devices
Drione* (Fairfield (American Corp.)				**NE: INA, D, DB** (Turner 1965)
Famphur			**NE**: 2.0mg (Treece 1964)	
Fenthion			**E**: 5mg **PVC** (Lloyd and Matthysse 1970)	**E**: 1% **BR** (Hair and Adkins 1965)
			E: 10mg (Ode and Matthysse 1964b)	**E**: 3% **D, DB** (Hair and Adkins 1965)
				NE: 5% **D, DB** (Kolach 1968)
				NE: 1% **BR** (Roberts 1963)
				NE: 2% **D, DB** (Turner 1965)
				E: 0.5% and 1.0% **BR** (Wrich 1970)
Fenvalerate		**NE**: 8% **ET** (Flannigan and Surgeoner 1984a; Knapp and Herald 1984)		
		E: 8% **ET** (Burton et al. 1984; Knapp and Herald 1981)		

Chemical [b]	Manual application entire animal	Facial treatments	Oral application	Self application devices
Flucythrinate		**NE:** 7.5% **ET** (Costello and Carter 1984) **E:** 7.5% **ET** (Flannigan and Surgeoner 1984c)		
GC 4072*	**E:** 0.5% **Sp + Su** (Granett et al. 1962)	**NE:** 0.5% **Sp** (Granett and Hansens 1961)	**E:** 1.0mg (Treece 1964)	
HRS 1422* (Hooker Chemicals and Plastics Corp.)			**NE:** 2.0mg (Treece 1964)	
Ivermectin (Merck and Co., Inc.)			**E:** 5ug oral dose (Miller et al. 1981)	
Lindane				**NE:** 2% **Br** (Dorsey et al. 1966)
Malathion	**NE:** **INA, Sp** (Bruce et al. 1960) **NE:** 4% **D** (Ode and Matthysse 1964a) **NE:** 25% **WP, D** (Ode and Matthysse 1964a)	**NE:** 5% **D** (Dorsey et al. 1966) **NE:** 1.6% **Sp + Su** (Fales et al. 1961b)	**NE:** 10mg (Ode and Matthysse 1964b)	**E:** 2% **BR** (Dorsey et al. 1966) **NE:** 2% **BR** (Hair and Adkins 1965) **NE:** 2.5% **BR + FR** (Roberts 1965)

Chemical [b]	Manual application entire animal	Facial treatments	Oral application	Self application devices
Malathion (cont'd.)				**E:** 5% **D, DB** (Seawright and Adkins 1968; Turner 1965)
Menazon			**NE:** 2.5mg (Treece 1964)	
Methoprene			**E:** 10% in sustained-release bolus (Miller et al. 1979)	
			E: 0.25mg and 1.0mg (Miller and Pickens 1975b)	
			NE: 0.02%, **E:** 0.12% **MB,** (Miller and Pickens 1975b)	
			E: 1mg (Miller and Ubel 1974b)	
			E: 0.07mg and 0.13mg (Miller et al. 1978)	
			E: 0.27% **MB** (Miller et al. 1978)	
			E: 0.5% **MB** (Wright 1973b)	

Chemical [b]	Manual application entire animal	Facial treatments	Oral application	Self application devices
Methoxychlor	**NE:** 0.5% **Sp** (Benson and Wingo 1963) **NE:** 50% **WP** (Dobson and Huber 1961) **NE:** 5% **D** (Ode and Matthysse 1964a) **NE:** 50% **WP, D** (Ode and Matthysse 1964a)	**NE:** 50% **WP, D** (Benson and Wingo 1963) **NE:** 1.6% **SuB** (Fales et al. 1961b) **NE:** 1% **SyB** (Granett et al. 1962)	**NE:** 5mg (Ode and Matthysse 1964b)	**NE:** 5% **BR** (Benson and Wingo 1963) **E:** 5% **BR** (Dobson and Huber 1961) **E:** 2% **BR** (Dorsey et al. 1966) **E:** 2% and 5% **D, DB** (Poindexter and Adkins 1970) **E:** 50% **WP** or **D, DB** (Roberts 1965)
Methoxychlor (2.5%) + Malathion (1%)				**NE:** **BR** (Barlow and Surgeoner 1979)
MGK 264* (5.0%) + MGK 1207* (2%)		**NE:** **BO** (Granett and Hansens 1961)		
MGK 326*		**NE:** 5% **Sp** (Fales et al. 1961b) **NE:** **INA, A** (Matthysse 1961)		
MGK 326* (8%) + Synergized Pyrethroids (0.06%)		**NE:** **BO** (Ode and Matthysse 1964a)		

Chemical [b]	Manual application entire animal	Facial treatments	Oral application	Self application devices
MGK 326* (0.2%) + Synergized Pyrethroids (0.075%)				**NE: D, DB** (Poindexter and Adkins 1970)
MGK 874*	**NE**: 2% **Sp** (Fales et al. 1968)			
MGK R 1207*		**NE:** 5% **Sp** (Fales et al. 1961b) **NE:** 2% **BO**, 2% **Sp** (Granett and Hansens 1961) **NE: A** (Matthysse 1961)		
MGK R 1207* (0.2%) + Synergized Pyrethroids (0.06%)		**NE: B** (Ode and Matthysse 1964a)		
MGK R 1207* (2.2%) + Synergized Pyrethroids (0.03%)	**NE: Sp** (Granett et al. 1962)			
Naled	**NE:** 1.0% **Sp, E:** 0.6% **Sp + Su** (Granett et al. 1962)	**NE:** 0.25% and 0.5% **Sp** (Granett et al. 1962) **E:** 0.5% **SyB** (Ode and Matthysse 1964a)		
Permethrin	**E:** 1% **Sp** (Lancaster and Simco 1981)	**E:** 10% **FT** (Flannigan and Surgeoner 1984b; 1985; Miller et al. 1984)		**NE:** 0.5% **BR** (Lancaster and Simco 1981)

Chemical [b]	Manual application entire animal	Facial treatments	Oral application	Self application devices
Permethrin (cont'd.)		**NE:** 10% **ET** (Hall and Fischer 1984; Krafsur 1984)		**NE:** 0.5% **DB** (Lancaster and Simco 1981)
		NE: 5% and 10% **ET** (Williams and Westby 1980; Williams et al. 1981)		**NE:** 1gm (tail tag) (Surgeoner and Gilhen 1982b)
				E: 0.5% **BR** (Surgeoner and Mollenbeek 1979)
				E: 0.5% **D, DB** (Surgeoner and Mollenbeek 1979)
Phenothiazine			**NE: INA** (Jones 1963)	
			NE: MB, INA (Miller and Pickens 1975a)	
			NE: 5mg (Treece 1964)	
Phosmet		**E:** 5% **D** (Dorsey et al. 1966)	**NE:** 0.5mg, **E:** 2.0mg (Treece 1964)	**NE:** 2% **BR** (Dorsey et al. 1966; Hair and Adkins 1965)
				NE: 2% **D, DB** (Dorsey et al. 1966)
Propoxur				**E:** 10% **D, DB** and **FR** (Dorsey et al. 1966)

Chemical [b]	Manual application entire animal	Facial treatments	Oral application	Self application devices
Prayamat* (Ciba-Geigy Limited)	**E:** 0.5% **Sp + Su** (Hansens and Granett 1963)			
Pyrethrins (Synergized)	**NE:** 0.1% **Sp** (Fales et al. 1961b)	**NE:** 0.06% **Sp** (Bruce 1960)		
	E: 7.5% **Sp** (Hansens and Granett 1963)	**NE:** 0.1% **BO** (Fales et al. 1961b)		
	NE: 0.2% **Sp** (Granett et al. 1962)	**NE:** 0.1% and 0.25% **Sp** (Granett and Hansens 1961)		
		NE: 0.5% **D** (Granett and Hansens 1961)		
		NE: 2% **A** (Matthysse 1961)		
RO 20-3600* (Hoffman-La Roche)			**E:** 10mg (Miller and Ubel 1974b)	
Ronnel	**NE: Sp, INA** (Bruce et al. 1960)	**NE:** 5% **Sp** (Granett and Hansens 1961; Ode and Matthysse 1964a)	**E:** 2.5mg and 5.0mg (Anthony et al.	**NE:** 2% **BR, FR** (Dorsey et al. 1966)
	NE: 25% **WP, D** (Ode and Matthysse 1964a)		**E:** 5.5% **MB** (Knapp 1965a; Ronald and Wingo 1973; Treece 1962; Wallace and Turner 1964)	**E:** 1% **FR** (Knapp 1965a)
				E: 5% **D, DB** (Seawright and Adkins 1968)
			NE: 0.25mg and 1.0mg (Ode and Matthysse 1964b)	

Chemical [b]	Manual application entire animal	Facial treatments	Oral application	Self application devices
Ronnel (cont'd.)			**NE:** 2.0mg (Treece 1962)	
Ryania* (Penick Crop.)			**NE:** 5.0mg (Ode and Matthysse 1964b)	
R-326* (Stauffer Chemical Co.)		**E: INA** (Bruce et al. 1960)		
R-326* (0.4%) + Synergized Pyrethroids (0.06%)		**E: Sp** (Bruce et al. 1960)		
R-1207*	**NE:** 2% **Sp** (Cheng et al. 1962)			
R-1207* (1.8%) + Dimethoate (0.9%) + Synergized Pyrethroids (0.27%)	**NE: A** (Cheng et al. 1962)			
Shell SD8447* (Shell Chemical Co.)				**E:** 3% **D, DB** (Seawright and Adkins 1968)
Shell SD447*			**E:** 0.5mg (Treece 1964)	
Shell SD448			**E:** 0.5mg (Treece 1964)	
Shell SD4294	**E:** 0.2% **Sp + Su** (Benson and Wingo 1963)		**E:** 2 and 5mg (Treece 1962)	

Chemical [b]	Manual application entire animal	Facial treatments	Oral application	Self application devices
Shell SD4294 (cont'd.)	**E:** 0.5% **Sp + Su** (Granett et al. 1962)			
Shell WL 42479*	**E:** 0.5% **Sp** (Surgeoner and Reilly 1979)			
Tabatrex		**E: INA, A** (Bruce et al. 1960) **NE:** 5% **BO** (Fales et al. 1961b) **NE:** 5% **Sp** (Granett and Hansens 1961)		
Tabatrex (2%) + Synergized Pyrethoids (1%)	**NE: Sp** (Ode and Matthysse 1964a)			
Tabatrex (1%) + Synergized Pyrethroids (0.06%)		**E: Sp** (Bruce 1960)		
Tabatrex + Synergized Pyrethoids		**NE: A, INA** (Matthysse 1961)		
Tetrachlorvinophos		**NE:** 13.7% **ET** (Krafsur 1984; Williams et al. 1981)	**E:** 1.94% **MB** (Gerhardt and Cook 1976)	**NE:** 3% **D, BR** (Barlow and Surgeoner 1979)

Chemical [b]	Manual application entire animal	Facial treatments	Oral application	Self application devices
Tetrachlorvinophos (cont'd.)		**E:** 13.7% **ET** (Lewis and Block 1982) **NE:** 14% **ET** (Surgeoner and Biberhofer 1981)	**NE:** 1.5mg (Miller and Pickens 1975a) **E:** 1% **MB** used in conjunction with sticky traps (Miller et al. 1984a) **E:** 60% in sustained release bolus (Riner et al. 1981) **NE: INA** (Surgeoner et al. 1982)	**E:** 3% **D, FR** (Gerhardt et al 1976) **NE: INA, D, DB** (Miller and Pickens 1975a)
Tetramethrin	**E:** 2% **Sp + Su** (Fales et al. 1968)			
Toxaphene	**NE:** 0.5% **Sp** (Benson and Wingo 1963; Ronald and Wingo 1973) **NE: INA** (Bruce et al. 1960)			**NE:** 5% **Br** (Benson and Wingo 1963; Roberts 1963; Ronald and Wingo 1973) **E:** 5% **BR** (Dobson and Huber 1961) **NE:** 6% **BR** (Kessler and Berndt 1971)
Toxaphene (14%) - DDT (7%)				**E: D, DB** (Hair and Adkins 1965)

Chemical [b]	Manual application entire animal	Facial treatments	Oral application	Self application devices
Toxaphene (5%) + DDT (5%) + Lindane (1%)				**E: D, DB** (Poindexter and Adkins 1970)
Trichlorfon	**E:** 1% **Sp + Su** (Fales et al. 1968)	**NE:** 0.8% **SuB** (Fales et al. 1961b)	**E:** 5mg **PVC** (Lloyd and Matthysse 1970)	**NE:** 1% **BR,** 1% **FR** (Dorsey et al. 1966)
		NE: 2% **Sp,** 2% **Sp + Su** (Granett and Hansens 1961)		
Zinc Oxide			**NE:** 10mg, **E:** 40mg (Ode and Matthysse 1964b)	

[a] = Effectiveness is based on the opinion of the cited investigator.

[b] = All chemicals are listed by common name according to Anon. (1985); if not available, the trade name is given as indicated by an asterisk.

laboratory-reared flies indicated that the face fly was in fact susceptible to a wide range of insecticides (Treece 1961; Bodenstein and Fales 1962; Turner and Wang 1964; Rousell 1965; Robinson et al. 1975; Knapp and Herald 1985). Laboratory studies were also conducted to determine the effectiveness of various compounds for repellancy and attractiveness (Frishman and Matthysse 1966; Dorsey 1968; Bodenstein et al. 1970). It was soon discovered that most of the repellents and attractants tested had limited practical use because of the short duration of their effectiveness when applied under field conditions (Miller and Pickens 1980).

A number of factors have been identified that may have contributed in some way to the erratic results reported in Table 3. Lack of isolation of treated farms and the lack of area-wide experiments resulted in reinfestation of treated herds from nearby untreated herds (Wallace and Turner 1962, 1964; Jones and Medley 1963, Treece 1964; Turner and Wang 1964; Knapp 1965a; Turner 1965; Surgeoner et al. 1982). Secondly, only a small proportion of the total fly population is on cattle at any one time and very little time is spent on cattle (Treece 1964; Turner and Wang 1964; Williams and Westby 1980). In contrast, insecticides applied on cattle are usually quite effective against horn flies which spend most of their time on cattle (Seawright and Adkins 1968; Williams and Westby 1980). Thirdly, face flies, when found on cattle, feed on protein sources (given the absence of blood) available from nasal and

eye secretions, which emanate from regions of the face which are extremely difficult to treat. The problem is exacerbated by the fact that face flies prefer to feed on the highly concentrated protein source of the mucoid layer around the eye (VanGeen and Broce 1985). When treatments are applied to the face they are frequently diluted by facial secretions or are removed during grazing, grooming or drinking (Hansens and Granett 1963; Treece 1964; Seawright and Adkins 1968). Insecticides applied with attractants such as sugar or syrup are often licked-off by other cattle (Fales et al. 1961b). In addition, compounds applied with baits usually require daily applications, which are tedious and expensive (Ode and Matthysse 1964a). Thus facial treatments are generally impractical under rangeland conditions and are more suited to dairy operations, where cattle are handled daily. A final problem stems from the discrepancies associated with sampling the size of the pre- and post-treatment fly populations. Many entomologists have evaluated the effectiveness of treatments by counting flies about the entire animal (Bruce et al. 1960; Decker 1961; Matthysse 1961; Granett and Hansens 1961; Cheng et al. 1962; Turner 1965; Wright 1971,1972c,1973a), while the majority have counted flies about the head or face. Hansens and Granett (1963) sprayed the faces, sides and backs of cattle with a number of insecticides alone or in conjunction with a bait and found that in almost all cases the reduction of flies was greatest on the body as opposed to the face.

Despite the limited effectiveness of self-application devices such as dust bags and back rubbers in controlling face fly activity about the facial region of cattle (Barlow and Surgeoner 1979), their usefulness to the producer can be justified because of their proven effectiveness for horn fly control (Roberts 1963,1965; Benson and Wingo 1963). These devices are easily and cheaply installed and are relatively maintenance free (Roberts et al. 1963). Self-application devices can be used either under forced or free choice situations. Forced use requires installation of the applicating apparatus in areas frequented regularly by cattle, such as watering holes, salt blocks or entries into adjoining pastures (Hair and Adkins 1965; Adkins and Seawright 1967). Dorsey et al. (1966) found that back rubbers work best when placed in favoured resting areas of cattle. Here a triangular arrangement of cables was set up with a salt box in the middle of the triangle. Free choice applicators, although not as effective as forced use in that cattle may not use them, should be placed in resting areas (Gerhardt et al. 1976). Forced use facial applicators such as dust bags should be set up in a manner which requires cattle to contact the bag with their head (Poindexter and Adkins 1970; Gerhardt et al. 1976). This form of control has met with some success (Table 3) but the lack of current research in this area seems to indicate skepticism.

Self-application devices should be placed in the field well in advance of the fly season, so that cattle become accustomed

to their presence and thus are likely to use them. The success of a self application control program can be greatly improved if it is conducted on an area wide basis.

Insecticide-impregnated ear tags have provided complete control of horn flies (Knapp and Herald 1981,1984; Flannigan and Surgeoner 1984a, 1984b,1984c,1985). However similar success has not been achieved for face flies (Table 3), despite the fact that they are now the most commonly used means of controlling face flies (Lancaster and Meisch 1986).

Knapp and Herald (1981) noted that if cattle were protected by fenvalerate-impregnated ear tags, face flies generally ceased alighting about their eyes, and focussed their attack on the nose area. Schmidtmann (1985a) noted a positive correlation between the ear flap rate of cattle and face fly abundance. Moreover, cattle bearing pendant identification tags on their ears had significantly fewer flies about the eyes than cattle lacking such tags. It was concluded that ear tags that were dependent on movement or contact for insecticide release and transfer would be most efficient. Commercial ear tags transfer insecticide to body surfaces contacted (Beadles et al. 1977), but release of the insecticide is a rate limited diffusion process (Miller et al. 1983a). Knapp and Herald (1984) found that face fly control was usually most efficient in the 5-7 week period following the early season application of ear tags to cattle. This efficiency corresponded to a period in which face fly populations were generally low and insecticide release rates

from ear tags were maximal. Toward the end of the season, populations tended to be higher and the insecticide release rate lower. Krafsur (1984) stated that although ear tags are effective in deterring or shortening the length of the flies' visit to the animal's face, they do not adversely affect face fly populations.

Despite their shortcomings for face fly control, ear tags can be considered effective if they can prevent face flies from feeding on eye tissue. In doing so, pinkeye and eyeworm infections can be greatly reduced. Ear tags are also generally inexpensive and easily applied.

15.1 Broadcast Spray Treatments

A number of researchers have attempted to control adult face fly populations using ultra-low volume sprays (ULV). Dobson and Sanders (1965) aerially applied a ULV spray of malathion (560 g per ha) to cattle and the surrounding pasture. Effective control was obtained for at least 1 week. Kantack et al. (1967) repeated this experiment and found that only 4 applications of malathion at 420 g per ha were required to provide full-season control of both face and horn flies. The control was more effective when both animals and surrounding pasture were treated than when only cattle were sprayed. Because of the success with malathion, ULV sprays using other

compounds were similarly tested. ULV sprays of trichlorfon at 210 g per ha gave excellent control of both horn and face flies for 24 h (Knapp 1966), but no assessment was made at a later time. Additional studies by Knapp (1967), in which the same chemical was applied at 840 g per ha resulted in only 11% reduction of fly populations, possibly due to immigration from surrounding untreated herds. Balsbaugh et al. (1970) tested ULV sprays of malathion at 840 g per ha, tetrachlorvinophos at 840 g per ha, trichlorfon at 560 g per ha, fenthion at 112 g per ha and naled at 70, 140 and 210 g per ha but were unable to properly evaluate the effectiveness of these compounds because of naturally low populations of face flies. More recently, Del Fosse and Balsbaugh (1974) tested stirofos at 203 g per ha, malathion at 798 g per ha and a 1:4 mixture of DDVP and tetrachlorvinophos at 231 g per ha. All of the preparations adequately suppressed horn and face fly populations for at least one week. No residual effect was observed past the first week; and the greatest reductions occurred when sprays corresponded with peak fly numbers. The use of either of these 3 organophosphates had no deleterious effects on members of the bovine dung community. Bruce et al. (1960) manually applied diazinon, dimethoate, malathion and ronnel to face fly resting areas such as fences, trees and sheds, and met with no success.

Because of the success obtained with ULV sprays in the American mid-west, this form of control for both face and horn flies has been recommended for North and South Dakota (Lofgren

1970). However, under test conditions in New Mexico, ULV treatments for horn fly control, with insecticides and concentrations similar to those previously mentioned for the face fly, were prohibitively more expensive than control by other conventional means.

15.2 Feed additives

Table 3 includes numerous insecticides, including insect growth regulators (IGR's), that have been given to cattle orally. These substances have been given with food, as concentrates, in mineral supplements, and have recently been administered in sustained-release boluses. Although not as efficient as adding larvicides directly to manure, the feed additive approach offers considerable advantages over conventional control methods. These include: relative simplicity of mixing an insecticide into animal rations or incorporating it into mineral supplement blocks, elimination of the labour and costs associated with applying insecticides directly to cattle or manure, and lastly, the potential control of a number of other dung breeding flies without additional cost or equipment modifications (Miller 1970).

To be used as a feed additive, a pesticide must pass through the animal with minimal degradation, allowing for maximum effectiveness in the resulting excrement; it must be

palatable to livestock and have no detrimental effect on it. Any build up of the original compound or its metabolites in tissues or milk must be within acceptable limits (Miller 1970). Few insecticides meet the above criteria. Compounds that degrade slowly or accumulate as residues in the animal have been improved upon with the use of polymer protectants. Lloyd and Matthysse (1966) indicated that of all the protectants tested, polyvinyl chloride formulated as a plastisol was the most promising. These conclusions were later substantiated by Lloyd and Matthysse (1970). Protectant-insecticides can pass rapidly through the animal's digestive tract, with minimal absorption or metabolism (Pitts and Hopkins 1964). Residues are minimized and the protected compound is gradually released into the manure.

Although many of the insecticides tested as feed additives were successful in controlling immature stages of the face fly, control of adult flies in most cases was erratic. This lack of adult control stems primarily from the dispersive nature of the face fly and the lack of isolation of treated from untreated areas (Miller and Pickens 1980). Problems may also arise when cattle do not consume sufficient quantities of insecticide-treated feed to obtain control (Knapp 1965a).

Insecticides incorporated into mineral blocks have also been throroughly investigated. However, problems similar to those with food additives have affected results.

Effectiveness of feed additives and mineral blocks, depends not only on the insecticide used but also on location in the

pasture. These materials should be strategically placed so that they are accessible and easy to find (Wallace and Turner 1964). Wallace and Turner (1964) also noted that in hot, dry weather, cattle consumed less insecticide-treated salt, resulting in a reduction of larval control. Cattle may also obtain sufficient amounts of their mineral requirements in their natural diets, and thus be unlikely to consume mineral supplements.

To reduce labour and pesticide costs and to prevent debilitation of cattle due to frequent insecticide applications, research is now being directed towards the use of sustained-release boluses (Miller et al. 1981). These devices depend on rention of a bolus formulated with a pesticide in the reticulum or rumen. A bolus is usually formulated from a blend of waxes with the addition of a compound such as barium sulphate to increase its specific gravity. Thus the bolus lodges and remains in the animal (Miller et al. 1981). Here, the active agent is slowly released, eventually passing through the digestive system to render the feces toxic (Riner et al. 1981). This form of control ensures a relatively uniform effective daily dose of insecticide. These boluses are easily administered using standard balling-guns. Depending on the size of the animal, the erosion rate of the bolus and the insecticide used, larval control can be maintained for up to 20 weeks (Miller and Pickens 1980).

Owing to the instability and tendency of many insecticides to accumulate as residues, emphasis has now been directed

towards the use of IGR's as feed additives. When compared to the more common insecticides, IGR's are generally not as toxic to cattle, are effective at lower dosages, and often pass through the digestive system unaltered (Chamberlain 1975). When absorbed into the blood system and tissues of animals, these compounds are easily metabolized (Chamberlain et al. 1975). A number of IGR's (in addition to those mentioned in Table 3) have been tested as larvicides (Miller 1974; Schwarz et al. 1974; Pickens and DeMilo 1977; Hall and Foehse 1980; Knapp and Herald 1983), and although some show potential, only methoprene has yielded consistent results. Almost all of the experiments using this compound in either sustained-release boluses, mineral blocks or incorporated into feed have proven successful (Table 3). Depending upon the dosage, methoprene is also effective against horn flies, stable flies and house flies (Harris et al. 1974; Miller and Ubel 1974).

When incorporated into sustained-release boluses, methoprene potentially offers the most practical and effective means of orally treating cattle for face fly control, although additional research is required to develop formulations which allow for more uniform erosion rates (Miller et al. 1979; Miller and Pickens 1980), and dosages that will control other dung breeding pests. Methoprene also has limited toxicity to non-target insects in manure (Pickens and Miller 1975). Methoprene is currently registered in the United States as a feed-through larvicide for horn fly control (Anon. 1985).

In addiion to the insecticides that have been tested as feed additives, substituted xanthene dyes have also been investigated (Anon. 1977; Fondren and Heitz 1978; Fairbrother et al. 1981). Only rose bengal and erythrosin B showed potential as replacements for the current array of oral pesticides. These dyes act in a manner similar to IGR's, but the exact mechanism that provides toxicity is not fully understood (Fairbrother et al. 1981).

Of considerable interest is the recent discovery and development of the antihelminthic, ivermectin (Merck MK933), a macrocyclic lactone produced by the soil microorganism Streptomyces avermitiles (Anon. 1981). It is said to be the most potent antiparasitic agent yet found; it is capable of controlling a wide range of external and internal parasites by either oral or subcutaneous applications (Anon. 1981; Miller et al. 1983b). A single injection of 200 ug of ivermectin per kg of body weight provided complete control of face fly larvae for 14 days (Meyer et al. 1980). Miller et al. (1981) later showed that depending on dosage, ivermectin was able to control both horn and face flies with injection and oral treatments. Drummond (1985) suggests that rangeland cattle would only have to be treated 1-3 times with a sustained release bolus implant of ivermectin to provide season-long control of face fly and horn fly larvae.

The use of orally administered insecticides for control of the face fly holds considerable promise, in that the face fly

breeds almost exclusively in fresh cattle manure. However, because of invasion of adult flies from surrounding untreated pastures, future attempts using this or any other method of control should be conducted over large areas.

Another problem with insecticides administered as feed additives is that they could have a significant impact on the entire insect community associated with cattle droppings. There is a risk of increasing the presence of insect-free, non-degraded dung pats in pasture and rangeland ecosystems (Anderson 1966). The ecological role of the microfauna and insect communities within dung should be closely examined if pesticides are to be used in such a fashion (Anderson et al. 1984). However, pesticides such as methoprene with minimal longevity may not prove to be very disruptive to a fecal-pat habitat.

15.3 Sterilants

Because of the failure of many insecticides to control the face fly, research interests were directed toward chemosterilants as possible control agents. A number of compounds including tepa (Hair and Adkins 1964; Killough and McClellan 1969), apholate (Hair and Adkins 1964; Hair and Turner 1966; Adkins 1968), heliotrine (Zapanta and Wingo 1968), hempa and metapa (Kaur and Steve 1969; Kaur and Wentworth 1972), oil

of Sterculia foetida seeds (Lang and Treece 1971), boric acid (Lang and Treece 1972) and diflubenzuron (Knapp and Herald 1982) have been tested for their potential as chemosterilants. These were applied either by way of feed rations, manure treatments or topical applications to adult flies. All treatments were generally effective, indicating that the face fly can be easily sterilized. However, the applicability of chemosterilants under field conditions has not been investigated (Pickens and Miller 1980). Investigations should be directed toward methods of sterilizing either laboratory-reared flies for mass release, or toward sterilizing field populations using traps baited with treated feeding attractants. The possibilities for mass release of sterilized flies holds potential as laboratory rearing procedures for the face fly are well established (Fales et al. 1961a; Wang 1964).

15.4 Trapping techniques

Visually-attractive materials have been used to lure face flies to traps for sampling and control purposes. Pickens et al. (1977) demonstrated the effectiveness of glossy white pyramidal sticky traps for sampling attracted face flies. This technique was further tested for area-wide control by Miller et al. (1984a). They used 1 trap per 3 head of cattle in conjunction with a feed additive contol program and were able to

suppress face fly populations effectively in a 225 km^2 area. Either control method alone met with limited success. In an attempt to improve the effectiveness of the tetrahedron-shaped traps, the Tack-Trap^R adhesive was replaced with a 10% solution of permethrin in acetone; however, the permethrin failed to remain toxic under field conditions. Miller et al. (1984a) suggested that an insecticide with a long residual life would make the traps more efficient. Pickens and Nafus (1984) combined 2 tetrahedron traps at the base to form an octahedron or diamond-shaped trap that was just as effective as the former type trap in capturing face flies, with the added advantage of also selectively capturing stable flies. To capture face flies effectively, traps should be placed ca 1 m from the ground and should be weighted to reduce movement due to wind (Pickens and Nafus 1984).

16.0 Conclusions

In 1976, ca 5 million kg of livestock insecticides were used in the United States (Eichers 1981). Of this amount, approximately 70% was used in the beef cattle industry to control face flies, horn flies and cattle grubs. Control of face and stable flies in dairy operations accounted for 18% of the total. The most commonly used insecticides in the beef cattle industry were toxaphene and methoxychlor, and in the

dairy industry DDVP followed by methoxychlor (Eichers 1981). Knapp et al. (1985) recently determined that the face fly has developed a low level of resistance to methoxychlor. In all probability this resistance developed because of the high selection pressure caused by the extensive use of this pesticide.

An updating of the published annotated bibliographies of the face fly (Smith et al. 1966; Smith and Linsdale 1967,1968,1969, 1971; and Smith and Krancher 1974) is recommended as an aid to future research.

Although the face fly is quite susceptible to the insecticides commonly used to control other fly pests on cattle, field performance of numerous pesticide formulations and control methods has been largely unsatisfactory. Low field efficacy can be attributed to such factors as: lack of isolation of treated areas from untreated areas, the highly dispersive nature of the face fly, its reluctance to enter buildings except to overwinter, the fact that only a small proportion of the total population is on cattle at any given time, and when there, they commonly attack the facial region, an area which is difficult to treat.

Future approaches to contol could exploit other aspects of face fly biology. Because the face fly breeds exclusively in the feces of cattle, feed additives hold considerable merit for controlling the face fly in addition to other manure breeding fly pests over wide areas. Sustained-release boluses containing

compounds such as methoprene or ivermectin, have recently provided the producer with a valuable management tool. Boluses are easily administered and are capable of providing better season-long control with less effort and expense than the more conventional forms of livestock pest control. Additional research should be conducted to develop improved formulations that provide more uniform release rates for control of both face flies and other manure-breeding pests. Mammalian toxicity must be addressed as well as the effect of insecticides on non-target organisms.

One potential insecticidal treatment is to induce cattle to produce watery feces in which face fly larvae cannot survive. This outcome might be achieved chemically or through altered forage grasses.

Methods to control adult flies also require further attention. Face rubbers and ear tags represent a possible means by which face flies can be prevented from feeding on eye tissues, thus reducing their capacity to transmit eye damaging organisms. Emphasis should be directed toward more persistent pesticides with greater repellancy. Such compounds would prevent feeding about the eyes and would better withstand removal from the facial region.

Aerial ULV pesticide treatments carried out on an area wide basis have been highly successful. Such treatments are expensive and undoubtedly affect a great many non-target insects. However, such a management tool might become necessary

if the face fly were to become a vector of a debilitating disease of livestock. Traps have considerable potential if they can be modified so that feeding attractants laced with either insecticides or chemosterilants can be used against populations. Such autocidal control may work best in the spring when post-hibernating flies behave as a uniform cohort. The factors leading to overwintering by face flies in the same buildings year after year need to be identified. It may then be possible to treat problem buildings or to direct overwintering face flies into buildings where they can be effectively dealt with.

A cost-benefit analysis of current control programs is required to justify the time, effort and expense currently being directed toward the management of the face fly which in the absence of pinkeye and eyeworm infections, appears to be more of an aesthetic problem to producers than an actual problem to livestock.

It should be noted that current research concerning the impact of the face fly on livestock productivity is inadequate and thus one cannot positively conclude the importance of this pest in North America.

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